Ecological features and processes of lakes and wetlands

Lakes are complex ecosystems defined by all system components affecting surface and ground water gains and losses. This includes the atmosphere, precipitation, geomorphology, soils, plants, and animals within the entire watershed, including the uplands, tributaries, wetlands, and other lakes. Management from a whole watershed perspective is necessary to protect and maintain healthy lake systems. This concept is important for managing the Great Lakes as well as small inland lakes, even those without tributary streams. A good example of the need to manage from a whole watershed perspective is the significant ecological changes that have occurred in the Great Lakes. The Great Lakes are vast in size, and it is hard to imagine that building a small farm or home, digging a channel for shipping, fishing, or building a small dam could affect the entire system. However, the accumulation of numerous human development activities throughout the entire Great Lakes watershed resulted in significant changes to one of the largest freshwater lake systems in the world. The historic organic contamination problems, nutrient problems, and dramatic fisheries changes in our Great Lakes are examples of how cumulative factors within a watershed affect a lake.

Habitat refers to an area that provides the necessary resources and conditions for an organism to survive. Because organisms often require different habitat components during various life stages (reproduction, maturation, migration), habitat for a particular species may encompass several cover types, plant communities, or water-depth zones during the organism's life cycle. Moreover, most species of fish and wildlife are part of a complex web of interactions that result in successful feeding, reproduction, and predator avoidance. Seemingly minor physical changes in a portion of a lake or neighboring upland watershed can disrupt the system and significantly influence species diversity and abundance of plants and animals within the lake ecosystem.

Water Quality

The quality of lake water depends on a variety of factors including the underlying geologic formations, landforms, soils, precipitation, evaporation, ratios of ground water to surface water drainage, and human influences caused by alteration of the landscape (Figure 3). These factors determine the inorganic and organic chemical constituents of lake water. Important components of water quality include phosphorous, nitrogen (ammonia, nitrate, and nitrite), water temperature, oxygen, carbon dioxide, pH, and a number of metals and salts. Typical water quality values for Upper Peninsula and northern Lower Peninsula Michigan lakes collected in 1984 are provided in Table 1.

Water temperature influences internal structure, chemistry, biological metabolism, and the types of aquatic organisms that live in lakes. Water temperatures in Michigan lakes vary from the southern portion of the state to the northern portion, a function of regional air temperatures. Internal lake water temperatures also vary. The warmest water temperatures are found near the surface of the lake (epilimnion) during summer months and near the bottom of the lake (hypolimnion) during winter months. This condition is called stratification. Stratification is most pronounced during summer months when temperature changes are the greatest. A zone of rapid temperature change occurs in the metalimnion (also called thermocline, generally 15–40 feet deep; Figure 4), and this often forms a physical barrier that prevents interchange of water, gases, organic material, and nutrients between the epilimnion and the hypolimnion. In spring and autumn, water temperatures become uniform throughout the water column for a period of time and these are referred to as “turnover periods.” Turnover periods are important in the cycling of organic matter and chemicals, especially nutrients, in many lakes. Stratification varies annually depending on solar radiation, wind, and the physical features of each lake. Shallow lakes often do not stratify and have relatively uniform water temperatures throughout the water column. Aquatic vegetation can affect water temperatures in the littoral zone. Shading by plants can create cooler water temperature microhabitats in the littoral zone that influence the distribution of aquatic organisms.

Michigan Surface Water Quality Standards (MAC R323.1041 – R323.1117 promulgated pursuant to Part 31, Water Resources Protection, of the Natural Resources and Environmental Protection Act, 1994, PA 451, as amended) provide water temperature limits for water discharges into lakes. These standards allow not more than a 3°F temperature increase at the edge of a discharge mixing zone in all lakes. The Great Lakes and inland lakes also have specific monthly temperature limits in various parts of the state.

Dissolved oxygen is important for sustaining aquatic life. The solubility of oxygen and other gases depend on water temperature. Colder water can contain more dissolved gases. Oxygen enters the water from the atmosphere and it is produced by aquatic plants during photosynthesis. Oxygen is used by all animals and microorganisms in lakes and it is removed by plants during respiration when sunlight is not available. Oxygen depletion can occur in lakes with high plant and animal oxygen demand, especially in areas of lakes where waters do not mix freely or come in contact with the atmosphere. Water quality standards (related to discharges) in Michigan require maintenance of 7 mg/l dissolved oxygen for all Great Lakes and connecting waters, designated trout streams, and coldwater inland lakes. The water quality standard for other water bodies is 5 mg/l. Minimum dissolved oxygen levels for suitable summer habitat are approximately 3.0 mg/l for coldwater and coolwater fish and 2.5 mg/l for warmwater fish (Schneider 2002). The influence of water temperature stratification, dissolved oxygen, and trophic status determine the types of aquatic organisms that live in a lake, and are discussed later under trophic status.

