ISLE ROYALE BIOSPHERE RESERVE:

Volume I

A HISTORY OF SCIENTIFIC STUDIES

U.S. MAN AND THE BIOSPHERE PROGRAM
U.S. MAB REPORT NO. 11

MaB

NATIONAL PARK SERVICE
Department of the Interior

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U. S. Man and the Biosphere Program
U. S. MAB Report No. 11
Volume I

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INTRODUCTION

The principal objectives of this report are to provide an overall assessment of the history of scientific study in Isle Royale National Park, and to compile a bibliography citing the numerous scientific studies that have taken place in the park and its immediate surroundings. A "Literature Cited" section has also been attached since there are a number of references cited which do not deal directly with Isle Royale and therefore are not in the bibliography, but are germane to the topic under discussion.

This report emphasizes scientific studies that have been conducted since the turn of the century. This qualification is necessary since in the middle of the nineteenth century Isle Royale was the site of numerous detailed mineralogical assessments undertaken as part of the region-wide studies associated with copper mining. While selected key references pertinent to this period are mentioned in this report and in the bibliography, no attempt has been made here to include all of the many specific mineralogical reports and surveys.

Isle Royale is located in the northwest quarter of Lake Superior, the largest (by surface area) freshwater lake in the world. It is the northern-most point in the state of Michigan and is located 21 km from Ontario, Canada, and 29 km from the Minnesota, USA mainland (Fig. 1).

Isle Royale is actually an archipelago consisting of a main island surrounded by over 200 smaller islands of greatly varying sizes. The main island is 72 km long and 14 km across at its widest point. In orientation it roughly parallels the north shore of Lake Superior with its long axis running in a southwest-northeast direction. The island is characterized by a series of ridges and valleys which run parallel to the long axis. Numerous inland lakes and hundreds of swamps, ponds and bogs are located between the ridges (Fig. 2).

The park boundaries extend 7.2 km out into Lake Superior. The total park area is 231,403 hectares. Of this (approximately one-quarter of the total) 54,143 hectares is land area. The highest elevation in the park is 242 meters above Lake Superior, or 425 meters above mean sea level.

Much of the land is thin-soiled with numerous rocky outcrops. The almost continuous and dense vegetation is characterized by discrete boreal conifer forest in near-lake locations and northern hardwoods at inland sites. The climate is typically mid-continental but greatly tempered by the surrounding waters of Lake Superior. The fauna consists of moose, wolves, beaver, snowshoe hare, and nine additional mammalian species.

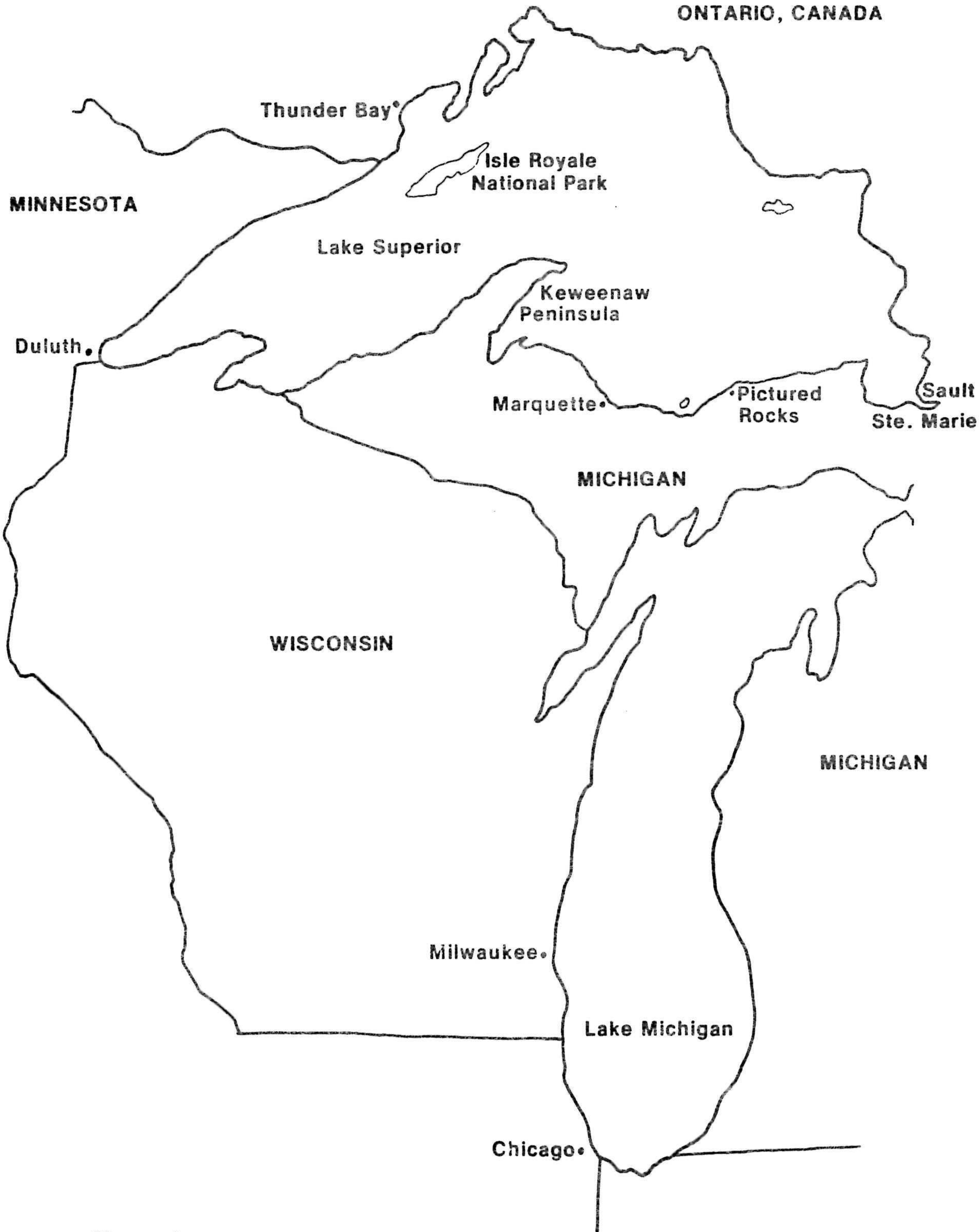

Figure 1

Lake Superior region showing location of Isle Royale National Park, Michigan.

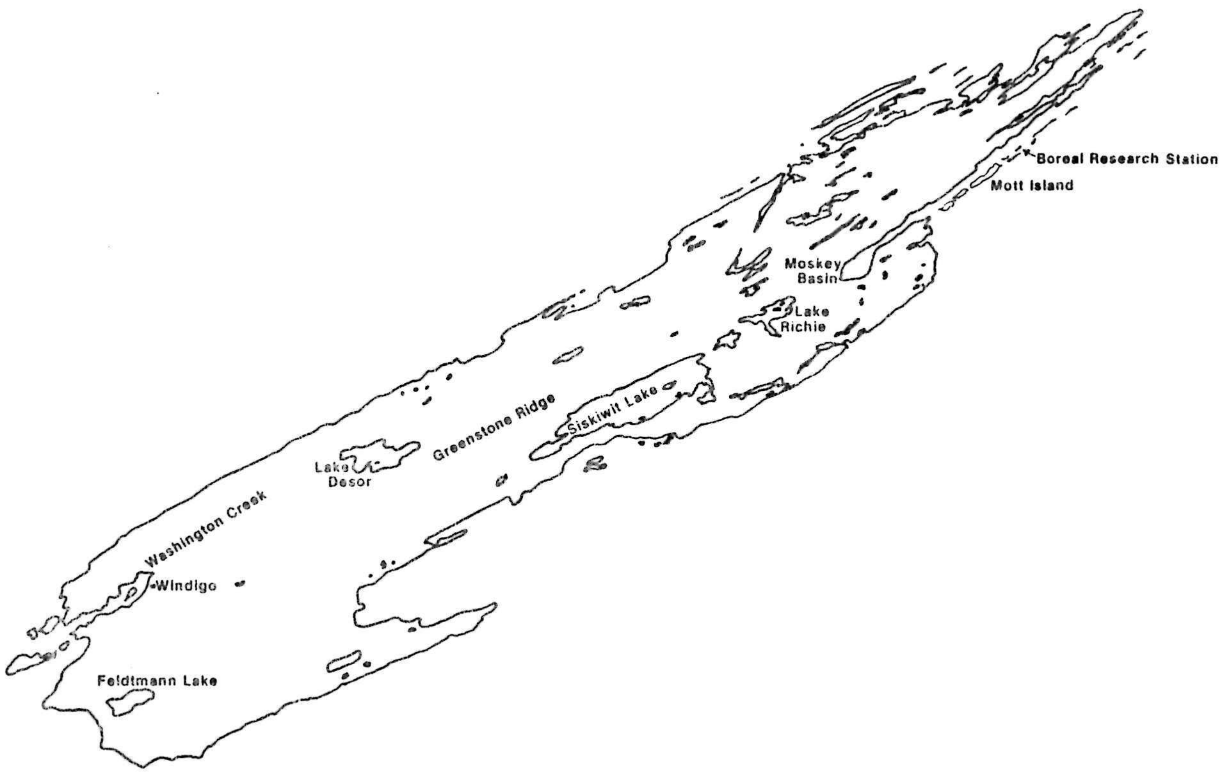

Figure 2. Map showing detail of Isle Royale National Park, Michigan.

HISTORY OF OBSERVATION AND RESEARCH ON ISLE ROYALE: A SUMMARY

Accumulated information concerning the physical and biotic components of the Isle Royale ecosystem date from as early as 1669, when Jesuit Fr. Claude Dablon entered observations into the Jesuit Relations (Dablon 1669-1671). A few other early accounts exist, such as other Jesuit writings, records of fur trading companies, and Agassiz' descriptions of the Lake Superior area (Agassiz 1850); these are of a general descriptive nature however.

In 1847, a General Land Office survey of Isle Royale was made by William Ives (Ives 1847). Ives' extensive notes and accurate survey provide good information about the natural ecological conditions existing at that time (Gilchrist 1968-69; McKaig 1978). Because mineral exploration commanded so much attention from the mid-1800s to the early 1900s, a wealth of early geological information was produced (Jackson 1849, 1850a, b, 1854; Foster and Whitney 1850, 1851; Lane 1898, 1899, 1911). Later contributions to geological knowledge were made by Stanley (1932) and Ferrand (1960, 1962, 1969) who contributed significantly to the understanding of the Quaternary of the Great Lakes area, and by Huber (1969, 1971, 1972, 1973a, b, c, 1975) who described and mapped in detail the bedrock geology of Isle Royale and vicinity. Huber's papers concerning Isle

Royale and Lake Superior geology (from the Precambrian to the Quaternary) are a complete and modern record, incorporating the latest techniques and theories.

Ecological studies have been conducted at Isle Royale from early in the history of the discipline. In 1904, a party from the University of Michigan Museum conducted an ecological survey of the Porcupine Mountains (on the south shore of Lake Superior in Upper Michigan) and a small portion of southwestern Isle Royale. Ten "stations" were established on Isle Royale at which plants, mammals, birds, and invertebrates were collected and their habits and interrelationships were studied (Ruthven 1906). In the following year, 1905, a second Museum party concentrated solely on Isle Royale, establishing five primary stations consisting of 38 substations which were located at Rock Harbor, Siskiwit Bay and Washington Harbor (northeast, central and southwest, respectively). Data similar to those of the first year were collected and analyzed to form a reasonably extensive compendium of basic ecological information (Adams 1909). In 1909 and 1910, William S. Cooper carried out field studies that described the climax forest of Isle Royale and the several successional pathways by which it became established. This he later published (Cooper 1913a) along with related studies on the moss flora and a list of the plant specimens he collected (Cooper 1912, 1913b, 1914). When Cooper returned to

Isle Royale in 1927, he failed to relocate most of his original study plots; nevertheless, he obtained sufficient information to publish his landmark, "Seventeen Years of Successional Change..." paper (Cooper 1928). Even though restricted to the northeastern portion of Isle Royale, Cooper's studies clearly delineated the nature of the climax spruce-fir and its several sub-climax and successional community types on Isle Royale.

In 1929 and 1930, another party from the University of Michigan Museum of Zoology and University Herbarium carried out field studies at Isle Royale. Some important changes had taken place since the first Museum party of 1904-05: caribou, which previously inhabited Isle Royale, had disappeared by about 1922; moose, which previously had not been present, arrived on Isle Royale in about 1912; lynx, previously present, had disappeared; and a movement had been on-again-off-again since the early 1920s to make Isle Royale a state or national park. The faunal changes resulted in vegetational changes, especially the near extinction of yew, which had formed nearly impenetrable thickets at the time of the Ruthven and Adams surveys. Also, the copper prospectors of the 1850-1900 period had burned off considerable portions of Isle Royale which by 1930 had reached various post-fire successional stages. Therefore, the surveys and studies of the 1929-30 period documented a crucial stage of conditions. Adolph Murie's "The

Moose of Isle Royale" (1934) initiated a long series of inquiry into the population dynamics of this species, and Clair Brown's "Ferns and Flowering Plants of Isle Royale, Michigan" (1936) remained the most important floristic listing up to the present time, succeeded only by Slavick and Janke's (1984) updated list. Other studies included fungi (Povah 1934), phytoplankton (Taylor 1935), bryophytes (Thorpe and Povah 1935), and lichens (Hedrick and Lowe 1936).

