WETLAND HABITATS *of* NORTH AMERICA

ECOLOGY AND CONSERVATION CONCERNS

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CHAPTER 13

Great Lakes Coastal Marshes

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Great Lakes Geology and Hydrology

The Great Lakes system consists of Lakes Superior, Huron, Michigan, Erie, and Ontario, as well as their connecting channels and the St. Lawrence River, which connects the lakes to the Atlantic Ocean (Fig. 13.1). The Great Lakes Basin includes the Canadian province of Ontario and the U.S. states of Minnesota, Wisconsin, Illinois, Indiana, Michigan, Ohio, Pennsylvania, and New York. The basin covers about 765,000 km^2, including the upper St. Lawrence River (Neff and Nicholas 2005).

The surficial geology of the Great Lakes Basin is highly variable. Lake Superior and northern Lake Huron are surrounded by metamorphic and igneous rocks of Precambrian age, with little or no overburden. The remainder of the basin is underlain by sedimentary rocks of Cambrian through Cretaceous ages (Wilcox, Thompson, et al. 2007) and covered by unconsolidated glacial deposits. Water chemistry of the lakes reflects the underlying geology; Lake Superior is less mineralized (specific conductance 95–100 uS/cm; pH 7.4–8.0; alkalinity 40–50 mg/L as $CaCO_3$) compared to the other lakes, which are more calcareous, with limestone and dolomite bedrock (specific conductance 200–300 uS/cm; pH 7.8–8.5; alkalinity 80–110 mg/L as $CaCO_3$) (Keough, Thompson, et al. 1999; Mechenich, Kraft, et al. 2006; www.ilec.or.jp/database/index/idx-lakes.html).

Lake Superior is at the upstream end of the Great Lakes and discharges to Lake Huron via the St. Marys River (Fig. 13.1). Lakes Huron and Michigan are one lake hydrologically because the connection between lakes at the Straits of Mackinac is very wide. Lake Huron discharges to Lake Erie by way of the St. Clair River, Lake St. Clair, and the Detroit River; Lake Erie connects to Lake Ontario largely via the Niagara River.

Mean annual precipitation ranges from 0.7 m north of Lake Superior to 1.3 m east of Lake Ontario. Snowbelt areas downwind from open waters of the lakes receive lake-effect snow that can average 3.5 m and exceed 8.9 m annually (Wilcox, Thompson, et al. 2007). Evaporation from the lake surface, especially when cooler dry air passes over warmer open water in fall and early winter, results in atmospheric outflows composing as much as one-third of the water balance in lakes Superior and Michigan-Huron (Wilcox, Thompson, et al. 2007).

Great Lakes water levels vary considerably on timescales from hours to millennia and are influenced by both natural processes and human activities. Storm surges, seiches, and barometric pressure changes can create localized changes in water levels that last hours to days. Wind-driven seiches with amplitudes of 10 to 30 cm are common across most Great Lakes and larger embayments within the lakes, but seiches with amplitudes of over 3 m have been recorded in Lake Erie. Seasonal and annual data systematically recorded by the U.S. and Canadian governments since 1860 show cycles of low winter levels and high summer levels that vary in magnitude by lake (Fig. 13.2). Based on the monthly average water levels, the magnitudes of unregulated seasonal fluctuations are relatively small, averaging about 0.4 m on lakes Superior and Michigan-Huron, about 0.5 m on Lake Erie, and about 0.6 m on Lake Ontario (Wilcox, Thompson, et al. 2007).

Longer-term (multiyear, decadal, and longer) fluctuations are recognizable in the historical lake-level record and show some similarities among lakes (Fig. 13.2). Pronounced low lake levels occurred in the mid-1920s, mid-1930s, mid-1960s, and starting again in 1999. Periods of higher lake levels generally occurred in the late 1800s, the late 1920s, the mid-1950s, and from the early 1970s to mid-1980s. However, Lake Superior water levels have been regulated since about 1914, and levels of Lake Ontario have been regulated since about 1960. Therefore, lake-level patterns on those lakes since regulation began do not reflect all of the natural variability that would have occurred. Other human activities affecting lake levels include diversions into or out of the basin, consumption of water, and dredging of outlet channels.

Water-level changes have also been recorded in the late Holocene geologic record as sequences of beach ridges of similar origin but different age (chronosequences) that formed during repeated occurrences of high lake levels, with intervening low levels. Baedke and Thompson (2000) used the elevations of foreshore deposits in these ridges coupled with radiocarbon dates from the wetlands between the ridges to develop a 4,700-year lake-level record for lakes Michigan-Huron (Fig. 13.3). The record shows a quasi-periodic behavior, with short-term fluctuations with a range of 0.5 to 0.6 m that occur about every 32 ± 6 years superimposed on longer-term fluctuations with a

FIG. 13.1. Map of the Great Lakes showing the extent of the drainage basin. Base from ESRI, 2001; U.S. Army Corps of Engineers, 1998; and Environment Canada, 1995; digital data sets at various scales. (From Neff and Nicholas 2005.)

range of 0.8 to 0.9 m that occur about every 160 ± 40 years. Over millennia, three high phases occurred from 2,300 to 3,300, 1,100 to 2,000, and 0 to 800 years ago.