The carbon dioxide content of lakes is affected by photosynthesis, respiration, and contact with the atmosphere. It is the basic carbon source from which plants produce sugar and more complex organic matter and is therefore a vital component of lake chemistry.

Alkalinity, hardness, and pH are measures of acidity and the buffering capacity of water. The acidity (hydrogen ion concentration) of water is measured by pH. A lower pH value indicates higher acidity. Alkalinity is a measure of the carbonate levels or acid buffering capacity in water. Buffering capacity increases with increasing alkalinity. Hardness is a measure of calcium and magnesium levels. Alkalinity and hardness generally are associated through calcium and magnesium carbonate reactions. High hardness generally indicates high alkalinity. Typical ranges of these parameters are listed in Table 2. A pH of 7 is neutral, and a pH of 3 or less is toxic to most fish. Species vary in their sensitivity to pH. The pH of most lakes ranges between 6 and 9. Hardwater lakes commonly are buffered strongly and have pH values above 8. Seepage lakes and lakes with an igneous rock catchment are less well buffered and may have pH values somewhat less than 7. Bog lakes typically have pH values of 3 to 5. Generally, hardwater lakes are more productive than softwater lakes because more inorganic carbon is available for photosynthesis. The majority of softwater lakes are in the Upper Peninsula. Underlying geological formations of the Lower Peninsula are predominantly deep glacial deposits over limestone bedrock, while much of the Upper Peninsula has a thin layer of glacial deposits underlain by igneous rock.

Chlorides, sulfate, sodium, and potassium generally are indicators of pollution or excessive drainage and runoff from the watershed. Generally these elements and their compounds are low in natural lakes. Typical land uses associated with these chemical constituents include septic tanks, polluted rainwater, road salting, animal waste, and fertilizer.

Trace metals are important to both human and animal health. In general, metals usually are not found at significantly elevated levels in lakes unless pollution was discharged into the lake. Most of these sites have been identified. Elevated mercury levels are found in many species of fish in Michigan lakes, resulting in general statewide consumption advisories. It is generally accepted that atmospheric inputs of mercury are the primary cause of the elevated mercury levels.

Phosphorous is an important nutrient for plant growth and most often is the limiting nutrient for plant growth in lakes. Naturally productive lakes have higher levels of phosphorous in the soils of the catchment than unproductive lakes. Human land-use practices presently are the principal source of phosphorus for most Michigan lakes. Phosphorous does not dissolve easily in water and forms insoluble precipitates with calcium, magnesium, and iron. This makes phosphorous less available for algal growth. These precipitates accumulate in the sediments where rooted aquatic macrophytes may extract the phosphorous. Hardwater lakes may have low algae and clear water with abundant macrophyte growth. When oxygen is not present, iron compounds release phosphorous to the water. This is an important mechanism for seasonal phosphorous recycling within deeper, stratified lakes.

Nitrogen is second only to phosphorous as a nutrient for plant growth. Nitrogen occurs in various forms in lakes. These forms include ions of nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), and organic compounds. Total nitrogen is determined by adding nitrate, nitrite, and Kjeldahl (organic plus ammonium) nitrogen. Rain can be a source of nitrogen for lakes, but human land-use practices presently are the principal source in Michigan lakes. Nitrogen can be the limiting nutrient for algal growth when the ratio of total nitrogen to total phosphorous is less than 10:1. Phosphorous is the limiting nutrient at values greater than 15:1. Nitrogen may be a factor in limiting rooted aquatic plant growth. It may also affect species composition and influence non-indigenous plant growth.

Transparency and chlorophyll-*a* are measures of productivity. Transparency, or water clarity, is measured visually using a Secchi disk (a 20–cm weighted white disk). Lower transparency generally indicates higher algal production in lakes. Chlorophyll-*a* is a component of the cells of most plants. High chlorophyll-*a* levels indicate high levels of algal growth and productivity in the water.