During the mid-1930s, several important events contributed to our overall understanding of the Isle Royale ecosystem. First, a large fire - resulting from a combination of a small lumbering operation at Siskiwit Bay, a series of very dry years, and probably lightning - burned between one-fourth and one-third of the forested area of the main island (mostly in the central portion). This fire produced a variety of successional stages that later became valuable study plots and provided a large amount of sorely-needed browse for the depauperate moose population. Paul Hickie's studies on the moose (Hickie n.d., 1936, 1937), served to augment the continued interest in this animal on its island home. Second, Civilian Conservation Corps (CCC) funds enabled a number of projects to occur (Isle Royale had three CCC camps), among which was a project to map the island's vegetation (Anon. 1937). At the end of the 1930s, the advent of World War II and the demise of the CCC essentially spelled the end of any important scientific inquiry until the 1950s. Third, 1941 witnessed the final Act establishing Isle Royale as a national park.

The acquisition of national park status made Isle Royale one of the few boreal conifer-northern hardwood areas in the United States that was relatively well protected from development and exploitation. This was a great attraction to those wishing to conduct long-term ecological studies. Continuing the studies of the moose (begun by Murie and Hickie in the early 1930s), Krefting (1946, 1949, 1951, 1956, 1960, 1974; Krefting and Lee 1948) established four moose exclosures at various island locations. He obtained data from these and from paired non-exclosed plots on a nearly annual basis for many years to obtain a fairly long record of moose browse conditions, along with observed moose population conditions. Sometime in 1947-49, the eastern timber wolf arrived on Isle Royale, either from Minnesota, or more probably, from Ontario. The newly-arrived wolf was studied during three winters (1953, 1956, 1957) by Park Service biologists (Cole 1953, 1954, 1956, 1957a; Hakala 1953; Linn 1956a, b.) and in 1958 Durward L. Allen began his long-term studies of the ecological relationships between the wolf and other island wildlife populations. Allen's program, as continued today by Rolf

Peterson, is a landmark of long-term ecological inquiry now in its 25th year. It has proven the indispensability of continuous study of ecosystems over long- and short-cycle environmental variables (Allen 1969a, b, 1974, 1979a, b, c; Allen and Mech 1963; Johnson 1969, 1970; Jordan 1964; Jordan et al. 1967; Mech 1963a, b, 1965, 1966, 1970; Peterson 1974, 1975, 1977, 1979; Peterson and Allen 1974; Peterson and Scheidler 1977; Scheidler 1979; Shelton 1966, 1979; Wolfe 1969; Wolfe and Allen 1973). These studies also spawned an interest in various peripheral aspects of moose and wolf ecology at Isle Royale (Belovsky et al. 1973; Belovsky 1978; Belovsky and Jordan 1978; Botkin et al. 1973; Jordan et al. 1971; Jordan et al. 1973; Karns and Jordan 1969; Rykiel and Kuenzel 1971; Stauber 1963, 1964; Wilson and Johnson 1971).

Renewed interest in the vegetation of Isle Royale began to emerge in the 1950s when Linn began a series of studies on forest succession and the environmental causes for the apparent existence of both boreal conifer and northern hardwood climax types on Isle Royale (Linn 1952, 1957, 1962). Linn has permanent quadrats from which data were initially collected in 1951 and resampled in 1974. These may prove valuable, along with the still extant moose exclosures of Krefting, for additional long-term successional and productivity studies.

Studies of the boreal conifer type on Isle Royale have been continued to the present time by various investigators. Janke, in particular, has investigated fire as a factor in the spruce-fir type and has studied the establishment of seedlings of dominant species and the effect of the island's faunal components on the vegetation (J. de Waal Malefyt 1974; S. de Waal Malefyt 1974; Janke 1979; Janke et al. 1976; Raymond et al. 1975a, b; Snyder and Janke 1976). Recently, studies of air and water quality have been initiated by Stottlemyer (1979, 1981, 1982) in an attempt to discern external threats emerging as a result of the near and far production of industrial and other airborne pollutants. Also, in progress are studies concerning the bryophyte flora, algae, aquatic invertebrates and plants, and studies on the role of lichens in bare rock successions along the shores.

GEOLOGY

The Region

The Great Lakes occur at the boundary between the Precambrian rocks of the Canadian Shield and the more southern, predominantly Paleozoic sedimentary formations. The Lake Superior Basin is entirely within the Canadian Shield. Lake Huron, to the east and south, is bordered on the north by Precambrian bedrock and its remainder by Paleozoic deposits. The remaining lakes are entirely within Paleozoic sedimentary deposits. The Silurian Niagra dolomite is a dominant structural feature in Lakes Michigan, Huron, Erie, and Ontario. Lake basin morphology differs considerably among these lakes due to the differences in geologic substrate. The benthic morphology of upper Lake Michigan, Lake Superior, and Lake Huron is quite rough while that of Erie and Ontario is quite smooth.

Much geologic study of the region has taken place since the 1850s. Primarily these studies relate to the native copper deposits of the Lake Superior Basin. These studies began with the survey by Agassiz (1850) of the physical character and biology of the basin. An interpretation of the Portage Lake Volcanics, especially along the south shore of Lake Superior, is presented in some detail by White (1960) who also provided a relatively recent summary of the nature and origin of the copper deposits in Michigan's Upper Peninsula (White 1968). Keweenawan geology of the Lake Superior region and the relationships of Keweenawan rock groups were reviewed by Halls (1966).

As is the case for perhaps all other sections of the North American continent influenced by Quaternary and Pleistocene glaciation, this region has witnessed much attention devoted to the events of these periods (Flint 1961). Bird (1972) described the physical landscape and the effects of glaciation on the Canadian Shield. Kelley and Ferrand (1967) provide a good summary of the glacial and post glacial lakes of the Lake Superior Basin. Much of this and the work of other investigators was subsequently summarized by Ferrand (1969). Dorr and Eschman (1970), in their excellent text on the geology of Michigan, provide a descriptive overview of the sedimentary and metamorphosed geologic substrates characteristic of most of the Lake Superior Basin, in particular its southern half.

For those interested in a more historical perspective relating man to the pursuit of native copper deposits, the work of Foster and Whitney (1850) provides interesting sketches of early explorations in the Lake Superior region. Griffin (1961) examined in detail the prehistoric activities of indian copper miners especially on Isle Royale. Rakestraw (1965) assessed the post-indian explorations for copper, again with emphasis on Isle Royale.

Geology of Isle Royale

The most extensive geologic study of Isle Royale is the contemporary work of Huber (1975). A series of publications authored and coauthored by Huber examines in detail the glacial and post-glacial geologic history of the park (Huber 1973a) and the islands' middle Keweenawan deposits of Portage Lake Volcanics and Copper Harbor Conglomerates (Huber 1973b, Wolff and Huber 1973). Huber also produced a detailed geologic map of Isle Royale (Huber 1973c). Additional publications deal, in some detail, with specific interesting minerals associated with the geological deposits of the park (Courter 1972, Huber 1971).

Most of Isle Royale's geologic substrate consists of interbedded volcanic and sedimentary rocks which include the Portage Lake Volcanics. This thick bedded layer forms the syncline beneath Lake Superior jutting up to form the bulk of the Isle Royale archipelago. Overlaying this extensive formation are the post-volcanic sedimentary rocks (the Copper Harbor Conglomerate is a member) which in this region are nearly completely covered by Lake Superior except for a narrow band on the north shore of the Keweenaw Peninsula and a relatively small portion of Isle Royale at Feldtmann Ridge and surrounding Siskiwit Bay. The thick series of flood basalts and sedimentary layers tilt (10^{o}-55^{o}) southeast toward the axis of the Lake Superior basin. The tilt is steeper on the north side of the Isle Royale archipelago (Huber 1975). That portion of the island between south-central Siskiwit Bay and Rock Harbor, to the northeast, is somewhat pushed up or domed and is an area of extensive faulting. These fault lines run predominantly in a northeast-southwest direction. The remainder of the Portage Lake Volcanics throughout the archipelago generally have less closely spaced fault lines running in a north-south direction. The erosion that has occured along these fractures creates the conspicuous ravines characteristic of the islands. Fault displacement along these fractures is almost always minor.

Foster and Whitney (1850) and Lane (1898) recognized that the geologic sequence on Isle Royale was similar to that of the Keweenaw Peninsula only in reverse. Thus they were able to deduce that the layers must be of the same origin and similar in age, and probably extended in an arch under Lake Superior.

As is characteristic of geologic information in any region affected by mineral exploitation, there is considerable detailed information on local mineralogy, while questions regarding the overall geology of the region still remain. The best general overviews of the region are probably provided by Dorr and Eschman (1970). The best general study of the geology of Isle Royale clearly is Huber (1975) who, based upon personal extensive surveys of the island and the synthesis of the work of many of his predecessors, provides a summary of the geologic history easily understood even by the layman. Both Dorr and Eschman's and Huber's texts provide a reasonably good synthesis of the effects of Pleistocene glaciation on changes in landforms, lake levels, and major soil variations. For details related to these subject areas, and in particular on matters dealing with the effects of Pleistocene glaciation at any specific geographical site, one should consult the references mentioned in this report.

SOILS

Information regarding soils, even in its most rudimentary descriptive form, is lacking for the Lake Superior basin and especially Isle Royale. As is the case for much of the United States, those counties having an agricultural or forestry base generally have soils maps produced by the Soil Conservation Service, USDA. However, for this region most of them are quite old, having been prepared in the 1920s and 1930s. General soils maps exist for Houghton and Keweenaw counties but have never been published (pers. comm., Soil Conservation Service, USDA, Hancock, Michigan).

Soils of Boreal/Northern Hardwood Ecotone

The widespread soil type in boreal regions is podzols. This soil type typically develops on sandy or more coarse substrates such as granite. During podzolization the very soluble monovalents potassium and sodium along with the divalent calcium ions are readily washed from the soil by water movement. Iron and aluminum are typically removed from the A horizon to the B horizon. Iron leaching is complex and involves chelaters found in the upper organic layers which help reduce iron into the mobile ferrous state. Biomass typically accumulates as litter on the soil surface, and considerable humus lenses may be found as deep as the B horizon. Northern coniferous species are especially rich in the compounds that promote podzolization, such as chelaters. Surface soil layers are typically of the mor type. The podzolization process is understood in concept but is poorly understood or defined in detail.

Boreal zone soils are interrelated to climate and vegetation, and one can not be considered without attention to the others. Podzol soils are not confined to just the boreal zone. But the podzolization process is particularly intense at the southern boundary of the boreal zone especially where precipitation is abundant, and in the Great Lakes region where there are acid sandy glacial deposits. In highly podzolized soils the upper A subhorizons are nearly depleted of all but organic and siliceous materials. Where there is less intense podzolization or where the substrate is not sandy a wide variation of soil characteristics will be found in the upper horizons. The time available for substrate weathering and subsequent soil formation is a significant factor. In areas of recent glaciation the time available for soil development has been very short as is the situation for much of the Upper Great Lakes region.

Within the boreal zone there are also soils that would be correctly described as regosols, peats, gleys, gray-and-brown-wooded soils, and azonal lithosols.

There are no clearly distinguishable changes in soil types or their formation processes at the southern (or northern) ecotone of the boreal zone. The gradual shift from deciduous to coniferous litter is one subtle factor along with the gradual decrease in litter decomposition rates with increasing latitude. In deciduous forests along the southern ecotone, litter decay rates are high. The litter is rich in bases which are in turn quickly recycled back into the living tissue of the tree. Upper soil horizons are zones of enrichment rather than zones of leaching. The resulting gray-wooded soils of the transition zone are distinctly different from the northern podzols.

A modification of the classic podzol formation exists where topography and parent material conditions inhibit leaching. Topography most often elevates the soil water table into the upper B or A horizon resulting in a gley mottling. The resulting soil is termed a bog soil or gley podzol. Conversely, immature podzol soils might be found in upland, well-drained areas where humus accumulation is very thin and horizon formation retarded. Natural or manmade forest perturbation, particularly on dry sites, can also result in poor podzol soil profile development.

Soils of Isle Royale

The soils of Isle Royale have never been extensively studied. They have not been mapped, nor does any type of systematic soil survey exist. What little is known about the soils has come from portions of largely unpublished vegetative research studies that included some soils data. Most of this work has been confined to the northeast section of the island and in particular soil differences among the spruce-fir, birch-aspen, and jack pine vegetation types (Janke unpub. Final Report to NPS, 1983). Linn (1957) examined soil moisture characteristics in the sugar maple forest type and selected transition vegetation zones in the southwest end of the island. Linn concluded that there was little discernable influence of soil physical and chemical properties on vegetation makeup in this portion of the island.