A preliminary paleo-record of Lake Superior water levels was also created, using dating of sand grains by a technique called optically stimulated luminescence to determine the age of the ridges (Argyilan, Forman, et al. 2005). It shows patterns similar to those of lakes Michigan-Huron until about 1,200 years ago because lakes Superior, Michigan, and Huron had been joined as one lake prior to that time (Johnston, Baedke, et al. 2004; Johnston, Thompson, et al. 2007). It appears that Lake Superior has taken on its own lake-level pattern following its split from the other lakes.

The hydrographs recording long-term patterns of lake-level change also reflect long-term patterns of vertical ground movement in response to glacial isostatic adjustment (GIA), in which the earth's crust is warping in response to the melting of the last glacial ice sheets that crossed the area. The glacial ice was thickest north of the Great Lakes Basin, so these areas of the earth's crust were depressed the most. Today, areas depressed the most are rising the fastest (Baedke and Thompson 2000; Mainville and Craymer 2005). GIA influences long-term lake levels by warping each lake's basin and changing the elevation of the lake's coastline in relationship to its outlet. Segments of coastline rebounding more rapidly than the lake's outlet experience a long-term lake-level fall, whereas coastlines rebounding more slowly than the outlet experience a long-term lake-level rise (Wilcox, Thompson, et al. 2007). In areas under a long-term rise, lake waters advance into river and stream valleys along the shoreline, creating drowned river mouths that are a major setting for wetland development.

Great Lakes coastal wetlands can be separated into three specific hydrogeomorphic systems—lacustrine, riverine, and barrier-protected—based on geomorphic position, dominant hydrologic source, and current hydrologic connectivity to the lake (Keough, Thompson, et al. 1999; Environment Canada 2002; Albert, Wilcox, et al. 2005). In addition to the three general hydrogeomorphic systems, this classification includes further breakdown into geomorphic type and geomorphic modifiers that reflect specific site conditions.

Lacustrine (lake-influenced) systems (Fig. 13.4a) are controlled directly by waters of the Great Lakes and are strongly affected by lake-level fluctuations, nearshore currents, seiches, and ice scour. Geomorphic formations such as embayments and sand spits along the shoreline provide varying degrees of protection from coastal processes. Open lacustrine wetlands are exposed to the full force of winds and waves, and they accumulate little organic sediment. Protected lacustrine wetlands have more organic sediments and typically have more extensive vegetation development (Environment Canada 2002; Albert, Wilcox, et al. 2005).

Riverine (river-influenced) system wetlands (Fig. 13.4b) occur in rivers and streams that flow into or between the Great Lakes. The water quality, flow rate, and sediment input are con-

