Great Lakes

“If we could first know where we are and whither we are tending, we could better judge what we do and how to do it…”

Abraham Lincoln

The Great Lakes region, as defined here, includes the Great Lakes and their drainage basins in Minnesota, Wisconsin, Illinois, Indiana, Ohio, Pennsylvania, and New York. The region also includes the portions of Minnesota, Wisconsin, and the 21 northernmost counties of Illinois that lie in the Mississippi River drainage basin, outside the floodplain of the river. The region spans about 9º of latitude and 20º of longitude and lies roughly halfway between the equator and the North Pole in a lowland corridor that extends from the Gulf of Mexico to the Arctic Ocean.

The Great Lakes are the most prominent natural feature of the region (Fig. 1). They have a combined surface area of about 245,000 square kilometers and are among the largest, deepest lakes in the world. They are the largest single aggregation of fresh water on the planet (excluding the polar ice caps) and are the only glacial feature on Earth visible from the surface of the moon (The Nature Conservancy 1994a).

The Great Lakes moderate the region’s climate, which presently ranges from subarctic in the north to humid continental warm in the south (Fig. 2), reflecting the movement of major weather masses from the north and south (U.S. Department of the Interior 1970; Eichenlaub 1979). The lakes act as heat sinks in summer and heat sources in winter and are major reservoirs that help humidify much of the region. They also create local precipitation belts in areas where air masses are pushed across the lakes by prevailing winds, pick up moisture from the lake surface, and then drop that moisture over land on the other side of the lake. The mean annual frost-free period—a general measure of the growing-season length for plants and some cold-blooded animals—varies from 60 days at higher elevations in the north to 160 days in lakeshore areas in the south. The climate influences the general distribution of wild plants and animals in the region and also influences the activities and distribution of the human population.

The wild plants and animals and the natural systems that support them in the Great Lakes region are valuable resources of considerable local, regional, and national interest. They are also, in part, transboundary resources that we share with our Canadian neighbors to the north. The way these resources are changing over time is inadequately known and is a cause for concern for resource users and for those charged with managing and protecting these unique and valuable resources. This chapter describes the wild plants and animals and the systems that support them in the Great Lakes region; addresses their condition; and points out the gaps in our knowledge about them that, if filled, would aid in their conservation and appropriate use.

Regional Setting

Geology and climate are the major physical factors that influence the distribution and abundance of native plants and animals on a broad scale across the Great Lakes region. Much of the Great Lakes watershed lies in the Michigan Basin, an area centered in the Lower Peninsula of Michigan where an ancient, massive sinking of the surface of the Earth occurred

Courtesy M. Mac, USGS

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Fig. 1. The Great Lakes are a major physical feature of the North American continent.

Courtesy National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan

(Hough 1958). In the center of this basin, Precambrian rocks more than half a billion years old are overlain to a depth of 3,000 meters with Paleozoic rock 185–520 million years old and also with newer sedimentary and glacial deposits (Dorr and Eschman 1970). The Precambrian rocks slope upward to form the Canadian Shield, which lies north of the Great Lakes and extends into Minnesota, Wisconsin, and the western portion of the Upper Peninsula of Michigan. These rocks, which are generally hard and dense, underlie Lake Superior and form much of its shoreline. They also underlie and form much of the shoreline of Georgian Bay on the northeastern side of Lake Huron. The softer Paleozoic rocks, which include limestones, dolomites, shales, and sandstones, were laid down in the Michigan Basin 185–520 million years ago when the area was covered with a shallow sea. These are the rocks that were most deeply eroded to form major surface features, including the basins of the four lower Great Lakes.

During most of the last million years, the climate in the region favored the formation of glaciers. These glaciers reshaped the Earth's surface in the region, creating a low-relief surface, with elevations ranging from 700 meters above mean sea level in the Minnesota highlands north of Lake Superior to about 220 meters below mean sea level at the bottom of Lake Superior.

The last Ice Age, which ended about 12,000 years ago, produced an ice sheet that pushed enormous amounts of glacial till across the surface of the land. This till ranged from boulders several meters in diameter to fine silt and lake clays with particle diameters of a fraction of a millimeter. The ice smoothed the landscape in some areas, grinding down bedrock highs and depositing till in valleys and other depressions

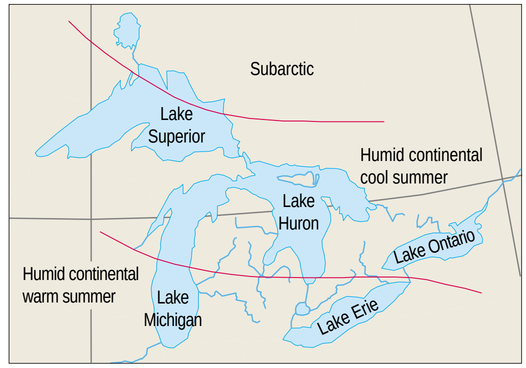

Fig. 2. Climate of the Great Lakes region.

between high areas of resistant bedrock. In other areas, including parts of the present basins occupied by the Great Lakes, the advancing ice sheet gouged the surface more deeply instead of filling and smoothing it. As the climate changed, the ice sheet stopped advancing and began to melt, and the till being transported by the ice was deposited in a variety of distinctively shaped ridges, hills, terraces, plains, and other landforms that provide much of the varied topography in the region. These landforms reflect both the thrust of the ice and the subsequent eroding action of the water that flowed out of the melting ice sheet.

The various tills or parent soils distributed broadly across the region by the ice sheet (Fig. 3) weathered differently to produce soils of varying fertility and water-holding capacity. The calcareous soils derived from limestone and related sedimentary bedrock were generally more suitable for colonization by plants than the sandy soils that were produced from sandstone and the harder crystalline bedrock from the northern part of the region. As the glacier retreated, water levels in the Great Lakes fell tens of meters and areas of former lake bed with sandy, silty, and clayey sediments became available to terrestrial plants and animals. Wind also redistributed the finer till, creating the silt-rich loess deposits in the southwestern portion of the region. The postglacial bedrock formations, elevation, local topography, precipitation patterns,

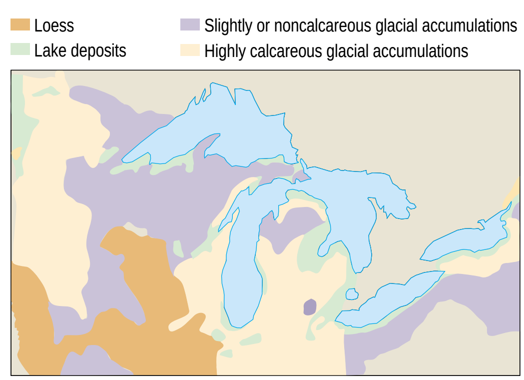

Fig. 3. Distribution of parent soils (glacial till) in the Great Lakes region (after Whitney 1994).

and soils also influenced the distribution of surface water, creating streams, lakes, and wetlands, which in turn influenced the local distribution of native plants and animals.

The plants and animals that colonized the area after the ice sheet retreated were from ice-free areas to the east, west, and south. Tundra vegetation was established in the northern portion of the region at least 10,000 years ago. As the climate moderated, tundra was replaced by a succession of larger plants, including coniferous and hardwood tree species typical of a warming environment. The forests were typically spruce and fir in the north, and beech, maple, oak, and other hardwoods in the south. Prairie grasslands developed at the region's drier western end and along its southwestern edge. Farther east, these prairie grasslands graded into savannah grasslands with sparse tree cover. Prairies and savannahs reached their greatest sizes in the region during the warmer, drier period that ended about 7,000 years ago (Barnes and Wagner 1981).

Animal communities became established in the area soon after the ice sheet retreated; their composition changed with the changing vegetation and climate. The muskox was an early inhabitant that lived near the ice front and moved north out of the region as the ice sheet retreated. A number of other large, now-extinct Ice Age mammals were also recorded in the region. Moose and caribou occupied the northern areas, elk occurred in some areas, and white-tailed deer were common in the south. Some coldwater aquatic species, including the whitefishes and the small mysid shrimp eaten by whitefishes, became established as the ice retreated. These relict glacial species are abundant today in the Great Lakes.

Archaeological evidence indicates that humans occupied portions of the region shortly after the last ice sheet retreated. Human occupation in the Saint Marys River valley at the north end of the region dates back 11,000 years (Conway 1977, 1980). These early people were hunters who moved frequently in search of food; they did not establish permanent villages (Cleland 1982). As these people's fishing implements improved and their spears and gorges (a primitive fishhook) were replaced with nets, fish became a more important food for them. Seasonal or permanent villages were established at sites containing concentrations of catchable fish. One such site in the Saint Marys River valley was occupied continuously by humans for about 2,000 years preceding the arrival of the first European explorers in the early 1600's.

About 1,000 years ago, four subsistence patterns based on domesticated plants, fishing, hunting, and wildrice had evolved in the region, and some people may have systematically exploited all of these resources in different seasons (Tanner 1986). In the south, where the growing season was longer and agriculture was an important contribution to subsistence, more permanent villages developed. The first introductions of nonindigenous species in the region, including domesticated forms of maize and beans from Central and South America, are attributed to these early cultures.

There is scholarly debate about the role of early humans in the extinction of some of the large Ice Age animals. Similar debate exists about the effects of the more recent and populous American Indian cultures on plants and animals, and their ecosystems. The local scarcity or extirpation of some food types and the deliberate use of fire to maintain some natural plant community types—particularly the prairie and savannah ecosystems in the western and southern portions of the region—have been attributed to these more recent Indian cultures.

Settlement of the region by the new Americans of European descent began in the late 1700's on the south shores of Lakes Ontario and Erie. Settlement spread rapidly westward, and by 1820 all of the drainage basin was settled from the south shore of Lake Ontario and Lake Erie and the west shore of Lake Erie to Detroit, Michigan. In 1835 settlements extended across southern Michigan, northern Ohio, Indiana, and Illinois, and into southern Wisconsin. By 1890 the entire region was settled except for the portion of Minnesota east of a line from Duluth to Lake of the Woods on the Canadian border.

Settlement brought about major changes in the landscape. Forest cover was removed to permit farming and for lumber and fuel (see chapter on Land Use), and streams were dammed to provide waterpower for mills and other industries (see chapter on Water Use). The vast eastern white pine forests in the lower peninsula of Michigan and northern Wisconsin were clearcut for lumber from 1850 to 1890. Large forest fires occurred in northern Michigan and Wisconsin during that same period, and the accumulation of branches and treetops discarded during logging contributed to intense, widespread fires that burned with such heat that they destroyed much of the humus in the sandy northern soils. The combined effect of the fires and logging led to the replacement of the pine forests with hardwood or mixed hardwood and pine forests. In the southern part of the region, nonforest areas—including grasslands, savannahs, and large wetlands in the lake plains—were also among the first lands converted to agriculture.

Settlement also affected the native animals, restricting their distribution and abundance and causing the extinction of a number of notable species. The extinction of the Atlantic salmon in the Lake Ontario drainage took place in the 1800's and was attributed to overfishing during spawning, the construction of mill dams that prevented fish from reaching their spawning grounds, and forest removal that reduced streamflow, increased stream temperatures, and made streams unsuitable nursery areas for young salmon (Smith 1972; Webster 1982). The arctic grayling, which had been abundant in streams in northern Michigan, became extinct in the early 1900's, probably through the combined effects of forest-cover removal, overfishing, and the introduction of trout into its habitat. The passenger pigeon, which had nested in aggregations of as many as several million birds in northern Michigan and portions of Wisconsin, was hunted intensively during its nesting season and suffered major population declines in the late 1800's. The species became extinct at about the turn of the century. Hunting for commercial markets and the conversion of wetland habitat to farming sharply reduced the number of waterfowl that nested in the region or migrated through it. Bison, which had inhabited the savannahs in the southwestern part of the region, disappeared with settlement. Likewise, white-tailed deer and wild turkeys had been common in the forests and savannahs of southern Michigan at the time of settlement, but by the late 1800's uncontrolled hunting had eliminated the turkeys and most of the deer in the southern part of the state. In northern Michigan, the last caribou was seen on an island in the lower Saint Marys River around 1900 (Bayliss and Bayliss 1955). Self-sustaining populations of elk, gray wolf, fisher, and marten in the region were lost because of hunting and trapping.

Settlement also brought into the region many nonindigenous species from various parts of the world. Many of these were domesticated species that were intensively cultured. Other introductions were often wild European species that were accidentally or deliberately introduced. Some of these introductions were beneficial and filled habitats that would no longer support extirpated native species, but many had substantial undesirable effects on native animals and plants.

The human population in the region increased markedly after 1850, when most of the region had been settled. In Illinois, for example, the population increased almost linearly from slightly less than 1 million people in 1850 to more than 9 million by 1970 (Illinois Department of Energy and Natural Resources and The Nature of Illinois Foundation 1994). About 95% of the population of Illinois lived in rural areas in 1850, but by 1970 about 85% of the population lived in urban areas. Similar rapid growth and urbanization occurred in other parts of the region, with the highest population density occurring in a band across the southern portion of the region. In Michigan, the inhabitant-to-land density in the 1970's exceeded that in China at the beginning of the twentieth century. The population of Michigan now exceeds that of about 170 nations in the world (Santer 1993). A similar demographic situation exists in the Canadian portion of the Great Lakes basin, which supports a population greater than half of the nations in the world. In 1990 the Great Lakes basin in the United States and Canada contained more than 95 metropolitan-sized communities of at least 50,000 inhabitants each. The U.S. population in the eight states bordering the Great Lakes was about 77 million, of which about 34 million resided in the Great Lakes region (U.S. Bureau of the Census 1994).

This brief description and history of the region is intended to provide a context in which the status and trends of the present plant and animal species, natural communities, and ecosystems of the region could be examined. The changes in the region, particularly those that have occurred since settlement, are reasonably well documented. Detailed knowledge of the processes that brought about these changes continues to elude us, but it is clear that dramatic change occurred in the plants and animals and their ecosystems during the first 10,000 years of human occupation and that humans contributed to this change. It is also clear that climate was the major instrument of change and that the change occurred extremely slowly when compared with the change that occurred during European settlement in the late 1700's–1800's and in the years between then and the present. It is evident that the change during and following settlement was the consequence of resource use patterns and species introductions that deliberately or incidentally resulted in the alteration or destruction of most preexisting natural ecosystems. The detailed and intriguing account by Whitney (1994) of resource use and its effects on natural systems in the region is recommended to the serious reader.

Regional Ecosystems

The Nature Conservancy (1994a) identified six major ecosystems that supported significant elements of biological diversity in the Great Lakes basin. Although the original classification was intended to describe only the ecosystems in the Great Lakes basin, the categories are broad enough to also include the major ecosystems in the portion of the region in Illinois, Minnesota, and Wisconsin that lies outside the Great Lakes basin. To aid presentation, the ecosystem designations and the grouping of ecosystem elements within each major category presented here were changed slightly from those given by The Nature Conservancy (1994a).

This discussion addresses in general, non-quantitative terms the status or health of each of the six major ecosystems in the Great Lakes region. The process of defining ecosystem health has just begun, and a more detailed assessment of the health of the ecosystems of the region will have to be delayed until an accepted procedure for doing so is developed. The International Joint Commission (1991) presents a condensed discussion of ecosystem health and proposes a useful framework for identifying physical, chemical, and biological indicators that could be used to measure ecosystem health in the Great Lakes region. Constanza et al. (1992) also present useful guidance for defining and measuring the region's ecosystem health.

Open Lake and Connecting Channels

All of the open lake and connecting channel ecosystems of the Great Lakes have been altered and stressed to some degree by human activities in the last 200 years. Lake Superior is the least altered water body in the system, whereas the large embayments and certain basins and harbors of the other lakes and the connecting channels are the most altered and stressed.

Commercial fishing and the introduction of nonindigenous aquatic plants and animals have permanently altered these ecosystems. Fishery management plans and goals are being developed to help assure that these interjurisdictional resources are managed as a sustainable resource supported largely by wild stocks of native fish species. Stocking of native and nonindigenous trout and salmon to support intensively managed recreational fisheries will probably continue indefinitely in all of the lakes, however. No practical way exists to control or eradicate most of the undesirable nonindigenous species that have become established in the Great Lakes; thus, most will probably become permanent members of the aquatic community. Efforts to control the sea lamprey, though, will continue as long as salmon, trout, and whitefish are managed to support major recreational and commercial fisheries. Control of rainbow smelt and alewife populations can probably be achieved in many areas by enhancement of the trout and salmon populations that prey on them. The zebra mussel may be impossible to control and may cause major changes, some of which may be beneficial. Western Lake Erie and Saginaw Bay of Lake Huron—once clear waters—became artificially enriched and plagued with high turbidity caused by runoff from agricultural lands. The filtering action of the zebra mussels in these areas may reduce turbidity and restore water clarity to historical levels, thus benefiting native fishes adapted to clear water. More comprehensive efforts by the United States and Canada will be needed to prevent further accidental or deliberate introductions of nonindigenous species into the Great Lakes region (International Joint Commission and Great Lakes Fishery Commission 1990).

Physical alteration of the Great Lakes and their connecting channels has had profound effects on the waters and their biota. The installation of dams and locks at the outlet of Lakes Superior and Ontario regulates the levels of those lakes and has significantly reduced the natural, seasonal, and between-year fluctuation in levels and interlake flows that sustain the pulsed stability of wetlands in the system (Jaworski and Raphael 1979). These dams have also fragmented the system by cutting off historical fish migrations between parts of the system. The commercial extraction of sand and gravel at the head of the Saint Clair River in 1908–1925 and dredging there in 1933–1962 to increase the depth of the navigation channel permanently lowered the levels of Lakes Huron and Michigan by 0.3 meters (Derecki 1985). The effect of this change on the coastal wetlands in those lakes is unmeasured but undoubtedly substantial and adverse.

Channel dredging and shoreline modification have permanently destroyed many coastal wetlands and large amounts of fish spawning habitat throughout the Great Lakes system, but particularly in the connecting channels. It is unlikely that such alterations of the system would be permitted now or in the future. Recent proposals to further regulate levels and flows in the system (to benefit navigation and hydropower interests and to reduce flooding and shoreline erosion in residential areas during high-water years) have been rejected. The decision to not further regulate the system expressly recognizes the ecological importance of retaining the natural fluctuations in levels and flows in the system.

Pollution has severely degraded portions of the Great Lakes system. Surface drainage from agricultural areas has added large amounts of silt to Lake Erie and to Saginaw Bay in Lake Huron. Herbicides and pesticides have also entered the system in large quantities from agricultural areas bordering Lake Michigan and Lake Saint Clair. Legal discharges of municipal and industrial wastes have overly enriched and polluted major embayments and other portions of the system. These discharges, together with spills of pollutants and frequent discharges of raw sewage into storm drains that flush directly into the Great Lakes system, are still problems in many municipal areas. Aerial inputs of some contaminants are also significant. Organochlorine compounds have reached high levels in Lakes Michigan and Ontario. These and other industrial pollutants, including oils and metals, occur at high levels in sediments in some areas of the connecting channels and in certain harbors throughout the system. The International Joint Commission has identified more than 40 such areas of concern in the Great Lakes system where the beneficial uses of the system have been substantially degraded by pollution. Remedial Action Plans are being developed to reduce the amount of incoming pollutants and to restore the affected areas to good ecological health.

Water withdrawals and out-of-basin diversions are subjects of major concern for the Great Lakes system. Most of the water withdrawals are made to provide cooling water for steam-electric power plants on the shoreline of the Great Lakes or the connecting channels. In some areas these withdrawals may approach 1% per day of the nearshore waters of Lake Michigan and western Lake Erie and 5% per day of the total flow in the connecting channels between Lakes Huron and Erie (T. Edsall, U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, Michigan, unpublished information). Fishes and invertebrates in the withdrawn water are killed by a combination of stresses, including physical collisions in the cooling system, elevated temperatures, and biocides used to clean the cooling system surfaces and to aid heat in exchange. Most steam-electric power plants built on the Great Lakes and connecting channel shorelines through the early 1970's operated with once-through cooling, a process that withdraws large volumes of water from the lake or channel, heats it 10°C–20°C, and then returns it to the water source. Steam-electric plants constructed after the early 1970's use closed-cycle cooling and are not a major threat to the aquatic resources of the Great Lakes system. Fish losses continue at the older plants, but these losses will eventually end when the older plants are retired from service and are replaced with plants using closed-cycle cooling.

Water withdrawals are also made for hydropower generation in plants in the connecting channels. The effects of these hydropower plants on Great Lakes fishes have not been extensively studied. A large pumped-storage hydropower facility on the Lake Michigan shoreline kills large numbers of fishes, and formal measures are now being taken to reduce the loss and provide mitigation (Manny 1984; Northwoods Call 1994). Out-of-basin diversions are occasionally proposed as a panacea for water shortages in the western states, but economic considerations and the governors of the Great Lakes states seem to have forestalled serious consideration of such transfers.

Wetlands

Wetlands are highly valued as recreational sites for hunting, fishing, bird watching, and general aesthetic enjoyment because they support a large number of plants and animals, including species that are not found elsewhere. Wetlands are transitional between terrestrial and aquatic systems (Cowardin et al. 1979). The wetland soil and sediments are saturated with water or covered by shallow water at some time during the growing season of each year and support mostly aquatic or water-loving plants. Included in this definition are bogs, fens, marshes, sloughs, and wet meadows.

Two major types of wetlands, coastal and inland, occur in the region. Great Lakes coastal wetlands are within 1 kilometer of the lakeshore or, if farther inland, are directly influenced by water level changes in the Great Lakes or their connecting channels (Herdendorf et al. 1981). These coastal wetlands are more dynamic, display a greater diversity of landforms, and are less influenced by groundwater inflow than are inland wetlands. Coastal wetlands, unlike inland wetlands, have mainly mineral sediments. They are also subject to short-term (hours-long) flooding and draining by storm tides (seiches), as well as to seasonal and years- or decades-long changes in lake levels (Fig. 4).