Trophic State

Several ecological processes are common to biological communities. Energy flow in food webs is initiated by photosynthesis and the rate of photosynthetic energy transfer is influenced by climate, nutrient cycling, hydrology, and succession. Natural and human-related disturbances can dramatically influence the energy flow process (Schindler and Scheuerell 2002). All components of a drainage basin influence the regulation of lake metabolism. Natural components of the watershed that influence the composition and production of the biotic community of a lake include the chemical composition of the water (including nutrients), the flow of water through the lake, organic inputs, and the morphometry of the lake basin. Other factors contributing to biological productivity include animal food (trophic) relations with plants and other animals and the competitive and predatory interactions that lead to greater success of one species over another.

The trophic state of a lake refers to the rate of organic matter supply and is a measure of its productivity. Generalized mechanisms regulating the trophic status of lakes are presented in Figure 5. Oligotrophic lakes are low in productivity and eutrophic lakes are high in productivity. Mesotrophic lakes have intermediate levels of productivity. Rates of productivity are regulated by natural and human-induced levels of carbon and inorganic nutrient inputs into the lake. Typical levels of phosphorous, chlorophyll-*a*, and transparency are provided in Table 3.

Oligotrophic lakes are typically deep with a relatively large hypolimnion and low biological productivity. They have clear water, with Secchi disk transparency readings of 15 feet or greater. Nutrients concentrations are low, with phosphorous concentrations generally less than 0.010 mg/l. Aquatic macrophyte populations are generally sparse, with some dense stands in scattered locations. Algal production is relatively low and chlorophyll-*a* concentrations remain below 0.002 mg/l.

Organic matter deposition into the hypolimnion is low, keeping microbial decomposition rates and oxygen use low. The hypolimnion remains aerobic, limiting nutrient recycling within the lake. These lakes have low biological diversity and usually support coldwater and coolwater fish populations. Typical coldwater fish include lake trout, lake whitefish, lake herring, burbot, and sculpins. Typical coolwater fish include smallmouth bass, rock bass, walleye, northern pike, lake chub, and emerald shiner.

Mesotrophic lakes are moderately productive, with Secchi disk transparencies of 6 to 15 feet. Phosphorous concentrations range between 0.010 mg/l to 0.030 mg/l. Aquatic plants occur at moderate levels, with dense stands common. Large algal blooms generally do not occur, especially blue-green algal blooms. Chlorophyll-*a* concentrations range between 0.002 mg/l and 0.010 mg/l. Oxygen depletion in the hypolimnion usually occurs in late summer and winter. Some recycling of nutrients from the sediments occurs during spring and fall turnovers. These lakes support coolwater and warmwater fish populations. Typical warmwater fish include largemouth bass, bluegill, black crappie, grass pickerel, channel catfish, longnose gar, bullheads, gizzard shad, and fathead minnow. Warmwater lakes typically are dominated by centrarchid fish communities.

Eutrophic lakes have Secchi disc transparencies usually less than 6 feet. Nutrient levels are high, with phosphorous concentrations greater than 0.030 mg/l. Aquatic macrophytes may be abundant in shallow waters. Significant algal blooms, including blue-green algae, may occur. Algae may limit light and restrict the depth distribution and abundance of macrophytes. Chlorophyll-*a* concentrations are usually greater than 0.010 mg/l. High organic matter deposition in the hypolimnion results in oxygen depletion for much of the year. Anaerobic conditions promote nutrient recycling from the hypolimnion and lower rates of organic matter deposition. Shallow eutrophic lakes frequently have extensive mortalities of fish during winter months ("winterkill"). This results from oxygen depletion under ice and snow cover. Eutrophic lakes are characterized by warmwater fish populations.

Marl lakes are categorized differently in that they generally are very unproductive, yet they may have summer-time depletion of dissolved oxygen in the bottom waters and very shallow Secchi disk depths, particularly in the late spring and early summer. Groundwater entering these lakes contains dissolved $CaCO_3$ that has been acquired from limestone in the soils. Chemical reactions within the lake allow the formation of particulate calcium compounds (marl) that form deposits on the bottom and can make the water have a white, turbid appearance.