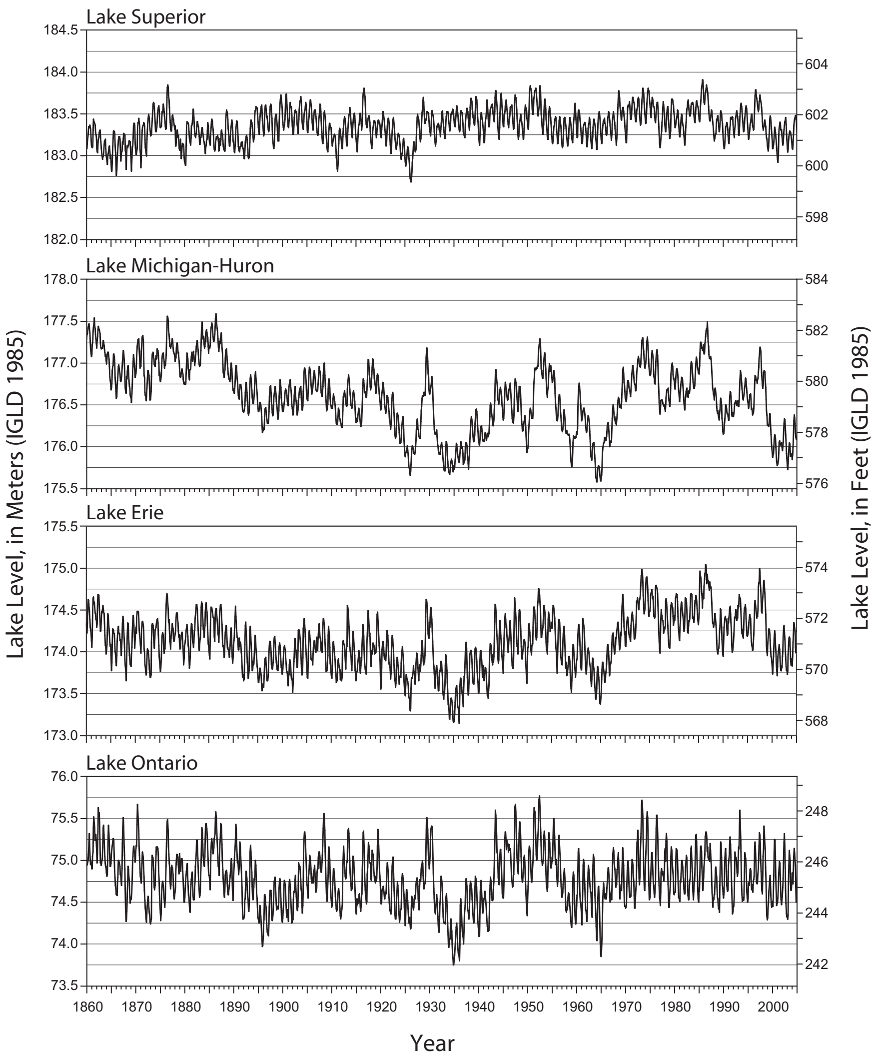


FIG. 13.2. Hydrograph showing historical lake levels for the Great Lakes, 1860–2005.

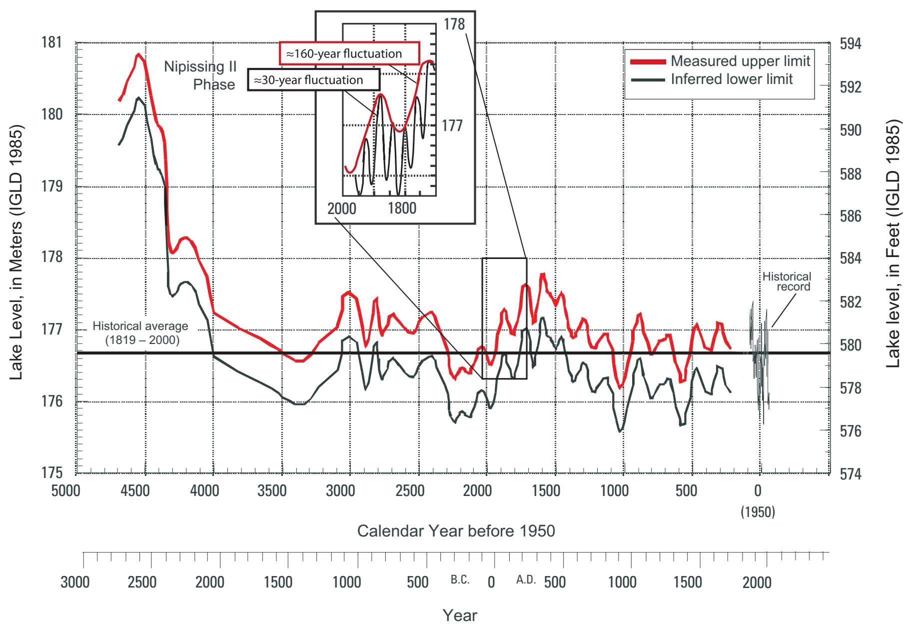


FIG. 13.3. Hydrograph of the late Holocene lake level and historical lake level for Lake Michigan-Huron. The upper line is interpreted from beach-ridge studies, whereas the lower line is an inferred lower limit using the range of the historical record as a guide. (From Baedke and Thompson 2000 as presented by Wilcox, Thompson, et al. 2007.)