Due to Pleistocene glaciation and the relative recent emergence of significant portions of Isle Royale from Lake Superior and its predecessors, it is thought that none of the soils on the island are derived from the Precambrian volcanic substrate. Rather, they have developed from the glacial till which was deposited on the island by the retreating glaciers. Glacial till deposits are extensive and deep on the southwestern one-third of the island, and extensive and scattered on the remaining two-thirds of the island. The tills are alkaline in character with a high carbonate content. They are probably derived from calcareous deposits brought south from Hudson Bay by glaciation.

Most of the published and unpublished soils information can be found in Shetron (1973), Snyder (1973), S. de Waal Malefyt (1974), and Janke (1981, 1982, unpub.). The only professional descriptions of soil profiles are those by Shetron (1972, unpub.) who studied 15 soil profiles in the northeastern section of the island and described them employing the Comprehensive System of Soil Classification. The soils were classified down to soil series, and the location of the sampling points is known. However, no soils map was prepared.

As part of the ongoing watershed studies by Stottlemyer (pers. comm.) on the northeast section of the island, soils within these drainages will be sampled and the watershed soil types mapped. In addition, much of the rather scarce quantitative soils information collected by other investigators in the past is being entered in computer files as part of this study. However, soils information has been identified by the park as one of its top information deficiencies for many years now.

Due to the relatively high cost of such a survey, this project has never been funded.

CLIMATE

The Region

As is the case with soils, there has been little systematic collection of meteorological data on Isle Royale up until very recently. Lake Superior has a profound influence on regional climatic conditions, and therefore, data collected by U.S. and Canadian weather stations within the Lake Superior basin cannot be easily extrapolated for determining conditions on Isle Royale. The relatively flat territory of central Canada offers the possibility of correlating air mass movement and frontal systems with general vegetation patterns since there are no major topographic features to divert air flow. Pacific air masses stream across the U.S. - Canada border into the Upper Great Lakes Region. Their swinging form, along with constant troughs and ridges, results in a high frequency of cyclonic passages which are particularly evident in the spring and fall (Hare 1968, Hare and Hay 1971) along the southern boundary of the boreal zone. Hare and Hay (1971) provide an excellent general summary of the boreal climate within North America.

The meteorological conditions that prevail on Isle Royale appear to be quite similar to those described for the southern boundary of the boreal zone. Historical data for select seasons, most notably about six weeks during the winter research season of January and February, and for about six months during the normal summer park operation season (Isle Royale is closed from November 1 to April 1) do exist, however, and allow for some comparison with regional mainland sites. Data collected by the National Park Service at Rock Harbor have been published since the 1960s in the state climatological records (NOAA, 1983). Unpublished Park Service seasonal records pertaining to basic meteorological conditions dating back into the 1950s are available from park files. These data are most complete for the Mott Island/Park Headquarters site, but are also reasonably complete for Windigo on the southwestern end of the island. About the only other systematically collected meteorological data from the 1950s is contained in Linn (1957).

The U.S. Geological Survey initiated stream discharge studies on Washington Creek near Windigo in 1964. As part of this study, daily stream water temperatures and annual precipitation input data were collected but have not been published. All their precipitation data have been recorded and placed on a computer file (Stottlemyer, pers. comm.). Additional historical data relating to climate were probably collected by the Coast Guard and quite likely by some of the very numerous passing ships carrying cargo to and from Thunder Bay. However, at present none of these data, if they exist, appear to be readily available.

Until 1980, daily meteorological data collected on a year-round basis did not exist for the park. In August of 1980 a National Atmospheric Deposition Program (NADP) station was located at Windigo, and daily precipitation quantity records since that time exist on computer files (Stottlemyer, pers. comm.). In addition, bulk precipitation quality data exist for this station since May 1979, and NADP precipitation quality data exist for this station for the periods of island occupancy from May until October of each year. All NADP data have been entered in computer files at the National Park Service Cooperative Research Unit at Michigan Technological University, and are published quarterly by the NADP (1982).

Bulk precipitation quantity and quality data exist for the northeastern end of the island beginning with 1979. However, these data were only collected during the time of island occupancy, and no data were collected during 1980. In 1981, the collection of daily hygrothermograph data was initiated at the recently established Boreal Research Station on Davidson Island. Similar data are also available for Windigo. Beginning in 1982, year-round daily precipitation and hygrothermograph data are available for Moskey Basin near the northeast end of the island. All these data are maintained on computer files at the National Park Service Cooperative

Research Unit at Michigan Technological University, and are part of the long-term boreal ecosystem monitoring data base being collected for Moskey Basin (Stottlemyer, pers. comm.).

An additional component of these long-term ecosystem studies has been the expansion of winter meteorological observations. Prior to 1979 snowpack density and moisture conditions and day to day temperature variation were monitored as part of the annual six-week winter moose/wolf research period conducted during January and February. These data go back to 1972. Since 1979, snowpack quality and quantity data have been gathered at about a half a dozen stations at the Windigo end of the island (Stottlemyer 1982). These stations have generally been located along a transect to observe variation in precipitation quality and quantity with changes in elevation above mean Lake Superior levels.

At present, year-round daily meteorological monitoring consists of a Remote Area Weather Station (RAWS) recording 6-8 channels of information in the Moskey Basin area, daily precipitation and hygrothermograph recordings at the Windigo station, and during the summer weekly precipitation quality samples at both ends (collected less frequently during the winter)(Stottlemyer, pers. comm.). In addition, the National Oceanographic and

Atmospheric Administration maintains two Remote Area Weather Stations collecting about 4 channels of information at the Passage Island and Rock of Ages lighthouses.

Within the Lake Superior basin, primary national meteorological stations are maintained by the Department of Fisheries and Environment of Canada at Thunder Bay (north shore); at Duluth, Minnesota; and at Houghton, Marquette, and Saulte Ste. Marie in Michigan by the National Oceanographic and Atmospheric Administration. Data collected by these agencies are part of the public record, and are available in annual publications from both countries.

VEGETATION

The Region

The geographic location of Isle Royale is paramount to an explanation of its vegetational components. Transeau (1948) was among the first to map the vegetation types of North America, and his map exists with only minor modification in present day plant geography literature. Transeau's map, which was privately published from his office at Ohio State University, is readily available and has been little changed over the years (Oosting 1956). On Transeau's map, Isle Royale lies in the transition zone between the hemlock-hardwood forests of the Great Lakes area and the boreal conifer forest of eastern Canada.

Cooper (1913a) compiled a map showing ranges and overlaps of the deciduous forest tree species and boreal forest tree species (data largely from Transeau, 1905). This map also clearly places Isle Royale within the transition zone between the two major vegetation associations.

Thirty-three major tree species are components of forest areas in the Lake Superior region. All thirty-three are present in varying degrees along the south shore, and twenty-six are present along the north shore. Twenty-four of these species are present on Isle Royale. Of the ten species which have failed to reach Isle Royale, four are found on both north and south shores and six are found only to the south of the Lake Superior basin.

Even though it is quite evident that Isle Royale lies within the transition zone, it is also clear that the discrete spruce-fir-birch forest on Isle Royale is a good representation of the boreal coniferous forest, and that the maple-birch forest is a fair representation of the hemlock-hardwood forest (now minus the hemlock). Cooper (1913a) was concerned that he may not have selected a good location for his studies of the spruce-fir forest. He said, "For a study of the northeastern conifer forest a more centrally located area might have been preferable; for instance, at some point midway between Lake Superior and James Bay. It will be shown, however, that Isle Royale affords a very fair sample of the forest growth of the northeastern region...", and "Important confirmation has recently been received from Dr. Robert Bell of Ottawa, the best authority upon the distribution of Canadian trees, who writes: 'The same type of upland forest which you describe on Isle Royale extends from the Great Lakes to James Bay and east and west of it, with modifications in parts.'" (from Cooper 1913a).

It is probable that those areas of Isle Royale in close proximity to Lake Superior have always experienced a climate somewhat ameliorated by Lake Superior and its postglacial ancestral lakes. This is somewhat supported by Potzger (1954), who suggested that fir did not decline to the levels observed in Quebec during the Xerothermic period.

Isle Royale

In 1847, William Ives conducted the original land survey of Isle Royale, Michigan (Ives 1847). Ives, who had a reputation as an extremely accurate surveyor, produced the earliest vegetation data for the island. The first interpretation of Ives' survey was accomplished by his granddaughter, Marie Gilchrist (1968-69). Later, McKaig (1978) reinterpreted Ives' work using more modern methods and statistics, and added information that enabled him to compare the vegetation of 1847 with that observed in the 1970s.

McKaig (1978) transcribed and tabulated forest data from the Original Land Office Survey of Isle Royale. This data set was then stratified and the boreal conifer association compared with three modern samples of this association. Survey data from the sugar maple-yellow birch association were compared with one modern sample of that type. Percent species composition (relative density), diameter distributions and point-to-tree distance distributions were utilized for these comparisons. Maps of the vegetation for both periods were prepared to facilitate aerial comparisons. A review of the suggested methods for the analysis of surveyor bias was also presented. The modern boreal forests show a marked reduction in the percent composition of balsam fir and a concomitant increase in paper birch. Aspen also has increased somewhat while cedar and tamarack have declined over this period of time. Some difficulties were encountered with the repeatability of the modern samples. The sugar maple-yellow birch association seems to have increased somewhat in the area which may be due to fire or climate modification. Modern forest species compositions indicate less mature conditions than in 1847, and this is attributed to the combined effects of fire, herbivory, and insect epidemics.

The first meaningful ecological survey of Isle Royale took place in 1905 by C.C. Adams (1909) who headed a party from the University of Michigan Museum of Zoology and Herbarium. One of the party, W.P. Holt, wrote, "large parts of the island...have remained quite free from man's invasion. That the present natural conditions are not likely to remain long undisturbed, and that the past summer's observations and records were made none too soon, is shown by the fact that contemporanious with the work of the Museum party there were at least three different parties of timber estimators working over large parts of the island looking toward the cutting off of the forests."(from Adams 1909.) Holt, being the principal botanical worker in the party, went to some length in describing the island's vegetation and included an annotated list of 364 plants (43 lichens, 38 mosses, 35 pteridophytes, and 248 spermatophytes).

In 1909 and 1910, William S. Cooper carried out his now-renowned field work on Isle Royale under the direction of Henry C. Cowles of the University of Chicago (Cooper 1912, 1913a, b, 1914). Cooper's research formed the basis for his Ph.D. dissertation, completed in 1911, and later for the series of papers he published in three successive numbers of Volume 55 of the Botanical Gazette (Cooper 1913a).

The purpose of Cooper's research was to "determine the climax forest of Isle Royale, its composition and character, and to trace the various lines of succession leading to it. It is thus a successional study of a small component portion of the northeastern conifer forest."(Cooper 1913a). Cooper's study plots (quadrats) were all located near the northeastern end of Isle Royale - principally on Smithwick Island, on Blake Point Peninsula, and in the Tobin Harbor area. His major description of the climax forest is from the Smithwick Island quadrats.

Cooper concluded that the climax forest of Isle Royale is composed of *Abies balsamea*, *Betula papyrifera*, and *Picea glauca*; that fir is the preponderant species because its seedlings can succeed in nearly any situation where enough light is available and because it reproduces freely by layering; that fir decreases the stand age because it is susceptible to windfall and fungal attack and because it competes with itself due to its abundant seedling survival; that paper birch does not germinate abundantly, but holds its own with fir because it is less susceptible to disease and windfall; that spruce is ecologically unimportant because of its relative scarcity; and that yew is the most important species of the undergrowth. Cooper also described, in some detail, the various primary and secondary successional stages.

Cooper returned to Isle Royale in 1926, and while he was unable to relocate his former quadrats, he described noticeable differences in the vegetation (Cooper 1928). He was able to duplicate a photo of a plot that he made in 1910. There was very little noticeable change in this plot over the 17-year period. This plot is located along the shore rocks in the Rock Harbor Lodge area, and today appears to have remained unchanged from its 1910 condition.

In 1929 and 1930, C.A. Brown was among those of the University of Michigan Herbarium who carried out field studies on Isle Royale. His published work (Brown 1936) is a compendium of Isle Royale species that had been reported by previous workers and added to by the herbarium party. It remained the most complete published annotated plant list for Isle Royale until the recently published list by Slavick and Janke (1984).

In addition to the invaluable annotated listing of ferns and flowering plants on Isle Royale in 1936, Brown included an excellent discussion of forest types and conditions existing at that time. Of particular value are the comparisons Brown made with the earlier accounts of Gleason and Holt (in Adams 1909) and Cooper (1914). For example, Brown noted the near disappearance of the once abundant Taxus as a result of extensive moose browsing, and the destruction of much aquatic vegetation by moose. This work is especially valuable since it fills an otherwise nearly complete void in the vegetational change record between Cooper's work in 1910 and the resurgence of interest in vegetation research in the 1950s. Very little evidence exists concerning the forest history of Isle Royale prior to the original land survey of Ives in 1847. The palynological work of Potzger (1954), however, makes it possible to describe the general forest history between the time that postglacial waters fell to expose the island surface and the present. Potzger's work centered on the pollen data collected from cores taken in bogs at three different elevations. The elevation differences coincided with known elevations of pre-Lake Superior lake levels. Potzger's data permits the association of gross forest history with a history of postglacial lakes ancestral to the present Lake Superior period.