Bogs, also called dystrophic lakes, have low production of phytoplankton. The production of organic matter within bogs is predominately by littoral plants. Bogs develop through the colonization and establishment of mosses, especially *Sphagnum*, as one of the dominant plants in the littoral zone, under low nutrient and humid conditions. This can occur in both shallow and deep lakes. The mosses increase the acidity of the system, resulting in decreased rates of organic matter decomposition within the water and in accelerated filling of the lake with organic matter.

The trophic state of a lake can naturally change over time. A lake can become more or less eutrophic as natural weathering processes and nutrient fluxes in the watershed change. Generally, once the surface soils of a drainage basin have undergone weathering for an extended period, nutrient inputs decline and become relatively stable. Lakes in Michigan are highly variable in trophic status between oligotrophic and extremely eutrophic. Human development tends to increase (cultural) eutrophication in our lakes through increased surface drainage, soil erosion, vegetation and wetland removal, and nutrient additions. Many lakes in Michigan, including the Great Lakes, have increased eutrophication resulting from human activities. This primarily results from increased nutrient concentrations in lake waters resulting from pollution. Historical industrial and municipal wastewater discharges into lakes were often poorly regulated and resulted in severe eutrophication, often allowing survival of only the most tolerant fish species, such as common carp and bullheads. Presently, non-point source nutrient pollution affects a significant number of lakes. Septic tanks, lawn and agricultural fertilizers, and animal waste are typical sources. In 1982, the Michigan Department of Natural Resources surveyed 656 inland lakes and found 12% to be oligotrophic, 62% mesotrophic, and 26% eutrophic (Michigan State University 1987). The majority of Michigan's eutrophic lakes were located in the southern part of the Lower Peninsula where agriculture, urban development, and lakeshore development were prevalent. An evaluation of 91 lakes in 2002 indicated the productivity of 25% were low, 62% moderate, 12% high, and 1% excessive (Harrison 2003). In 1996, Lake Superior was classified oligotrophic, Lake Huron was oligotrophic (except for the eutrophic Saginaw Bay), Lake Michigan was oligotrophic to mesotrophic, and Lake Erie was mesotrophic except for the western basin which was eutrophic (Bredin 1998).

Uplands, Including the Shoreline Ecotone

The uplands of the watershed include all of the landscape contributing surface water and groundwater drainages to the lake. Precipitation, geology, soils, and landscape morphology determine the drainage patterns, flow rates, and chemical composition of drainage waters. Forests, fields, lakes, swamps, marshes, and streams moderate surface drainage, chemical composition, and organic matter flow through the system.

The uplands of lake watersheds affect productivity of lakes through nutrient and organic matter inputs. Generally lakes with large watersheds are more productive. Watersheds rich in nutrients will naturally result in productive lakes. Organic matter, especially the dissolved forms, is an important contribution of the uplands affecting lake productivity.

The zones immediately adjacent to the lake are important transition areas between land and water, and are also referred to as ecotones and riparian areas. Riparian areas supply both particulate organic matter for the food web through leaf deposition, and large deadwood (Christensen et al. 1996b; Guyette and Cole 1999), important as a long-term carbon source and as cover for aquatic organisms. The shoreline ecotone provides critical habitat components for most amphibians, reptiles, mammals, and birds that require or use lacustrine systems. Seasonal and diurnal movements between various habitat components within the shoreline ecotone are necessary for survival of many animals. Management and maintenance of natural riparian areas is very important to the ecological integrity of lakes.

Littoral Zone

The littoral zone encompasses the area of a lake between the open water pelagial zone and the uplands of the drainage basin (Wetzel 1975). It generally extends from the depth of rooted plant growth, usually 15 to 25 feet deep, shoreward to the beach area affected by waves at the high water elevation. Submersed plants generally do not grow below a depth of 30 feet due to light and pressure limitations. Some lakes have very small littoral zones and some lakes are comprised entirely of littoral zone. Lakes St. Clair and Erie have relatively large littoral zones compared to the other Great Lakes. Houghton Lake, the largest inland lake in Michigan, is entirely littoral zone. In most lakes, the littoral complex of macrophytes and associated microflora is foremost in regulation of eutrophication rates and in the functional dynamics of the system as a whole.