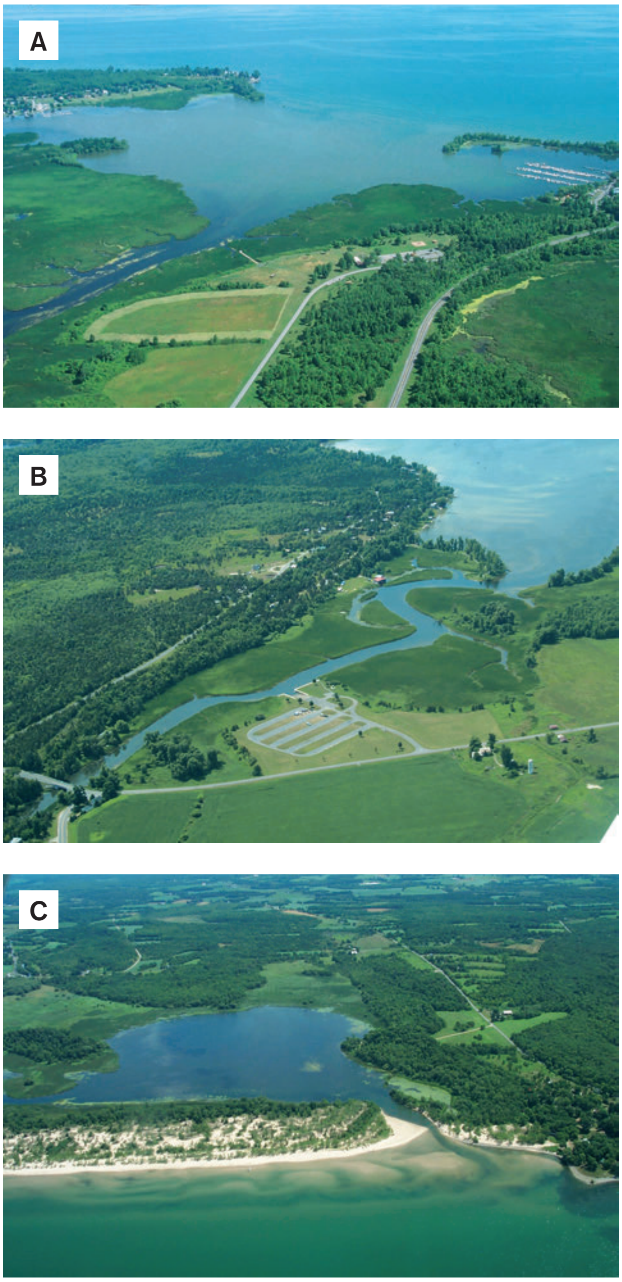


FIG. 13.4. Oblique aerial photographs of Lake Ontario wetlands of differing geomorphic type. A. Braddock Bay, open embayment; *lacustrine.* B. Stony Creek, drowned river mouth; *riverine.* C. South Colwell Pond, barrier-beach lagoon; *barrier-protected.*

trolled in large part by their individual drainage basins. However, water levels and fluvial processes in these wetlands are also determined by the Great Lakes because lake waters flood back into the lower portions of the drainage system (drowned river mouth wetlands). Protection from wave attack is provided in the river channels by bars and channel morphology. Riverine wetlands also include those wetlands found along large connecting channels, such as the St. Marys and St. Clair Rivers. In addition, delta wetlands formed from alluvial materials that extend into the lake or connecting channel are also included as riverine; they may be extensive and typically have well-developed organic soils (Environment Canada 2002; Albert, Wilcox, et al. 2005) .

Barrier-protected system wetlands (Fig. 13.4c) may have originated from either coastal or fluvial processes. However, due to nearshore processes, the wetlands have become separated from the Great Lakes by a barrier beach or series of beach ridges. Barrier-beach lagoon wetlands are protected from wave attack but may be periodically or continuously connected directly to the lake by a channel or inlet crossing the barrier. When connected to the lake, water levels in these wetlands are determined by lake levels, while during isolation from the lake, groundwater and surface drainage from the basin of the individual wetland provide the dominant source of water input. Inlets to protected wetlands may be permanent or temporary due to nearshore processes that can close off inlets from the lake. Swale complexes are wetlands that occur between recurved fingers of sand spits or relict beach ridges. Oftentimes, only the first few swales are directly connected to the lake, but groundwater discharges related to lake levels often supply water to swales farther from the lake (Environment Canada 2002; Albert, Wilcox, et al. 2005).

Plant Communities

Wetland plant communities in the Great Lakes vary according to factors that include underlying geology and resultant water chemistry, lake-level variability, geomorphic type, human disturbance, and location within the geographic range of the basin. Differences can be seen even among wetlands of the same geomorphic type from northern Lake Superior to the more southerly lakes. A lake-by-lake tour of selected wetlands illustrates this point, with descriptions reflecting plant communities commonly found when lake levels are not at extreme high or low levels.

Bark Bay is a lake-connected, barrier-beach lagoon wetland with two small inflowing streams on the Bayfield Peninsula in western Lake Superior (Fig. 13.5a). Behind the protective barrier beach is a large, shallow lagoon containing pondweeds (*Potamogeton* spp.), common watermilfoil *(Myriophyllum sibiricum),* stonewort (*Chara* spp.), and other submersed plants. The perimeter of the lagoon has a narrow band of emergent marsh containing broad-leaf cattail *(Typha latifolia),* lake sedge *(Carex lacustris),* bur-reed (*Sparganium* spp.), rushes (*Juncus* spp.), three-way sedge *(Dulichium arundinaceum),* and increasing amounts of common reed *(Phragmites australis).* Large areas also consist of floating fen mat—peatland where slow decomposition of plants allows development of deep organic soils. Rhizomes of wool-fruited sedge *(Carex lasiocarpa)* intertwine to form the mat, which supports other sedge species, as well as mat-forming leatherleaf *(Chamaedaphne calyculata)* and peatland plants such as sphagnum moss (*Sphagnum* spp.), sundew (*Drosera* spp.), small cranberry *(Vaccinium oxycoccos),* and pitcherplant *(Sarracenia purpurea).* The shrub sweet gale *(Myrica gale)* is also common on the floating mats (Epstein, Judziewicz, et al. 1997; Wilcox, Meeker, et al. 2002).