During the 1950s Linn (1952, 1957) carried out botanical work at several sites on the island. His study attempted to discern the causes for existence of sugar maple and yellow birch, both where they form a definite climax community and where they occupy transitional positions, and causes for the distribution of the spruce-fir-birch forest on the island. Emphasis was placed on obtaining temperature differences among the seedling strata of various transitional and climax communities, soil moisture and soil physical characteristics of the communities, and vegetational characteristics. This work hypothesized that generally two distinct climates exist on the island: one near the lake, and the other within the island's interior locations, particularly in the wider southern portions of the island. Linn detailed the then-existing environmental differences among climax spruce-fir habitat, climax maple-birch habitat, and spruce-fir and maple-birch in the transition zone. Several of Linn's quadrats, established and mapped in 1951, were resampled in 1974. These data, unpublished at present, suggest that sugar maple is increasing in dominance where it has existed in the past, white pine also appears to be increasing where it exists, and paper birch appears to be holding its own in areas where fir is decreasing. A partial explanation of the survivability of maple in such a location at the extreme northern end of its range may lie in the studies of allelopathy by Flora (1977) who found that maple root extracts proved to inhibit the seed germination of other species.

During the summers of 1967 and 1968 T. Thurston, under the supervision of R.A. Janke from Michigan Technological University, studied the distribution and habitat preferences of devil's club (Oplopanax horridus) on the island. This member of the Araliaceae family is a disjunct on Isle Royale. Its only occurrences east of the Rocky Mountains are a few discreet locations on the Isle Royale archipelago and Porphory Island near Thunder Bay, Ontario. This species is most abundant on Passage Island. Earlier recordings of the occurrence of the species can be found in Cooper (1914).

Devil's club distribution was subsequently studied by Cebelak during the summers of 1980-81 as the subject of a masters thesis. During this study all known occurrences of devil's club were mapped and described, and were studied as to phenology, morphology, and general growth habits of selected individuals at selected locations. Cebelak's work was completed in 1983, and copies of his thesis are available in the park and at the Michigan Technological University library (Cebelak 1983).

Devil's club is the epitome of disjuncts in the Lake Superior basin, a region in which there are many. While the ameliorating effect of Lake Superior during postglacial times may have shepherded the species through the Xerothermic period and other events of stress, the true causes for the existence of these species are unknown. Botanical science could well profit from a more extensive study of the occurrence of devil's club on Isle Royale.

Moose-Forest Relationships

The arrival of moose to the island occurred sometime between 1905 and 1913 (Murie 1934; Hickie 1936). One needs only to walk briefly through the forests of Isle Royale to witness the striking impact of moose on the vegetation. A study in 1969 undertook to document the changes that moose have made on the boreal forest of Isle Royale since their arrival in the Park

(Snyder and Janke 1976). This arrival occurred sometime between 1905 and 1913 (Murie 1934; Hickie 1936).

The study took place on the northeast end of the park from Rock Harbor to Passage Island. This area was selected since the browsing intensity for several sites had been reasonably well documented since the 1930s. In addition, the nearby islands differed considerably from one another with respect to the amount of moose habitation and differences in forest age due to other factors such as fire. The study indicated that the tree species composition has been drastically altered by moose browsing in the past. This is especially true for species such as balsam fir (Abies balsamea), mountain ash (Sorbus decora), and white spruce (Picea glauca). In general, moose browsing has significantly reduced the tree density compared with control sites, but the basal area per tree has increased (Snyder and Janke 1976). Additional detailed data regarding the effects on shrub layers were also covered in this study.

Reports describing the forested conditions of Isle Royale prior to the establishment of moose on the island can be found in Adams (1909) and Cooper (1913a). Perhaps the most striking effect of the long-term moose browsing has been the near elimination of Taxus on the main island. Bergerud and Manuel

(1968) and Pimlott (1953) considered yew a reliable indicator of the presence or absence of moose browsing. The data summarized by Snyder and Janke (1976) also address the dynamic process of windthrow and its effect on the forest vegetation of Isle Royale. They suggested the possibility that the accelerated windthrow observed on many of the islands has been agravated by the intensity of moose habitation, and that the moose browsing in Isle Royale boreal forests has resulted in tree stands that are more open with fewer and larger trees, particularly in the understory. Also, the shrub layer has become lower and contains a greater abundance of low ground cover vascular plants with a greater ratio of windfalls to standing trees.

Fire Ecology and Post-Fire Succession in the Boreal Forest

During the 1970s a considerable amount of research on the role of fire in natural ecosystems was carried out in numerous national parks. Such a study was initiated during the late 1970s on the boreal forest type of Isle Royale (Janke 1983). The study's emphasis was on post-fire succession, the effect of fire on tree species reproduction, the susceptibility of several forest successional stages to fire, and adaptations of dominant species to fire. Post-fire succession was studied by collecting data from approximately 200 forest plots with stand ages varying from 40 to about 230 years in age. This study was approached from two directions: a direct comparison of species density means for five different ranges of forest stand age, and by deducing trends in the density of each species from the diameter class structure of that species in stands of the same age range. Results of this study show that birch and aspen are the most abundant post-fire invaders with jack pine locally important. With passing time, balsam fir and white spruce both increase in density, with indications that white spruce will increase in importance more so in the future. Ground cover diversity was also addressed in considerable detail for each of the successional forest stands.

The final report, summarizing the results of this five year study initiated in 1977, was prepared in 1983, and has been submitted to the National Park Service. Copies of the report are also available in the Department of Biological Sciences, Michigan Technological University. Janke possesses a copy of the map showing the approximate locations of transects and plots. However, most of these sites could probably not be located by anyone other than the principal investigator. Approximately 25 of these plots were located, photographed, and permanently marked with a stainless steel stake in 1982. Most of these plots are on the northern end of the island. It is hoped additional effort will be spent in 1984 or 1985 to locate an array of additional plots.

Janke's 1983 report also includes a number of additional plant ecological investigations. Site germination preferences for several species were investigated, as was the relative importance of revegetation by sprout or seed source. Additional work was also undertaken regarding the earlier stages of forest succession in a study initiated by Janke in 1981. This study compared three distinct post-fire forest stand types each dominated by different post-fire pioneer species namely paper birch, quaking aspen and jack pine. The aim was to characterize these stand types and to determine what factors favor one or another of them. This study sampled thirty stands for each vegetation type, and the sample sites included an array of topographic variability, soil characteristics, tree density, low vascular plant ground cover, and windfall abundance.

In the middle 1970s the National Park Service changed its policy regarding the absolute suppression of all fires in National Parks. Subsequent to this, two small natural fires occurred in forested areas of Isle Royale. Neither exceeded four hectares. In 1977 Janke established vegetation plots in both burns. Live, dead, and fallen trees were sampled in an effort to construct the pre-burn forest, and tree seedlings, shrubs, and herbs were sampled in the plots on an annual basis for four years in an effort to study reinvasion and succession. These relatively small disturbed sites provide the only data regarding vegetation re-establishment immediately following fires on Isle Royale. A partial summary of the results of this study can be found in the 1983 final report (Janke 1983). It is evident that some plant species (birch, aspen, fire weed) thrive only under the conditions associated with early stages of succession, while others (balsam fir, white spruce, twin flower) thrive only in later stages. The same may be said of animal species which utilize these plants. Moose and snowshoe hare, for example, do best in earlier stages of succession while woodpeckers and red squirrels do best in later stages. Maximum diversity of the flora and fauna of the boreal forest ecosystem is best maintained, therefore, by the presence of a mosaic of forest stands at different stages of succession. Maximizing diversity should be important in northern ecosystems where diversity tends to be inherently low. The increase in flammability of this forest type with time helps ensure that each stand will eventually burn and return to earlier stages of succession. This may be the natural mechanism by which the mosaic is maintained. If this boreal forest ecosystem is to be maintained in its natural state, it is important that this mechanism be permitted to operate in a natural way.

The Rock Shore Plant Communities

During 1979 and 1980 Janke undertook a study (Janke 1983) of the vascular plant life along the outer shoreline of Isle Royale. The substrate for this environment is largely made up of metamorphosed precambrian volcanics. Much of this environment has relatively recently emerged from Lake Superior and its predecessors as a result of isostatic rebound. Wave and ice action keep this environment relatively devoid of soil and it is quite sparsely vegetated. Janke's study took place on several study sites located in the northeastern portion of the main island and on several of the smaller northeastern islands. Vegetation was sampled along a gradient of differing elevations above the lake, and the data recorded include the percentage of the area covered by soil, average soil depth, presence or abscence of crevices, and other minor topographic features. The percent relative cover of the most abundant plant species in this environment is recorded in great detail. This was, in effect, a study of primary plant succession following emergence of the substrate above the lake level. Results of the study (Janke 1983) show that the vegetation in this environment does demonstrate primary succession, that the environment harbors many plant species not found elsewhere in the park, and it contains many arctic tundra species found far south of their normal distribution range. The results indicate that the rock shore communities are one of the outstanding natural features of the park and, properly interpreted, they should be highly attractive to visitors. Yet, because of the severity of the environment, they are a very fragile system, and without proper management visitor impact could be quite detrimental.

TERRESTRIAL FAUNA

Free-Living Terrestrial and Parasitic Invertebrates

Members of the invertebrate phyla Arthropoda and Mollusca were carefully surveyed in 1904 and 1905 by the expedition from the University of Michigan. An annotated list of species and comments on relative abundance in relation to plant successional patterns was published in Adams (1909).

The parasitic fauna of vertebrates on Isle Royale has not yet been systematically compiled. The only vertebrate species for which adequate records exist is the moose, which supports 3 ectoparasites (the winter tick, moose fly, and one species of leech) and several internal parasites, notably alternate stages of cestode parasites of the wolf (Peterson 1977).

In midsummer bloody lesions have been commonly observed on the rear hocks of moose. These appear to result from fly enlargement of wounds initially made by leeches as moose feed in aquatic environments (cf. Grosnick 1976).

Incidence of the winter tick appears quite variable, though ticks are commonly noted whenever substantial numbers of moose have been found dead from apparent malnutrition. Ticks appear to be associated with high densities of moose and have been frequently recorded at times of winter dieoffs of moose. The possible contributing role of ticks to moose mortality is the subject of current research in Alberta (W. Samuel, pers. comm.). Ticks were found on almost all carcasses of moose dying in the early 1970s (when malnutrition was evident), but were rare 10 years later after moose density had been reduced 50% (Peterson, unpubl. data).

Prominent in the parasitic fauna of the moose are 2 species that exploit the predator-prey relationship between wolves and moose. Taenia hydatigena up to 2 meters long were recovered from a wolf dying of natural causes, and the encysted stage is commonly present in low numbers in the liver of moose. Another common wolf-moose taeniid, Taenia krabbei, has never been recorded on Isle Royale.

Echinococcus granulosus has received the most attention at Isle Royale, since it may figure prominently in wolf-moose interactions and is a potential parasite of humans. The encysted stage has been found in lungs of all moose examined older than 3 years of age. Several dozen cysts measuring 2-3 cm in diameter may accumulate in moose that reach advanced age. Mech (1966) surmised that an accumulation of cysts probably reduced the ability of moose to resist wolf attack. There is some evidence that moose harboring Echinococcus cysts are more vulnerable to human hunters (Rau and Caron 1979), implying the existence of subtle behavioral responses in moose that would probably be readily detected by experienced wolves.

Terrestrial, Avian, and Semi-Aquatic Vertebrates

Isle Royale vertebrates are typical of temperate north latitudes, but the number of species is greatly reduced by the insular character. This is true especially for the mammalian fauna. Fortunately, those terrestrial vertebrates that are of greatest ecological significance (due to total biomass, turnover, or biotic effects on plants and other vertebrates) are present at Isle Royale: moose, snowshoe hare, beaver, and wolf. Thus, Isle Royale provides a simplified microcosm of boreal vertebrate fauna, though certain peculiarities (primarily due to the high density of moose) arise from the island character.

The fauna of Isle Royale is most comparable to the mainland to the north. At this northern latitude members of Amphibia and Reptilia are not of great ecological significance and relatively few species exist. Established at Isle Royale are 9 of the 14 amphibian species found on the northern shore of Lake Superior and 3 of the 4 reptiles (an additional reptile recorded only south of Lake Superior may exist at Isle Royale) (Jordan 1982). In boreal regions most of the vertebrate fauna are endothermic mammals, with 47 species recorded for the northern shore of Lake Superior. Only 14 mammalian species are known to occur presently at Isle Royale.

In spite of the reduced fauna, Isle Royale maintains natural food chains representative of boreal regions. The island is unique among Biosphere Reserves in North America outside Alaska in that top carnivores (i.e., gray wolf) still exist and are naturally-regulated.