The littoral zone of a lake can be broken down into a number of smaller zones. Typically, the lower littoral zone contains predominantly submersed macrophytes, the middle littoral zone contains floating-leaved rooted macrophytes, the upper littoral zone is dominated by emergent vegetation, and the eulittoral-supralittoral zones are areas influenced by waves. As discussed earlier, other terms used to describe these areas of a lake include swamp, marsh, deepwater or submerged wetland, fen, bog, and wet meadow. Hydrology, particularly water depth and duration, determine the dominant type of vegetation

Submersed macrophytes and aqueous portions of emergent and floating macrophytes provide an enormous surface area that is colonized by microflora (algae and bacteria). In addition, all other surfaces within the littoral zone are colonized by microflora that are more or less attached. An extremely diverse spectrum of microhabitats occurs in the littoral zone among substrates of sand, rock, organic sediments, and macrophytes. The massive surface area available for colonization, especially among submersed macrophytes, can result in very high contributions of attached littoral algae to the total primary productivity of many freshwater systems. When this productivity is coupled with the very high rates prevalent among the emergent macrophytes, the littoral primary productivity can form a major input of organic matter to lake systems. The littoral zone provides diverse habitats for aquatic organisms, and its components are highly important in the overall production and regulation of the lake ecosystem (Wetzel 1975).

Typical indigenous plant species found in Michigan lakes are classified within the following architectural groups:

- Low-growing: muskgrass *Chara* (a macroalgae), southern naiad, Robinson pondweed, and bladderwort.
- Mid-water: large-leaf pondweed, water star-grass, flat-stemmed pondweed, sago pondweed, eel grass (wild celery), smartweed, and waterweed.
- Full water column: American pondweed, Richardson's pondweed, variable pondweed, white-stemmed pondweed, Illinois pondweed, coontail, and water-milfoil.
- Floating-leaved: water-lilies, floating-leaf pondweed, and watershield.
- Emergent: arrowhead, bur-reeds, swamp loosestrife, arrow arum, pickerelweed, cat-tail, wild-rice, reed canary grass, spike rush, bulrush, and sedge.

Aquatic macrophytes are an essential habitat component of lake ecosystems and contribute many benefits to aquatic communities. Natural plant species composition and distribution within lakes are influenced by lake size and depth, wave energy, water currents, ice-scour, bottom slope, sediment composition, and water chemistry and clarity. The heterogeneity of sediment composition is influenced by the physical characteristics of a lake. Sediment composition combined with depth strongly influences both species composition and biomass of the plant community (Duarte and Kalff 1988; Johnson and Ostrofsky 2004). Canopy-erect species (e.g., coontail, water-milfoil, pondweeds) dominate where nutrients are abundant, and bottom-dwelling species (e.g., eel grass, water marigold, muskgrass, naiads, water star-grass) dominate where sediments are infertile. Areas of lake where physical conditions (wave, ice-scour, water currents) are more severe have a tendency to be poorer in nutrients.

Generally, macrophyte production tends to be lower in oligotrophic lakes and higher in mesotrophic-eutrophic lakes. However, naturally oligotrophic lakes often have dense stands of macrophytes as part of the overall plant community.

Macrophytes are important in determining type, structure, and production of fish communities, and they influence fish behavior (Hall and Werner 1977; Werner and Hall 1977; Miranda and Hubbard 1994; Randall et al. 1996). Aquatic plants play a key role in different life stages of many fish species, including serving as substrates for eggs and providing habitat for some species that require plants for their existence (Scott and Crossman 1973; Trautman 1981; Becker 1983). Janacek (1988) provided a literature review of 119 papers in relation to fish interactions with aquatic macrophytes. He found that 44 species of fish were found to spawn in, on, or near macrophytes, and 84 species of fish utilized macrophytes to satisfy some habitat need. Most of these species are found in Michigan and include the principal game fish. Fish that inhabit the littoral zone are known to segregate predominantly by habitat (Werner et al. 1977; Schneider 1981; Keast 1984; Weaver et al. 1997). Submerged macrophytes create areas favorable to invertebrates that are a principal source of food for many fish (Keast 1984; Wiley et al. 1984; Engle 1985). Macrophytes offer spatial diversity for fish providing both open and complex areas for foraging and predator avoidance (Keast 1984; Kilgore et al. 1989; Smith 1993).