Long-term changes in water level cause coastal wetlands to advance lakeward or retreat landward over a period of years. Species lists of

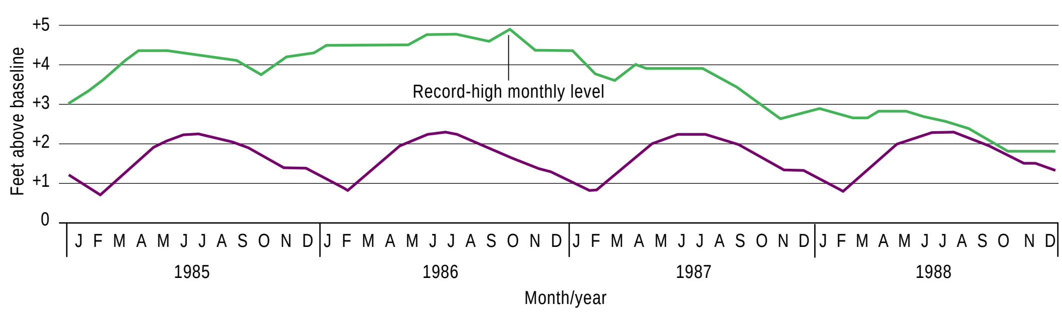

Fig. 4. Seasonal and interannual variation in water levels in Lake Saint Clair, 1985–1988. Lake Saint Clair is a segment of the connecting channel between Lake Huron and Lake Erie. The green line is the recorded monthly level, and the purple line is the 90-year average level (after Edsall and Gannon 1991).

plants and animals of Great Lakes coastal wetlands have been developed by Herdendorf et al. (1981). Brady and Burton (1995) and Wilcox (1995) provide recent descriptions of Great Lakes coastal wetland ecosystems in Lake Huron.

Presettlement wetland area in the United States was estimated at 87 million hectares (Roe and Ayres 1954; Dahl 1990) and, between 1780 and the mid-1980's, about 53% of the total had been drained and converted to other uses (Mitsch and Gosselink 1993). A total of about 14,600 hectares of wetlands was present in Michigan, Minnesota, and Wisconsin in 1780, but by the mid-1980's, about 54% of that had been converted to other uses. Losses in Illinois, Indiana, and Ohio were also high as a result of the draining of the Great Kankakee Marsh on the northern Indiana–Illinois border and the draining of the Great Black Swamp that covered 4,000 square kilometers at the Michigan–Ohio border. Inland wetlands remaining in 1955 were much more abundant in Michigan, Minnesota, and Wisconsin than in the rest of the region (U.S. Fish and Wildlife Service 1971). Much of the remaining inland wetland habitat is in private ownership, and its fate in the face of pressures to develop the land for other uses is uncertain. All the states in the region except Illinois, Indiana, and Ohio have laws to regulate wetland use (Tiner 1984). Existing legislation in the other Great Lakes states presently offers a reasonable degree of protection for these wetlands, but legislative changes currently being considered by the federal government could further reduce the amount of wetlands held by the private sector.

There are no reliable estimates of the total area originally occupied by Great Lakes coastal wetlands, but fewer than 1,200 square kilometers may remain within the United States (Herdendorf et al. 1981). The mean size of these wetlands varies from about 0.3 square kilometers along Lake Ontario to about 1.4 square kilometers along Lake Huron. The largest total number of coastal wetlands and the largest total wetland area occur along the perimeter of Lake Michigan. A unique set of coastal–deltaic wetlands occurs in Lake Saint Clair and in the Saint Clair delta at the mouth of the Saint Clair River on Lake Saint Clair (Edsall et al. 1988). The international border divides the lake and delta. In the United States in 1873, there were 7,200 hectares of wetlands around the lakeshore and on the delta but by 1973, 73% of these had been lost (Jaworski and Raphael 1979). On the Canadian side, about 3,570 hectares of wetlands remained in 1965, but by 1973 about 30% of those had been lost (McCullough 1985). Urbanization and residential or recreational development were responsible for most of the loss on the U.S. side of the border, and conversion to agriculture was the major cause of wetland loss in Canada. Diking of wetlands—a practice that had been common in this portion of the system in areas managed intensively for waterfowl hunting—reduces wetland productivity and withdraws habitat previously used for spawning by Great Lakes fishes. Additional diking of coastal wetlands is unlikely.

Rivers and Streams

The Great Lakes watershed has been divided into river basin groups and flow measurement areas (Great Lakes Basin Commission 1975). The largest catchment basins are the Maumee River in Ohio and Michigan (17,100 square kilometers) and the Nipigon River in Canada (25,258 square kilometers). The numerous small streams that flow directly into the Great Lakes each have catchments of only a few square kilometers. For example, Michigan has 513 of these small coastal streams (flows of 1 cubic meter per second or less) and only 100–150 larger streams (Hudson et al. 1992). In the Precambrian shield bedrock areas in Minnesota, Michigan, northern Wisconsin, and in Canada, the glacial deposits are thin or altogether lacking, and the streams have relatively steep gradients. Glacial drift and glacial landforms dominate the topography in much of the rest of the basin, although there are areas where calcareous bedrock reaches the surface and affects streamflow and the character of the streambed. Streams with relatively steep gradients occur throughout this portion of the region, even in the till plains where an undulating land surface and moraines produce local relief of up to 30 meters (Hudson et al. 1992). The topography and soils, which create many lakes and wetlands in the basin, tend to slow runoff and sustain flow throughout the year. The maximum flow of larger unregulated streams in the basin is usually only about three to seven times greater than their mean flow.

Drainages with clayey soils have higher loads of suspended solids and phosphorus and are more susceptible to flooding than those drainages with sandy soils. Streams with clayey soils occur in the west–southwestern end of the Lake Superior basin, parts of the drainage to southern Lake Michigan, the western basin of Lake Erie, and parts of the Lake Ontario drainage. Sandy soils are dominant in north–central Wisconsin and in northern Michigan in Lake Michigan and Lake Huron drainages; water quality in streams in these areas is high (Sonzgoni et al. 1978; Manny and Owens 1983). Northern streams with good groundwater inflow generally support cool or coldwater fish communities. Other streams usually support warmwater fish communities.

Many streams that are not dammed have runs of fishes that enter them seasonally from the Great Lakes.

The quality of the stream ecosystems is generally highest in undeveloped portions of the region where damming, channelization, sedimentation, and pollution have not occurred and is lowest in areas where there is extensive agricultural, industrial, and urban development. In Illinois, for example, where the land is intensively developed, more than 25% of the total length of sizeable streams in some main river basins has been channelized, and almost every sizeable stream in the state has at least one dam (Illinois Department of Energy and Natural Resources and The Nature of Illinois Foundation 1994). Peoria Lake, the largest, deepest bottomland lake on the Illinois River, lost 68% of its capacity because of sedimentation that occurred between 1903 and 1985. Of the species present in Illinois streams at the turn of the century, about one in five fishes, one in three amphibians and reptiles, more than half the freshwater mussels, and one in five crayfishes have been extirpated or are threatened by extinction. Water quality in Illinois streams is improving, but the quality of stream ecosystems remains low. In 1988 about 66% of the total stream length in the state was in fair to very poor condition and 34% was in good to excellent condition.

Hydropower development creates significant problems in many of the larger stream and river ecosystems in the region. Most of the dams were built early in this century, and few have fish ladders or other devices that allow fishes to pass over or through the dams unharmed. Recent evaluations show that these dams fragment and substantially degrade the stream ecosystem and limit the use of the stream system by resident fishes and by anadromous fishes that migrate up Great Lakes tributaries to spawn. Most of the dams in the region were built in high-gradient stream reaches, which were areas of permanent residence for some fish species and spawning areas for other migratory species. Generally, these high-gradient reaches were also sites of the groundwater inflow that was required to support coolwater and coldwater fish species. Stream fishes in the flooded areas above the dams were replaced by species better suited to a warm lake environment. Stream fishes below the dams were also adversely affected. The dams were usually operated in a daily peaking mode to supply power when it was in greatest demand, usually in the morning, evening, or both. As a result, exceptionally high flows occurred once or twice a day when power was needed, and water was held back at other times. The high flows eroded the streambed, and the intervening low flows drained it. The temperature variation in the stream below the dam was also significantly altered. In Michigan alone, there are 113 operating hydropower plants (Whelan and Houghton 1991). These plants produce only about 1.5% of the existing power demand while impounding about 750 kilometers of riverbed, adversely affecting another 1,200 kilometers of river, and blocking anadromous fishes from 3,300 kilometers of mainstream river habitat.

Many of these dams in the Great Lakes region that are licensed to operate by the Federal Energy Regulatory Commission are now under consideration for relicensing. Relicensing agreements recently reached in Michigan between resource advocates and the power companies will greatly lessen the adverse effects of the dams and should help set an environmentally beneficial precedent for relicensing in other states. Under the agreements, the water release patterns from the dams will closely mimic the inflow pattern to the reservoirs above the dams. In addition, effective upstream and downstream fish passage facilities will be installed in each dam consistent with fishery management plans for the area. These changes will significantly improve habitat quality below the dams and reduce the fragmentation effect that the dams have had on the river ecosystem. The relicensing agreements also provide for dam removal when the dams are declared obsolete.

A number of federally listed endangered freshwater mussels occur in tributaries throughout the Great Lakes region, but the Hungerford's crawling water beetle is the only federally listed endangered insect that is found in Great Lakes basin tributaries. The beetle is only known to occur in the Maple River in the northern Lower Peninsula of Michigan and in one or two other streams in that part of the basin.

Coastal Shore

The coastal shore is a relatively narrow strip of land bordering the Great Lakes shorelines (The Nature Conservancy 1994a). It directly adjoins with and is strongly influenced by the lake environment, including wave action, wind, temperature, water level, humidity, and precipitation. In some areas even the soils of the coastal shore are strongly influenced by the lake environment. Physical features of the zone include bedrock shorelines and gravel, rubble, cobble, and sand beaches. Sand dunes are major features in some areas.

The Great Lakes region contains some of the most extensive freshwater sand dunes on Earth. Some occur near river mouths, others are perched on wave-cut bluffs of glacial till. Dunes and sand beaches reflect sediment transport

Habitat Change in a Perched Dune System Along Lake Superior

Pitcher's Thistle and Lake Level Change

Pitcher's thistle (Fig. 1), listed as a threatened species by the U.S. Fish and Wildlife Service, inhabits the sandy shores of the upper Great Lakes. Its life cycle requires a dynamic habitat that periodically provides both highly disturbed, open patches (affording sites for seed germination on mineral soil in high light under limited competition) and more stable patches for flowering, seed set, and seedling establishment before burial or other site destruction (McEachern 1992). Since water levels of the lakes greatly influence the effects of waves upon the shore, the fine-scale history of lake-level change is relevant to understanding past habitat change, the persistence of Pitcher's thistle, and habitat requirements for restoration and protection of the species.

Fig. 1. Pitcher's thistle.
Courtesy K. McEachern, USGS

Recent studies of lake-edge dunes and beach ridges (Fraser et al. 1990; Lichter 1995; Thompson and Baedke 1995) suggest that because of climatic variation, past levels of Lake Michigan have differed from those of the present by as little as several tenths of a meter to as much as a meter or more. These changes have taken place periodically over decades to centuries during the past 5,000 years. The growth of open habitat patches through dune building in lake-edge dunefields is greatest as low lake levels bare broad sand flats, expanding the source of sand for transport by the wind (Fraser et al. 1990). Perched dunefields, which form high atop lake-facing bluffs, also respond to lake-level change (Marsh and Marsh 1987; Anderton and Loope 1995) but in a mirror-image fashion to those on the lake edge (Olson 1958). In perched dunefields, growth of open habitats (dune building) occurs as rising lake levels destabilize lake-facing bluffs, creating active colluvial slopes and increasing sand supply to the bluff tops.

For both lake-edge and perched dunes, the mix of habitat change may depend upon smaller-scale episodes of lake-level change that are *nested* within larger, longer-term trends (Fraser et al. 1990; Thompson and Baedke 1995; Fig. 2). Lake-level changes, then, have probably mediated expansion and contraction of habitat patches suitable for Pitcher's thistle on several scales (Snyder 1985; Businski 1992; McEachern et al. 1994) since the appearance of the Great Lakes about 10,000 years ago.

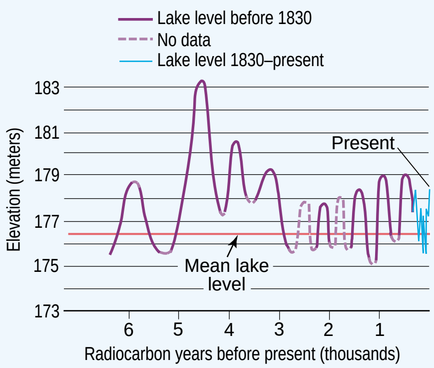

Fig. 2. Hypothetical late Holocene hydrograph proposed for Lake Michigan (Fraser et. al. 1990) in relation to historical lake levels.
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Episodes of habitat change, driven by changes in levels of the Great Lakes, must be considered when assessing human effects upon coastal vegetation and rare species (Schultz 1988; Businski 1992). Paleoecological studies, baseline inventories, and long-term monitoring programs within the Grand Sable Dunes, a perched-dune system along Lake Superior, provide a window on vegetation change at different spatial and temporal scales and also provide an illustrative case study.

Vegetation Change

The modern Grand Sable Dunes are characterized by a shifting mosaic of plant communities and physical dune forms periodically disturbed as sand builds, stabilizes, and erodes away from the dune system (Fig. 3). Exhumed forests and buried soils in this landscape (Fig. 4) attest that vegetation cover has varied significantly over hundreds to thousands of years and give us a crude picture of coarse-scale changes (Anderton and Loope 1995). Analysis of present-day vegetation and plant population dynamics helps reveal how plant communities may change within tens to hundreds of years and allows us to predict habitat suitability for disturbance-adapted species like Pitcher's thistle for the next few decades.

a. Courtesy W. L. Loope, USGS
b. Courtesy W. L. Loope, USGS
c. Courtesy W. L. Loope, USGS

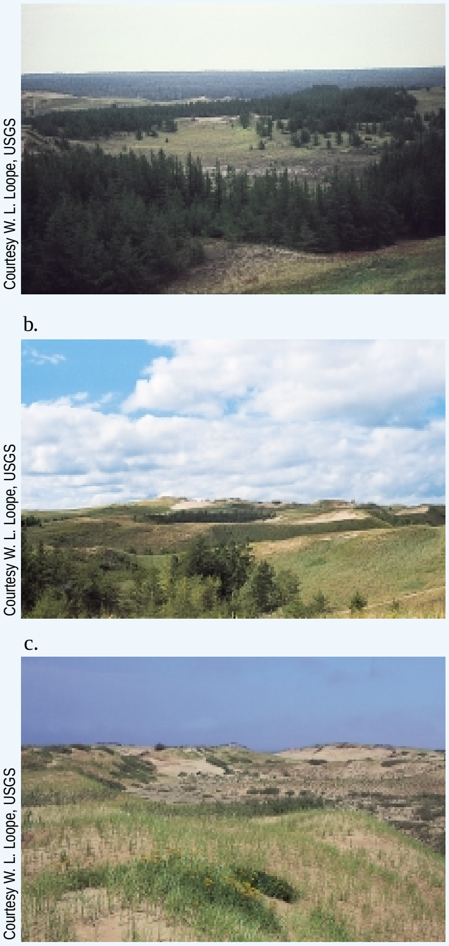

Fig. 3. Grand Sable Dunes vegetation mosaic: a) pine forest, b) grassland, and c) dunes.

Courtesy W. L. Loope, USGS

Fig. 4. Buried soil in a perched dunefield.

Paleoecological Change

The presence of buried soils within Grand Sable Dunes implies sharply contrasting rates of sand supply to the dunefield. Radiocarbon dating of buried soils suggests that at least 5 and perhaps as many as 11 episodes of soil burial have occurred there over the past 5,500 years (Anderton and Loope 1995). Soil burial events were probably related to a much greater supply of sand than that of the present (Fig. 5a), which occurred as lake-facing bluffs were destabilized by the rising waters of Lake Superior (Fig. 5b). Periods of bluff stability during low water on Lake Superior (Fig. 5c) allowed vegetation to invade sand-starved dunes. Whether each buried soil represents complete forestation of Grand Sable Dunes is questionable, but the presence of charcoal in several soil profiles supports the possibility that vegetation occasionally became continuous enough to carry a fire. During periods of afforestation, Pitcher's thistle would have been restricted to small, isolated, and disturbed areas along the bluff edge or in rare inland blowouts. During periods of high sand supply and dune building, Pitcher's thistle would have been afforded a broader spectrum of open habitat. Rapid dune building may also have limited the availability of *intermediate sites*, which were stable long enough to permit completion of the flowering cycle of Pitcher's thistle but were open enough to permit germination of new seedlings.

Contemporary Vegetation Change

The most striking evidence of contemporary vegetation change within Grand Sable Dunes is the increase of jack pine forest over the last several hundred years. An aerial photo time series shows a fivefold increase in forest cover over the past 50 years. Snyder (1985) and Businski (1992) report similar results at Sleeping Bear Dunes, a perched dune system along Lake Michigan. Stand-age structure within forest patches at Grand Sable Dunes suggests that afforestation began at the landward edge of the dunes at least 125 years ago. The plant species richness in the forest increases with stand age and is strikingly higher than in the fire-influenced pine stands to the south and east of Grand Sable Dunes. Although charcoal from ancient soil profiles (Anderton and Loope 1995) suggests fire-prone vegetation occurred there in the past, burned snags and species usually associated with fire, such as blueberries, wintergreen, and bracken, are absent from modern pine patches.

Within the large-scale trend toward increasing forest cover, open patches are still being created on a smaller scale just landward of the lake bluff and in inland blowouts. Species composition and cover within open patches are determined by proximity to the lake-facing bluff edge and by fine-scale patterns of stability along the bluff face. Dominance of American beachgrass and wormwood along the bluff edge, both of which tolerate burial, reflects a high sand supply and fast patch turnover because of periodic sloughing of the bluff face. Shrubs such as woolly beachheather and bearberry and the bunch-grass, little bluestem, dominate more stable, open patches farther landward of the lake bluff, where there is less blowing sand.

Linking Nested Episodes of Change

Coastal geomorphology is important in understanding and predicting species persistence (Pavlovic et al. 1991). Periods when open habitats become rare or inaccessible to disturbance-adapted species (the *bottlenecks* of Loveless and Hamrick 1988) must have occurred at Grand Sable Dunes during nested landscape changes beginning about 5,500 years ago and continuing into the present.

Repeated episodes of both afforestation and soil burial at Grand Sable Dunes imply varying habitat quality for Pitcher's thistle over late Holocene time. Depending on the magnitude and duration of lake-level changes, open habitats may have been restricted to the bluff edge during low water. During high water, advancing dunes may have limited the extent of intermediate habitat required for the 8- to 10-year life cycle of Pitcher's thistle. The temporal and spatial details of landscape history can be linked

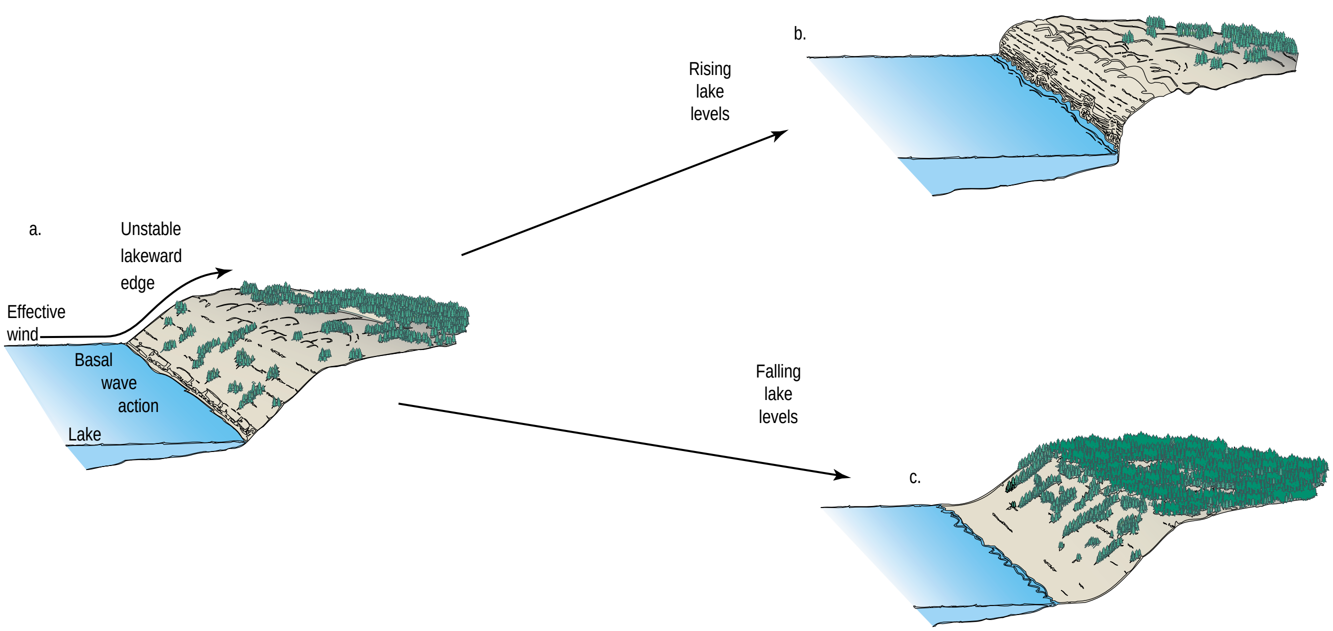

Fig. 5. Drivers of change a) within the modern Grand Sable Dunes, b) under a dune-building future, and c) under a stabilization future.

with species' life histories, which allows for more realistic and spatially explicit population models.

Present successional trends at Grand Sable Dunes seem to be toward increasing forest cover. The landward half of Grand Sable Dunes preserves a record of successional change since the last major destabilization about 500 years before the present; the lakeward half presents a composite picture of changes over the last several hundred years in response to localized changes along the bluff. The same characteristics of perched dunes that make them valuable for studying buried soils and vegetation change over the last 5,000 years also make them valuable for studying recent vegetation trends. The perched dunes are remote from direct wave action and apparently respond only to more sustained changes of lake levels.