An impressive number of extirpations and colonizations by new species have occurred during the present century. In 1904 the "representative mammals of the island" were the red squirrel, deermouse, snowshoe hare, and lynx (Adams 1909). At that time beaver had apparently been trapped to extirpation, woodland caribou existed at very low density, and wolf, moose, and red fox had never been recorded. Coyotes, unrecorded by Adams (1909), were reported present in the early 1900s by island residents (Mech 1966). Extirpations during the 1900s include the caribou, lynx, coyote, and probably the marten. New arrivals include moose and wolves; red fox, otter, and beaver were either colonizers or increased from very low levels in the early 1900s. The role that humans play in the extirpation of caribou, lynx and marten is unclear because there were substantial ecological changes that occurred simultaneously due to the rapid irruption of moose. Several trappers were active on the island in the early 1900s, and some trapping was continued by the Michigan Department of Conservation into the

1930s (Mech 1966). There is no mention in the literature of marten after 1912 (only 2 trapper reports of this species exist prior to that time); elsewhere in the Lake Superior region this species was extirpated by overharvest. Substantial numbers of lynx and coyote were trapped as late as the early 1930s (Mech 1966).

The colonization of the island by moose caused substantial changes in the structure of its forests, and likely influenced the distribution and abundance of other species considerably. Shrub density declined markedly and the understory took on a more open appearance, and evergreen Canada yew was replaced by deciduous thimbleberry in the understory. We speculate that a rapid rise in the moose population during the 1920s was responsible for the reduced density of snowshoe hare after about 1930. Hares were formerly the most numerous mammal on the island. There is considerable overlap in forage preferences of moose and hare, and moose browsing undoubtedly reduced the understory cover for hares. Snowshoe hares were probably key prey species for marten and lynx. Lynx in turn are highly capable predators of caribou calves (Bergerud 1971), and the role of lynx predation and harvest by humans in the dynamics of the small caribou population present in the 1920s is unknown.

Coyotes disappeared 8-9 years after wolves colonized the island in the late 1940s. Interspecific killing by wolves was undoubtedly the cause for the coyote's demise, and there is some likelihood that, prior to the arrival of wolves, coyotes were able to locally reduce red fox density. In the 1960s and 1970s several long-time island residents reported that foxes were more common than in the 1930s and 1940s. Presently, wolves kill foxes opportunistically, but coexistence is apparently possible because of the greater difference in body size between wolves and foxes than between wolves and coyotes (Peterson, unpubl. data).

Reptiles and Amphibians

The number of species of reptiles and amphibians is low because of the northern location of Isle Royale and its isolation. It is evident from Jordan (1982) that little is known of these species at Isle Royale beyond mere "presence or absence." Existing species lists may not be complete; e.g., the mudpuppy was collected in 1904 and 1905 but has not been reported since, and the speculative presence of the black rat snake is as yet unconfirmed.

Small Mammal Community and Associated Food Web

The small mammal community at Isle Royale is dominated by 3 terrestrial species--the snowshoe hare, red squirrel, and woodland deermouse. Johnson (1969) presented data on aspects of population density and biomass relationships for these three species. The snowshoe hare is the most important small mammal in total standing crop and annual turnover in biomass and is the principal prey of the red fox. Other predators of this group are seasonal and/or uncommon (short-tailed weasel, raptors, owls).

Woodland deermouse. The presence of only one small rodent species is most unusual for a boreal community. Johnson (1969) determined from live-trapping in 1966-68 that deermouse density on Isle Royale was similar to mainland areas. Since more than seven other small herbivores are absent from Isle Royale (Johnson 1969), one might suspect an enlarged ecological niche for the single deermouse species. However, Johnson's work suggested otherwise. There are evidently many vacant niches in the small mammal community.

Red Squirrel. This species is abundant and apparently fluctuates relatively little in total numbers, although detailed trends in density have not been documented. While reproductive success seems highly dependent on annual cone crops, the longevity of the red squirrels lends some stability to total numbers. Density and survival were determined by W. Johnson in 1966-68 on a live-trapping grid north of Conglomerate Bay. The same grid was live-trapped by R. Peterson in 1975 and density was found to be similar to that of 1966-68. The Isle Royale red squirrel (*Tamiasciurus hudsonicus regalis*) is a unique sub-species, differing slightly in color and skull parameters from mainland populations. The taxonomic relationships among squirrels from Isle Royale and both north and south shores of Lake Superior were determined from skull characters by Kramm et al (1975).

Snowshoe hare. Snowshoe hares on the main island at Isle Royale do not oscillate in dramatic 10-year cycles, as is typical of mainland populations. Rather, they seem to exist at relatively constant, low density. Johnson (1969) documented a 2-fold difference between hare density in 1962 at Chippewa Harbor compared to 1968, and suggested that peak density in the early 1960s was comparable to peak mainland populations. However, high hare numbers were not observed in the early 1970s, at least relative to mainland populations. Notably, extensive barking of preferred forage species in winter has not been observed at Isle Royale recently, while this is common on the mainland during peak snowshoe hare numbers.

Snyder and Janke (1976) determined relative densities of moose and snowshoe hares on a series of offshore islands that showed a gradient in winter moose density. They found an inverse correlation between the two species, supporting the idea that high moose density has precluded periodic build-up of snowshoe hares through effects on food and cover.

Aerial observations of relative track density in winter indicates that during the 1970s snowshoe hares reach locally high densities only in dense thickets of white cedar in the southwestern third of the island, especially within the 1936 burn. Perhaps intensive predation by red foxes prevents expansion of hares into surrounding habitats with less cover.

Red fox. Red foxes at Isle Royale rely heavily on snowshore hare for prey year-round. In late summer fruit of sarsaparilla (*Aralia nudicaulis*) is prominent in their diet. In winter foxes scavenge wolf-killed moose, the only available food at that time of year other than snowshoe hare.

There are no accurate estimates of population size for Isle Royale foxes. There are undoubtedly several dozen families of foxes, as most major campgrounds and settlements have a family associated with it. The foxes are largely unafraid of people and regularly solicit handouts of food from humans. For purposes of biomass estimation, we have used an estimate of 1 fox/mi^2 (0.39/km^2) as a "best guess" of fox density. R. O. Peterson (unpubl. data) recorded an index to winter aerial observations of foxes during 1972-82. These data show no consistent trend in observation frequency, from which we infer a relatively stable population. In light of the dramatic changes in wolf density during the same period, this suggests that intraspecific predation by wolves on foxes is of little consequence to the fox population. The greater difference in body size between wolves and foxes facilitates coexistence that never developed between wolves and coyotes.

Avian Community

With relatively few exceptions, bird diversity at Isle Royale is similar to the adjacent mainland. Avian mammals (bats) total only 4 species, and little is known of density, relative abundance, and wintering habits.

Early studies of birds at Isle Royale include McCreary (1909) and Peet (1909a,b), who compiled observations of bird species in relation to vegetation types and during fall migration, respectively. Adams (1909) provided a discussion of bird diversity in relation to plant successional patterns. Krefting et al. (1966) compiled an annotated listing of birds at Isle Royale, which was updated by Johnsson and Shelton (1960, rev. 1964) and Jordan (1982). Because there are inadequate observations, actual reproduction remains unconfirmed for most summer residents.

While Isle Royale contains elements of both northern hardwood and boreal forests, it has not been established to what extent this may enhance bird diversity. In 1982, K. Dodge (pers. comm.) studied habitat factors that affected the distribution of 7 species of warblers, concentrating on the conifer gradient from the shoreline to higher elevations.

Disappearance of bald eagle [Haliëtus leucocephalus (Linn.)], osprey [*Pandion haliaetus carolinensis* (Linn.)], and peregrine falcon (*Falco peregrinus* Tunstall) from Isle Royale in the last 2 to 3 decades corresponded with regional and even continent-wide reductions in these species due to biological magnification of biocide residues. R. Janke (pers. comm.) reports that peregrine falcons last nested successfully in the late 1950s, while eagles and ospreys persisted into the 1960s. Unsuccessful nesting attempts of both latter species were recorded in the early 1970s. Bald eagle populations in the Great Lakes area are recovering slowly, but successful nesting in the Lake Superior watershed is still rare.

Breeding of some bird species is restricted to only a few localized areas. Great blue herons nest in 3-4 rookeries on small offshore islands. Sharp-tailed grouse, common in 1905 (Adams 1909), presently are known to breed in only two locations (Mt. Siskiwit and Mt. Ojibway) where moose browsing maintains an open habitat with occasional shrubs. Cormorants, said to be a common nesting species during the heyday of commercial fishing in the 1940s (Jordan 1982), no longer nest at Isle Royale. Pied-billed grebes, also said to be a common nesting species in 1905, also are absent now in summer at Isle Royale.

Peregrine falcons are the prime candidate for reintroduction. There have been no successful nesting attempts by this species in the Great Lakes area since the 1960s, yet successful reintroduction is proceeding in areas of the eastern U. S. Bald eagle and osprey are still present in the region surrounding Lake Superior and presumably could recolonize naturally if/when conditions again become suitable.

Large Mammal Community

A simplified large mammal food web exists involving the wolf as predator and moose and beaver as prey. The lack of additional species of predator and prey and the protection from harvest by humans are key features that underlie long-term studies of the predator-prey relationship between wolves and moose. Research on these species was initiated and directed by Durward L. Allen, Purdue University, from 1958 to 1975, and continued by Rolf O. Peterson, Michigan Technological University, from 1975 to the present. Findings have been summarized by Mech (1966), Jordan et al. (1967), Jordan et al. (1971), Wolfe and Allen (1973), Wolfe (1977), Peterson (1977), and Allen (1979c).

Moose population history before the establishment of wolves was characterized by rapid increase followed by a large dieoff. Following colonization early in the 1900s, moose initially increased to about 3,000 by 1930. Estimates ran as high as 5,000 moose during the initial peak. At this time Adolph Murie (1934) recorded as many as 28 moose at a mineral lick at one time, and other observers reported observations of as many as 30 moose at Lake Richie in one day. With their forage supply devastated, the moose population crashed by 1936, with the largest dieoff apparently occurring in the winter of 1933-34. A second increase through the 1940s led to an apparently lower population peak, and another major dieoff in 1948 was reported by Krefting (1951). Forage renewal followed the 1936 fire and a smaller burn in 1948.

Wolves colonized Isle Royale around 1948-49 and apparently rapidly increased to a level of 20-25 wolves. Moose increased a third time during the 1950s and 1960s, to a level of approximately 1,200-1,300 animals. During the moose increase the wolf population remained stable.

By 1969 the moose population was at a peak level, recent burns had become unimportant to moose due to secondary forest succession, forage throughout the island was heavily utilized, and there began a series of 4 severe winters. Moose vulnerability increased dramatically, and in 1969-76 the wolf population exhibited an immediate functional response followed by a longer-term numerical response. Kill rates doubled, and calves were especially vulnerable during periods of deep snow (Peterson and Allen 1974). Many young adult moose falling prey to wolves were found to be growth-retarded, probably due to in utero malnutrition (Peterson 1977). The moose population declined about 50% in 1969-77 due to high mortality and low recruitment.

The wolf population increased steadily in the 1970s, reaching a high of 50 animals in 1980 (Peterson and Page 1982). By that time the island was partitioned into 5 pack territories; prior to 1972 only 1 to 2 packs were typically present. The rapid increase of wolves in the early 1970s may have been facilitated by a high beaver population, which furnished an important alternate source of food for wolves in summer. High wolf predation was circumstantially linked to a 75% beaver decline during 1974-80 (Shelton and Peterson 1983).

In 1980 wolves on Isle Royale reached a density of $1/11km^2$, more than twice the density beyond which wolves were formerly thought not to exceed ($1/25km^2$, Pimlott 1967). This is perhaps the most impressive demonstration of the lack of absolute numerical limits to wolf density; rather, wolf density is regulated in a long-term sense by food supply, with complex social behavior providing the mechanism for short-term changes in relation to food (Packard and Mech 1980). Significantly, wolves do not respond to moose density per se, but rather the density of vulnerable prey (Peterson 1977).

In 1980-82 the wolf population declined by 72% due to high mortality from malnutrition, and interspecific killing coupled with poor pup survival. Simultaneously moose calf survival reached the highest level ever documented at Isle Royale, and the moose population appeared to be poised for rapid recovery. These correlations suggest that wolf predation was instrumental in limiting calf recruitment during the late 1970s. Peterson and Page (1983) hypothesize that fluctuations (on a 20-30 year scale) of wolves and moose are characterized by a predator-prey cycle of exceptionally long duration.

Data being collected at Isle Royale on wolves and moose are summarized below, together with the duration of data collection:

1. total count of wolves in winter, 1959-85.
2. estimated moose population in winter, 1970-85; earlier estimates to 1930.
3. moose adult sex ratio and calf proportion in autumn.
4. wolf kill rate and food availability.
5. age and sex structure of wolf-killed moose (1959-85), plus incidence of pathology (1959-85), body size (1970-85), and bone marrow fat content (1968-85).
6. incidence of twinning from summer ground observations, 1959-85.
7. number of litters of wolf pups and minimum litter size, 1974-85.
8. wolf food habits in summer, from analysis of scats, 1959-62 and 1973-85.
9. wolf travel per day in winter, 1959-61 and 1971-85.
10. analysis of wolf social organization, pack sizes, 1959-85.

11. total count, every 2 years, of active beaver colonies, 1978-85, with previous counts in 1965 and 1974.