The Kakagon River flows into Chequamegon Bay, on western Lake Superior near Ashland, Wisconsin (Fig. 13.5b). Seiches with amplitudes of 30 cm occur regularly and cause reverses in river flow direction as much as 2 km upstream in this drowned river mouth wetland. A dominant wetland plant is northern wild rice *(Zizania palustris),* a tall annual grass with large nutrient requirements that benefits from the nutrient-rich sediment deposited in response to flow reversals (Meeker 1996). Other dominant plants include pondweeds, waterweed *(Elodea canadensis),* coontail *(Ceratophyllum demersum),* bullhead pond lily *(Nuphar variegata),* white water lily *(Nymphaea odorata),* and pickerelweed *(Pontederia cordata)* in the aquatic zone and Canada bluejoint grass *(Calamagrostis canadensis)* and wool-fruited sedge in the peatlands (Meeker 1993).

A narrow fringe of wet meadow and emergent marsh follows long stretches of the St. Marys River (Fig. 13.5c), with beds of submersed vegetation, including stonewort, naiads (*Najas* spp.), quillworts (*Isoetes* spp.), and pondweeds, along the outside border. The emergent zone in these connecting channel riverine wetlands contains bulrushes (*Schoenoplectus* spp.) and spike-rushes (*Eleocharis* spp). The wet meadow at slightly higher elevation contains Canada bluejoint grass, tussock sedge *(Carex stricta),* wool-fruited sedge, lake sedge, broad-leaf cattail, and water knotweed *(Polygonum amphibium)* (Albert 2003; D. Albert pers. comm.).

Duck Bay is a protected lacustrine wetland in an embayment on Marquette Island, in the Les Cheneaux Islands of northern Lake Huron (Fig. 13.5d). Protection from wave action allows development of broad bands of emergent plants and wet meadows, with beds of submersed vegetation extending to depths of about 2 m. Submersed plants include pondweeds, naiads, waterweed, watermilfoil, and wild celery *(Vallisneria americana);* floating white water lily and spatterdock *(Nuphar advena)* are also common. The emergent community contains wave-tolerant hardstem bulrush *(Schoenoplectus acutus)* and spike-rushes along the outer edge and bulrushes, horsetails (*Equisetum* spp.), arrowhead *(Sagittaria latifolia),* pickerelweed, and bur-reed closer to shore. Wet meadows are dominated by Canada bluejoint grass and sedges, with scattered marsh fern *(Thelypteris palustris),* marsh bellflower *(Campanula aparinoides),* marsh pea *(Lathyrus palustris),* marsh cinquefoil *(Potentilla palustris),* and other forbs. At slightly higher elevations, a narrow band of shrubs includes speckled alder *(Alnus incana),* sweet gale, and willows (*Salix* spp.) among grasses and sedges, giving way to northern white cedar *(Thuja occidentalis)* swamp above the highest lake level (Albert 2003).

Limestone bedrock underlying open embayments, such as El Cajon Bay, along the shores of northern Lake Huron (Fig. 13.5e), supports development of highly minerotrophic fens with thin organic soils and marl flats. Standing water may contain lawns of stonewort and sparse stands of hardstem bulrush, but slightly higher elevations support plants such walking sedge *(Eleocharis rostellata),* Indian paintbrush *(Castilleja coccinea),* Kalm's lobelia *(Lobelia kalmii),* grass-of-Parnassus *(Parnassia glauca),* and insectivorous butterwort *(Pinguicula vulgaris),* pitcherplant, and sundews. Characteristic shrubs are sweet gale and shrubby cinquefoil *(Potentilla fruticosa);* common trees are northern white cedar and tamarack *(Larix laricina)* (Albert 2003).

Saginaw Bay, on Lake Huron, is an open lacustrine wetland (Fig. 13.5f). Seiches with an amplitude of 10–20 cm are routine, and they can be greater following storm events. The very gradual slope of the wetland basin thus allows seiches to flood and dewater large areas of wetland, affecting seed germination and the extent of submersed vegetation (Wilcox and Nichols 2008). The southern portion of Saginaw Bay is characterized by a 200- to 300-m-wide band of emergent marsh along much of its perimeter. Lakeward from the marsh and interspersed within it are submersed plants such as stonewort, naiads, common watermilfoil, water star-grass *(Heteranthera dubia),* and wild celery. The emergents are dominated by three-square bulrush *(Schoenoplectus pungens)* and softstem bulrush *(S. tabernaemontani),* with invading cattails and, more recently, common reed (Wilcox and Nichols 2008).

FIG. 13.5. Map of the Great Lakes showing locations of wetlands for which plant and animal communities are described. a. Bark Bay, Lake Superior. b. Kakagon River, Lake Superior. c. St. Marys River. d. Duck Bay, Lake Huron. e. El Cajon Bay, Lake Huron. f. Saginaw Bay, Lake Huron. g. Arcadia Lake, Lake Michigan. h. Dickinson Island, St. Clair River. i. Metzger Marsh, Lake Erie. j. South Colwell Pond, Lake Ontario. k. Kents Creek, Lake Ontario.