Grand Sable Dunes has experienced relative stability for the last 150 years, allowing jack pine to invade portions of the central and eastern dunes. An episode of dune building about 500 years ago buried the red pine and other early successional species that had begun to invade the dunes during a previous stable period. The duration and timing of such episodes have constrained the distribution of dunes-adapted plants during the late Holocene, alternately favoring species adapted to open sites with high sand supply and then favoring those adapted to shaded sites in early stages of succession. These changes in the dunefield habitat mosaic appear controlled by changes in the water levels of Lake Superior.

Regional reconstructions of paleolandscape dynamics have implications for studies of evolutionary ecology of narrowly distributed plants along the shores of the Great Lakes. Current research suggests that the hypothetical multiple successional pathways of Bach (1978) have indeed been a part of the recent history of Grand Sable Dunes. The turnover rate for small patches is presently quite rapid along the lakeward edge of the dunefield and decreases inland. The present turnover rate depends on a relatively low volume of sand along the lake-facing bluff. The sizes, distribution, and turnover rates of patches seem to have changed significantly throughout the late Holocene.

See end of chapter for references

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along the lakeshore. Sand discharged into the lakes from streams and sand moving alongshore near stream mouths form spits and bars that shelter wetlands in drowned river mouths. Some of the best examples of these dunes and drowned river-mouth coastal wetlands occur on the eastern shoreline of Lake Michigan. The larger coastal dunes were formed during periods of higher lake levels that closely followed melting of the ice sheet 10,000–14,000 years ago. Nearly 30% of the globally significant species and communities identified by The Nature Conservancy (1994a) in the basin occur in the coastal shore zone; the coastal dunes alone support more endemic species than any other part of the basin. The unique natural communities of the Great Lakes dunes include the open dunes, the interdunal wetlands, the jack pine barrens, and the sand beaches. The largest dune areas are on Lakes Huron, Michigan, and Superior. Some of the finest dunes occur in the federally owned Sleeping Bear Dunes National Lakeshore and the Indiana Dunes National Lakeshore on Lake Michigan, as well as in the Pictured Rocks National Lakeshore on Lake Superior. Commercial sand and gravel mining is still allowed in some dune areas, and commercial, residential, and recreational developments pose threats in other coastal shore zone areas.

Most of the plants that colonized the dunes came from populations native to the Atlantic coast and to the prairies to the west. Plant species that evolved in the dunes and are unique to them include Pitcher's thistle and Houghton's goldenrod. These two species are federally listed as threatened or endangered. Other unique plant species found in the Great Lakes coastal shore environment include the ram's head lady's slipper and the federally listed dwarf lake iris. The Lake Huron locust, a grasshopper, is also unique to the coastal shore in the basin.

Lake Plains

The lake plains are postglacial Great Lakes lakebeds. They have sandy, silty, or clayey soils, flat topography, and a high water table (The Nature Conservancy 1994a). Sandy ridges marking the locations of previous shorelines are apparent in some areas. At the region's southern end, prairies, savannahs, swamps, wet meadows, sand barrens, and Coastal Plain ponds occupied the lake plains. Most of the prairies, savannahs, and barrens occur near Saginaw Bay on Lake Huron, the Saint Clair delta, and the shores of southern Lake Huron and Lake Michigan and western Lake Erie. In the northern lake plains, fens and wet swales are present in the low areas between old beach ridges. Most of the alkaline shrub–grassland communities (alvars) in the basin occur in the lake plains. During periods of high lake levels, the lake plains probably served as refuge habitat for coastal species and communities that had been displaced by flooding. Groundwater movement and fire probably were important in maintaining savannahs and prairies and the Coastal Plain pond communities. Manipulation of surface- and groundwater movements to aid agricultural development and urban growth has extensively affected the ecosystems of the lake plains, especially in the southern portion of the basin. Much of the southern lake plain system was developed for agriculture and urban growth, but some large tracts remain near the lakes and on particularly sandy soils. The northern lake plain system is relatively more intact but is vulnerable to development.

The lake plain system supports the largest number of globally significant elements in the Great Lakes basin, and 22% of those restricted to the basin occur only on the lake plains or have their best examples there (The Nature Conservancy 1994a). Globally imperiled species include the eastern prairie fringed orchid and the Karner blue butterfly in the southern lake plain system, and the Michigan monkeyflower and the alvar community in the north. The Michigan monkeyflower is also federally listed as endangered.

Terrestrial Inland

The terrestrial inland system occupies most of the land mass in the region, particularly in that portion lying outside the Great Lakes basin in Minnesota, Wisconsin, and Illinois. The inland terrestrial system is the main catchment area for the region, and its geology, soils, and plant cover determine the basic quality of the surface and groundwaters in the region. The system supports a variety of forest types and most of the region's remaining prairie and savannah lands. Relatively large blocks of public land held by the state and federal governments and managed for recreation or for forest products provide some protection for terrestrial inland systems in northern portions of Michigan, Minnesota, and Wisconsin. In many other areas, however, agriculture, urban development, and construction of highways and recreational homes have fragmented the system, changing the vegetation and making those areas less suitable for use by animals who are intolerant of humans.

Before settlement, most of the region, except the prairie and savannah lands on its western and southern borders, was covered with virgin forest (Fig. 5). By 1920, though, substantial patches of virgin forest remained only in northern Minnesota, Wisconsin, and Michigan (Greeley 1925). Today, the total amount of forestlands in Minnesota, Wisconsin, and

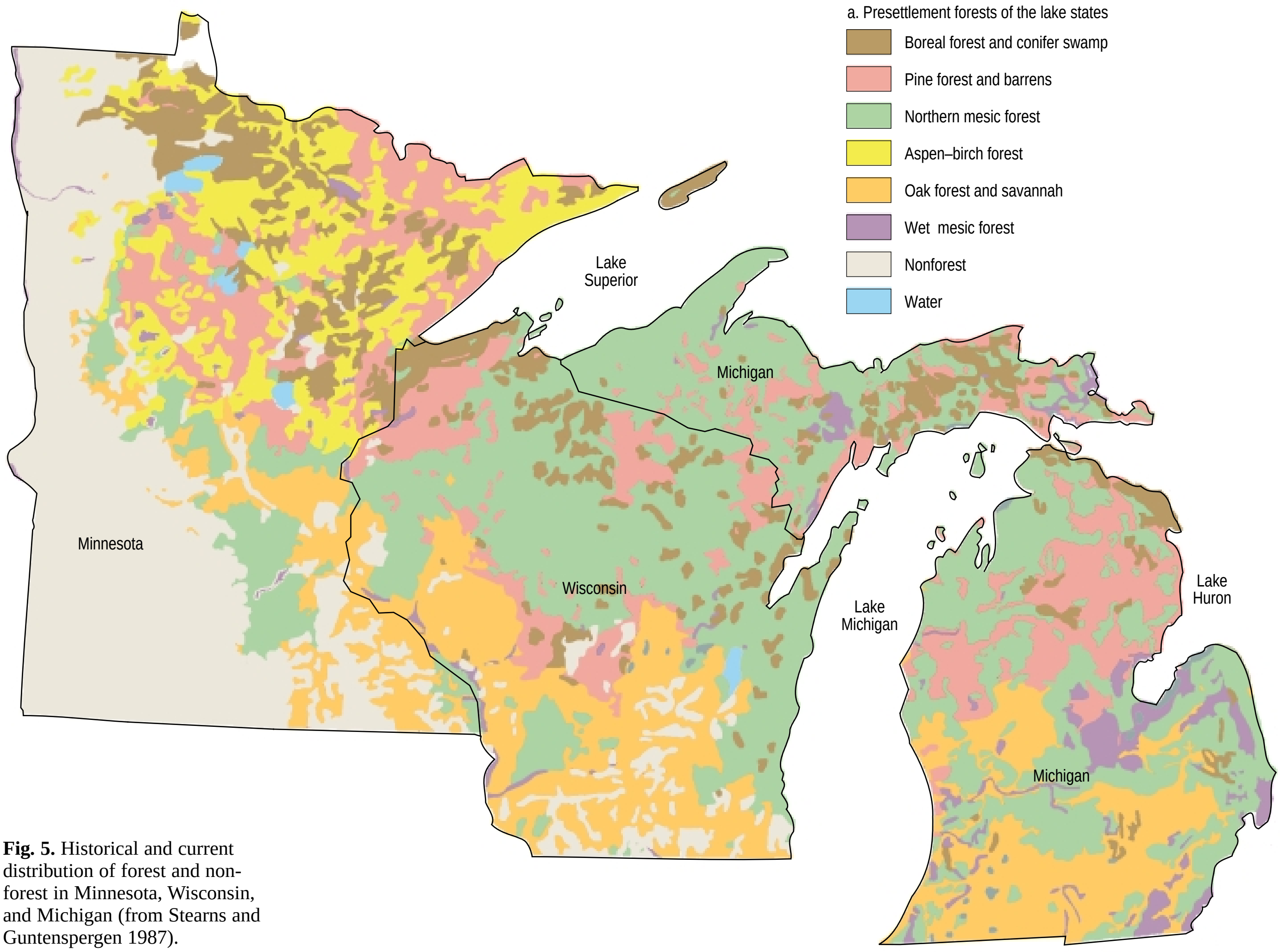


Fig. 5. Historical and current distribution of forest and non-forest in Minnesota, Wisconsin, and Michigan (from Stearns and Guntenspergen 1987).

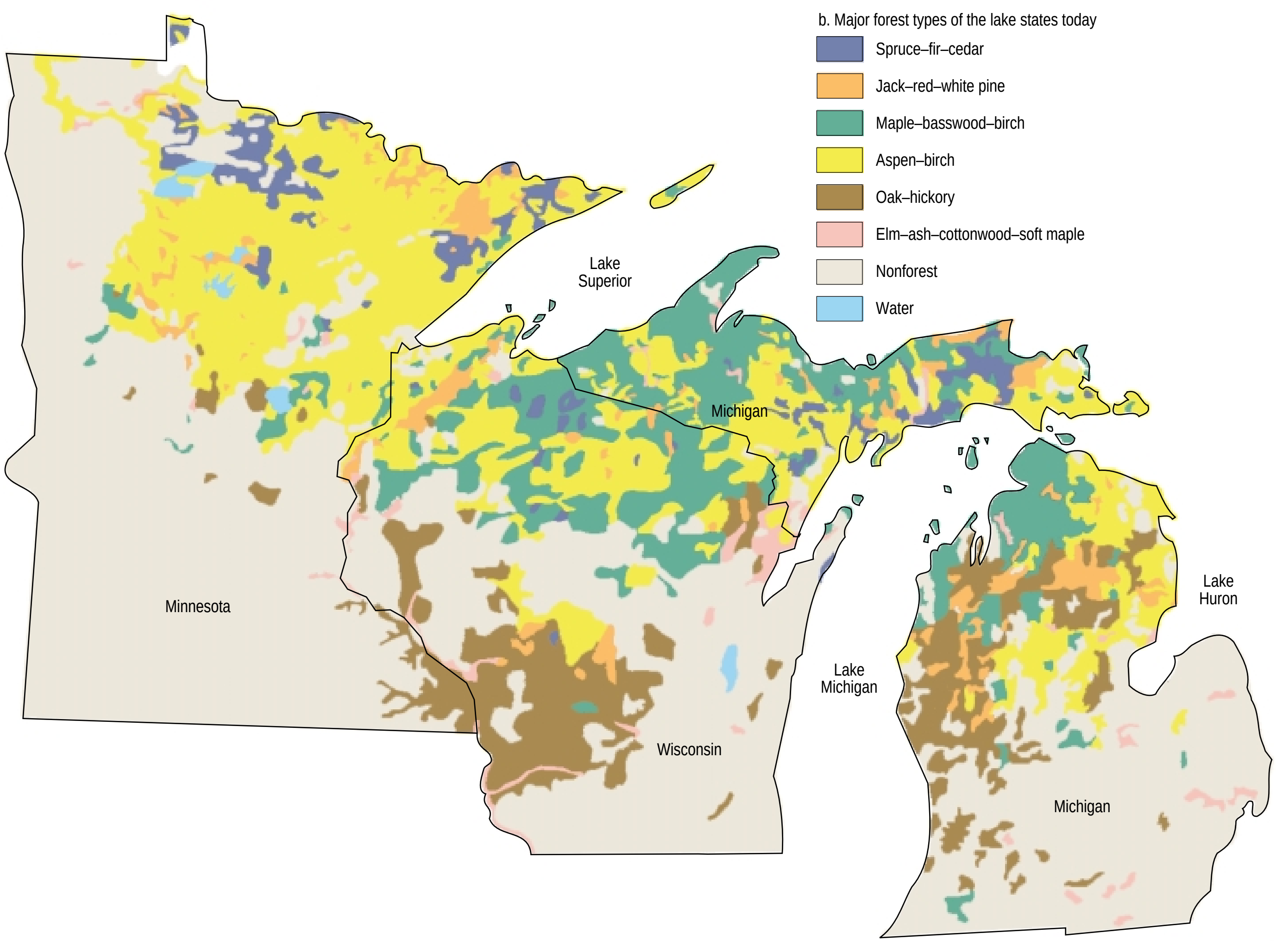
Michigan is substantially less than at the time of settlement, particularly in the southern portions of those states (Fig. 5), and virgin forests occupy only small patches of land in parks and other reserves. The forest in the north has also changed from one dominated by maple–basswood–birch (northern mesic forest), jack–red–white pine (pine forest and barrens), and spruce–fir–cedar (boreal forest and conifer swamp) to one largely dominated by aspen–birch. The large expanses of oak forest and savannah that dominated the southern portions of these three states have also disappeared and are now nonforest, and the area has been converted to other use.

In the Great Lakes basin, only about 8% of the globally significant elements are exclusively or mostly restricted to the terrestrial inland system (The Nature Conservancy 1994a). Still, the terrestrial inland system in the region contains some excellent elements of northern hardwood forest—for example, in the Porcupine Mountains, Huron Mountains, and Sylvania Recreation Area in northern Michigan. Three species of moonwort (a small fern) are globally significant elements in the system. Oak and pine barrens on sandy outwash plains in northern Wisconsin and Michigan are distinct and important community types. Neotropical birds and large mammals are major components of the woodland fauna of the system. In Michigan, the pine barrens support the federally listed Kirtland's warbler. Other federally listed threatened and endangered species that occur in the system include the gray wolf, Indiana bat, bald eagle, and the arctic and American peregrine falcons.

Status and Trends of Plants and Animals

Early Information

The earliest information on the status of the biota and their ecosystems in the Great Lakes region is fragmentary and includes written accounts by the first European explorers and traders. Later records compiled in the 1700's by the Hudson Bay Company and other fur-trading companies showed substantial natural fluctuations in populations of some northern mammals



that frequented the region (Clarke 1954). Information reflecting the status of regional ecosystems and biota during settlement is available from accounts by settlers and early expeditions and resource surveys of the U.S. Government.

The first systematic records of commercial fish production in the Great Lakes were collected in 1867 in Canada and in 1879 in the United States (Baldwin et al. 1979). These records provide an interesting look at the early condition of Great Lakes ecosystems and their fish communities and probably faithfully reflect major declines in abundance of some species that were overfished or subjected to other major environmental stresses brought about by human activities.

Presettlement and later land surveys provided information that has permitted creation of large-scale maps showing the presettlement distribution of regional vegetation and plant community types. Large-scale maps of the vegetation at the time of settlement have been made for most of the region from data provided by either federal land surveys or surveys by the states and others (for example, [Wisconsin] Curtis 1959; [Illinois] Anderson 1970; [Ohio] Hutchins 1979; [Pennsylvania] Brenner 1985; [New York] Andrle and Carroll 1988; [Minnesota] Coffin and Pfannmuller 1988; [Michigan] Albert 1994).

Table 1. Federally listed endangered and threatened plants and wildlife with historical ranges in the Great Lakes region.[a]

Mammals
Indiana bat
Woodland caribou
Gray wolf
Birds
Bald eagle
American peregrine falcon
Arctic peregrine falcon
Piping plover
Least tern
Kirtland's warbler
Freshwater mussels
Clubshell
Winged mapleleaf
Higgins' eye
White cat's-paw
Fat pocketbook
Northern riffleshell
Snails
Chittenango ovate amber snail
Insects
American burying beetle
Hungerford's crawling water beetle
Karner blue butterfly
Mitchell's satyr
Flowering plants
Northern wild monkshood
Mead's milkweed
Decurrent false aster
Pitcher's thistle
Leafy prairie-clover
Minnesota dwarf trout lily
Lakeside daisy
Dwarf lake iris
Small whorled pogonia
Prairie bush-clover
Michigan monkeyflower
Fassett's locoweed
Eastern prairie fringed orchid
Leedy's roseroot
Houghton's goldenrod
Running buffalo clover
Ferns
American hart's-tongue fern

[a]Sources: Coffin and Pfannmuller (1988); Heckert (1991); Cummings and Mayer (1992); Rhodes and Klein (1993); Evers (1994); The Nature Conservancy (1994a); U.S. Fish and Wildlife Service (1994); N. Conrad, New York Natural Heritage Program, personal communication; S. Crispin, The Nature Conservancy, personal communication; T. Freitag, U.S. Army Corps of Engineers, Detroit, Michigan, personal communication.

Contemporary Status and Trends Information

Much of the contemporary status and trends information for the region can be linked to the passage of the Federal Endangered Species Act of 1973 and similar subsequent legislation passed by the states in the region. The federal legislation resulted in the development of lists of species that were, based upon best scientific judgment, either endangered or threatened within the United States. This legislation carried with it provisions for protecting the critical habitat needed to maintain viable populations of the listed species. The federal listings contain species of threatened or endangered plants and animals (U.S. Fish and Wildlife Service 1994) with historical ranges in the Great Lakes states, including 3 mammals, 6 birds, 6 freshwater mussels, 1 snail, 4 insects, 16 flowering plants, and 1 fern (Table 1). Recovery plans (U.S. Fish and Wildlife Service 1992) have been developed for many of these listed species, and substantial progress has been made in restoring some of them to levels of abundance that will permit their removal from the federal lists of threatened or endangered species.

The Great Lakes states developed lists of species that they believed were threatened or endangered in their states. The states also listed communities and ecosystems they believed were threatened or endangered, rare, or otherwise deserving of special attention and protection. These lists (for example, Indiana Department of Natural Resources 1993; [Michigan] Evers 1994; Illinois Endangered Species Protection Board 1994; Minnesota Department of Natural Resources 1994; Pennsylvania Department of Environmental Resources 1994; Wisconsin Department of Natural Resources 1995) are available from the individual states or are in the published literature.

Much of the recent information used by the states to develop and update their listings was collected through Natural Heritage programs (The Nature Conservancy [n.d.]) established in each state. These are independent, cooperating programs that use a technology developed and supported by The Nature Conservancy. The Natural Heritage program staff compiles data from historical records and the literature and conducts field surveys to document locations of rare species and high-quality natural communities. The individual Natural Heritage programs retain precise location data. Global information on species and communities is compiled in and available from The Nature Conservancy data base in Arlington, Virginia. States in the Great Lakes region have some of the largest and most mature Natural Heritage programs and data bases in this network. The first Natural Heritage program in the region was developed in Ohio in 1977 and the last in Illinois in 1987.

The Nature Conservancy Great Lakes Program staff and others in the Great Lakes region recently used the Natural Heritage program data bases prepared by the states to produce a document (The Nature Conservancy 1994a) that provides a basinwide evaluation of biological diversity. The document identifies elements in the U.S. portion of the Great Lakes basin that are of special concern. Each element—including animal and plant species and natural communities—was ranked on a global basis as critically imperiled, imperiled, or rare. The ranking system, which was developed by Natural Heritage scientists and other experts, includes consideration of the world distribution of an element and its occurrence or abundance, health or condition, and vulnerability to disruption or loss. The document comments on the remarkably high biological diversity in the basin and attributes it to the basin's glacial history and to the influence of the Great Lakes on the basin, which together create a diverse and unique environment capable of supporting a diverse biota. Elements judged of greatest concern in the basin were those that occurred only in the basin and whose continued existence there was most in doubt. Elements whose distributions lie mostly in the basin or whose best examples occur there were also of high concern. Elements with 10%–50% of their known distribution in the basin and those that had 10% or less of their known distribution in the basin were judged of lesser concern. The document identifies 131 globally significant elements, of which 100 are species and 31 are communities. Twenty-two of the 131 were ranked as critically imperiled, 30 as imperiled, and 79 as rare.

Plants and Fungi

Green plants form the foundation of major food chains on Earth by capturing energy from the sun and converting it into organic matter. In the process, they generate the oxygen animals require for respiration. Fungi (molds, lichens, and mushrooms) do not contain chlorophyll but play an equally vital role in the breakdown of organic matter and the recycling of nutrients.

Plants and fungi include the oldest and largest living things on Earth. As such, they contribute to ecological stability in environments where other elements, including most animals, have life spans of less than 1 year. Most woody plants have life spans that are decades long, but some have even longer life spans. For example, individual bristlecone pines as old as 2,435 years have been discovered in rugged habitats in the Rocky Mountains in western North America (Brunstein and Yamaguchi 1992). The quaking aspen, which is the most widely distributed tree in North America (and a common species in the Great Lakes region) has a habit of clonal growth that may qualify it as long-lived (Engle 1991). A grove of aspen may consist of hundreds of trees that are all genetically the same individual, because they are produced from root sprouts of the founding clone tree. Stable clonal groves may reach a hectare in size in the western United States and some may be more than 1,000 years old. Smaller, younger clonal groves are probably more typical of aspen in the Great Lakes region. Fungi also develop underground clonal complexes that are large and long-lived. A clonal mass of the honey mushroom was recently identified in a northern Michigan hardwood forest; it covers more than 15 hectares, weighs more than 10,000 kilograms, and is estimated to be more than 1,500 years old (Smith et al. 1992).