12. moose distribution in midwinter, 1960, 1967, 1969, 1970, 1972, 1974, 1979-85.

Moose-Forage Interaction. Initial studies of moose at Isle Royale focused on the relationship between moose and vegetation, for the effects of heavy moose browsing were obvious. A. Murie spent the summers of 1929 and 1930 studying moose at Isle Royale, and predicted that a population crash was imminent (Murie 1934). Later studies by Hickie (1936), Kellum (1941), and Coburn (1934) documented the moose die-offs of the 1930s, and summarized successful attempts to remove about 70 moose for re-stocking the Upper Peninsula of Michigan.

L. W. Krefting, of the U. S. Fish and Wildlife Service, began studies of Isle Royale moose in about 1945. His focus was again on the relationship between moose and forage. In 1948-52 Krefting established 4 exclosures measuring 50 feet square; these were sampled for stem density, size and species presence at intervals until 1972 (Krefting 1974). Characteristics of forest structure were summarized by Hansen et al. (1973). Browse transects provided trend information on availability and utilization of forage by moose in 1950-70 (Krefting 1974). During this time Krefting documented a decline in availability of all major forage species except balsam fir. Simultaneously, counts of moose pellet groups increased consistently, from which Krefting (1974) inferred that the moose population increased steadily. However, the extent to which higher pellet density might have reflected reduced digestibility of browse is unknown.

Since 1970 there have been several moose-vegetation studies. These findings, together with aspects of Krefting's work, are reviewed below.

Food Habits. Food habits of moose on Isle Royale have been estimated indirectly using browse utilization transects (Krefting 1974, J. de Waal Malefyt 1974), from actual observations of feeding moose (Edwards 1978), or from a combination of these techniques (Belovsky and Jordan 1978, Miquelle 1979).

These studies have been confined to either the southwestern end of the island where a sugar maple-yellow birch forest predominates or to the northeastern portion of the island where a paper birch-balsam fir-white spruce association is dominant. Because these areas differ in canopy and understory species, they provide moose with varying amounts of available browse, and consequently, direct comparisons of results are difficult.

Summer food habits of moose were estimated by Krefting (1974) using browse utilization transects at 3 different areas on

Isle Royale. Data for the sugar maple-yellow birch climax forest (southwest) suggest that a shift in moose diets occurred from 1946 to 1971. In 1946, diets were composed primarily of sugar maple, mountain maple, mountain ash, paper birch and trembling aspen. When Krefting sampled these areas again in 1971, 80% of the diet was composed of mountain ash and mountain maple.

Belovsky and Jordan (1978) found similar diets for moose inhabiting the southwestern end of the island during 1972-74. Using browse utilization transects and direct feeding observations, they calculated that 84% of moose diets consisted of mountain ash and mountain maple. Miquelle (1979), working in the same area in 1977-78, also found mountain maple and mountain ash to be the main components of summer moose diets. Miquelle suggested that the apparent shift in diet preference to primarily mountain ash and mountain maple may be a reflection of change in species composition or abundance resulting from years of heavy utilization by moose during all seasons of the year. His data also indicated that mountain ash and particularly mountain maple were more tolerant of utilization by moose than were other species.

Food preferences of moose inhabiting the northeastern portions of Isle Royale have been reported by Krefting (1974), who found that 78% of moose diets consisted of trembling aspen, mountain alder, juneberry, and beaked hazelnut.

Winter food habits of moose on Isle Royale have been estimated only from browse utilization transects run in spring. Belovsky (1981) reported that mountain ash, yellow birch, and mountain maple comprised 83% of winter moose diets on the southwestern portion of Isle Royale. Krefting (1974) also reported the importance of mountain ash along with trembling aspen, balsam fir, and paper birch.

Krefting's (1974) data for the northeastern portion of the island indicate that balsam fir and trembling aspen are important winter foods. J. de Waal Malefyt (1974) reported that 72% of all twigs removed were balsam fir.

The usefulness of browse utilization transects in estimating available biomass, biomass consumed, diet preferences, and the status of a population in relation to "carrying capacity" is very limited. To produce even reasonable results requires large numbers of randomly placed transects and, due to variability, statistically adequate sampling intensity is usually around 50%. Certain areas are overutilized every year due to heavy concentrations of animals (i.e., winter range), while other areas receive little or no use because they are avoided for other reasons (i.e., predator evasion).

For this reason, data presented by Krefting (1974), J. de Waal Malefyt (1974), and to some extent Belovsky and Jordan (1978) is of limited value. For example, using Krefting's figures, his winter sampling intensity was 0.0032% in 1945 and 0.0046% in 1971 in the spruce-fir-birch type (1.42 acres divided by 44,000 acres). Belovsky's data on winter diet selection was based on a total of 2,000 twigs. Although Miquelle (1979) provided good estimates of summer dietary preferences (at least in the Windigo area), no reliable data exist on winter diets of moose on Isle Royale.

Several recent studies have attempted to examine various aspects of the feeding strategies of moose on Isle Royale. Edwards (1978), working in the northeastern end of the park, compared diet selection of different sex-age classes of moose. She concluded that summer habitat selection and diet of lactating and barren (non-lactating) cow moose differed as a result of their different metabolic and energy requirements. Cows with calves limited their activities to areas in close proximity to water and commonly frequented islets as an anti-predator strategy against wolves. Barren cows were able to utilize areas farther away from water and therefore could be more selective in their diet.

Belovsky and Jordan (1978) attempted to quantify a number of parameters associated with time-energy budgets of moose, including daily intake rates, diet preferences, and the availability of different forage items. These data were then used to construct constraint equations for optimization models that were used to predict optimal diets, habitat selection and activity patterns (Belovsky 1978, 1981; Belovsky and Jordan 1981).

Miquelle (1979) also measured intake rates and diet selection of moose in summer. He concluded that although sufficient biomass existed for moose to meet their quantitative intake requirements by feeding on a monotypic diet of a preferred species, they chose a diverse diet of several preferred species.

Although many of the ideas presented by Edwards (1978) have interesting implications and make "biological sense," the data presented lend little support to her conclusions. When data were presented, sample sizes were generally small and confidence intervals ignored in analysis.

The limited work of Belovsky and Jordan (1978), which has given rise to subsequent publications (Belovsky 1978, 1981; Belovsky and Jordan 1981), is unfortunately flawed by numerous poor and inaccurate assumptions and is based largely on weak data that lacks statistical significance. Belovsky's assumption that maintenance and reproductive requirements for bulls and barren cows were equal is contrary to data available in the literature. He also overestimated the metabolic requirements of moose by approximately 30%. In addition, several of his constraint equations (concerning sodium requirements and ruminant digestion) are not supported by data. In summary, because the initial collection of data was very unorthodox and partially based on unreasonable assumptions, the subsequent models produced are of doubtful biological value. Miquelle (1979), who attempted to duplicate some of Belovsky's methods, discovered that at least 3 of Belovsky's assumptions were either invalid or could not be duplicated.

Although Miquelle (1979) provides data on summer feeding strategies of moose in terms of diet selection, we still know relatively little about use patterns, and nothing about home range size and the importance of optimal diets and its role in seasonal energy balance. Significant aspects of moose abundance and distribution remain poorly understood.

<u>Sodium Dynamics of Moose</u>. As a result of recent attention concerning the lower relative amounts of sodium in terrestrial versus aquatic plants, Jordan et al. (1973) hypothesized that moose on Isle Royale are obligated to feed on aquatic vegetation in order to meet their sodium requirements. This idea was further developed by Belovsky (1978). Belovsky estimated the sodium requirements of moose by accounting for the loss of sodium through defecation, urination, body growth, fat deposition, reproduction, and lactation, and by assuming that this amount must be replaced if moose are to remain in sodium balance. Results from diet optimization modeling which was

constrained by estimated sodium requirements suggested that 15% of a moose's diet should come from aquatic plants to meet these needs.

Aho (1978) measured the production of aquatic biomass and its utilization by moose at Isle Royale. In addition, he collected samples of aquatic plant species and analyzed them to determine sodium concentrations. Results indicated that sodium concentrations varied among and between species and among sites. Also he found that production of aquatic biomass was quite variable among ponds. Moose did not select feeding sites based on the availability of biomass, suggesting that other factors were involved (i.e., sodium concentration, palatability, ease of movement).

However, moose feeding on aquatics did not select for species with the highest sodium concentrations. Also, moose appeared to feed indiscriminantly within patches, suggesting that palatability was unimportant. Aho also could find no evidence suggesting that ease of movement was a problem for moose feeding on aquatics. Although sample sizes were small, Aho's data indicated that 74% of the total standing crop of aquatic vegetation was provided by lakes and that moose were removing an estimated 22% of aquatic plant production annually.

In view of findings by Aho (1978), it appears that there are other factors influencing the use of aquatic vegetation beyond those presented by Belovsky (1978) or Jordan et al. (1973). Although there is no question that sodium is an important mineral for moose, there is no evidence that supports Belovsky's (1978) contention that sodium is the limiting factor for moose on Isle Royale.

Finally, Belovsky's claim that sodium requirements can be met only from aquatic vegetation are unfounded. Natural mineral licks are used extensively by most ungulates in North America and apparently provide the sodium needs for species which do not ingest aquatic plants. Risenhoover and Peterson (unpubl. data) found that sodium was obtained in significant quantities from natural licks at Isle Royale.

AQUATIC SYSTEMS

The Great Lakes form a large drainage system which culminates in the St. Lawrence River. Mean discharge from the drainage is 6,600m^3/sec (Ragotzkie 1974). Lake Superior (185 m above sea level) is at the head of the drainage, and it is the largest and deepest of the Great Lakes. It also has the largest surface area of any freshwater lake in the world. Owing to the relative absence of anthropogenic influences and very erosion resistant substrate, Lake Superior is the "purest" of the Great Lakes. Its water contains an average of only 52 ppm total dissolved solids. Due to its large volume relative to its watershed area, the lake water residence time is 450-500 years.

The physical and biological characteristics of Isle Royale's aquatic systems, both streams and the numerous lakes, are considerably influenced by the immediate proximity of Lake Superior. Physical characteristics of aquatic systems such as temperature, seasonal variability in runoff, and to some extent aquatic chemistry, are the direct result of influences from Lake Superior. In addition, the aquatic biota composition, in particular fish species, are determined to some extent by the coterminous Lake Superior.

Physical and Chemical Properties of Water

Very little basic research on the environmental components of the aquatic system had taken place on Isle Royale prior to 1979. The most comprehensive long-term data base regarding physical characteristics of stream water is that from the U.S. Geological Survey's Hydrologic Benchmark Station located on Washington Creek, a third order drainage culminating in Washington Harbor near Windigo. Stream water chemistry and discharge data have been gathered on this watershed since 1964, and are published annually (State of Michigan's Water Resources Reports). Stream water quality, including occasionally trace and heavy metals, has been determined at this site an average of six times per year since 1967. These analyses also include an occasional survey of plankton species and pesticides. However, the level of resolution employed in determining pesticide concentrations and heavy and trace metals has been such that few trends, even if they were present, would be detectable.

During the latter half of the 1970s and very early 1980s, additional water quality data were gathered by Jordan et al. (1981, Univ. of Minnesota personal communication) on water chemistry in a few selected streams located in the southwest section of the park. This monitoring was done in conjunction with the research being conducted on the significance of sodium in the diet of moose. Subsequent to, but somewhat related, are the unpublished studies by Peterson (pers. comm.) regarding the cation concentrations, and especially sodium concentrations, of natural salt licks scattered around Isle Royale.

During the summer of 1979 Bowden (1981) collected cation data at selected upstream and downstream stations for three low-order streams in the southwest portions of the park, a region dominated by alkaline glacial till. In addition to the collection of routine cation data, field data included flow, pH, alkalinity, and conductivity along with replicate samples of macroinvertebrates. The latter have been keyed out to the genera or species level, and examples of all specimen groups have been made available to the Park Service and are currently housed at Michigan Technological University.

Several additional studies have placed emphasis on the deposition and levels of organics and heavy and trace metals in surface waters on Isle Royale. Beginning in the late 1970s and continuing up to the present, Gschwend and Hites (1981) have been conducting studies on the deposition rate and sedimentation rate of polycyclic aromatic hydrocarbons (PAH) in lake Siskiwit, the largest and deepest inland lake on the island. Fluxes of 10 PAH have been calculated for the site for time periods corresponding to the present, 1950, and 1900.

This survey, which has been done in conjunction with monitoring stations located on the south and the north shores of Lake Superior by the same investigators, will be completed in 1984. The research has been supported by the National Science Foundation, and annual progress reports are available at the park. Isle Royale was selected because of its isolation which provides the ideal substrate for looking at ambient deposition rates. The research record of these investigators strongly suggests that the data will be published in the near future.

During the summer of 1983 W. Strong (1983) located replicate precipitation event samplers on Mott Island to measure the atmospheric deposition of organic pollutants, specifically toxaphene, polychlorinated biphenyls (PCB's), and lindane. This was part of a region-wide study of organic pollutant deposition funded by the Canadian government through the Canada Center for Inland Waters. This was a once-only sampling effort, and unfortunately took place during what was probably the driest summer of the last 50 years in the Lake Superior basin. A progress report on the findings of this survey is available at park headquarters, but at present no publications have resulted from this work.