Arcadia Lake contains a drowned river mouth wetland in which three tributary creeks coalesce and enter a small lake formed in the now-flooded river valley before exiting to Lake Michigan along its eastern shore (Fig. 13.5g). Much of the wetland is dominated by a sedge/grass meadow plant community composed of Canada bluejoint grass and tussock sedge, with jewelweed *(Asclepias incarnata),* marsh bellflower, and invading reed canarygrass *(Phalaris arundinacea)* also prominent. A short emergent community occurs along the water's edge that contains arrowhead, softstem bulrush, bur-reed, rice cutgrass *(Leersia oryzoides),* spike-rushes, and several sedges. The aquatic zone contains bullhead pond lily, pondweeds, waterweed, and other submersed aquatic plants. Unsuccessful attempts to ditch and drain the wetland allowed some of the emergent wetland to be invaded by narrow-leaf cattail *(Typha angustifolia).*

Dickinson Island is a riverine delta wetland that is part of the St. Clair River delta, which formed where the river flows into Lake St. Clair (Fig. 13.5h). Topographic relief varies across the island, with beaches, beach ridges, natural levees, and shallow swales and pools (Jaworski, Raphael, et al. 1979). Dominant plants include buttonbush *(Cephalanthus occidentalis),* Canada rush *(Juncus canadensis),* rice cutgrass, Canadian St. John's wort *(Triadenum fraseri),* bur-reed, pickerelweed, common arrowhead, stonewort, white water lily, pondweeds, and sedges. Common reed is a more recent invader (Albert 2003; unpublished data).

Metzger Marsh formed as a barrier-beach lagoon wetland in western Lake Erie (Fig. 13.5i), but the protective barrier was lost to erosion during a high lake-level period in the 1970s (Kowalski and Wilcox 1999; Wilcox and Whillans 1999). A dike was constructed in the 1990s to mimic the protective function of a barrier beach, with inclusion of a water-control structure to maintain hydrologic connection to the lake. Large areas of submersed vegetation are dominated by coontail, waterweed, Eurasian watermilfoil *(Myriophyllum spicatum),* and naiads. Emergent vegetation has changed periodically since the 1990s and is now dominated by areas of cattail, arrowhead, softstem bulrush, and invasive common reed, flowering rush *(Butomus umbellatus),* and reed canarygrass. American lotus *(Nelumbo lutea),* which begins as a floating-leaf plant but matures as an emergent, is also very prevalent (Kowalski and Wilcox 2002).

South Colwell Pond is a barrier-beach lagoon wetland on the eastern shore of Lake Ontario (Fig. 13.5j). The native plant community of much of the wetland was meadow marsh dominated by Canada bluejoint grass, with jewelweed, sensitive fern *(Onoclea sensibilis),* spinulose woodfern *(Dryopteris carthusiana),* and shrubs such as red-osier dogwood *(Cornus sericea).* Following regulation of Lake Ontario water levels when the St. Lawrence Seaway began operation in 1960, the narrow emergent marsh along the edge of the lagoon expanded, with domination by hybrid *(Typha × glauca)* and narrow-leaf cattail, but also containing bur-reed, arrowhead, and European frogbit *(Hydrocharis morsus-ranae).* The adjacent aquatic zone contains emergent northern wild rice and pickerelweed, submersed vegetation such as coontail, bladderwort (*Utricularia* spp.), nodding waternymph *(Najas flexilis),* and stonewort, and floating white water lily, bullhead pond lily, and duckweeds (*Lemna* spp.). The meadow marsh at higher elevations has been invaded by hybrid cattail, along with reed canarygrass and multiflora rose *(Rosa multiflora)* (Wilcox, Ingram, et al. 2005; Wilcox, Kowalski, et al. 2008).

Kents Creek is a drowned river mouth wetland in northeastern Lake Ontario near the outlet into the St. Lawrence River (Fig. 13.5k). The native sedge/grass–dominated meadow marsh contains Canada bluejoint grass, tussock sedge, forbs such as jewelweed, and shrubs such as red-osier dogwood. Following regulation of Lake Ontario water levels, the emergent marsh along the creek's edge expanded both landward and toward the water. Narrow-leaf cattail now dominates the lower-elevation emergent zone, with European frogbit floating among the stems. The adjacent aquatic zone contains submersed vegetation such as pondweeds, coontail, wild celery, and stonewort, as well as floating white water lilies. The meadow marsh at higher elevations has been invaded by hybrid cattail, along with reed canarygrass (Wilcox, Ingram, et al. 2005; Wilcox, Kowalski, et al. 2008).

Animal Communities

Great Lakes wetlands also provide valuable habitat for fish and wildlife (Wilcox 1995; Environment Canada 2002). Many invertebrates are closely associated with macrophyte beds; waterfowl, aquatic mammals, and small fish are attracted to these areas because they provide food and shelter. When water levels change, habitats and biotic interactions change as well. Flooding of emergent plant communities allows access for spawning fish, reduces mink *(Mustela vison)* predation on muskrats *(Ondatra zibethicus),* and increases the interspersion of vegetated and open-water areas preferred by waterfowl. Flooded, detrital plant materials are also colonized by invertebrates that are consumed by waterfowl. Low water levels can jeopardize fish spawning and reduce waterfowl nesting areas; yet they provide the opportunity for regeneration of the plant communities that are the foundation of the habitat.