Despite the relative stability of some plants and plant communities, there is clear evidence of major regional changes on a geologic time scale. Changes in vegetation over the past 11,000 years in the eastern United States can be deduced from the pollen grains preserved in the stratified sediments of lakes, bogs, and rivers that have been aged by their carbon-14 content (Webb 1981). Such vegetation changes reflect geological and climatic influences and can be used to trace postglacial changes in climate and to examine changes in animal populations in the Great Lakes region. Contour maps showing the present distribution of spruce, pine, oak, and herbaceous pollen for the Great Lakes region are vastly different from those for the same area 11,000 years ago. The early maps based on pollen evidence show an open spruce woodland with herbaceous ground cover that grew over much of the northern portions of the region. About 10,000 years ago, the forest canopy closed and pine moved westward to replace the spruce. About 9,000 years ago, oak forests gained dominance in southern Michigan, and the prairie moved eastward across Minnesota and into southwestern Wisconsin. By 8,000 years ago, the spruce-dominated woodland had shrunk to a narrow band just in front of the retreating ice front. After the full retreat of the ice sheet from the region 5,000–8,000 years ago, the spruce forests increased both northward and southward, and pine, oak, and prairie all moved westward in the northern Midwest. Conifer–hardwood forests separated the oak-dominated forests from the pine-dominated forests. Finally, the prairie moved westward and reached its present position about 2,000 years ago. These movements reflect both long-term changes in climate established after the final disappearance of the ice sheet from North America and intermittent drought in Minnesota 5,000–7,000 years ago.

The presettlement forest in Minnesota, Wisconsin, and Michigan ranged from boreal, or spruce–fir–cedar, in the north to mesic, or elm–ash–cottonwood–soft maple, in the south. Tallgrass prairie (nonforest) dominated the landscape in western Minnesota and northern Illinois, and oak forest and savannah dominated southern Wisconsin, the southern portion of the Lower Peninsula of Michigan, and northwestern Indiana (Anderson 1990).

Great Lakes vegetation is being studied by The Nature Conservancy and by the Natural Heritage programs supported by Great Lakes states. Trend data are not generally available, but plant listings recently found in the area are being prepared or are available for Illinois, Michigan, Minnesota, and Ohio. The Nature Conservancy and the Natural Heritage network have also collaborated in the production of recent reports describing the biological diversity of the Great Lakes region with emphasis on the region's rare species and plant communities (The Nature Conservancy 1994a,b). Plant communities are emphasized by The Nature Conservancy because species information alone is not sufficient for managing ecosystems to protect biological diversity. These reports show that the region has many poorly known and interesting species and communities that are unique to the region. Thirty-three rare plant community types in six classes have been listed by The Nature Conservancy (1994b) for the Great Lakes states. These include 6 forest, 12 woodland, 2 shrubland, 2 sparse shrubland, 1 sparsely vegetated, and 10 herbaceous community classes. In addition, 40 rare or imperiled plant species are identified in the basin.

Introduced plant species outnumber all other groups of introduced organisms in the Great Lakes region, but the effect of only a few of these are known (Mills et al. 1993; Edsall et al. 1995). Purple loosestrife has spread throughout the Great Lakes basin and is replacing the cattail and other native plants and is reducing plant and animal diversity in basin wetlands. Eurasian watermilfoil has also had a substantial effect in lakes in the Great Lakes basin. Massive beds of the plant often make boating and swimming impossible and reduce fish and invertebrate populations. Some introduced species of algae have become dominant members of the algal community of the Great Lakes, but their ecological effects are generally unknown. Major nonindigenous terrestrial plants that have become established in the region include garlic mustard in forests, spotted knapweed in prairies, and buckthorn in certain wetlands and upland areas.

Invertebrates

About 90% of the nearly one million species of animals in the world are terrestrial or aquatic invertebrates—animals without backbones. In the Great Lakes region the larger, more easily seen invertebrates include insects and mollusks (snails, mussels, and clams). Insects are the most diverse group of animals (Wheeler 1990), and globally they may have the largest collective biomass of all terrestrial animals (Holden 1989). Some insects are considered beneficial because they pollinate useful plants. Others, like the nonindigenous gypsy moth, which is undergoing a population explosion in parts of the region, are pests. Some insects are terrestrial and others are largely aquatic, emerging from the water only briefly to mate, deposit eggs, and die. There is little status and trend information for most invertebrates in the region (Messer et al. 1991). Taxonomic problems that impede the development of status and trends information for insects are discussed by Hodges (1995).

Lepidoptera

Lepidoptera (butterflies and moths) are among the better-known insects, because most are large, conspicuous, and have aesthetic appeal. The Lepidoptera are the major group of plant-feeding insects, and they are important in plant pollination. Knowledge of the status of the lepidopteran community can reflect the stability and diversity of local plant communities (Powell 1995). There are about 11,000 described species of Lepidoptera in North America, but there is no complete inventory of Lepidoptera species for any state, county, or locality in North America. Compiling an inventory is impeded, in part, by the lack of reliable taxonomic keys. The larger species, including butterflies and larger moths, are well described, but the smaller species are not. In the Great Lakes region, state lists are available for Illinois, Michigan, New York, Ohio, Pennsylvania, and Wisconsin.

Abundance and range data are also scarce for Lepidoptera. The Xerces Society began the Fourth of July Butterfly Count in 1975; the North American Butterfly Association has administered the count since 1993, when participation increased to 209 counts (Swengel 1995). Count data are published annually. Although the data set is still relatively small, it is growing in size and potential utility.

An assessment of the butterfly community of the tallgrass prairie that occupies the western border of the Great Lakes region in Minnesota, Wisconsin, and Illinois and extends into Iowa and Missouri (Swengel and Swengel 1995) revealed about 81,000 individuals of 90 species at 93 sites of 1 to 445 hectares from 1988 to 1993. The species fell into four categories: prairie specialist, grassland, generalist, and invader. The prairie specialists showed a pronounced decline that seemed to persist for 4 years or more after burning of the prairie vegetation. Invaders were most abundant in recently burned areas and least abundant in areas left unburned the longest. Grassland and generalist species were intermediate in their response to fire. Light grazing or mowing every year or two and removal of the cut vegetation seemed to increase butterfly diversity while avoiding the sharp declines noted in some species after a fire. Fragmentation and large-scale destruction of prairie habitat have reduced the habitat available for the prairie-specialist butterflies (Swengel and Swengel 1995), which rarely leave their habitat patches. Fragmentation can lead to small populations, reduced gene flow, local extinctions, and a low probability of recolonization of sites where these butterflies have experienced local extinction.

Despite the major loss of prairie habitat, however, there is cause for optimism. No known prairie butterfly species has yet become extinct, and the potential for management and preservation of habitat required to maintain a high diversity of prairie butterflies is good, particularly in western Minnesota and adjacent areas to the west of the Great Lakes region. The Karner blue (Fig. 6) and Mitchell's satyr butterflies are the only federally listed threatened or endangered lepidopterans in the Great Lakes region.

Aquatic Insects

Aquatic insects are highly productive, highly specialized animals that represent less than 12% of the total animal diversity in the world (Pennak 1978). About 11,000 species of aquatic insects occur in North America (Merritt and Cummins 1984), many in the Great Lakes region.

The burrowing mayfly is one of the most important and easily identified aquatic insects in the Great Lakes region (Fig. 7). It lives as a nymph burrowed in the stream or lakebed for up to 2 years before emerging as a winged adult. Usually within 2 days after emergence, the mayfly molts, mates, deposits eggs in the water, and dies. The burrowing mayfly nymph eats decaying plant matter and is important in the transfer of energy from the detrital food chain (that is, decaying plants) to fishes, amphibians, reptiles, and birds in the Great Lakes ecosystem.

The best long-term records for changes in the distribution and abundance of the burrowing mayfly in the Great Lakes region are from Lake Erie. Analysis of sediment core samples collected in the central basin of Lake Erie showed that burrowing mayfly larvae tusks (jaw parts) preserved in the sediment provided a useful record of the abundance of the species extending back to about 1740 (Reynoldson and Hamilton 1993). Abundance varied little until about the late 1800's, when the 4,000-square-kilometer Black Swamp at the southwestern end of the lake was drained (Fig. 8). Abundance increased sharply following draining, probably due to temporarily increased nutrient inflow to the lake. In the 1930's, abundance again increased, reflecting a gradual enrichment of the lake as a result of human activities in the drainage area. A sharp decrease in abundance of burrowing mayflies occurred in the central basin after about the early 1950's. This agrees with the decline and near extinction of nymphs that was observed directly in the western basin in 1953 and attributed to anoxic conditions there (Britt 1955a,b). Other pollutants, including metals and oils, have also been shown to reduce the abundance and production of burrowing mayfly nymph populations in the Great Lakes (Edsall et al. 1991; Schloesser et al. 1991). Massive water cleanup efforts beginning in the 1960's sharply reduced the amount of nutrients and toxic pollutants reaching the lake, and there is evidence (Kreiger et al. 1996) that recovery of the burrowing mayfly in western Lake Erie is well under way.

Freshwater Mussels

The United States has the greatest diversity of freshwater mussels in the world (Williams et al. 1992; Williams and Neves 1995). Of the nearly 1,000 species that occur worldwide, about one-third are found in the United States. There are about 50 species of freshwater mussels in the portions of Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio that lie in the Great lakes region (Cummings and Mayer 1992). Freshwater mussels are an important component of the biota in the area. Woodland Indians ate mussels and used their shells as tools and jewelry. Freshwater mussels are also eaten by freshwater drum and wetland mammals, and they are important in the food chains of the region. Historically, freshwater mussels were harvested for their shells, which were cut into buttons. Presently, the shells of harvested mussels are cut into beads that are inserted into oysters to serve as nuclei for cultured pearls.

Freshwater mussels, though, are one of the most endangered groups of animals in North America (Cummings and Mayer 1992). The significant declines in mussel populations that have occurred over the past several decades are attributed to siltation from agriculture, channelization, impoundments, pollution, and competition with nonindigenous species. At the turn of the century, the Saint Clair–Detroit River system and western Lake Erie had 39 species of freshwater mussels—one of the richest known freshwater mussel faunas in North America (Goodrich and van der Schalie 1932). Pollutants entering the Detroit River from the Detroit area in the 1940's and 1950's caused declines in the mussel population downstream from Detroit, but the populations upstream from Detroit in Lake Saint Clair seemed to have been largely spared. In the early 1990's, however, the native mussel populations declined rapidly when the zebra mussel, an invading species from Eurasia, appeared (Schloesser and Nalepa 1995). By 1992 native mussels were virtually or totally extirpated from southern Lake Saint Clair and the offshore waters of Lake Erie. The zebra

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Fig. 6. Karner blue butterfly larva on lupine with tending ants (top), adult male, and adult female (bottom).

Fig. 7. Adult burrowing mayfly.

Courtesy M. Steingraeber, U. S. Fish and Wildlife Service

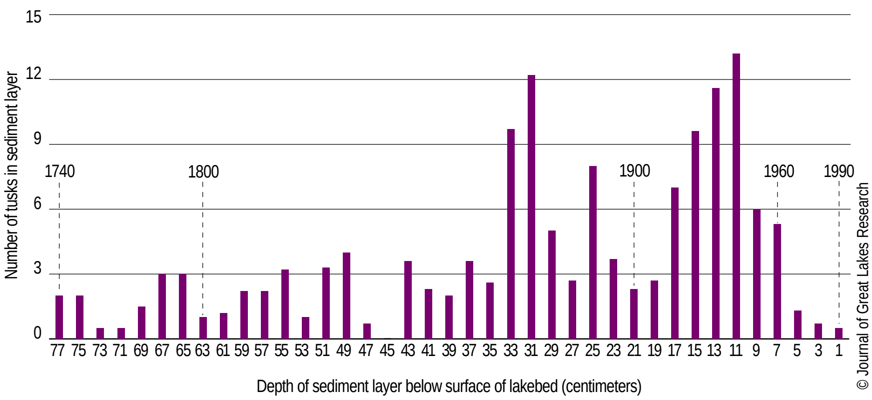

Fig. 8. Abundance of burrowing mayfly nymphs in central Lake Erie from about 1740 to 1990. Abundance was determined from counts of preserved mayfly tusks (jaw parts) in stratified and dated sediment core samples. Draining of the Black Swamp in the late 1880's increased nymphal abundance as shown in sediment layers 33–25 (after Reynoldson and Hamilton 1993).

mussel kills the native mussels by attaching in large numbers to native mussel shells (Fig. 9), causing them to suffocate or starve. Attachments averaging 7,000 zebra mussels per native mussel have been reported (Schloesser and Kovalak 1991; Nalepa and Schloesser 1992).

There are presently six species of federally listed endangered mussels in the region (Table 1). The last known world population of white cat's paw pearlymussels occurs in a tributary of the Maumee River, which enters Lake Erie near Toledo, Ohio.

Fig. 9. Native Great Lakes mussel and small, woody debris with heavy infestations of zebra mussels.

Fishes

The fish fauna of the Great Lakes basin is relatively large and diverse, despite the northerly location of the lakes at 40°–50°N latitude and the relatively short time for colonization following the retreat of the glaciers from the region (Bailey and Smith 1981). The native fish fauna of the basin is composed of 153 species in 64 genera and 25 families. The Nipigon system in Canada, which is tributary to the northeastern end of Lake Superior, contains substantially fewer species than the other five systems (Table 2); this probably reflects the shorter growing season and the lower diversity of habitats in the Nipigon system relative to the other systems to the south. The Saint Clair system also has a relatively low number of species, probably because it is small and supports only warmwater species during much of the year.

Some debate has occurred about the origins of the fish fauna that colonized the Great Lakes basin. At different times during the last glacial period, the outlet of the Great Lakes basin connected with the Mississippi River drainage and thus with glacial Lake Agassiz to the northwest, the central United States, and the coast of the Gulf of Mexico. On more than one occasion the outlet also connected with the Northeast and the Atlantic coast via the Saint Lawrence River drainage. Some scientists (for example, Hubbs and Lagler 1964) believed that the fishes that colonized the Great Lakes after the last glaciers retreated came from ice-free areas to the northwest of the basin. More recent analysis suggests that the species present in the basin at the time of European settlement basically entered from the Atlantic and Mississippi drainages at various times in the last 14,000 years. Thirty-six species may have entered the Great Lakes basin from the Atlantic drainage, 134 from the Mississippi drainage, and 22 from both drainages. These species and their origins are detailed in Bailey and Smith (1981).

Table 2. Number of fish species in the Great Lakes basin by drainage system component (after Bailey and Smith 1981).

System	Number of species		
	Lake	Tributaries	Both
Nipigon	-	-	40
Superior	53	82	135
Michigan	91	135	226
Huron	90	113	203
Saint Clair	-	-	108
Erie	106	125	231
Ontario	95	125	220

The whitefishes are a major element of the native coldwater fishes of the Great Lakes and require special mention here. At the time of European settlement, whitefishes were abundant and ecologically important as food for lake trout and burbot and as food for humans. As many as 40 species and subspecies of ciscoes (whitefishes most closely related to the lake herring) were identified by biologists working in the basin. Most of the whitefish group probably evolved locally; there are no records for any of them, other than the lake herring, from outside the basin. Bailey and Smith (1981) present evidence that the reproductive isolation (absence of interbreeding) that had developed among these species and subspecies over the 10,000 years was unstable and broke down as populations were reduced by commercial fishing and predation by the sea lamprey. Interbreeding among the survivors then caused their offspring to become genetically more

Sea Lamprey in the Great Lakes

The sea lamprey is an invading nonindigenous species that has had an immense impact on fish communities, fisheries, and fishery management in the St. Lawrence River and the Great Lakes of North America. Native to the Atlantic Ocean, sea lampreys probably entered the Great Lakes via the Hudson River and its artificial extension, the Erie Canal, which was opened to Lake Ontario in 1819 (Fig. 1).

Adult sea lampreys, which are shaped like eels, feed by attaching on other fish with their suctorial mouths and extracting blood and other body fluids from the fish. Each sea lamprey may kill as much as 18 kilograms of fish during the 12–20 months of its adult life. The sea lamprey gained access to Lake Erie when the Welland Canal around Niagara Falls was completed in 1829, but they were not noted in Lake Erie until 1921, almost a century later. Thereafter, the invasion quickened; sea lampreys were found in Lake Huron in 1932, in Lake Michigan in 1936, and in Lake Superior in 1946.

Life Cycle

Sexually mature sea lampreys, which are about 46 centimeters long, ascend the tributaries of the Great Lakes in the spring and summer to seek stony, gravelly riffles where they excavate redds, saucerlike depressions that serve as nests. Mating takes place on the redd, where individual females deposit up to 60,000 eggs each. Luckily for the lamprey's prey, the adult dies after spawning. The eggs hatch into larvae, barely visible to the naked eye. These larvae are blind, toothless, and have a fleshy hood overhanging the mouth. For several years the larvae live as filter feeders in burrows they construct in soft sediments of the tributaries. Larvae later transform (metamorphose) into free-swimming juveniles. Transformation involves the disappearance of the hood, the emergence of eyes, and the development of teeth on the tongue and the sucking disk, which surrounds the mouth (Fig. 2).

These *transformers*, silvery in color and about the size of a 13- to 15-centimeter-long pencil, move downstream to the Great Lakes, where they quickly attach to prey fish. The duration of attachment varies, but the site of attachment on the fish's body, the time of year, and the size of the sea lamprey relative to the size of its prey determine whether the attack will be fatal to the prey fish. Captured lake trout sometimes bear wounds and scars indicating that they have survived several attacks by small sea lampreys (Fig. 3). Over their 12–20 months of predatory existence, sea lampreys mature sexually and then repeat the life cycle.

Effects on the Fisheries

Commercial fishermen on Lakes Huron and Michigan went through the grim experience of seeing increasing numbers of sea lamprey wounds on their catch (Fig. 4). Storms also rolled growing numbers of lamprey-killed lake trout into bottom net sets. At the same time the combined annual catch of lake trout, which had averaged 5.9 million kilograms, declined sharply. Despite this alarming decline in lake trout abundance, fishermen tried to maintain the level of their catch because of the food shortage created by World War II and because of their fear that sea lamprey would kill all the lake trout anyway.

The lakewide decline of the fishery in relation to the invasion of sea lamprey was best documented in Lake Superior, where lake trout production held at 1.8 million kilograms from 1930 to 1952. In the following decade, though, production dropped 90%, while the number of sea lampreys caught in a fixed number of assessment weirs rose from 1,000 to 70,000.

Fig. 2. The mouth of an adult sea lamprey.

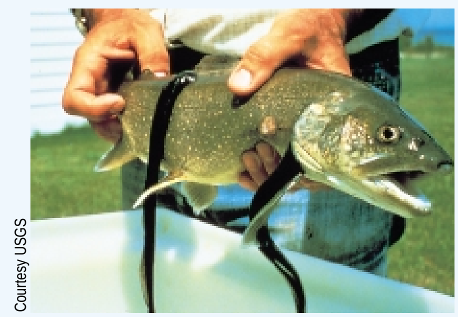

Fig. 3. Sea lampreys attached to a lake trout.

Fig. 1. Jurisdictional boundaries in the Great Lakes. The boundary between Ontario and various states is also the international boundary between Canada and the United States. The natural and artificial waterways between the lower lakes and the Atlantic Ocean are also shown.


Courtesy U.S. Fish and Wildlife Service

Fig. 4. Lake trout with wounds caused by sea lamprey attacks.

Lake trout were the favorite prey of sea lampreys and were also the top predator in the Lake Superior system. As the number of lake trout dropped, the sea lamprey turned to preying on lake whitefish and other members of the whitefish family, the chubs and lake herring. As the top predator in Lakes Huron and Michigan was eliminated, the population of another invader from the salty Atlantic, the predatory alewife, exploded. Alewives became very abundant, and though they were vulnerable to massive spring die-offs, they had adverse effects on many valuable native fish species.

Early Control Efforts

In 1948 a committee representing the governments of the United States and Canada, eight U.S. states, and Ontario—the jurisdictions bordering the Great Lakes (Fig. 1)—was established to begin a sea lamprey control program. The U.S. Fish and Wildlife Service, the state of Michigan, and the province of Ontario led research in defining the life history and distribution of sea lampreys and installing and testing physical barriers designed to prevent sea lampreys from entering streams to spawn. Very early in the program, the committee decided that a chemical selectively more toxic to sea lamprey larvae (lampricide) in streams than to nontarget fishes and other aquatic organisms would be invaluable. The U.S. Fish and Wildlife Service intensively screened some 6,000 chemicals in laboratory tests over 7 years before TFM™ (3-trifluoromethyl-4-nitrophenol) and Bayer™ 73 (2',5-dichloro-4'-nitrosalicylanilde) were chosen for field testing. These effective chemicals are still the major control agents today.

An International Commission

Meanwhile, Canada and the United States realized that to control and manage the sea lamprey and rebuild the Great Lakes fishery, coordination and stable, adequate funding were needed. Thus, the Convention on Great Lakes Fisheries was ratified in 1955, and the Great Lakes Fishery Commission was formed and charged to improve the fisheries, develop and coordinate research, advise governments, and control the sea lamprey. The commission assumed responsibility for ongoing sea lamprey control programs and selected the U.S. Fish and Wildlife Service and the Canadian Department of Fisheries and Environment as its agents to carry out sea lamprey control and research.

Further Control Efforts

By 1959 mechanical weirs and electrified barriers were installed in 135 Great Lakes tributaries. These devices, which contained traps, were generally effective at preventing sea lampreys from reaching spawning areas and also provided information on the number of sea lampreys in the area. During high water and power failures, though, sea lampreys could bypass these devices. Both systems were gradually phased out. The use of electricity was abandoned in the late 1970's, and research into effective electrical blocking systems was delayed by many years. The mechanical barrier program has since been refined and enlarged.

Subsequently, the commission concentrated on chemical control programs, which experienced great success following initiation of chemical treatments in all the lakes (Fig. 5). Information for Lake Michigan, where chemical treatment started in 1960, has not been summarized, but it followed a pattern similar to that of Lake Huron in the early years of treatment (1960–1982; see Lake Huron graph in Fig. 5). Lamprey numbers have increased recently in Lake Michigan, but not nearly as dramatically as in Lake Huron.