An extensive suite of heavy and trace metals, analyzed using Inductively Coupled Plasma Emission (ICPE), have been determined for precipitation and selected stream and lake samples within the Sumner and Wallace watersheds since summer 1983. These watersheds are located adjacent to Moskey Basin in the northeast section of the park, and the analyses are part of the long-term ecological monitoring of the effects of atmospheric deposition on watershed ecosystems (Stottlemyer 1983). Progress reports regarding this research are available at park headquarters, and the data base is maintained on computer files at Michigan Technological University. Publications regarding this research are just beginning to be submitted, and in time the data base will be part of the national data base being maintained by the Environmental Protection Agency (EPA) through contract at Brookhaven National Laboratories on Long Island.

There are very few data regarding bedload transport, or the stream transport of suspended sediments. The only such data known at present are those periodic samples that have been collected by the U.S. Geological Survey (USGS) since 1967 on sediment transport from Washington Creek near Windigo. These data are also available in the annual USGS data summaries published as part of the State of Michigan's Water Resources Survey.

Aquatic Biology

Until recently there also has been relatively little study of stream biota in the park. Isle Royale has long been recognized as a prime location for fishing, both commercial and recreational. Excellent accounts of the early commercial fisheries and fishermen that inhabited the island have been compiled by Rakestraw (1968) and Oikarinen (1979). Good references regarding the fishes of the Great Lakes Region are also available (Hubbs and Lagler 1964, Scott and Crossman 1973). The earliest study of the fishes of Isle Royale was conducted by Ruthven (Adams 1909), but the first intensive investigation of the fish fauna was performed by Koelz in 1929. Reference to these works can be found in Linn (1966). These studies found that many of the mainland species were lacking, and pointed out what possibilities Isle Royale might present in preserving a sample of aboriginal fish populations. At least eight taxa, 3 subspecies of minnow and 5 species of Coregonid fishes, are endemic to Isle Royale. Because of its isolation the Isle Royale fish fauna have been extensively studied by other investigators (Lagler and Goldman 1959, 1982; Wallis 1960). The latest edition of "Fishes of Isle Royale" (Lagler and Goldman 1959) states that a total of 49 species and 28 genera in 14 families are present in the waters of and immediately surrounding Isle Royale. Exotic fish species consist of brown and rainbow trout, sea lamprey, alewife, rainbow smelt, and several types of salmonids. These fishes reach the waters of the island by natural dispersal after introduction into other locations of the Great Lakes. The Isle Royale fishes represent less than one-fourth of the fishes indigenous to the Great Lakes as a whole (Lagler and Goldman 1959). The low diversity of fishes is explained by the isolated location and formidable cold water barriers between mainland shore fauna and the island. Those who have studied the fishes of Isle Royale have been surprised and puzzled by the presence of warm water mainland species (Linn 1966). Lagler and Goldman (1959) suggest that the northward dispersal of "southern" fishes came during the generally warmer period in the region which followed the last retreat of the glaciers.

Numerous streams on the island are periodically surveyed for the presence of the sea lamprey, and when found control measures are undertaken by the Fish and Wildlife Service. Limited additional physical and biological data are collected by the FWS as part of this program, but normally are not published. At best they would only represent conditions in selected streams on random and quite isolated dates. This work, conducted as part of the control program throughout the Lake Superior basin, is managed by the FWS in Marquette, Michigan. Their address is available from park headquarters.

A limited number of additional aquatic studies have been undertaken on the island. These deal with stream benthic invertebrates, lake macrophytes, and plankton populations and primary production rates. Bowden (1979) conducted a one year survey of benthic invertebrate populations in three streams of the southwest portion of the island. An additional aquatic invertebrate study has been conducted in the Siskiwit River by Johnson (1980).

Investigations of the aquatic vegetation have been few in number and quite general in nature. Perhaps the most comprehensive work on the inland lakes was by Cain (1962). His investigation was primarily from the air over an eight day period of time with minimal excursions on the ground. Cain's chief interest was to classify the lakes based upon their aquatic vegetation (both submerged and emergent macrophytes). He also considered macrophytes in proximity to the shoreline in this classification. Cain's work was not published, but both reports are available at the park's library. An earlier study by Koelz (1929), while principally devoted to a survey of fish species, also included considerable data on shoreline vegetation and emergent and submergent lake macrophytes. As with Cain this material also was never published, but a report exists in the park library.

More recently, taxa lists have been developed for a number of the lakes in the central and southern portions of the main island (Toczydlowski et al. 1980). This rather extensive unpublished report, conducted by advanced undergraduates at Michigan Technological University with support from the National Science Foundation, includes tabular data on the limnology, phytoplankton, insects, and aquatic plants (macrophytes) of eight island lakes and Chippewa Harbor. Copies of this report are available at park headquarters and the Michigan Technological University Department of Biological Sciences. In addition, Janke (1979-82) has collected and listed many aquatic plants as part of a project to produce an annotated list of Isle Royale plants which was recently published (Slavick and Janke 1984).

DISTURBANCE HISTORY

Introduction

Being a large island ecosystem, Isle Royale does not have many of the usual current anthropogenic impacts. There are no road vehicles, very few planes, few opportunities for establishment of exotic species, and no coterminous land use since the park is surrounded by Lake Superior. In addition, visitor ingress and egress is carefully controlled since park access is generally by boat and access points are few in number. Also, the park has one of the lowest levels of visitor use in the system with current annual visitation running about 13,000. This low visitor use is probably a factor of the relative difficulty of access, but more importantly perhaps is the hostility of the climate and environment during much of the year. Because of the impracticalities of access during winter, the danger to humans associated with this hostile environment, and the need to protect the endangered eastern timber wolf during the stressful winter season, the park is closed from November 1, to April 15 each year.

Visitor Impacts

On the whole, visitor impacts within the park seem to be minimal. Administrative authority presently appears adequate to regulate any activity should it be found a threat to the park's resources. Most of the park's visitors are backpackers who follow a network of trails and campgrounds. Due to the very dense nature of the vegetation, the widespread occurence of wetlands, and the topography, cross-country hiking is not popular. However, the presence of wetlands and shallow depth-to-bedrock in many areas does result in trails giving out and/or widening due to detour use. This has resulted in numerous instances of trail relocation to both reduce resource impact and maintenance costs (C. Axtell, Isle Royale National Park, per. comm.).

Visitor distributions in the park have been studied by Crowther (1980) and by the park staff. In addition, campground degradation has been studied by Axtell and Meldrum (1983, Isle Royale National Park, per. comm.). The latter study primarily centered around establishing photo plots and monitoring changes in bulk density of the soils in and about the campgrounds. In addition, during 1983-84 a water quality monitoring program was established at nine sites in the park where visitor use is most frequent (Bagley and Stottlemyer, per. comm.). This study also includes the monitoring of the sewage treatment plant outflow. Total coliform, fecal coliform, and fecal streptococci are monitored weekly. In addition, several sites are located along a stream above, in, and just below the most heavily used campground in the park. Stream water chemical quality is determined along with bacterial surveys at these stations in an attempt to correlate visitor use levels with stream water quality.

Historical Anthropogenic Impact

The history of man-caused effects on the island has been studied by numerous investigators in recent time. The effects of man-caused fires especially during the 19th century has been documented by Janke et al. (1978). The objective of this study was to examine how the man-caused fires associated with the very limited attempts at mining for copper on the island have effected the forest vegetation. Hansen et al. (1973) studied the role of fire and the fluctuating moose populations on the forest vegetation of the island. The objectives of this research were to identify and describe major forest types according to tree regeneration, shrub, and herbaceous components; and to associate primary and secondary successional trends in forest types with their consequences to wildlife populations, in particular moose. Complementing these studies and putting them in a more historical context is the paleolimnological work of Raymond et al. (1975) and of Stottlemyer (1984, MTU, per. comm.).

In addition to these more recent studies and syntheses, Potzger (1954) studied the post-Algonquin and post-Nipissing forest history of Isle Royale, upper Michigan, and northern Wisconsin. Rakestraw (1964) pulled together a historical background for preparation of a historical base map of the park outlining the extent of mining attempts during the 19th century. Rakestraw (1965, 1967) also documented in some detail the history of mining and mining families in the park prior to this century.

Despite these early attempts at mining copper much of the park escaped significant impact, and today significant portions of the park's vegetation are mature or old-aged. Numerous additional studies, reports, and publications regarding the effects of fire on vegetation can be found in Janke (1975, 1976, 1977, 1979, 1983).

Air and Water Pollution

Potentially the most significant impact to the natural resources of Isle Royale is the external input of atmospheric contaminants to the terrestrial and aquatic ecosystems. Many of the studies mentioned in the preceding sections on aquatics and climate contain some baseline information of possible value in the long-term assessment of change in anthropogenic atmospheric inputs into park ecosystems. Additional studies relate directly to this problem and are discussed below. As previously mentioned the oldest continuous indirect environmental monitoring of atmospheric pollutants are the data from the Washington Creek USGS Hydrologic Benchmark Station. These data serve as an indication of atmospheric input since there are no local sources of airborne contaminants.

The next oldest record of atmospheric inputs into the park is that started by the National Park Service and Michigan Technological University at Windigo in 1979 (Stottlemyer 1980, 1982). This continuing record is from bulk samples collected year-round at the Windigo Ranger Station near the southwest end of the park. This record was expanded with the addition of a monitoring station near the Moskey Basin in 1980. Both stations continue to operate to provide input data for the ongoing lake/watershed ecosystem study on the ecological effects of atmospheric contaminants. In August of 1980 a National Atmospheric Deposition Program site was established at Windigo, and the results from this station are published quarterly in the NADP reports from Ft. Collins, Colorado. This site is operated by park staff, and it is run in conjunction with the National Trends Network site at Michigan Technological University (MTU). The sites' supervisor is R. Stottlemyer, Department of Biological Sciences, MTU. All precipitation data from these stations are maintained on computer files at MTU. The primary objective in maintaining these stations is to provide baseline monitoring data for ongoing research on ecological effects. Most of the data relate to inorganic constituents including an array of heavy and transition metals.

Additional monitoring studies have been undertaken by Gschwend and Hites (1981), Strong (1983), and Stottlemyer (1982, 1983). These were discussed in the earlier section "Physical and Chemical Properties of Water".

SCIENCE FACILITIES AT ISLE ROYALE NATIONAL PARK

Environmental Monitoring

Currently there are two year-round monitoring stations located on the island. These are located at Windigo and in the Moskey Basin area in the Wallace Lake watershed. At Windigo there is a continuous recording rain gauge which has been in operation since 1980, a long-term recording hygrothermograph, and an event precipitation collector operated as part of the NADP program. Also, during the time the park is occupied daily weather records are taken as part of the NPS fire weather data program. In addition, the USGS has operated a precipitation collector ("rocket gauge") at Windigo since 1967 which provides the only historical annual precipitation data for the entire park. This station is operated in conjunction with the USGS Hydrologic Benchmark Station on Washington Creek. Finally, there is a bulk precipitation collector used for chemical analyses at Windigo which has been in operation since May 1979. This unit is ran as a "paired" collector with the NADP collector, and provides the only year-round precipitation quality data.

The Moskey Basin site contains a ten-channel Remote Area Weather Station (RAWS) which replaced an older station in operation since 1981. There is a nearly continuous record from a recording rain gauge, a long-term recording hygrothermograph, and bulk precipitation collector which has been used for determining precipitation quality. In addition, at the Wallace site and nearby Sumner Lake watershed there are four Parshall flume installations complete with Stevens Digital recorders which record year-round discharge from four first-order streams. Two of these stations continuously record stream temperature, and on a periodic basis have continuously recording pH meters installed.

There are two additional Parshall flume installations complete with stage height recorders at two other locations within the park. These are Moskey Stream, a first-order stream flowing into Moskey Basin from the north; and Washington Tributary (WATR), a first-order tributary flowing into Washington Creek from the north. The latter stream has about a five-year record while the former about four.

Two canopy throughfall and soil lysimeter plots have also been installed in the Wallace Lake watershed, and another plot on the Greenstone ridge at Windigo.

Since 1979 a qualitative and quantitative snow course has been sampled about six times each winter. This course follows a gradient of increasing elevation, and is located just outside the Windigo area.

Finally, the National Oceanic and Atmospheric Administration (NOAA) operates two RAWS stations in immediate proximity to the operating lights on islands just off the main island to the northeast and southwest. These were installed during the last year (1984), and record a partial basic weather data set.

Laboratory Facilities

In the park there are two facilities. At Windigo there are tent frames available for overnight use and limited field processing of samples. There are 9 x 12 foot tents available, and on occasion even larger units depending on current NPS needs for seasonal housing.