Fish biomass is directly related to aquatic macrophytes in inland lakes (Schneider 1975, 1978, 1981; Durocher et al. 1984; Wiley et al. 1984; Kilgore et al. 1989; Bettoli et al. 1993; Hinch and Collins 1993). Schneider (1975, 1978) determined that submersed macrophyte abundance was one of four principal components regulating the biomass of fish in Michigan lakes. Schneider (1981) also determined that the better fishing lakes in Michigan contained moderate densities of aquatic macrophytes. Fishing quality was related to size structure and growth rates of game fish. Durocher et al. (1984) found that any reduction of aquatic macrophytes below 20% of total lake surface area resulted in a reduction in the bass fishery. He had data only to a maximum of 20% of lake surface area, so he was not able to evaluate higher levels of plant coverage. Wiley et al. (1984) estimated 36% macrophyte coverage was optimal for bass populations in Illinois ponds. Theiling (1990) related growth rates of bluegill in Michigan lakes to percent macrophyte coverage of total lake surface area. Growth index values were always positive below 33% macrophyte coverage. Bluegill growth index values at higher levels of macrophyte coverage ranged from negative to positive. This information indicates that above average bluegill growth is common in lakes with macrophyte coverage up to 33% of total lake surface area. Lakes with higher levels of macrophyte coverage can have above average bluegill growth, but usually have average or below average growth.

Macrophytes are equally important for determining a lake's value to wetland wildlife. The distribution and abundance of plants in shallow zones of lakes can directly influence use by species of dabbling ducks and wading birds (Kaminski and Prince 1981; Monfils 1996; Soulliere and Monfils 1996). Areas having a "mosaic" or mixture of aquatic plants and open water often have the highest species diversity and overall use by these bird groups. Some species of shorebirds also prefer shallow water areas with macrophytes, whereas others depend on the mudflats commonly found in the upper littoral zone (Helmers 1992). Submerged plant leaves and roots (tubers) are used as food by several species of wildlife. In addition these plants act as substrate for aquatic invertebrates like insects and snails, important food sources for many waterbirds. Emergent plants provide both food and protective cover, plus nest-building material for birds and aquatic mammals (Baker 1983). A variety of amphibians and reptile species depend on the littoral zone, and they represent additional critical elements of these complex lake communities.

Pelagial and Profundal Zones

The pelagial and profundal areas of a lake are important in processing dissolved and particulate organic compounds critical to energy flow in the system, the annual cycling of nutrients, producing phytoplankton and zooplankton, and as feeding and refuge areas for small invertebrates, fish, and birds. Diving ducks are especially obvious on open water lakes where they feed on mollusks, crustaceans, and submerged aquatic plant leaves and tubers. Loons, grebes, and terns commonly fish the pelagial zone of lakes. Some lakes have no true pelagial zone and others have very large open water areas. Waters of the epilimnion are usually well mixed and oxygenated during summer months. The hypolimion may be depleted of oxygen during summer months, and sometimes during winter months.

Lakes Superior, Michigan, Huron, and some inland lakes have very large, deep pelagial zones. The hypolimnion contains cold, well-oxygenated water throughout the summer months. These types of lakes are typically oligotrophic and low in nutrients and productivity, and the profundal zone remains aerobic with high rates of organic matter decomposition. Coldwater and coolwater aquatic communities are supported in these lakes because the cold waters of the hypolimnion remain oxygenated.

Most large inland lakes have moderately large pelagial zones and hypolimnions relative to the littoral zone. The hypolimnions of many of these often become devoid of oxygen during summer. The hypolimnion and profundal zones become anaerobic and organic matter decomposition rates decrease. Typically these lakes have warmwater aquatic communities.

Bogs

Bogs are unique because their nutrient-poor, acidic nature promotes high organic matter accumulation (refer to the Trophic state section). The rapid accumulation of organic matter can turn an open water lake into a forested wetland at a greater rate than a typical lake.

Relatively few aquatic animals have adapted to the extreme acidity and low salinity of bog waters. Species diversity is very low and entire groups of animals are lacking or poorly represented, including mollusks and fish.

Bogs support a specific group of carnivorous plants such as pitcher plants, sundews, and bladderworts that eat insects and are able to retain water from precipitation. Common shrubs include leatherleaf, bog laurel, bog rosemary, and Labrador tea. Blueberries and cranberries are also common. American goldfinch, song sparrow, American woodcock, alder and willow flycatchers, and golden-winged and chestnut-sided warblers are birds found using bogs. Ruffed grouse eat the catkins of bog birches, which often grow around the edges of bogs and fens, and migrating ducks use the open pools of bogs for resting. Because bogs support insects, shrews, mice, frogs, toads, and other species in the food chain, they also attract mink, raccoons, herons and other predators. A unique species occurring in bogs and adjacent meadows is the southern bog lemming.