Since 1975 the commission, concerned that the control program was overly dependent on chemicals, has emphasized that the chemical control program alone can never bring the sea lamprey under complete control. The success of the chemical applications and the development of a

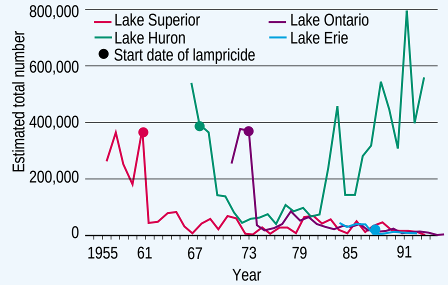

Fig. 5. Numbers of feeding-phase sea lamprey in Lakes Superior, Huron, Erie, and Ontario before and after initiation of lampricide applications in tributaries. Dot indicates start date of lampricide use (G. Christie, Great Lakes Fishery Commission, Ann Arbor, Michigan, unpublished data).

world-class recreational fishery, though, have led the public and the U.S. and Canadian governments to consider the lamprey problem in the Great Lakes solved. Thus, funding for research that was needed to investigate supplemental and alternative control methods, and even funding for maintenance of control programs, was curtailed. The sea lamprey control program directly benefited the fishery and therefore was better funded than the research program.

In 1982 the commission began applying integrated pest management concepts to sea lamprey management. Concern about the introduction of chemicals into the environment has led the commission to fund extensive testing of the environmental safety of lampricides. Although no long-term detrimental effects to the ecosystem have been detected, public apprehension about pesticides is a compelling reason to seek alternatives to lampricides. Therefore, the commission's integrated management of sea lamprey includes establishing target levels of sea lamprey abundance (Fig. 6) and reducing lampricide use by 50% by the year 2000 (Great Lakes Fishery Commission 1992). The sea lamprey controls now in use include low-head barrier dams, stream velocity barriers, safer and more effective electrical barriers, mechanical trapping, and the

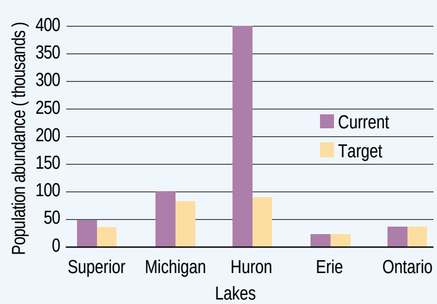

Fig. 6. The 1995 status of sea lamprey populations in the Great Lakes and control program targets for sea lamprey suppression (G. Christie, Great Lakes Fishery Commission, Ann Arbor, Michigan, unpublished data).

release of sterile male sea lampreys, which compete with normal males for mates but produce no offspring. The development of spawning attractants and repellents, which took a large part of the research budget for several years, has not yet yielded a useful control tool.

The St. Marys River, which connects Lake Superior and Lake Huron, contributes an estimated 400,000 sea lampreys a year to Lake Huron, with disastrous effects on the lake trout population there (Figs. 5 and 6). Although a multiphase attack program on sea lampreys spawning in the St. Marys has been developed, it may not be implemented soon.

Rebuilding the Great Lakes Fishery

As sea lampreys became sufficiently controlled, Ontario, state, and U.S. Fish and Wildlife hatcheries produced large numbers of lake trout for stocking. These hatcheries, though, were unable to produce enough fish to fully take advantage of the carrying capacity of the lakes with their huge populations of forage fish. After evaluating the opportunity, the Michigan Department of Natural Resources introduced chinook salmon and coho salmon, which can be grown in hatcheries to stocking size in greater numbers and in shorter times than lake trout. The salmon were first stocked in Lake Michigan, where they survived in excellent numbers, grew quickly on a diet of alewives, were relatively resistant to lamprey attack, and provided an excellent offshore and inshore recreational fishery. Other states around the lakes soon followed Michigan's lead.

Thus, the fishery has been rebuilt through sea lamprey control, water-quality improvement, habitat protection, stocking, establishment of sanctuaries, and enforcement of regulations. At the fishery's peak in the mid-1980's, the annual regional economic effect of the commercial fisheries was estimated at $270 million, and that of the recreational fisheries at $2.0–$4.0 billion (Talhelm 1988). Some 55 million angler-days were spent in pursuit of Great Lakes fish annually, and the fishery-related industries provided employment for between 37,500 and 75,000 people.

The commercial catch of lake whitefish, a valuable species that was also decimated by the sea lamprey, is at historic levels. Lake trout populations have been declared recently to be self-sustaining in Lake Superior, and natural reproduction is finally occurring in the other lakes. Alewife populations are under control, and native species of forage fish are rebuilding. Keeping sea lamprey populations at levels that allow adequate survival of desirable fish communities seems to be the key to success. With adequate funding for current control strategies and further research into innovative alternative control techniques and their application, further declines in sea lamprey populations seem achievable and economically feasible.

See end of chapter for references

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alike. Today the ciscoes are represented only by the lake herring and one to three other closely related deepwater species or subspecies that are extinct, approaching extinction, or simply merging their genetic identities by interbreeding. Similar evolution of subspecies also occurred in lake trout in the Great Lakes proper (Brown et al. 1981; Goodier 1981; Goodyear et al. 1982; Krueger and Ihssen 1995) and in New York's Finger Lakes, which are in the Lake Ontario drainage (Royce 1951).

At least 25 nonindigenous fishes have become established in the Great Lakes since the region was settled, and nearly half of them have had substantial ecological and economic effects (Bailey and Smith 1981; Mills et al. 1993; Edsall et al. 1995). The sea lamprey, a marine species, contributed to the loss of native Atlantic salmon and lake trout in Lake Ontario. Sea lamprey probably entered Lake Ontario from the Hudson River via the Erie Barge Canal, which was opened to barge traffic in 1819 and connects the Hudson River and Lake Ontario drainages via Lake Oneida. Sea lamprey later moved into the upper four Great Lakes, probably through the Welland Canal, which allows ships to go around Niagara Falls. In the upper four lakes, sea lamprey contributed directly to the decline of lake trout and several other large fish species that supported the sport and commercial fisheries of those lakes. Millions of dollars are now spent annually on sea lamprey control in an effort to restore the damaged fish populations.

The alewife is another nonindigenous marine species that has become established in the Great Lakes. It was present in Lake Ontario in 1873 and probably entered the lake and spread throughout the rest of the basin following the same route used by the sea lamprey. It reached Lake Michigan in 1949 (Smith 1972) and by the 1960's had caused major changes in the plankton community (Wells 1970). The alewife also suppressed the native whitefishes, yellow perch, emerald shiner, deepwater sculpin, and spoonhead sculpin, probably through predation on the youngest life stages and competition with the older life stages (Potter and Fleischer 1992). The alewife also may have suppressed the rainbow smelt, a nonindigenous marine forage species that had been deliberately introduced into the Great Lakes in the early 1900's to provide forage for trout and salmon. Researchers generally believe that the alewife would not have reached such high levels of abundance and dominated the fish community in any of the Great Lakes if the large, native predatory fishes had not been destroyed by overfishing and predation by sea lamprey. Eventually, though, the alewife became a major prey species for trout and Pacific salmon and was considered a beneficial addition to the forage base. Recent information (Fisher et al. 1995a,b), however, shows that an enzyme carried by the alewife destroys vitamin B_1 in Atlantic salmon that eat alewives. Thus, female Atlantic salmon that feed extensively on alewives become B_1-deficient, and the fry that hatch from their eggs die when they are only a few weeks old. Consequently, the invasion of the Lake Ontario drainage by the alewife is strongly implicated in the extinction of the native populations of Atlantic salmon there in the 1800's. The alewife can also cause B_1 deficiency in lake trout and may contribute to the general failure of stocked lake trout to reproduce in Lakes Michigan, Erie, and Ontario, where the alewife is a major food of lake trout (Fisher et al. 1996).

The nonindigenous blueback herring, a marine species closely related to the alewife, is one of the newest additions to the fish fauna of the Great Lakes. This species was recently documented entering the Lake Ontario drainage from the Hudson River via the Erie Barge Canal (L. R. Wedge, New York Department of Environmental Conservation, personal communication)—the same entry route postulated for the sea lamprey and the alewife. This species' effect on the Great Lakes fishes and ecosystems is expected to be similar to that of the alewife, which it closely resembles.

The ruffe, a small perchlike fish from Eurasia (Fig. 10), is another recent addition to the Great Lakes. In the early to mid-1980's it reached the Saint Louis River estuary in Lake Superior via ballast water (Simon and Vondruska 1991; Pratt et al. 1992). Ruffe abundance increased sharply in 1993, and the species spread to other parts of the lake. Yellow perch numbers in the Saint Louis River estuary declined markedly as ruffe abundance increased. Researchers are concerned that similar declines could occur elsewhere in the Great Lakes if the ruffe expands its range and competes with yellow perch for thermal habitat (Edsall et al. 1993) and food (Ogle et al. 1995). The ruffe could potentially occupy nearly 7 million hectares of habitat in the Great Lakes that is presently suitable for use by yellow perch (Edsall et al. 1993). In 1995 two ruffe were captured in Thunder Bay, Lake Huron, near Alpena, Michigan.


Courtesy T. Edsall, USGS

Fig. 10. The ruffe, a small, perch-like Eurasian fish that recently became established in the western end of Lake Superior.

Round and tubenosed gobies are also among the recent ballast-water additions to the Great Lakes. They were first reported from the Saint Clair River in 1990 (Jude et al. 1995). They are expected to compete strongly with native sculpins and other small, bottom-feeding fishes and are considered highly undesirable additions to the region.

The successful stockings of Pacific salmon, rainbow trout, and brown trout in the Great Lakes during the present century had profound and largely beneficial ecological and economic effects on the region. They are large predators that feed extensively on the introduced alewife and rainbow smelt. They also support popular fisheries that contribute significantly to the Great Lakes fishery, which is valued at more than $6.8 billion annually (U.S. Fish and Wildlife Service 1995). There are self-sustaining populations of these fishes in some areas, but in most areas stocking substantially augments the naturally produced fishes.

Status and trend information is available for a number of fishes commonly found in the Great Lakes. The longest set of records is for fish species that were of commercial value and entered the commercial catch. The commercial fishery in the Great Lakes dates back to the 1700's in some areas, but the earliest records are fragmentary or anecdotal and are not useful for demonstrating trends. Continuous records of the commercial fishery in the Great Lakes began in 1867 in Canada and in 1879 in the United States (Baldwin et al. 1979). Because the records do not report the amount of fishing effort expended to catch fishes or the amounts of some fish species that were caught but not brought to land for sale, they must be interpreted carefully. The records for the high-value, intensively fished species like the lake whitefish probably fairly reflect the trends in abundance, whereas records for low-value species like freshwater drum do not. Freshwater drum were often taken incidentally in large numbers in nets set for other high-value species such as yellow perch and walleye. The market price for freshwater drum and the size of the catch of high-value species made by the individual fisherman on any given day probably determined how many freshwater drum were brought ashore for sale and how many were simply dumped back into the lake. Thus, the records for freshwater drum and other low-value species are generally not good indicators of abundance trends. There were, however, periods in particular areas or lakes when the high-value species had been fished to extinction or near extinction, and the only species left to catch were those of low value. In those situations, the records for the low-value species probably more closely reflect actual trends in abundance.

If these caveats for interpreting the catch data are applied, the history of the early commercial fishery in the Great Lakes can be seen as one of intensive, selective fishing that eventually caused stocks of high-value species to decline and, in some cases, to become extinct.

The lake sturgeon (Fig. 11), a long-lived species that does not reproduce until it is about 25 years old, was one of the first species to approach extinction in the Great Lakes. Annual catches in the U.S. waters of Lake Erie fell from an all-time high of 2.1 million kilograms in 1885 to about 13,000 kilograms in 1917 (Fig. 12). Thereafter, catches never exceeded 10,000 kilograms, and after 1966 the catch fell to zero. Early in the fishery the lake sturgeon was considered a nuisance species because it destroyed nets set for other smaller fish. Later, as markets developed, it became a sought-after species. The construction of dams that denied the lake sturgeon access to its spawning grounds in Great Lakes tributaries also helped accelerate its decline.

The blue pike, another high-value species, was lost to overfishing. Annual catches as high as 9 million kilograms occurred in the mid-1930's in the U.S. waters of Lake Erie, but by the early 1960's the species had been fished to extinction (Fig. 13). The walleye, a closely related species, was also severely overfished in Lake Erie. Catches declined from annual highs of about 2.3–2.8 million kilograms in the late 1940's–late 1950's to about 25,000 kilograms in 1971. The decline was largely attributed by commercial fishing interests to deteriorated environmental conditions. Closure of the fishery because of mercury contamination in the early 1970's, followed by the imposition of more stringent catch regulations, allowed walleye numbers to rapidly increase, and the species again supports a healthy, self-sustaining, and high-value fishery.

High-value coldwater fishes that declined to virtual extinction in all or some of the Great Lakes include the lake trout, lake whitefish, and lake herring. Native populations of lake trout were nearly extinguished in the Great Lakes as a combined result of overfishing and predation by the introduced sea lamprey. The native lake trout populations in Lakes Michigan, Erie, and Ontario were lost, and only a small population survived in a remote area of Lake Huron. In Lake Superior, the nearshore populations of native fishes were sharply reduced by the late 1950's when commercial fishing ended and the sea lamprey was controlled. Lake whitefish populations reached record lows during the 1950's and the 1960's in Lake Huron and in the 1950's in Lake Michigan but have since recovered. In Lake Erie, for example, the U.S. catch fell gradually from a high of 1.6 million kilograms in the late 1800's to zero in the early 1960's, although a recovery may have begun in the late 1980's (Fig. 14). In the U.S. waters of Lake Huron and in Lake Michigan, the catch of lake herring fell to zero in the 1970's. Catches also fell to record lows in Lake Superior in the 1970's. These declines in lake herring populations have been attributed to overfishing and predation of young lake herring by rainbow smelt.

The more recent records of commercial catch in the Great Lakes have not been published but are available from the U.S. Geological Survey, Biological Resources Division. The commercial fishery in the U.S. waters of the Great Lakes is presently quite restricted. Better information on the status and trends of Great Lakes fish populations is now compiled annually for each of the lakes by committees whose memberships represent biologists and managers from the Great Lakes states, the Province of Ontario, Department of Fisheries and Oceans—Canada, the U.S. Geological Survey, and the Native American tribes with treaty fishing rights. These reports reveal the following major trends.

In Lake Superior, the lake trout fishery is presently maintained by stocking and by natural reproduction from wild fishes (Hansen 1994).

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Fig. 11. Biologist with a lake sturgeon. The largest lake sturgeon caught in the Great Lakes weighed 140 kilograms.

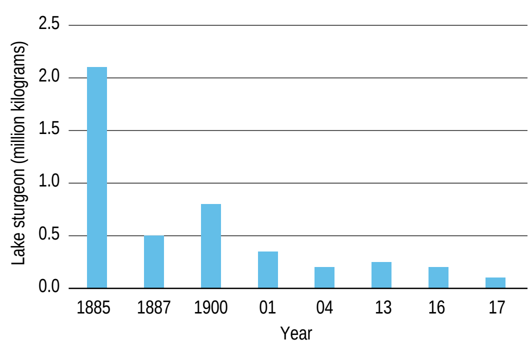

Fig. 12. Commercial catch of lake sturgeon in U.S. waters of Lake Erie, 1885–1917 (Baldwin et al. 1979).

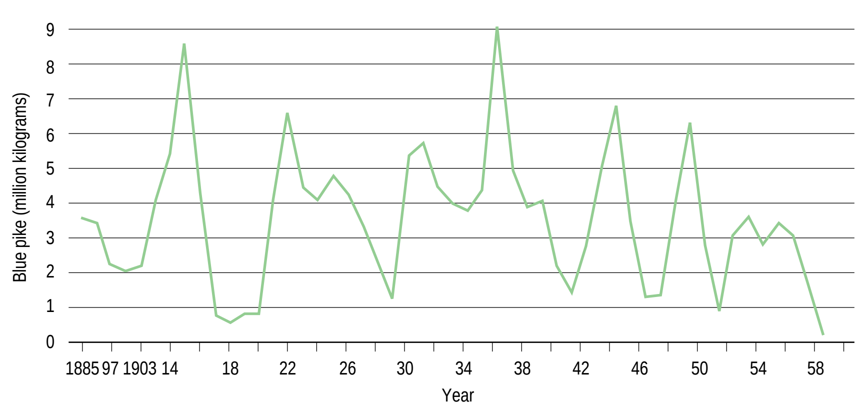

Fig. 13. Commercial catch of blue pike in U.S. waters of Lake Erie, 1885–1960 (Baldwin et al. 1979).

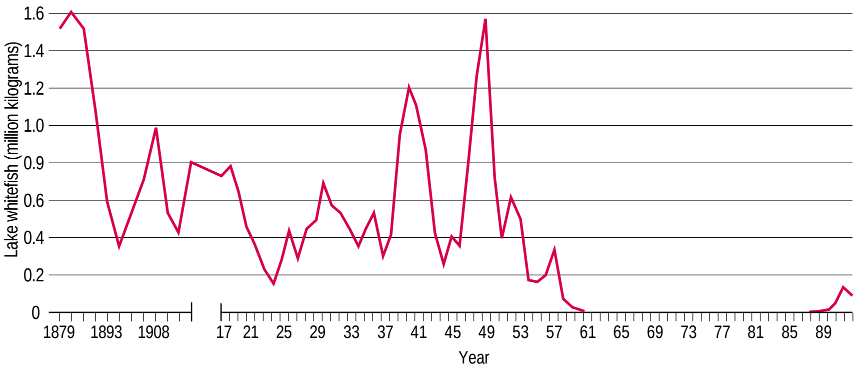

Fig. 14. Commercial catch of lake whitefish in U.S. waters of Lake Erie, 1879–1992 (Baldwin et al. 1979).

Introduced species of trout and salmon support a stable fishery, whereas brook trout and lake sturgeon populations have not recovered from earlier exploitation and are still at low levels. Lake herring numbers are recovering strongly and rainbow smelt are reduced from earlier levels of peak abundance. Deepwater cisco populations have declined, and lake whitefish are abundant and support a productive fishery. The sea lamprey is reduced to about 10% of its former peak abundance, but the ruffe is increasing in abundance.

In Lake Huron, the fish community is recovering but remains unstable after decades of overharvest and the effects of introduced species (Ebener et al. 1995). Modest numbers of stocked lake trout are once again reproducing in the lake, and populations of lake whitefish and deepwater ciscoes are more abundant than at any other time in this century. Walleye and yellow perch are once again abundant. Rainbow smelt and alewife populations are stable but are still reduced over former peak levels in the 1970's. In the 1980's, the sea lamprey increased in abundance in the northern end of the lake, imposing high mortality and reversing recent gains in lake trout restoration in that area.

In Lake Michigan, substantial numbers of stocked, breeding-age lake trout are present in lake trout refuges at several locations throughout the lake (Holey et al. 1995). Spawning and fry production by stocked fish have been recorded at several locations in the lake, and wild yearling and older lake trout have been found in the lake, but substantial numbers of adult wild fish have not been produced. Pacific salmon abundance is sharply reduced over peak levels reached in the 1970's to the mid-1980's. The causes for the decline are complex and not fully understood. Mortality of coho salmon fry soon after hatching has been observed. This mortality can be alleviated by treatment with vitamin B_1, suggesting there is a vitamin B_1 deficiency in the female parent that causes mortality in the fry. Mortality of adult Pacific salmon in the lake is correlated with an incidence of bacterial kidney disease, a pathogen that has been introduced to the Lake Michigan basin. A linkage between virulence of the pathogen and nutritional status of the salmon is being investigated.

The biomass (a measure of abundance expressed as weight) of the three major prey fishes in Lake Michigan has changed significantly since the early 1970's (U.S. Geological Survey, Biological Resources Division, unpublished data). Alewives made up more than 80% of the biomass in catches in the 1970's but declined to about 10% in the mid-1980's–1990's. The biomass of bloaters, a deepwater cisco, increased from less than 10% in the 1970's to more than 80% in the 1980's–1990's, and rainbow smelt decreased from 15%–20% in the 1970's and early 1980's to less than 10% in the mid-1980's and 1990's. Deepwater sculpins were abundant in the late 1970's and the early 1980's but then declined sharply in the 1990's, perhaps in response to competition from the increased biomass of bloaters and to predation by burbot, which have increased substantially in abundance since 1984. Slimy sculpin abundance peaked in the late 1970's but in the 1980's–1990's declined to less than 20% of peak 1970's levels, probably in response to predation by trout, salmon, and burbot.

In Lake Erie, lake trout restoration goals are being met and lake whitefish are showing signs of a recovery (Great Lakes Fishery Commission 1995a). Walleye and yellow perch are intensively managed to provide productive recreational and commercial fisheries in the United States and Canada (Great Lakes Fishery Commission 1995b). The abundance of the major forage fish species in Lake Erie—rainbow smelt, spottail shiners, emerald shiners, gizzard shad, and alewives—seems to be declining.

In Lake Ontario, the fish community has improved considerably from a low point in the 1960's (Kerr and LeTendre 1991; Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation 1994). Reductions in nutrients and other pollutants entering the lake, aggressive sea lamprey control, and stocking of trout and salmon brought about major improvements in the lake's fish community by the 1980's. Water quality had improved, levels of toxic contaminants in fish had decreased, and valuable recreational fisheries were established. Alewife and rainbow smelt abundance declined in the 1980's in response to trout and salmon predation and to reduced nutrient input to the lake, and in the 1990's, stocking of trout and salmon was reduced to bring them into better balance with their food supply. In addition, some native fishes are recovering from low levels observed in the 1960's. For example, lake whitefish, which typically had been most abundant in the eastern end of the lake, were nearly absent there from the catch in the 1970's. In the 1980's, however, the species began increasing and were 30- to 40-fold more abundant there in the 1990's.