The Boreal Research Station, established in 1981, located on Davidson Island in the northeast portion of the park is the main in-park facility. It was established largely to support research needs associated with establishment of the park as an International Biosphere Reserve. It is the site where most of the work associated with the ongoing long-term ecosystem study is conducted. The main facility has room for approximately seven persons. An additional walled tent platform can accomodate four. There is a 300+ square foot laboratory facility equipped with sinks, a dry lab area, drying oven, Muffle furnace, Wiley mill, pH meters, titration facilities, spectrophotometer, and other water quality instruments, and bacteria incubator. The lab routinely is used to partially process soil, plant tissue, and water samples.

The Boreal Research Station is self-supported. It maintains two research boats, 16' and 18' Lunds equipped with 40 and 50hp motors. The facility has adequate storage facilities, and is conveniently located to both air and boat access to and from the park.

Support facilities are located principally at Michigan Technological University in Houghton about 65 miles to the south. A National Park Service Cooperative Studies Unit (CPSU) is located at the university, and the university is well equipped to handle most analysis needs relatively efficiently through the CPSU. The CPSU maintains a laboratory equipped to process and do detailed inorganic and organic analyses of soil, plant tissue, and water samples. In addition, the university has the best research library in the region with ready access to additional libraries through a computer service.

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TABLES

TABLE: GEOLOGY

Objective/Subject	Remarks	Location	Sampling Date	Reference
Regional explorat/ copper deposits Lake Superior	Earliest survey of region with objective being mapping of stratigraphy and location of copper deposits. Some	Great Lakes Basin	——	Agassiz (1850)
Mapping and interpretation volcanics	Detailed interpretation of Portage Lake volcanics on south shore. Same formations found on Isle Royale but these not mapped.	Lake Superior south shore in particular	——	White (1960)
Define nature and origin copper deposites	Integration and summary of origin of of copper deposits in Michigan's Upper Peninsula.	Michigan's Upper Penin.	——	White (1968)
Keweenawan geology	Relationship of Keweenawan rock groups in Lake Superior Basin described. Largely a review of earlier work.	Lake Superior Basin	——	Halls (1966)
Glaciation on land forms	Description of effects of Pleistocene Glaciation on landforms especially area along north shore of Lake Superior.	Upper Great Lakes Basin	——	Bird (1972)
Ancient lake levels	Summary of previous research on glacial and post-glacial lake levels in Lake Superior Basin. Diagrammed.	Lake Superior Basin		Kelly and Ferrand (1967)
Synthesis/interpretation of geology	Relatively recent comprehensive interpretation of geologic history and deposites in the State of Michigan.	State of Michigan	——	Dorr and Eschman (1970)
Native copper mining	Accounts of man's early pursuit for native copper in the Lake Superior Basin. One of earliest documents.	Upper Great Lakes Basin	——	Foster and Whitney (1850)
Prehistoric mining	Accounting of prehistoric man's mining activities in Lake Superior Basin and especially Isle Royale.	Upper Great Lakes Basin	——	Griffin (1961)
Post-indian copper mining	Summary and evaluation of post-indian mining activities, especially 19th century, on Isle Royale.	Lake Superior Basin and Isle Royale	——	Rakestraw (1965)

TABLE: GEOLOGY				
Geology of Isle Royale	Most comprehensive mapping and interpretation of the geology and glacial deposits on Isle Royale. One of a series of publications by author on Isle Royale and Lake Superior Basin.	Isle Royale and some of Lake Superior Basin	---	Huber (1975)
Geologic map of park	Detailed map of precambrian metamorphos--ed bedrock on island, its isolated and rare veins of sedimentary material, and map of glacial till deposits on southwest portion of island.	Isle Royale	---	Huber (1973)
Geology of Lake Superior area	Recognized relationship between bedrock of south shore of Lake Superior and that on Isle Royale.	Lake Superior Basin	---	Lane (1898)

TABLE: SOILS

Objective/Subject	Remarks	Location	Sampling Date	Reference
Description of thin organic soils	Sampled seven locations on northeast end of island. Detailed physical descriptions (SCS), but no chemistry. Sampling only in boreal forest. Written report at MTU.	Isle Royale, North east boreal forest	1976	Shetron (1977) [unpub]
Soil fractions and chemistry, three forest types	Soil fractions and complete chemistry for 30 samples collected under three foest types: jack pine, aspen, w. birch. Written report filed at Dept. Biol. Sci. and with NPS, Houghton.	Northeast Isle Royale	1981	Janke (1981) [unpub]
Soil description and chemistry in boreal forests	Complete description and chemistry forest soils under spruce, birch, and maple. Data collected as part of soil anion mobility study in high and low organic soils. Written report at MTU.	Isle Royale and Keweenaw Peninsula	1983-84	Stottlemyer (1983) [unpub]

TABLE: CLIMATE

Objective/Subject	Remarks	Location	Sampling Date	Reference
State climate summaries	State climatological summaries by year and month. Standard physical data, no chemistry. No multi-year summaries.	Mott Island on Isle Royale and Houghton County Airport	----	NOAA (1965-84)
Daily weather collection	Standard "fire weather" data collected on daily basis during occupancy of Island. Data recorded by month and is kept in NPS files at headquarters. Same data used by NOAA.	Mott Island, Windigo, Isphming Tower	----	NPS (1956-84) [unpub]
Winter season weather conditions	Observations of temperature, precip, relative humidity, snowpack depth and density. Some data published but most in personal files at MTU.	Windigo on Isle Royale	1972-84	Peterson (1975)
Seasonal and annual precip. and temp.	Precipitation and stream temperature data to support study at Hydrologic Benchmark Station on Washington Creek. Data published annually in State Geological Survey Annual Report. Data include stream discharge.	Washington Creek and Windigo.	1968-84	USGS (1968-84)
Weekly quality and quantity of prec.	Precipitation quality and quantity, max/min. temp., RH, wind speed and direct., snowpack accum. and chemistry. Some data published, vast majority maintain. in computer files at MTU.	Windigo, Moskey Basin, Davidson Island	1979-84	Stottlemyer (1979)
Monthly precip. quality and quant.	Precipitation chemistry and amount, one tation. Sponsoring program unknown as is investigator. Data file maintained by Stottlmyer at MTU. Data quality very suspect.	Windigo, Isle Royale	1976	Annon. (1976)
Meteorological summary	Annual meteorological summaries for north shore of Lake Superior about 32km to NW of Isle Royale. Best data set for north shore which is relatively less affected by lake. No chemistry.	Thunder Bay, Ontario	1936-84	Environment Canada

TABLE: AQUATICS

Objective/Subject	Remarks	Location	Sampling Date	Reference
Role of aquatic Na in plants/moose	Looked at sodium content of water in streams, aquatic plants, and moose.	Mostly southwest end of park.	1975-1980	Jordan et al.(1981
Stream chemistry	Relationship of stream water chemistry and benthic invertebrates.	Washington Creek, Little Siskiwit, Grace Creeks	1979-1980	Bowden (1981)
Remote deposition of PAH	Deposition rates (historical) of PAH in remote sites as indicator of ambient input levels.	Siskiwit Lake	1981-1984	Gschwend and Hites (1983)
Atmospheric input of anthropogenic organics	One-season study of organic deposition remote sites without local point sources.	Mott Island	1983	Strong (1983)
Atmospheric input inorganics	Anthropogenic inputs of inorganics including heavy metals to gaged watersheds for input/output budgets.	South and north ends of island	1979-1984	Stottlemyer (1983)
Precipitation input	Maintain precipitation collector on year basis for baseline data to merge with stream data from Hydrologic Benchmark Station at Washington Creek.	Windigo	1967-1984	USGS (1983)
First analytical fish survey	Comparison of island's fish species to those found on mainland to hypothesize on migration.	Island-wide esp. margins	1927?	Koelz (1929)
Taxonomy of island's fish	Taxonomic study to assess effects of isolation on fish populations of park.	Island-wide	1956-1958	Lagler and Goldman (1959, 1982)
Baseline aquatic survey.	Lake aquatic baseline surveys for six lakes including water chemistry, plankton, macrophyte data.	South and southwest end of island	1979-1980	Toczydlowski et al. (1979)

Plant Surveys/Ecological Studies

Objective/Subject	Comments	Location	Sampling Dates	Reference
Original land survey	map and survey notes	Isle Royale	1847	Ives (1847)
Ecology of Mosses	Describes ecological succession of mosses	Northeastern Isle Royale	1909-1910	Cooper (1912)
Description of climax forest and its succession	Traces successional changes through to climax (boreal forest stands)	Northeastern Isle Royale	1909-1910	Cooper (1913a)
Catalogue of moss species	List of mosses collected	Northeastern Isle Royale	1909-1910	Cooper (1913b)
Catalogue of vascular plant species	List of vascular plants collected	Northeastern Isle Royale	1909-1910	Cooper (1914)
Successional change	Compares 1910 with 1926 vegetation	Northeastern Isle Royale	1909-1926	Cooper (1928)
Study moose of Isle Royale	Qualitative observations; stomach analysis, measured physical dimensions of carcasses	Isle Royale	1929-1930	Murie (1934)
Catalogue of vascular plants	Annotated list of vascular plants found to date and a description of vegetation	Isle Royale	1929-1930	Brown (1936)

Livetrap moose and transport to Upper Peninsula of Michigan	Summarized history of moose on Isle Royale and describes the live trapping operation	Isle Royale	1934-1937	Hickie (1936)
Postglacial forest history	Bog pollen profiles	Isle Royale	1950	Potzger (1954)
Climax forest causal factors	Describes some causes for both boreal and deciduous forest climax types on Isle Royale	Isle Royale	1951-1956	Linn (1952, 1957)
Interpretation of Original Land Survey	Interpretation of Land Survey notes	Isle Royale	--	Gilchrist (1968-69)
Effects of moose on boreal forest type on Isle Royale	Compared moderately browsed, heavily browsed and unbrowsed areas in northeast end of park.	Isle Royale	1969-1970	Snyder and Janke (1976)
Postfire succession	Interactions of fire, forest tree species and moose	Isle Royale	1975-1981	Janke (1978, 1979, 1980)
Vegetational change	Vegetational changes between Ives 1847 survey and later work in the 1970s	Isle Royale	1975-1979	McKaig (1979)
Disjunct species	Describes rockshore plant communities	Northeastern Isle Royale	1979-1980	Janke (1981)

Disjunct species	Describes occurrence of *Oplopanax* *horridus* on Isle Royale	Northeastern Isle Royale	1980-1981	Cebelak (1983)
Catalogue of vascular plants	Annotated list of vascular plants found to date, description of environment and vegetation, and traces botanical history	Isle Royale	1962-1983	Slavick and Janke (1984)

Terrestrial Faunal Surveys/Ecological Studies

Objective/Subject	Comments	Location	Sampling Dates	Reference
Zoological survey	Annotated list of vertebrates and invertebrates, U. of Mich.	several fixed sites	1904-5	Adams (1908)
Leech survey	Annotated list of species, N. Michigan Univ.	interior lakes throughout island	1974-5	Grosnick (1976)
Snowshoe hare, red squirrel, woodland deermouse	Study of small mammal community and associated food web	hares- Chippewa Harbor squirrels- n. Conglom. Bay Deermice- n. Conglom. Bay	1967-9	Johnson (1969)
Snowshoe hares - density on offshore islands	Found inverse relation between hare numbers and moose numbers	selected islands at NE end	1976	Snyder and Janke (1976)
Taxonomic status of red squirrels	Compared skulls of IR and mainland squirrels		1975-6	Kramm et al. (1978)
List of bird species	Focused on relation of birds seen to vegetation types			McCreary (1908)
List of bird species	Focused on birds seen during fall migration			Peet (1908)
Bird density in relation to plant successional stages				Adams (1908)
Annotated list of Isle Royale birds				Krefting et al. (1966)

Objective/Subject	Comments	Location	Sampling Dates	Reference
Updated list of Isle Royale birds				Shelton and Johnsson (1964)
Updated list of Isle Royale birds				Jordan (1982)
Habitat factors affecting distribution of 7 species of warblers		SW end of IR	1982	Dodge (1983)
Predator-prey studies			1958-present	Mech (1966) Jordan et al. (1967) Wolfe and Allen (1973) Wolfe (1977) Peterson (1977) Allen (1979)
Ecological studies of beaver	Population study	NE end	1962-4	Shelton (1966)
Moose-forage interaction	Moose at peak; crash predicted	NE 1/3 of IR	1929-30	Murie (1934)
	Natural history studies; moose removal to mainland			Hickie (1936)
	Moose feeding experiments			Kellum (1941)
	Moose necropsied during 1934 die-off			Coburn (1934)
	25 year exclosure study	4 sites		Krefting (1974)
	Vegetation history with reference to moose requirements			Hansen et al. (1973)

Objective/Subject	Comments	Location	Sampling Dates	Reference
Food habits of moose	Browse utilization transects	NE end		deWaal Malefyt (1974)
	Summer feeding on Aralia nudicaulis	Tobin Harbor		Edwards (1978)
	Summer feeding strategies	SW end		Belovsky and Jordan (1978)
	Moose diet diversity in summer	SW end		Miquelle (1979)
Sodium dynamics of moose	Summer feeding study	Washington Harbor		Belovsky (1978)
	Moose use of aquatic plants	Washington Harbor		Aho (1978)
Moose population estimates	Reviewed aerial and ground techniques			Stephens (1979)