Beaver Impoundments

A high proportion of the small (<5 acres) inland lakes found in northern Michigan are created by beaver. Beaver ponds are usually temporary, lasting from a couple years to a couple decades, until food depletion (particularly poplar and willow trees) encourages abandonment by a beaver colony (Baker 1983). Following beaver emigration, dams deteriorate and associated impoundments drain, which results in stands of aquatic macrophytes being replaced by herbaceous plants adapted to dryer soils. Trees eventually return to most “beaver basins,” and the cycle begins again, increasing temporal diversity to local plant and wildlife communities.

The use of beaver impoundments by wildlife is greater than for other small natural lakes in northern Michigan. Beaver droppings and the materials pulled from uplands provide fertilizing agents and structure to wetlands that can otherwise be generally sterile and unproductive, especially in the Upper Peninsula. Various characteristics of beaver impoundments, such as excavated channels, shallow and deepwater zones, aquatic macrophytes, and woody debris (lodges, food caches, dams and feeding sites) result in a diversity of micro-habitat for many wildlife and some fish species. A recent study completed in northern Minnesota revealed that productive and diverse fish assemblages (non-trout species) in headwater streams required the entire mosaic of successional habitats associated with beaver activity, including those due to the creation and abandonment of beaver ponds (Schlosser and Kallemeyn 2000). Thus, the diversity of site-level and landscape-level features associated with beaver lakes can result in wildlife and fish diversity and abundance that surpasses that found on other small northern lake basins.

Wetland Habitats

At the time of European settlement, the area that is now the conterminous United States contained an estimated 221 million acres of wetlands. In 1997, there were an estimated 105.5 million acres left (Dahl 2000). The rate of wetland loss was estimated for several periods as follows: mid 1950s to the mid 1970s – 485,000 acres/yr; mid 1970s to the mid 1980s – 290,000 acres/yr; and 1986 through 1997 – 58,500 acres/yr. Between 1986 and 1997, the net loss of wetlands was 644,000 acres. Ninety-eight percent (633,500 acres) of all losses were to freshwater wetlands. In 1997, there were an estimated 100.2 million acres of freshwater wetlands remaining, including 50.7 million acres of forested wetlands, 25.2 million acres of freshwater emergent wetlands, 18.4 million acres of freshwater shrub wetlands, and 5.5 million acres of freshwater ponds. Since the 1950s, freshwater emergent wetlands have declined by the greatest percentage of all wetland types with nearly 24% lost. Freshwater forested wetlands sustained the greatest overall loss in area, declining by 10.4 million acres. National wetland losses were attributed to urban development (30%), agriculture (26%), silviculture (23%) and rural development (21%). Dahl (2000) concluded that substantial progress had been made in reducing the rate of wetland loss, but the goal of no net loss of wetlands had not been achieved.

Michigan's landscape has been modified extensively from conditions present prior to European settlement. Logging, farming, residential, urban, industrial, and recreational development have removed wetlands through draining and filling. Wetland losses in Michigan, compared to conditions at the time of European settlement, have been estimated as high as 70% (Herman et al. 2001). Wetlands along the shorelines of lakes have been severely depleted in many instances as a result of human development. It should be emphasized that estimated wetland losses only indicate losses of aquatic vegetation in the portion of a lake's littoral zone containing emergent plants. Losses of aquatic vegetation from dredging, filling, and removal programs in the remaining portion of the littoral zone in Michigan lakes have not been determined.

The Michigan Natural Features Inventory has described a number of natural communities in Michigan using a wetland classification system. They have described 30 specific palustrine communities as of March, 2003 (www.michigan.gov/dnr). Many of these have unique plant or animal communities, often containing species threatened or endangered.