Amphibians and Reptiles

The amphibians and reptiles of the Great Lakes region are an interesting and diverse group that includes 83 species (Table 3). Salamanders, frogs, turtles, and snakes are represented by the greatest number of species (11–28), and toads (4) and lizards (6) by the fewest. There are also another dozen or more subspecies and hybrids, mostly snakes, that are not represented in Table 3. Species richness is highest in Illinois (63 species) and lowest in New York (44). The high richness in Illinois, Indiana, Ohio, and Pennsylvania is remarkable because the areas that are included in the Great Lakes region in those states are relatively small. Minnesota and Michigan, states with large land masses in the region, have relatively low species richness (48 and 51 species, respectively) because the climate is generally less suitable for amphibians and reptiles in those states than in the other states in the region. Many of the amphibians and reptiles that occur in Minnesota are at the northern end of their range. Amphibians are generally less abundant in the drier western portions of Minnesota, and the number of reptiles is low in the colder northern portions of Minnesota and Michigan.

Species that occur throughout the region include the eastern newt, eastern red-backed salamander, mudpuppy, American toad, chorus frog, spring peeper, gray treefrog, bullfrog, green frog, pickerel frog, northern leopard frog, wood frog, common snapping turtle, Blanding's turtle, painted turtle, common map turtle, smooth green snake, racer snake, rat snake, milk snake, common garter snake, Dekay's brown snake, red-bellied snake, and northern water snake. The lizards have the most restricted distributions; their highest richness occurs in the four westernmost states in the region.

Amphibians in many parts of the world have recently declined in number and geographic ranges (Blaustein and Wake 1990; Phillips 1990, 1991; Wake 1991; Livermore 1992). The situation is complex, but many scientists believe that a global problem faces amphibians and that this problem is largely the result of habitat modification by humans. Acid precipitation, shifts in precipitation patterns, intensive agriculture, deforestation, urbanization, highway construction, wetland draining, dam construction, pollution by pesticides and heavy metals, and the introduction of fishes and other predators

Table 3. Numbers of species of amphibians and reptiles in the Great Lakes region.[a]

	Total by state								Total by region
	MN	WI	IL	IN	MI	OH	PA	NY	
Amphibians									
Salamanders	5	7	10	11	11	15	13	12	17
Toads	3	1	2	2	2	2	2	1	4
Frogs	11	11	10	9	10	9	9	8	11
Reptiles									
Lizards	3	4	4	3	1	1	0	1	6
Turtles	9	11	14	10	9	8	9	9	17
Snakes	17	20	23	18	18	20	16	13	28
Total	48	54	63	53	51	55	49	44	83

[a]Sources: Ruthven et al. (1928); Smith (1961); Minton (1972); Pentecost and Vogt (1976); Vogt (1981); Conant and Collins (1991); Shaffer (1991); Oldfield and Moriarity (1994).

can all adversely affect amphibians. Baseline information on the status and health of U.S. populations of amphibians and reptiles is remarkably scarce (McDiarmid 1995), and there are no long-term, quantitative data on amphibians or reptiles in the Great Lakes region. Amphibians in the Midwest do not seem to be experiencing the drastic declines occurring elsewhere (Illinois Department of Energy and Natural Resources 1994), but local declines are apparent for both amphibians and reptiles. Sensitive species—including the spotted salamander, eastern red-backed salamander, four-toed salamander, wood frog, pickerel frog, northern cricket frog, wood turtle, and queen snake—are usually the first to disappear following reductions in water quality, other physical alterations of the environment, and pesticide use (Minton 1972).

Better descriptions of the status of amphibians and reptiles in the region will require more intensive surveys, monitoring, and data-base development. None of the reptile or amphibian species in the Great Lakes region are federally listed as threatened or endangered.

Birds

Birds contribute significantly to the biological diversity of the Great Lakes region. They are visible and valued elements of the regional ecosystems, and collectively they represent substantial recreational resources. Many books and articles have been written about the birds of the Great Lakes region to meet the needs and interests of bird watchers and other nature observers, resource managers, and scientists.

Broad-scale national programs—such as the U.S. Geological Survey's Breeding Bird Survey, annual waterfowl surveys, wintering surveys, and the annual National Audubon Society's Christmas Bird Count—provide status and trend information on as many as 75% of the bird species in the United States (Hall 1995). The information collected for the more abundant species is sufficient to detect large-scale population changes. Specialized surveys provide information on some of the less

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abundant species and on those species whose habits make them more difficult to census. The newer status and trends information for individual species is organized in various ways, with much of it being stored in state and national data bases in a geographically referenced manner. Breeding bird atlases or other general texts prepared for each state (for example, [Indiana] Mumford and Keller 1984; [New York] Andrle and Carroll 1988; [Illinois] Bohlen 1989; [Michigan] Brewer et al. 1991; [Ohio] Peterjohn and Rice 1991; [Wisconsin] Robbins 1991; [Pennsylvania] Brauning 1992) also provide useful, detailed information on breeding birds. These books contain species accounts and background information describing the distribution, habitats, and breeding habits. Some of them also describe the status and the trends in abundance of bird species found in the state and provide explanations for observed changes in distribution and abundance.

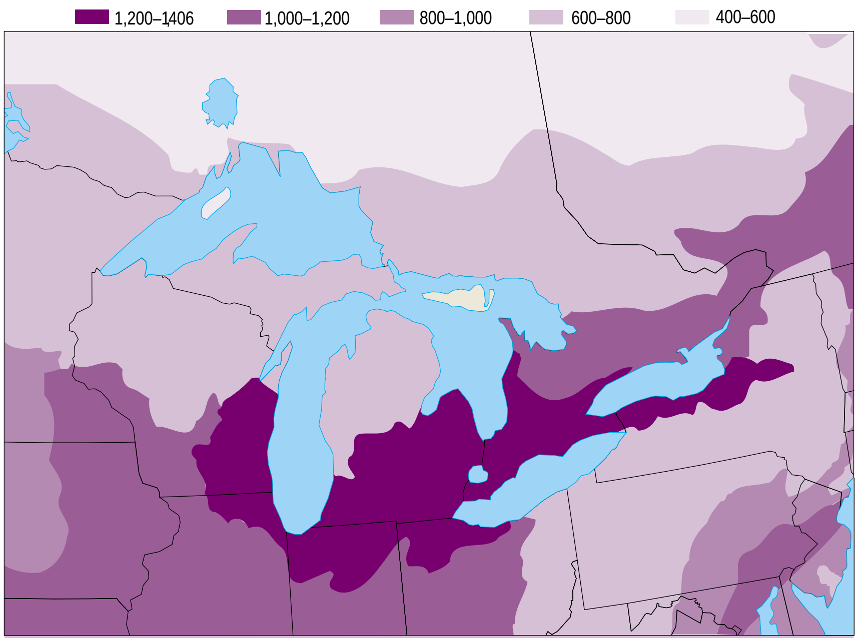

Fig. 15. Relative abundance of breeding birds across North America by physiographic region. Abundance expressed as mean number of individuals per 50-stop Breeding Bird Survey route, 1965–1980 (after Robbins et al. 1986).

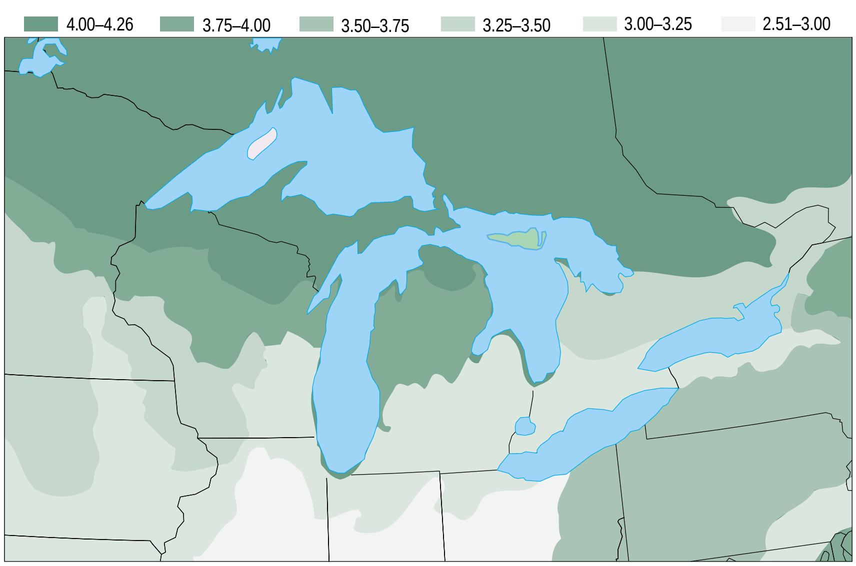

Fig. 16. Species diversity index (H′) for breeding birds across North America by physiographic region. $H' = \sum p_i, \ln p_i$, where p_i = the proportion of all birds that belong to the *i*th species (after Robbins et al. 1986).

Birds are a large and highly diverse group, and it is probably inappropriate to generalize too broadly about the status of the group, although aggregating species data functionally can be useful. On a national scale, such data suggest that many species are presently stable, that some generalist species that can adapt to altered habitats are increasing, and that species less able to adapt to habitat degradation and habitat loss are decreasing (Hall 1995).

The North American Breeding Bird Survey documents species distributions and population trends of about 250 species on national, regional, and local scales. The survey data for 1965–1980 (Robbins et al. 1986) show that the relative abundance of breeding birds (mean number of individuals counted) in 1965–1980 in the southern portion of the Great Lakes region and along the south shore of Lake Ontario was among the highest in the nation (mean of 1,200–1,406 individuals per 50-stop counting route; Fig. 15). Abundance was lower to the west in Illinois and southern Wisconsin (1,000–1,200 individuals), and lowest (600–800) elsewhere in the region. Species diversity in 1966–1979 was lowest (species diversity index H′ = 3.00–3.25) in the southern part of the region where relative abundance was highest and was highest in the region and nationally (4.00–4.26) in the northern portions of the region, where relative abundance was lowest (Fig. 16).

The Breeding Bird Survey data collected since 1979 have not been published in detail. Peterjohn et al. (1995), however, presented a brief summary and evaluation of the data for 1966–1992, showing that 130 species decreased in abundance, 57 of which were confirmed by statistical testing. Some species in all families decreased in abundance, but decline was most common among the Mimidae (mockingbird, catbird, thrashers) and sparrows. Increases in abundance were exhibited by 115 species; 44 of these increases were confirmed by statistical testing. Flycatchers and warblers were prominent among those species that increased nationally. Functional groupings of the species breeding in the United States revealed other trends (Peterjohn et al. 1995). Grassland species showed the most declines nationally and in the Great Lakes region (Fig. 17).

Shrubland and old-field birds also seem to be declining nationally, but the increases and

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decreases seem to roughly balance out in the Great Lakes region (Fig. 18). Woodland birds are increasing nationally and in the Great Lakes region as well (Fig. 19). Neotropical migrants show regional declines balanced by increases in other parts of the nation. In the Great Lakes region, Neotropical migrant populations are increasing in some areas and decreasing in others; the net change seems to be positive (Fig. 20). Short-distance migrants are declining nationally and in the southern portions of the Great Lakes region (Fig. 21). Permanent residents are also declining nationally, but seem to be generally increasing in the Great Lakes region (Fig. 22).

Trend data for 106 individual species from the Breeding Bird Survey displayed statistically significant trends in abundance from 1966 to 1992 (Table 4). Fifty-two species increased in abundance over the 26-year period, and 54 decreased. Most rates of annual change were small. The abundance of 57 species changed only 1%–2% per year; 43, 3%–11%; 4, 15%–20%; and 2, 51%–53%. Some of the changes can be related to natural or human-mediated range expansions, changes in habitat availability, competition with introduced species like the starling, and mortality resulting from severe and unusual weather conditions. The largest changes shown in Table 4 occurred

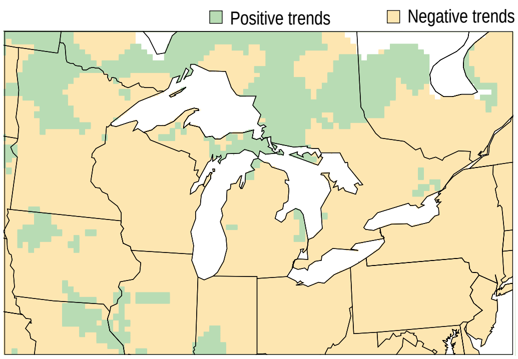

Fig. 17. Geographic patterns in mean trends for grassland bird species, 1966–1992 (from Peterjohn et al. 1995).

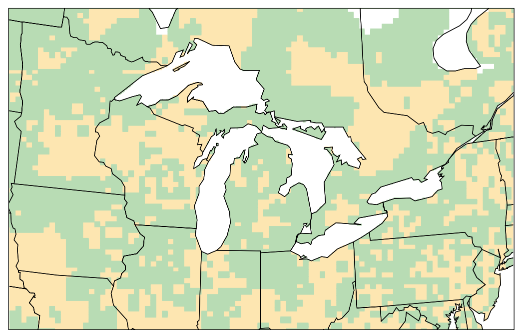

Fig. 20. Geographic patterns in mean trends for Neotropical migrant birds, 1966–1992 (from Peterjohn et al. 1995).

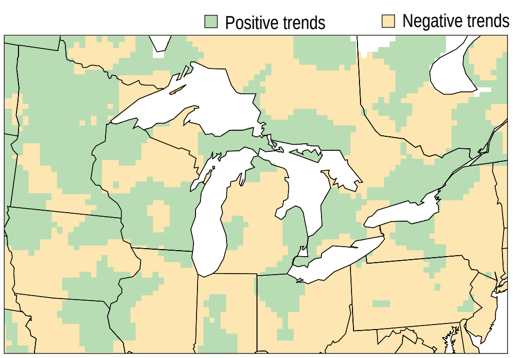

Fig. 18. Geographic patterns in mean trends for shrubland and old-field birds, 1966–1992 (from Peterjohn et al. 1995).

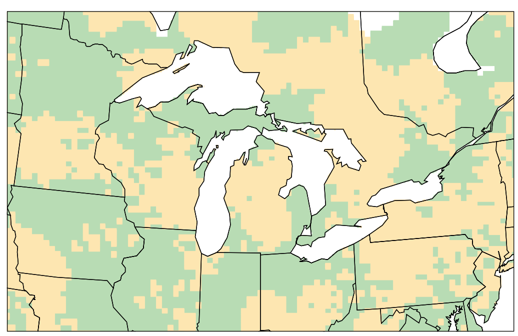

Fig. 21. Geographic patterns in mean trends for short-distance migrant birds, 1966–1992 (from Peterjohn et al. 1995).

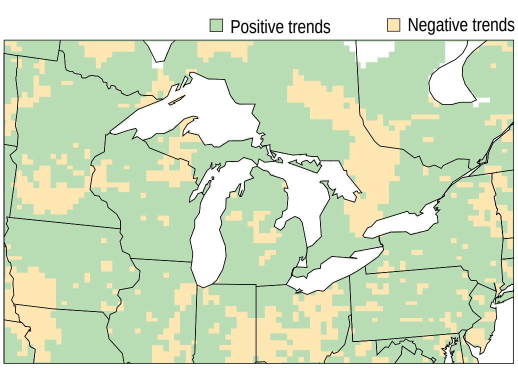

Fig. 19. Geographic patterns in mean trends for woodland birds, 1966–1992 (from Peterjohn et al. 1995).

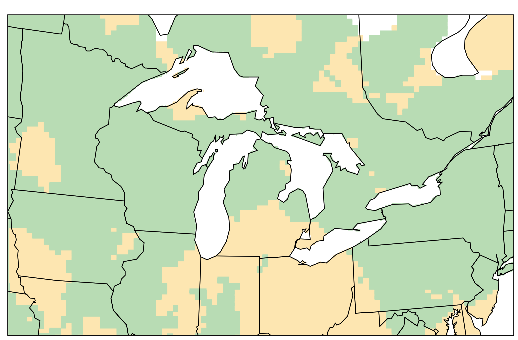

Fig. 22. Geographic patterns in mean trends for permanent resident birds, 1966–1992 (from Peterjohn et al. 1995).

Table 4. Trends in abundance (percent change per year) of birds breeding in the Great Lakes region, 1966–1992.[a]

Group and species[b]	Trend
Loon to heron (10)	
Common loon	3.3
Double-crested cormorant	6.3
Great blue heron	3.2
Swan to duck (14)	
Canada goose	51.1
Wood duck	9.2
Green-winged teal	-2.2
Mallard	3.1
Red-breasted merganser	-5.3
Vulture to hawk (11)	
Turkey vulture	11.9
Osprey	9.1
Bald eagle	7.1
Red-tailed hawk	2.6
American kestrel	1.0
Merlin	18.9
Partridge to quail (7)	
Gray partridge	-7.0
Ring-necked pheasant	-2.1
Sharp-tailed grouse	2.9
Northern bobwhite	-6.4
Rail to plover (11)	
Virginia rail	-7.2
Common moorhen	-20.5
Sandhill crane	15.6
Common snipe	-1.4
Tern and gull (7)	
Ring-billed gull	5.7
Common tern	-8.8
Black tern	-5.9
Dove to cuckoo (4)	
Mourning dove	1.0
Black-billed cuckoo	-1.4
Yellow-billed cuckoo	-2.4
Owl to kingfisher (8)	
Chimney swift	-1.3
Belted kingfisher	-2.9
Woodpecker (8)	
Red-headed woodpecker	-5.3
Red-bellied woodpecker	5.4
Downy woodpecker	2.1
Hairy woodpecker	2.5
Black-backed woodpecker	8.0
Northern flicker	-2.1
Pileated woodpecker	6.0
Flycatcher to swallow (18)	
Olive-sided flycatcher	-2.3
Eastern wood-pewee	-1.0
Alder flycatcher	1.2
Least flycatcher	-2.3
Eastern phoebe	2.0
Eastern kingbird	-0.7
Purple martin	-2.5
Barn swallow	-1.2
Jay and crow (5)	
American crow	1.3
Common raven	3.4
Titmouse to wren (11)	
Black-capped chickadee	2.5
Boreal chickadee	-5.3
Tufted titmouse	4.3
Red-breasted nuthatch	4.4
House wren	0.6
Winter wren	4.1
Sedge wren	2.2
Kinglet to thrush (10)	
Ruby-crowned kinglet	-1.6
Blue-gray gnatcatcher	9.0
Eastern bluebird	3.0
Veery	-1.9
Swainson's thrush	-2.2
Hermit thrush	2.0
Wood thrush	-3.3
American robin	0.6
Catbird to starling (5)	
Brown thrasher	-2.7
Cedar waxwing	1.5
European starling	-1.6
Vireo (6)	
Solitary vireo	4.6
Yellow-throated vireo	2.9
Warbling vireo	-1.0
Red-eyed vireo	1.2
Warbler (32)	
Northern parula	1.2
Yellow warbler	1.3
Magnolia warbler	1.8
Yellow-rumped warbler	1.9
Pine warbler	6.6
Bay-breasted warbler	-4.9
Black and white warbler	1.3
Canada warbler	-2.3
Yellow-breasted chat	-5.0
Tanager to towhee (6)	
Northern cardinal	2.5
Rose-breasted grosbeak	-1.0
Indigo bunting	0.6
Dickcissel	8.3
Eastern towhee	-2.0
Sparrow (15)	
Field sparrow	-2.7
Vesper sparrow	-3.3
Savannah sparrow	-1.8
Grasshopper sparrow	-6.9
Henslow's sparrow	-10.0
Song sparrow	-0.6
White-throated sparrow	-1.8
Junco to oriole (12)	
Slate-colored junco	-3.1
Bobolink	-1.8
Red-winged blackbird	-1.5
Eastern meadowlark	-3.4
Western meadowlark	-7.4
Brewer's blackbird	2.1
Common grackle	-2.1
Brown-headed cowbird	-3.4
Orchard oriole	4.3
Baltimore oriole	-0.8
Finch (9)	
Pine grosbeak	-17.8
Purple finch	-2.8
House finch	53.0
Red crossbill	10.1
Evening grosbeak	-3.8
House sparrow	-1.9

[a]Data provided from the Breeding Bird Survey data bank by J. Sauer, U.S. Geological Survey, Patuxent Wildlife Research Center. The Breeding Bird Survey lists trend information for 209 species for the Great Lakes region; of these, statistically significant trends were detected for the 106 species listed here.
[b]To aid in presentation, groupings may include more than one family (for example, "Loons to herons" includes loons (Gaviidae), grebes (Podicipedidae), cormorants (Phalacrocoracidae), and bitterns and herons (Ardeidae). Number in parentheses is number in group on Breeding Bird Survey list.

among house finch (53% per year) and Canada goose (51% per year) populations and are easily interpreted. The house finch, which is native to the western United States, was introduced to the east coast and is rapidly expanding its range to include most of the eastern and midwestern United States. The resident populations of Canada geese have developed in the Great Lakes region in response to management efforts to improve hunting opportunities. These populations now breed widely in urban and rural areas throughout the region. Causes for the changes in abundance of some other individual species listed in Table 4 are discussed in Robbins et al. (1986) and in bird atlases for the individual states.

Many species overwinter in portions of the United States; the National Audubon Society Christmas Bird Count, which began in 1900, provides data that can be used to describe population trends outside the breeding season. An atlas of North American wintering birds (Root 1988) gives data on distribution and abundance for more than 600 species in count years 1963–1973. More recently, Root and McDaniel (1995) examined national count data collected in 1959–1989 for 50 songbird species whose northern range is limited by low winter temperature. Twenty-seven of these species exhibited a trend in at least one state, and 16 had declining populations in more than half of the states where they occurred. Meadowlarks, sparrows, and other species that eat seeds from grasses and forbs showed a more widespread decline than those that eat berries or seeds from woody vegetation. This supports the finding by Peterjohn et al. (1995) of a nationwide decrease in the grassland species. An analysis by state for the Great Lakes region revealed that more species were increasing than were decreasing.