Fish

Fish use Great Lakes wetlands for spawning, rearing, and adult feeding habitat. Some species, such as northern pike *(Esox lucius),* deposit their eggs in early spring in flooded grasses, thus taking advantage of warmer shallow-water temperatures and the higher dissolved oxygen concentrations required for egg respiration. Other species, such as largemouth bass *(Micropterus salmoides),* spawn in late spring or early summer. The male remains with the eggs while fanning them to increase oxygen availability and guarding both eggs and juveniles from predators. Many young-of-year fish remain in wetlands, taking advantage of the protective cover of the vegetation and feeding on plentiful invertebrates. Some adult fish use wetlands seasonally but abandon them when warm water and decomposing vegetation reduce dissolved oxygen levels. Others, such as bowfin *(Amia calva),* are more tolerant and remain in the wetlands throughout the summer (Environment Canada 2002).

Fish common to Bark Bay in Lake Superior (Fig. 13.5a) include rock bass *(Ambloplites rupestris),* black bullhead *(Ameirus melas),* northern pike, and spottail shiner *(Notropis hudsonius),* as well as mottled sculpin *(Cottus bairdi)* and central mudminnow *(Umbra limi)* (Wilcox, Meeker, et al. 2002; unpublished data). The emergent bulrush marshes of Saginaw Bay (Fig. 13.5f) support many alewife *(Alosa pseudoharengus)* (young-of-year), pumpkinseed *(Lepomis gibbosus),* white bass *(Morone chrysops),* yellow perch *(Perca flavescens),* blacknose shiner *(Notropis heterolepis),* and largemouth bass, as well as longnose gar *(Lepisosteus osseus),* spottail shiner, and other species (Wilcox, Meeker, et al. 2002; unpublished data). Prominent fish in the Arcadia Lake drowned river mouth wetland (Fig. 13.5g) are largemouth bass, pumpkinseed, rockbass, brown bullhead, yellow bullhead *(Ameiurus natalis),* yellow perch, and common carp *(Cyprinus carpio)* (Wilcox, Meeker, et al. 2002; unpublished data). Abundant fish species in Metzger Marsh of western Lake Erie (Fig. 13.5i) include gizzard shad *(Dorosoma cepedianum),* bluegill *(Lepomis macrochirus),* pumpkinseed, largemouth bass, common carp, and white bass; other prominent species are spottail shiner, emerald shiner *(Notropis atherinoides),* goldfish *(Carassius auratus),* and white perch *(Morone americana)* (Wells, McClain, et al. 2000; Johnson, Braig, et al. 2004). Kents Creek and adjacent Mud Bay in Lake Ontario (Fig. 13.5k) support golden shiner *(Notemigonus crysoleucas),* yellow perch, pumpkinseed, largemouth bass, black crappie *(Pomoxis nigromaculatus),* and banded killifish *(Fundulus diaphanous),* as well as spotfin shiner *(Cyprinella spiloptera),* rockbass, brown bullhead *(Ameiurus nebulosus),* round goby *(Neogobius melanostomus),* and northern pike (J. Farrell pers. comm.). Other fish species found in Great Lakes wetlands include shortnose gar *(Lepisosteus platostomus),* muskellunge *(Esox masquinongy),* walleye *(Sander vitreus),* smallmouth bass *(Micropterus dolomieu),* logperch *(Percina caprodes),* trout-perch *(Percopsis omiscomaycus),* johnny darter *(Etheostoma nigrum),* ninespine stickleback *(Pungitius pungitius),* fivespine stickleback *(Culaea inconstans),* threespine stickleback *(Gasterosteus aculeatus),* channel catfish *(Ictalurus punctatus),* tadpole madtom *(Noturus gyrinus),* brindled madtom *(N. miurus),* white sucker *(Catostomus commersonii),* shorthead redhorse *(Moxostoma macrolepidotum),* quillback *(Carpiodes cyprinus),* fathead minnow *(Pimephales promelas),* bluntnose minnow *(P. notatus),* common shiner *(Luxilus cornutus),* and rainbow smelt *(Osmerus mordax)* (Goodyear, Edsall, et al. 1982; Jude and Pappas 1992; Wilcox 1995; Uzarski, Burton, et al. 2005; Seilheimer and Chow-Fraser 2007).

Other Animals

Invertebrates in Great Lakes wetlands range from microinvertebrates commonly termed zooplankton to macroinvertebrates such as insects, clams, and crayfish. Wetland invertebrates provide an important food source for fish and wildlife, both in aquatic habitats and, if emerging from larval life stages, on land or in the air. The large numbers of invertebrate taxa and difficulty in identifying many of them often result in broad taxonomic classifications. Published lists of taxa are available in Burton and Uzarski (2009).