Inland swamps and marshes occur within the littoral zone of lakes, along stream margins, and in isolated locations with saturated soils. Michigan swamps are often dominated by conifer trees (white cedar, black spruce, balsam fir, white pine, and hemlock) in the north and deciduous trees (silver and red maple, swamp white oak, tupelo, black ash, and basswood) in the south, but with mixed swamps in both regions. Common marsh plants include narrow- and broad-leaved cat-tails, sedges, species of arrowhead, bulrush, water-lily, eel grass (water celery), rushes, and pondweeds. Reed canary grass, woolgrass, a variety of sedges, big bluestem, prairie cordgrass and blue-joint grass are examples of wet meadow plants that can withstand occasional, temporary flooding. As soils become more saturated, red-top grass, goldenrod, Joe-pie-weed, marsh aster and other marsh plants begin to dominate wet meadows. Sedges like bottlebrush sedge and lake sedge dominate where the soils are saturated most of the year. Southern Michigan marsh often grades into shrub swamp dominated by dogwood and willow.

Swamps and marshes provide habitat for wildlife, including mammals such as muskrat, raccoon, mink, cottontail rabbit, and white-tailed deer. Wading birds (herons and bitterns), shorebirds, waterfowl, terns and many species of songbirds seek nest sites and food in marshes and swamps. Shorebirds commonly found using marsh mudflats include greater and lesser yellowlegs, killdeer, common snipe, and solitary sandpiper. Less common bird species that live in marshes include the black tern, American bittern, least bittern, and king rail. Dense cattail stands provide quality winter habitat for ring-necked pheasants. They also supply food and cover to leopard frogs, chorus frogs, snapping turtles, red-eared slider turtles, northern water snakes, and ribbon snakes.

Swamps and marshes have significant fisheries values. Typical fish that use swamps and marshes for spawning or nurseries include northern pike, yellow perch, bluegill, largemouth bass, and a variety of minnow species.

Various types of wildlife rely on springs and seeps when rivers, creeks, ponds and other water sources are absent. Because they do not readily freeze during winter months, they offer a dependable source of flowing water year around. In addition, the ground water that percolates at lower elevations often creates a snow-free area in winter and provides wildlife with access to green vegetation. In spring and summer, reptiles and amphibians, including several kinds of salamanders favor the constantly moving shallow water of springs and seeps.

Coastal wetlands are found along the Great Lakes, their connecting waters (e.g., St. Mary's River, St. Clair River), and in lakes connected by streams (drowned river mouth lakes) and tributary estuaries influenced by Great Lakes water levels. Great Lakes wetlands are considered to be the some of the most productive natural systems in the temperate zone of North America. Some of the special communities found within Great Lakes wetlands are very rare and considered globally imperiled.

Typical plant species associated with Great Lakes wetlands include: button bush, silky dogwood *Cornus amomum*, red-osier dogwood *Cornus racemosa*, and willow in the shrub swamps; hardstem bulrush, three-square, softstem bulrush, *Phragmites*, giant bur-reed, common arrowhead, water plantain, pickerel weed, and cattail in the shallow emergent plant zone; and Eurasian water-milfoil, pondweed, wild celery (eel grass), naiad, and common waterweed in the submerged zone. Muskgrass *Chara* (a species of macro-algae) is also commonly found growing on the bottom of the submerged zone.

Great Lakes wetlands provide habitat for a wide diversity of animal species. Thirty-nine species of amphibians and reptiles and 15 species of mammals occur in the St. Clair system (Hendendorf et al. 1986). Typical waterfowl species observed on Michigan wetlands include: 3 species of swan, 2 species of geese, and 21 species of ducks. Birds other than waterfowl that may be found in the Great Lakes system include: grebes, rails, herons, plovers, sandpipers, gulls, terns, hawks, bald eagle, osprey, American kestrel, short-eared owl, belted kingfisher, and an extended list of perching birds (Edsall 1988). More than 48 species of fish and several species of invertebrates are known or presumed to use the coastal wetlands of the Great Lakes.

The lake-plain prairie system typically occupies the position between the shallow emergent marsh zone of the Great Lakes marsh community and the adjacent uplands. It also can occur inland on the glacial lake-plain landform in shallow depressions. Lake-plain prairie and lake-plain oak openings are considered globally imperiled by The Nature Conservancy. The majority of wet prairie along or near the shorelines was drained in the mid-late 1800s and converted to agriculture or developed. At present, the amount of remaining lake plain prairie is approximately 1,000 acres or 0.7% of the original prairie present at the time of European settlement (Comer et al. 1995). The St. Clair area contains 25% of the lake-plain prairie in Michigan. Statewide, 53 plant species, 6 insect species, 2 bird species, and 1 species of snake associated with lake-plain prairies are state listed as endangered, threatened, or special concern.