The Breeding Bird Survey and Christmas Bird Count data are collected in different manners and cannot be compared directly as equivalents. Together, however, they show clearly how species distribution changes between the breeding and wintering seasons. The only such published comparison (Robbins et al. 1986) was made for 1979 (Figs. 23 and 24). The number of breeding species per route in 1979 for the Great Lakes region was 60–67 in the northern portions of the region, 50–60 in the southern portions of the region, and 40–50 in the western portions. The mean number of species during the Christmas Bird Count in 1979 for the Great Lakes region was less than 40 in the northern portion of the region, 40–60 in most of the region, and 60–80 along southern Lake Michigan and most of Lake Erie and Lake Ontario. Many of the species counted along the shorelines of eastern Lake Erie and western

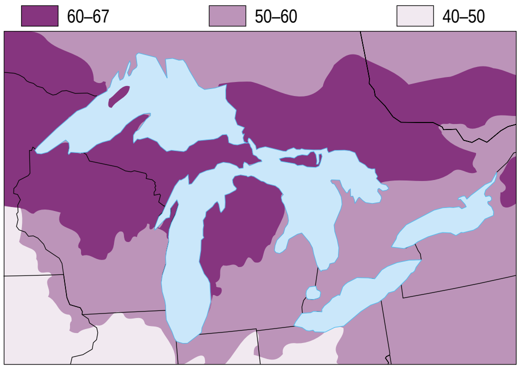

Fig. 23. Mean number of breeding birds across North America per 50-stop Breeding Bird Survey route by physiographic region, 1979 (after Robbins et al. 1986).

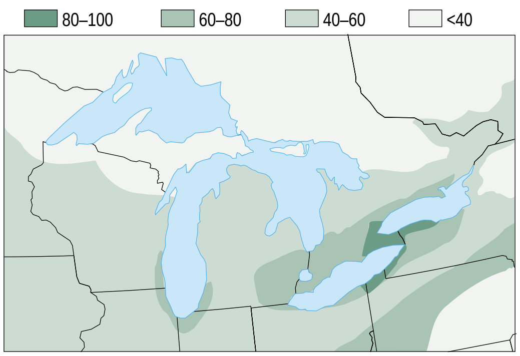

Fig. 24. Mean number of bird species per Christmas Bird Count, 1979, for comparison with distribution during the 1979 breeding season shown in Fig. 23 (after Robbins et al. 1986).

Lake Ontario were wintering waterbirds. The less complex winter distribution suggests that the habitat requirements in winter are simpler than during the breeding season and are probably strongly related to temperature and food availability.

Federally listed threatened and endangered bird species in the Great Lakes region include the bald eagle, American and arctic peregrine falcons, piping plover, Kirtland's warbler, and least tern (U.S. Fish and Wildlife Service 1994). Two of these species, the bald eagle and Kirtland's warbler, are responding favorably to recovery plans designed to restore productive populations and remove them from the list of threatened and endangered species.

The bald eagle is a large, predatory bird that feeds mainly on fishes and waterbirds. The bald eagle was once relatively abundant in the Great Lakes region, but reproductive failure caused by high levels of organic pesticides in its diet caused the species to decline to record low numbers in the 1960's. Contaminant levels have been declining in the region since the 1970's, and the bald eagle is now staging a substantial recovery in some parts of the region (Best et al. 1990). For example, the number of bald eagle breeding territories in Minnesota increased from 115 in 1973 to 400 in 1989 and, in Michigan, breeding pairs increased from 88 in 1977 to 165 in 1989. Despite the observed increases, habitat-related problems remain. Inland populations have expanded and birds produced in those populations have occupied breeding territories along Great Lakes shorelines in the 1980's. The shoreline populations, however, produce substantially fewer young than the inland populations (Table 5). The lower reproductive success of the bald eagle populations near the lakeshore has been attributed to a diet that is higher in contaminants than the diets of inland populations. Human activity, which tends to be higher in lakeshore areas than in inland areas, has been shown to limit the feeding activity of fledgling eagles in shoreline populations and may be a mortality factor. Adult mortality may also be higher among lakeshore populations than among inland populations. The recovery goals for bald eagle populations in the Great Lakes region have been met in Minnesota and Michigan and will probably soon be met in Wisconsin (Table 5). Recovery in the other Great Lakes states is less advanced.

The osprey, another fish-eating bird, is also recovering from reproductive failure and severe population declines caused by organochlorine pesticides in the 1950's–1960's (Ewins et al. 1995). The annual production of fledged ospreys has increased throughout the Great Lakes region since the use of organochlorine pesticides was reduced. Osprey populations nesting within 5 kilometers of the north shore of Lake Huron showed annual increases in abundance of up to 13% per year. On average, almost one young is now produced for each occupied nest—the level believed necessary to maintain a stable population.

The Kirtland's warbler, a Neotropical migrant, is federally listed as endangered. It nests only in young jack pine forest, mainly in the north-central portion of the lower peninsula of Michigan, but limited nesting also occurs in Wisconsin. In Michigan, more than 400 singing males were counted in 1951 and about 500 in 1961 (Fig. 25). The counts stabilized at about 200 from 1971 to 1989 and then increased steadily to slightly more than 600 in 1994.

Table 5. Bald eagle recovery goals and status by Great Lakes state (after Best et al. 1990).[a]

	Number of occupied breeding areas			Number of young per nest	
		Present status			
State	Recovery goal	Inland	Great Lakes	Inland	Great Lakes
Illinois	20	9	0	0.4	
Indiana	5	2	0	0.0	
Michigan	140	163	44	1.0	0.7
Minnesota	300	390	0	1.1	
New York	50	10	0	1.1	
Ohio	20	12	11	0.8	0.6
Pennsylvania	10	9	0	0.7	
Wisconsin	360	336		1.4	

[a] Zeros are measured values; blanks indicate no information available.

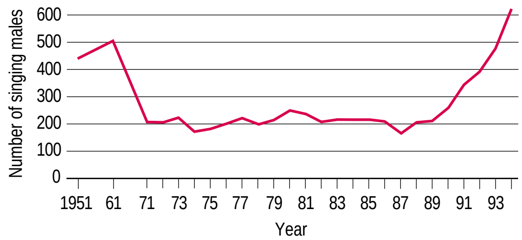

Fig. 25. Counts of singing male Kirtland's warblers in Michigan, 1951–1994 (Weinrich 1995).

Because Kirtland's warblers nest on the ground in stands of immature jack pine, their increase in abundance may be a response to habitat improvements that included an accidental burning of mature jack pine forests and reestablishment of large stands of immature jack pine.

Mammals

As a result of environmental changes and extinctions at the end of the Ice Age, the mammalian fauna of North America about 11,000–10,000 years ago generally resembled the present fauna (Hibbard et al. 1965; Lundelius et al. 1983). A description of the recent native mammals of the Great Lakes region (Burt 1967) listed 74 species living wild in the region. Of these 74 species, 28 ranged widely throughout the region; their areas of geographic origin could not be determined. Seventeen of the other species were southern forms that reach the northern limits of their ranges in the region, 16 were northern forms at the southern limits of their ranges, 8 were at their eastern limits, and 5 at their western limits. This confluence of range limits in the Great Lakes region indicates the region is a transition area, especially on a north-to-south axis. Northern boreal species do not seem to penetrate farther south than the limits of the coniferous forest that occupies the northern portion of the region, and southern species do not seem to move farther north than the northern edge of the deciduous forest in the southern portion of the region. The Great Lakes also seem to be barriers to distribution for some of the other species whose range limits occur in the region.

A more recent description of the native mammalian fauna of the north-central United States (Jones and Birney 1988) lists 99 species and covers Minnesota, Wisconsin, Illinois, Indiana, Ohio, and Michigan. This newer work extends coverage to the prairie and grassland communities bordering the western end of the Great Lakes region, but it excludes the portions of Pennsylvania and New York that compose the eastern end of the region. Jones and Birney (1988) found substantial faunal similarities among the states. The same seven taxonomic orders were represented in all six states, and the number of species in each order was generally similar in each state. The only marsupial in the region, the Virginia opossum, occurred in all six states. The number of insectivores (shrews and moles) was similar among the states (7–9). The number of bat species varied within the region and was fewest in Minnesota (7 species) and highest in Ohio (13 species). Rabbits or hares or both (2–3 species) occurred in each state. The number of rodents also varied within the region and was highest in Minnesota (31 species), largely because of the inclusion of grassland and northern faunas; in the other five states the numbers were similar (20–24 species). There were 18–20 species of carnivores, including one or more of the following in each of the six states: coyote; gray wolf; fox; black bear; raccoon; marten and fisher; ermine, weasel, and mink; wolverine; badger; skunk; river otter; and mountain lion, lynx, and bobcat. Slightly more antlered and horned animal species—including elk, deer, moose, pronghorn, and bison—occurred in Minnesota (7 species) than in Wisconsin and Michigan (5 species each) or in Illinois and Indiana (3 species each). There were more mammal species in Minnesota (78) because it has both grassland and northern species; the other five states have 65–70 species. Rodents and carnivores made up 58%–67% of the total mammal species in the six states.

Changes in the region's mammalian fauna that began with European settlement will almost assuredly continue as the human population grows and the habitat is further fragmented by development and more intensive land use. Species that have been extirpated from most or all of their former range in the region (for example, the bison, wolverine, pine marten, fisher, mountain lion, caribou, moose, elk, and gray wolf) will find it difficult to spread from any wild source populations that remain in the region or to become reestablished by emigration from wild source populations in bordering regions. Successful reintroduction is possible for some species, however, as evidenced by the relatively recent reestablishment of self-sustaining populations of pine marten, moose, and elk in portions of the region where the habitat can still support them and where human interaction can be controlled. The reintroduced population of elk in the northern portion of the Lower Peninsula of Michigan now supports a limited annual hunt. Gray wolves migrate intermittently from Canada into the Upper Peninsula of Michigan; natural reproduction now occurs there as well as in neighboring areas of Wisconsin (Ann Arbor News 1995). Fifty-nine moose were captured in Ontario and released in the Upper Peninsula of Michigan in 1985 and 1987. They bred successfully, and the herd is now estimated at 400–500 animals (Gwizdz 1995).

The mammalian fauna will also continue to change as the human population in the region continues to increase and species that are tolerant of human presence replace those that are not. The coyote, for example, probably had been extirpated in the region, but it now occurs widely and has even been seen in urban areas. The Virginia opossum, eastern cottontail, and the fox squirrel are other examples of species whose range extensions in the region are related to favorable environmental changes brought about by humans. Although the future of the region's mammalian fauna is difficult to predict, it is clear that many species—and particularly the larger species that are intolerant of human presence—will continue to be at a major disadvantage unless special efforts are made to protect them. Most of the small mammals that occurred in the north-central region 400 years ago still occur there today, and their future as a group presently seems secure (Jones and Birney 1988). In contrast, the region's larger carnivores and the antlered and horned species have undergone extinctions, extirpations, and large range changes as a result of human activities. The future of these species is not certain unless special measures are taken to assure their presence in the area's faunal communities.

The Indiana bat is federally listed as endangered in all states in the Great Lakes region except Minnesota. The species seems to be recovering in Indiana. The major threat to the Indiana bat is human disturbance of populations hibernating in caves. The gray wolf is listed as endangered in Michigan and Wisconsin and as threatened in Minnesota. The populations in northern Michigan and Wisconsin are growing slowly but need protection from humans.

Information Gaps and Research Needs

Areas that should be given particular attention in developing an initiative designed to protect biological diversity and support healthy ecosystems in the Great Lakes region are listed next. The list provides consideration of species of traditional management interest including game species and other species with economic or aesthetic values as well as species and communities that have become regionally or globally rare or are threatened with extinction.

- Field inventories and field and laboratory research should be conducted as demonstration projects to show how the ecosystem approach can be successfully applied to protect biological diversity and resources of management interest in the Great Lakes region.
- Formal, empirically based approaches for measuring ecosystem health need to be developed and tested for use in the region.
- Contaminant levels should be monitored as a component of ecosystem health.
- Research is needed to determine the effects of contaminants on specific ecosystem components.
- Introduced species should be monitored and studied as a component of and threat to ecosystem health.
- The function and performance of native species and communities in healthy Great Lakes ecosystems should be studied to provide baseline information that can be used to assess the health of stressed or threatened ecosystems and particular ecosystem components and to guide protection, management, and restoration activities.
- Research should be conducted to determine and better demonstrate the value of undisturbed communities and ecosystems as voucher or baseline elements for use in assessing ecosystem health.
- The role and value of long-lived, old-aged, large-sized individuals as components of healthy aquatic populations and ecosystems should be recognized and documented.
- More status and trend information is needed for many plant and animal groups in the region. Invertebrate, fish, amphibian, and reptile species and communities are underrepresented in most regional data bases.
- There is uneven geographical representation among regional data bases. Some states are more advanced than others in developing resource inventories and assessments.
- State data bases need to be more fully developed so that data can be easily and effectively aggregated to aid ecosystem management at multistate, regional, or national levels.
- Assessment of information in existing data bases may not be keeping pace with data-base construction. Additional field research may be needed to permit interpretation of observed changes in distribution and abundance of species of interest.
- Aquatic community classification systems should be developed as a framework for understanding and managing regional aquatic resources in the Great Lakes, connecting channels, and tributary ecosystems.
- Aquatic and terrestrial ecosystems should be described in terms that permit them to be linked for analysis.
- Considerable research is needed to understand the effects of a variety of specific land- and water-resource use practices and projects on species and communities so that adverse effects can be minimized or avoided and biological diversity and ecosystem health can be maintained.
- The effect of measures or practices employed to control undesirable introduced species (such as the sea lamprey) should be assessed in the context of ecosystem health, as should the role of hatcheries and artificial propagation in the management of game species.

- The effect of commercial or recreational enhancement and harvest on the health of plant and animal populations and communities should be assessed and related to the health of the ecosystems to which these elements belong.
- Field research and surveys at the watershed and landscape scales are needed to better identify ecosystems and ecosystem elements that are particularly susceptible to perturbation by human activities common to the region.
- Methods should be developed for restoring aquatic habitats damaged by pollution and physical alteration.
- Governments and private sector organizations with resource management authority should be encouraged to cooperate in developing land-use inventories and guidelines or regulations that reflect the ecosystem approach to resource management.

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Cited References

Albert, D. 1994. Michigan's landscape. Pages 5–81 *in* D. C. Evers, editor. Endangered and threatened wildlife of Michigan. University of Michigan Press, Ann Arbor. 412 pp.

Anderson, R. C. 1970. Prairies in the Prairie State. Transactions of the Illinois State Academy of Science 63:1724–1734.

Anderson, R. C. 1990. Illinois prairies: a historical perspective. Pages 384–391 *in* L. M. Page and M. R. Jeffords, editors. Our living heritage: the biological resources of Illinois. Illinois Natural History Bulletin 34. 477 pp.

Andrle, R. F., and J. R. Carroll. 1988. The atlas of breeding birds in New York state. Cornell University Press, Ithaca, N.Y. 551 pp.

Ann Arbor News. 1995. Wolves resurge in U.P. without man's influence. 16 April 1995, Ann Arbor, Mich.

Bailey, R. M., and G. E. Smith. 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 38:1539–1561.

Baldwin, N. S., R. W. Saalfeld, M. A. Ross, and H. J. Buettner. 1979. Commercial fish production in the Great Lakes, 1867–1977. Great Lakes Fishery Commission Technical Report 3. Ann Arbor, Mich. 187 pp.

Barnes, B. V., and W. H. Wagner, Jr. 1981. Michigan trees. University of Michigan Press, Ann Arbor. 384 pp.

Bayliss, J. E., and E. L. Bayliss. 1955. River of destiny, the Saint Marys. Wayne State University Press, Detroit. 328 pp.

Best, D. A., M. Gilbertson, and H. Hudson, editors. 1990. Proceedings of the expert consultation meeting on bald eagles. International Joint Commission, Great Lakes Regional Office, Windsor, Ontario. 33 pp.

Blaustein, A. R., and D. B. Wake. 1990. Declining amphibian populations: a global phenomenon? Trends in Ecology and Evolution 5:203–204.

Bohlen, H. D. 1989. The birds of Illinois. Indiana University Press, Bloomington. 221 pp.

Brady, V. J., and T. M. Burton. 1995. The microcrustacean community of a Saginaw Bay coastal emergent marsh. Pages 325–341 *in* M. Munawar, T. Edsall, and J. Leach, editors. The Lake Huron ecosystem: ecology, fisheries, and management. Ecovision World Monograph Series, S.P.B. Academic Publishers, Amsterdam, The Netherlands.

Brauning, D. W., editor. 1992. Atlas of breeding birds in Pennsylvania. University of Pittsburgh Press, Pa. 484 pp.

Brenner, F. J. 1985. Aquatic and terrestrial habitats in Pennsylvania. Pages 7–17 *in* H. H. Genoways and F. J. Brenner, editors. Species of special concern in Pennsylvania. Carnegie Museum of Natural History Special Publication 11. Pittsburgh, Pa.

Brewer, R., G. A. McPeek, and R. J. Adams, Jr. 1991. The atlas of breeding birds of Michigan. Michigan State University Press, East Lansing. 594 pp.

Britt, N. W. 1955a. *Hexagenia* (Ephemeroptera) population recovery in western Lake Erie following the 1953 catastrophe. Ecology 36:520–522.

Britt, N. W. 1955b. Stratification of western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. Ecology 36:239–244.

Brown, E. L., Jr., G. W. Eck, N. R. Foster, R. M. Horrall, and C. E. Coberly. 1981. Historical evidence for discrete stocks of lake trout (*Salvelinus namaycush*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Science 38:1747–1758.

Brunstein, F. C., and D. K. Yamaguchi. 1992. The oldest known Rocky Mountain bristlecone pines *Pinus aristata* Engelm. Arctic Alpine Research 24:253–256.

Burt, W. H. 1967. Mammals of the Great Lakes region. University of Michigan Press, Ann Arbor. 246 pp.

Clarke, G. L. 1954. Elements of ecology. John Wiley & Sons, New York. 534 pp.

Cleland, C. E. 1982. The inland shore fishery of the northern Great Lakes: its development and importance in prehistory. American Antiquity 47:761–784.

Coffin, B., and L. Pfannmuller, editors. 1988. Minnesota's endangered flora and fauna. University of Minnesota Press, Minneapolis. 473 pp.

Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians: eastern and central North America. Peterson Field Guide Series, Houghton Mifflin Company, Boston. 450 pp.

Constanza, R., B. G. Norton, and B. Haskell, editors. 1992. Ecosystem health. Island Press, Washington, D.C. 269 pp.

Conway, T. A. 1977. Whitefish Island: a remarkable archeological site at Sault Sainte Marie. Ontario Ministry of Culture and Recreation, Data Box 310, Toronto, Canada. 69 pp.

Conway, T. A. 1980. Heartland of the Ojibway. Pages 1–28 *in* D. S. Melvin, editor. Collected archeological papers. Ontario Ministry of Culture, Recreation, and Archeological Research Report 13. Toronto, Canada.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service FWS/OBS-79/32. 103 pp.

Cummings, K. S., and C. A. Mayer. 1992. Field guide to freshwater mussels of the Midwest. Illinois Natural History Survey Manual 5. 194 pp.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 pp.

Dahl, T. E. 1990. Wetlands losses in the United States, 1970s–1980s. U.S. Fish and Wildlife Service, Washington, D.C. 22 pp.

Derecki, J. A. 1985. Effects of channel change in the Saint Clair River during the present century. Journal of Great Lakes Research 11:201–207.

Dorr, J. A., Jr., and D. F. Eschman. 1970. Geology of Michigan. University of Michigan Press, Ann Arbor. 476 pp.

Ebener, M. P., J. E. Johnson, D. M. Reid, N. P. Payne, R. L. Argyle, G. M. Wright, K. Krueger, J. P. Baker, T. Morse, and J. Weise. 1995. Status and future of Lake Huron fish communities. Pages 125–169 *in* M. Munawar, T. Edsall, and J. Leach, editors. The Lake Huron ecosystem: ecology, fisheries, and management. Ecovision World Monograph Series, S.P.B. Academic Publishers, Amsterdam, The Netherlands.

Edsall, T. A., and J. E. Gannon. 1991. A profile of Lake Saint Clair. Michigan Sea

Grant College Program MICHU-SG-91-701. Ann Arbor. 15 pp.

Edsall, T. A., B. A. Manny, and N. C. Raphael. 1988. The Saint Clair River and Lake Saint Clair, Michigan: an ecological profile. U.S. Fish and Wildlife Service Biological Report 85(7.3). 130 pp.

Edsall, T. A., B. A. Manny, D. W. Schloesser, S. J. Nichols, and A. M. Frank. 1991. Production of *Hexagenia limbata* nymphs in contaminated sediments in the upper Great Lakes connecting channels. Hydrobiologia 210:353–361.

Edsall, T. A., E. L. Mills, and J. H. Leach. 1995. Exotic species in the Great Lakes. Pages 442–444 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Edsall, T. A., J. H. Selgeby, T. J. DeSorcie, and J. R. P. French III. 1993. Growth–temperature relation for young-of-the-year ruffe. Journal of Great Lakes Research 19:630–633.

Eichenlaub, V. L. 1979. Weather and climate of the Great Lakes region. University of Notre Dame Press, Notre Dame, Ind. 335 pp.

Engle, E. 1991. The tremble tree. American Forests 97:54–56, 69–70.

Evers, D. C., editor. 1994. Endangered and threatened wildlife of Michigan. University of Michigan Press, Ann Arbor. 412 pp.

Ewins, P. J., S. Postupalsky, T. Weise, and E. W. Addison. 1995. Changes in the status, distribution, and biology of ospreys (*Pandion haliaetus*) breeding on Lake Huron. Pages 273–290 *in* M. Munawar, T. Edsall, and J. Leach, editors. The Lake Huron ecosystem: ecology, fisheries, and management. Ecovision World Monograph Series, S.P.B. Academic Publishers, The Netherlands.

Fisher, J. P., J. D. Fitzsimons, G. F. Combs, Jr., and J. M. Spitsbergen. 1996. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and Great Lakes lake trout. Transactions of the American Fisheries Society 125:167–178.

Fisher, J. P., J. M. Spitsbergen, R. Getchell, J. Symula, J. Skea, M. Babenzein, and T. Chiotti. 1995a. Reproductive failure in landlocked Atlantic salmon from New York's Finger Lakes: investigations into the etiology and epidemiology of the 'Cayuga syndrome.' Journal of Aquatic Animal Health 7:81–94.

Fisher, J. P., J. M. Spitsbergen, T. Iamonte, E. E. Little, and A. DeLonay Chiotti. 1995b. Pathological and behavioral manifestations of the 'Cayuga syndrome,' a thiamine deficiency in larval landlocked Atlantic salmon. Journal of Aquatic Animal Health 7:269–283.

Goodier, J. L. 1981. Native lake trout (*Salvelinus namaycush*) stocks in the Canadian waters of Lake Superior prior to 1955. Canadian Journal of Fisheries and Aquatic Science 38:1724–1737.

Goodrich, C., and H. van der Schalie. 1932. The naiad species of the Great Lakes. University of Michigan Occasional Papers of the Museum of Zoology 238:8–14.

Goodyear, C. D., T. A. Edsall, D. M. Ormsby-Dempsey, G. D. Moss, and P. E. Polanski. 1982. Atlas of spawning and nursery areas of Great Lakes fishes. Volumes 1–14. U.S. Fish and Wildlife Service FWS/OBS-82/52. 1314 pp.

Great Lakes Basin Commission. 1975. Great Lakes basin framework study. Appendix 14: floodplains. Great Lakes Basin Commission. Ann Arbor, Mich. 327 pp.

Great Lakes Fishery Commission. 1995a. Report of the coldwater task group to the Lake Erie committee, 22 March 1995. Great Lakes Fishery Commission, Ann Arbor, Mich. 15 pp.

Great Lakes Fishery Commission. 1995b. Report of the Lake Erie yellow perch task group to the Lake Erie committee. Great Lakes Fishery Commission, Ann Arbor, Mich. 52 pp.

Greeley, W. B. 1925. The relation of geography to timber supply. Economic Geography 1:1–14.

Gwizdz, R. 1995. Moose herd grows in U.P. Ann Arbor News, 25 February 1995. 2 pp.

Hall, R. J. 1995. Birds. Pages 15–17 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Hansen, M. J., editor. 1994. The state of Lake Superior. Great Lakes Fishery Commission Special Publication 94-1. Ann Arbor, Mich. 110 pp.

Heckert, J. R. 1991. Endangered and threatened species of Illinois: status and distribution. Illinois Endangered Species Protection Board, Springfield. 158 pp.

Herdendorf, C. E., S. M. Hartley, and M. D. Barnes. 1981. Fish and wildlife resources of the Great Lakes coastal wetlands within the United States. U.S. Fish and Wildlife Service FWS/OBS-82/02-V2-6. 5023 pp.

Hibbard, C. W., D. E. Ray, D. E. Savage, D. W. Taylor, and J. E. Guilday. 1965. Quaternary mammals of North America. Pages 509–525 *in* H. E. Wright and D. G. Frey, editors. The Quaternary of the United States. Princeton University Press, N.J.

Hodges, R. W. 1995. Diversity and abundance of insects. Pages 161–163 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Holden, C. 1989. Entomologists wane as insects wax. Science 246:754–756.

Holey, M. E., R. W. Rybicki, G. W. Eck, E. H. Brown, Jr., J. E. Marsden, D. S. Lavis, M. L. Toneys, T. N. Trudeau, and R. M. Horrall. 1995. Progress toward lake trout restoration in Lake Michigan. Pages 128–151 *in* J. H. Selgeby, R. L. Eshenroder, C. C. Krueger, J. E. Marsden, and R. L. Pycha, editors. International conference on restoration of lake trout in the Laurentian Great Lakes. Journal of Great Lakes Research 21 (Supplement 1).

Hough, J. L. 1958. Geology of the Great Lakes. University of Illinois Press, Urbana. 313 pp.

Hubbs, C. L., and K. F. Lagler. 1964. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor. 213 pp.

Hudson, P. L., R. W. Griffiths, and T. J. Wheaton. 1992. Review of habitat classification schemes appropriate to streams, rivers, and connecting channels in the Great Lakes drainage basin. Pages 74–107 *in* W.-D. N. Busch, and P. G. Sly, editors. The development of an aquatic habitat classification system for lakes. CRC Press, Boca Raton, Fla.

Hutchins, E. F. 1979. The Ohio country. Pages 5–15 *in* M. B. Lafferty, editor. Ohio's natural heritage. Ohio Academy of Science, Columbus.

Illinois Department of Energy and Natural Resources. 1994. The changing Illinois environment: critical trends assessment project. Volume 3. Ecological resources. Champaign, Ill. 242 pp.

Illinois Department of Energy and Natural Resources and The Nature of Illinois Foundation. 1994. The changing Illinois environment: critical trends assessment. Summary report. Springfield, Ill. 89 pp.

Illinois Endangered Species Protection Board. 1994. Checklist of endangered and threatened animals and plants of Illinois. Springfield, Ill. 20 pp.

Indiana Department of Natural Resources. 1993. Indiana's rare plants and animals: a checklist of endangered and threatened species. Indianapolis, Ind. 26 pp.

International Joint Commission. 1991. A proposed framework for developing indicators of ecosystem health for the Great Lakes region. International Joint Commission, Windsor, Ontario. 47 pp.

International Joint Commission and Great Lakes Fishery Commission. 1990. Exotic species and the shipping industry: a special report to the governments of the United States and Canada. International Joint Commission, Windsor, Ontario. 74 pp.

Jaworski, E., and N. C. Raphael. 1979. Impact of Great Lakes water level fluctuations on coastal wetlands. U.S. Office of Water Resources Technology, East Lansing, Mich. 351 pp.

Jones, J. K., and E. C. Birney. 1988. Handbook of mammals of the north-central states. University of Minnesota Press, Minneapolis. 346 pp.

Jude, D. J., J. Janssen, and G. Crawford. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the Saint Clair and Detroit rivers. Pages 447–460 *in* M. Munawar, T. Edsall, and J. Leach, editors. The Lake Huron ecosystem: ecology, fisheries, and management. Ecovision World Monograph Series, S.P.B. Academic Publishing, The Netherlands.

Kerr, S. J., and C. G. LeTendre. 1991. The state of the Lake Ontario fish community in 1989. Great Lakes Fishery Commission Special Publication 91–3. Ann Arbor, Mich. 38 pp.

Contents Article Page

Kreiger, K. A., D. W. Schloesser, B. A. Manny, C. E. Trisler, S. E. Heady, J. H. Ciborowski, and K. N. Muth. 1996. Evidence of the recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia*) in western Lake Erie. Journal of Great Lakes Research 22:254–263.

Krueger, C. C., and P. E. Ihssen. 1995. Review of genetics of lake trout in the Great Lakes: history, molecular genetics, physiology, strain comparisons and restoration management. Pages 348–363 *in* J. H. Selgeby, R. L. Eshenroder, C. C. Krueger, J. E. Marsden, and R. L. Pycha, editors. International conference on restoration of lake trout in the Great Lakes. Journal of Great Lakes Research 21 (Supplement 1).

Livermore, B. 1992. Amphibian alarm: just where have all the frogs gone? Smithsonian 23:113–120.

Lundelius, E. L., Jr., R. W. Graham, E. Anderson, J. Guilday, J. A. Holman, D. W. Steadman, and S. D. Webb. 1983. Terrestrial vertebrate faunas. Pages 311–353 *in* H. E. Wright, Jr., and S. C. Porter, editors. Late-Quaternary environments of the United States: the late Pleistocene. University of Minnesota Press, Minneapolis. 407 pp.

Manny, B. A. 1984. Potential impacts of water diversion on fishery resources in the Great Lakes. Fisheries 9(5):19–23.

Manny, B. A., and R. W. Owens. 1983. Additions of nutrients and major ions by the atmosphere and tributaries to nearshore waters of northwestern Lake Huron. Journal of Great Lakes Research 9:403–420.

McCullough, G. B. 1985. Wetland threats and losses in Lake Saint Clair. Pages 201–208 *in* H. H. Prince and F. M. D'itri, editors. Coastal wetlands. Lewis Publishers, Chelsea, Mich.

McDiarmid, R. W. 1995. Reptiles and amphibians. Pages 117–118 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Merritt, R. W., and K. W. Cummins. 1984. Introduction. Pages 1–3 *in* R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects of North America. 2nd edition. Kendall-Hunt Publishing Company, Dubuque, Iowa.

Messer, J. J., R. A. Linthurst, and W. S. Overton. 1991. An EPA program for monitoring ecological status and trends. Environmental Monitoring 17:67–78.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1–54.

Minnesota Department of Natural Resources. 1994. Proposed revisions to Minnesota's endangered, threatened, and special concern species. Saint Paul, Minn. 20 pp.

Minton, S. A. 1972. Amphibians and reptiles of Indiana. Indiana Academy of Science, Indianapolis. 346 pp.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York. 722 pp.

Mumford, R. E., and C. E. Keller. 1984. The birds of Indiana. Indiana University Press, Bloomington. 376 pp.

Nalepa, T. F., and D. W. Schloesser. 1992. Zebra mussels: biology, impacts, and control. CRC Press, Boca Raton, Fla. 810 pp.

Northwoods Call. 1994. Historic pact worth 70 miles of frontage, tens of millions. 41(22) October. Charlevoix, Mich.

Ogle, D. H., J. H. Selgeby, R. M. Newman, and M. G. Henry. 1995. Diet and feeding periodicity of ruffe in the Saint Louis River estuary, Lake Superior. Transactions of the American Fisheries Society 124:356–369.

Oldfield, B., and J. J. Moriarity. 1994. Amphibians and reptiles native to Minnesota. University of Minnesota Press, Minneapolis. 237 pp.

Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation. 1994. Ecosystem watch: status of the Lake Ontario ecosystem. Ontario Ministry of Natural Resources, Napanee, Ontario, and New York State Department of Environmental Conservation, Albany. 8 pp.

Pennak, R. W. 1978. Fresh-water invertebrates of the United States. 2nd edition. John Wiley & Sons, New York. 803 pp.

Pennsylvania Department of Environmental Resources. 1994. Pennsylvania natural diversity inventory of biota of special concern in Pennsylvania. Harrisburg, Pa. 29 pp.

Pentecost, E. D., and R. C. Vogt. 1976. Environmental status of the Lake Michigan region. Volume 16. Amphibians and reptiles of the Lake Michigan drainage basin. Argonne National Laboratory, Argonne, Ill. 69 pp.

Peterjohn, B. G., and D. L. Rice. 1991. The Ohio breeding bird atlas. Ohio Department of Natural Resources, Columbus. 416 pp.

Peterjohn, B. G., J. R. Sauer, and S. Orsillo. 1995. Breeding bird survey: population trends 1966–92. Pages 17–21 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Phillips, C. A. 1990. Where have all the frogs and toads gone? BioScience 40:422-424.

Phillips, C. A. 1991. Geographical distribution: *Ambystoma jeffersonianun* (Jefferson salamander). Herpetological Review 22:133.

Potter, R. L., and G. W. Fleischer. 1992. Reappearance of spoonhead sculpins (*Cottus ricei*) in Lake Michigan. Journal of Great Lakes Research 18:755–758.

Powell, J. A. 1995. Lepidoptera inventories in the continental United States. Pages 168–170 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Pratt, D. M., W. H. Blust, and J. H. Selgeby. 1992. Ruffe, *Gymnocephalus cernuus*: newly introduced in North America. Canadian Journal of Fisheries and Aquatic Sciences 49:1616–1618.

Reynoldson, T. B., and A. L. Hamilton. 1993. Historic changes in populations of burrowing mayflies (*Hexagenia limbata*) from Lake Erie, based on sediment tusk profiles. Journal of Great Lakes Research 19:250–257.

Rhodes, A., and W. Klein. 1993. Vascular flora of Pennsylvania: annotated checklist and atlas. American Philosophical Society, Philadelphia. 636 pp.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965–1979. U.S. Fish and Wildlife Service Resource Publication 157. 96 pp.

Robbins, S. D., Jr. 1991. Wisconsin birdlife. University of Wisconsin Press, Madison. 702 pp.

Roe, H. B., and Q. C. Ayres. 1954. Engineering for agricultural drainage. McGraw-Hill, New York. 501 pp.

Root, T. L. 1988. Atlas of wintering North American birds. University of Chicago Press, Ill. 312 pp.

Root, T. L., and L. McDaniel. 1995. Winter population trends of selected songbirds. Pages 21–23 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Royce, W. F. 1951. Breeding habits of lake trout in New York. Fishery Bulletin 52:59–76.

Ruthven, A. G., C. Thompson, and H. T. Gaige. 1928. The herpetology of Michigan. University of Michigan, Ann Arbor. 229 pp.

Santer, R. A. 1993. Geography of Michigan and the Great Lakes basin. Kendall-Hunt Publishing Company, Dubuque, Iowa. 422 pp.

Schloesser, D. W., T. A. Edsall, B. A. Manny, and J. S. Nichols. 1991. Distribution of *Hexagenia* nymphs and visible oil in sediments of the upper Great Lakes connecting channels. Hydrobiologia 219:345–352.

Schloesser, D. W., and W. P. Kovalak. 1991. Infestation of unionids by *Driessena polymorpha* in a power plant canal in Lake Erie. Journal of Shellfish Research 10:355–359.

Schloesser, D. W., and T. F. Nalepa. 1995. Freshwater mussels in the Lake Huron–Lake Erie corridor. Pages 179–182 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Shaffer, L. L. 1991. Pennsylvania amphibians and reptiles. Pennsylvania Fish Commission, Harrisburg. 160 pp.

Simon, T. P., and J. T. Vondruska. 1991. Larval identification of the ruffe, *Gymnocephalus cernuus* (Linnaeus) (Percidae: Percini) in the Saint Louis River estuary, Lake Superior drainage basin, Minnesota. Canadian Journal of Zoology 69:1036–1039.
Smith, M. L., J. N. Bruhn, and J. B. Anderson. 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. Nature 356:428–431.
Smith, P. W. 1961. The amphibians and reptiles of Illinois. Illinois Natural History Survey Bulletin 28. 298 pp.
Smith, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. Journal of the Fisheries Board of Canada 29:717–730.
Sonzgoni, W. C., T. J. Monteith, W. N. Bach, and V. G. Hughes. 1978. United States Great Lakes tributary loading. Prepared by the Great Lakes Basin Commission staff for the Pollution From Land Use Activities Reference Group, International Joint Commission, Windsor, Ontario. 187 pp.
Stearns, F. W., and G. Guntenspergen. 1987. Maps of the presettlement forests of the lakes states and major forest types of the lakes states. *In* W. E. Shands, editor. The lakes states forest: a resource renaissance. The Conservation Foundation, Washington, D.C. 185 pp.
Swengel, A. B. 1995. Fourth of July Butterfly Count. Pages 171–172 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.
Swengel, A. B., and S. R. Swengel. 1995. The tall-grass prairie butterfly community. Pages 174–176 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.
Tanner, H. H. 1986. Atlas of Great Lakes Indian history. University of Oklahoma Press, Norman. 186 pp.
The Nature Conservancy. n.d. The Great Lakes biodiversity data system. The Nature Conservancy of Canada, Toronto, Ontario, and The Nature Conservancy Great Lakes Office, Chicago. 16 pp.
The Nature Conservancy. 1994a. The conservation of biological diversity in the Great Lakes ecosystem: issues and opportunities. The Nature Conservancy Program, Chicago. 118 pp.
The Nature Conservancy. 1994b. Rare plant communities of the conterminous United States. The Nature Conservancy, Arlington, Va. 604 pp.
Tiner, R. W., Jr. 1984. Wetlands of the United States: current status and recent trends. U.S. Fish and Wildlife Service, Washington, D.C. 59 pp.
U.S. Bureau of the Census. 1994. County and city data book. Washington, D.C. 928 pp.
U.S. Department of the Interior. 1970. The national atlas of the United States. U.S. Geological Survey, Washington, D.C. 417 pp.
U.S. Fish and Wildlife Service. 1971. Wetlands of the United States. Their extent and their value to waterfowl and other wildlife. U.S. Fish and Wildlife Service, Washington, D.C. 67 pp.
U.S. Fish and Wildlife Service. 1992. Report to Congress: Endangered and Threatened Species Recovery Program. U.S. Fish and Wildlife Service, Washington, D.C. 279 pp.
U.S. Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants. 50 CFR 17.11 & 17.12. Washington, D.C. 42 pp.
U.S. Fish and Wildlife Service. 1995. Great Lakes fishery resources restoration study. A report to Congress. U.S. Fish and Wildlife Service, Washington, D.C. 198 pp.
Vogt, C. R. 1981. Natural history of amphibians and reptiles in Wisconsin. Milwaukee Public Museum, Wis. 205 pp.
Wake, D. B. 1991. Declining amphibian populations. Science 253:860.
Webb, T., III. 1981. The past 11,000 years of vegetational change in eastern North America. BioScience 31:501–506.
Webster, D. A. 1982. Early history of the Atlantic salmon in New York. New York Fish and Game Journal 29:26–44.
Weinrich, J. 1995. The Kirtland's warbler in 1994. Michigan Department of Natural Resources, Wildlife Division Report 3222, Lansing. 13 pp.
Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnology and Oceanography 15:556–565.
Wheeler, Q. D. 1990. Insect diversity and cladistic constraints. Annals of the Entomological Society of America 83:1031–1047.
Whelan, G., and W. Houghton. 1991. The Michigan DNR, hydrodams and FERC. Michigan Trout II (3). September.
Whitney, G. G. 1994. From coastal wilderness to fruited plain. Cambridge University Press, England. 451 pp.
Wilcox, D. A. 1995. The role of wetlands as nearshore habitat in Lake Huron. Pages 233–245 *in* M. Munawar, T. Edsall, and J. Leach, editors. The Lake Huron ecosystem: ecology, fisheries, and management. Ecovision World Monograph Series, S.P.B. Academic Publishers, Amsterdam, The Netherlands.
Williams, J. D., and R. J. Neves. 1995. Freshwater mussels: a neglected and declining aquatic resource. Pages 177–179 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.
Williams, J. D., M. L. Warren, Jr., K. S. Cummings, J. L. Harris, and R. J. Neves. 1992. Conservation status of freshwater mussels of the United States and Canada. Fisheries 19:6–22.
Wisconsin Department of Natural Resources. 1995. Wisconsin's biodiversity as a management issue. Wisconsin Department of Natural Resources, Madison. 240 pp.

Habitat Change in a Perched Dune System Along Lake Superior

Anderton, J. B., and W. L. Loope. 1995. Buried soils in a perched dunefield as indicators of late Holocene lake-level change in the Lake Superior basin. Quaternary Research 44:190–199.
Bach, D. P. 1978. Plant communities, habitats and soil conditions of Grand Sable Dunes, Pictured Rocks National Lakeshore, Michigan. M.S. thesis, Michigan Technological University, Houghton. 180 pp.
Businski, S. A. 1992. Airphoto interpretation of vegetative cover change on the Sleeping Bear Dunes Complex, Leelanau County, Michigan, 1938–1987. M.S. thesis. Michigan State University, East Lansing. 115 pp.
Fraser, G. S., C. E. Larsen, and N. C. Hester. 1990. Climatic control of lake levels in the Lake Michigan and Lake Huron basins. Pages 75–89 *in* A. F. Schneider and G. S. Fraser, editors. Late Quaternary history of the Lake Michigan basin. Geological Society of America Special Paper 251.
Lichter, J. 1995. Lake Michigan beach-ridge and dune development, lake level, and variability in regional water balance. Quaternary Research 44:181–189.
Loveless, M. D., and J. L. Hamrick. 1988. Genetic organization and evolutionary history in two North American species of *Cirsium*. Evolution 42:254–265.
Marsh, W. M., and B. D. Marsh. 1987. Wind erosion and sand dune formation on high Lake Superior bluffs. Geografiska Annaler 69A:379–391.
McEachern, A. K. 1992. Disturbance dynamics of Pitcher's thistle (*Cirsium pitcheri)* populations in Great Lakes sand dune landscapes. Ph.D. dissertation, University of Wisconsin, Madison. 216 pp.
McEachern, A. K., M. L. Bowles, and N. B. Pavlovic. 1994. A metapopulation approach to Pitcher's thistle (*Cirsium pitcheri*) recovery in southern Lake Michigan dunes. Pages 194–218 *in* M. L. Bowles and C. J. Whelan, editors. Restoration of endangered species. Cambridge University Press, Cambridge, England.
Olson, J. S. 1958. Lake Michigan dune development 3. Lake level, dune and beach oscillations. Journal of Geology 66:473–483.
Pavlovic, N. B., M. L. Bowles, S. R. Crispin, T. C. Gibson, K. D. Herman, R. T. Kavetsky, A. K. McEachern, and M. R. Penskar. 1991. Draft pitcher's thistle (*Cirsium pitcheri*) recovery plan. U.S. Fish and Wildlife Service, Region 3, Minneapolis, Minn. 111 pp.
Schultz, J. L. 1988. Inventory of several rare plant species within the Grand Sable Dunes area of Pictured Rocks National Lakeshore.

Report to U.S. Department of the Interior, National Park Service, Omaha, Nebr. 40 pp.

Snyder, F. S. 1985. A spatial and temporal analysis of the Sleeping Bear Dunes complex, Michigan. Ph.D. dissertation, University of Pittsburgh, Pa. 204 pp.

Thompson, T. A., and S. J. Baedke. 1995. Beach-ridge development in Lake Michigan: shoreline behavior in response to quasi-periodic lake-level events. Marine Geology 129:163–174.

Sea Lamprey in the Great Lakes

Great Lakes Fishery Commission. 1992. Strategic vision of the Great Lakes Fishery Commission for the decade of the 1990's. Great Lakes Fishery Commission, Ann Arbor, Mich. 38 pp.

Talhelm, D. R. 1988. Economics of Great Lakes fisheries. Great Lakes Fishery Commission Technical Report 54. 54 pp.