Amphibians depend on the mix of land and water provided by wetlands, feeding on insects that emerge en masse from aquatic larval forms to flying adults. The amphibians, in turn, provide important food for wading birds and fish. Wetlands also provide habitat and food for many reptiles, and these turtles and snakes are important predators in the wetland ecosystem (Environment Canada 2002). Published lists of taxa are found in Maynard and Wilcox (1997), Hecnar (2004), Price, Howe, et al. (2007), and Burton and Uzarski (2009).

Just as Great Lakes wetlands vary in vegetation, invertebrate assemblages, and physical conditions, so too do these habitats vary in bird community composition. During spring and fall migration, coastal wetlands provide critical habitat for literally millions of birds as they forage along shorelines, marshes, and swamps (Diehl, Larkin, et al. 2003; www.jstor.org/stable/4090180). During winter, on the other hand, Great Lakes coastal wetlands can be nearly devoid of birds, especially at northern latitudes. More than 150 bird species are known to use Great Lakes coastal wetlands during the breeding season, the majority breeding or feeding extensively within wetland habitats (Howe, Regal, et al. 2007). Published lists of taxa are available in Maynard and Wilcox (1997), Hanowski, Danz, et al. (2007), Howe, Regal, et al. (2007), and Miller, Niemi, et al. (2007).

Muskrat and beaver *(Castor canadensis)* are keystone mammals in Great Lakes wetlands. Muskrats cut emergent wetland plants (especially cattails) for food and to build lodges, thus opening the canopy and enhancing habitat for many bird species. The lodges also serve as nesting habitat for some bird species. Beaver act on a grander scale by cutting woody vegetation for food and to build lodges and dams. The dams may alter water levels in some drowned river mouth wetlands. Many other mammals reside in Great Lakes wetlands or include them within their larger habitat. Published lists of taxa are available in Maynard and Wilcox (1997) and Burton and Uzarski (2009).

Key Ecological Processes

Coastal wetlands of the Great Lakes are, by nature, stress-controlled systems. An understanding of human-induced stresses to these wetlands requires an initial understanding of natural stresses.

Water-Level Change

The major stressor and key ecological process affecting Great Lakes wetlands is water-level change, which is caused by a combination of seasonal and longer-term weather conditions and climate changes. Water-level fluctuations are the primary driver affecting wetland vegetation, as even small changes in lake level can shift large areas from flooded to exposed conditions and vice versa. Individual plant species and communities of species have affinities and physiological adaptations for certain water-depth ranges and durations, and their life forms may show adaptations for different water-depth environments. Changes in water level add a dynamic aspect to the species-depth relationship and result in shifting mosaics of wetland vegetation types. In general, high water levels kill trees, shrubs, and other emergent vegetation, and low water levels following these highs result in seed germination and growth of a multitude of species (Keddy and Reznicek 1986; Maynard and Wilcox 1997) (Fig. 13.6). Some species are particularly well suited to recolonizing exposed areas during low water phases, and several emergents may coexist there because of their diverse responses to natural disturbance.

In the first year following a reduction in water levels, the distribution of new seedlings is due to the distribution of seeds in the sediments. In ensuing years, the distribution of mature plants is due to seedling survival dictated by competitive interactions and changes in abiotic conditions (Welling, Pederson, et al. 1988; Seabloom, van der Valk, et al. 1998; Seabloom, Maloney, et al. 2001; Keddy 2000). If one species is favored in early colonization, its density may be great enough that it can maintain dominance of an area. In most cases, early-colonizing species or communities are later lost through competitive displacement, but the opportunity to go through a life cycle allowed them to replenish the seed bank in the sediments (van der Valk and Davis 1978; Keddy and Reznicek 1982). Occasional low water levels are also needed to restrict growth of plants that require very wet conditions.

The magnitude of water-level fluctuations is of obvious importance to wetland vegetation because it directly results in different water-depth environments (Environment Canada 2002). The different plant communities that develop in a Great Lakes wetland shift from one location to another in response to changes in water depth. Flooding/dewatering history largely determines the species composition of a particular site at a given point in time, with resultant zonation patterns sometimes becoming obvious (Environment Canada 2002; Wilcox and Nichols 2008) (Fig. 13.7).

In general, elevations that have not been flooded for many years are dominated by shrubs, grasses, and old-field plants. If flooding has been more recent, small shrubs may be present, as well as grasses, sedges, and forbs (Keddy and Reznicek 1986). Elevations that are flooded periodically, each 10 to 20 years, and dewatered for successive years between floods have the greatest diversity of wetland vegetation. These plant communities contain the most wetland taxa and the highest diversity of plant structural types. Dominants include grasses, sedges, forbs, rushes, short emergent plants, and submersed aquatic vegetation. At elevations that are rarely or never dewatered, submersed and floating plants are dominant, with emergent plants also occurring at some sites (Keddy and Reznicek 1986; Maynard and Wilcox 1997; Environment Canada 2002).

The frequency, timing, and duration of water-level fluctuations are important for several reasons. Effects of seiches are poorly understood, although they can affect zonation of plant communities by keeping soils wet and limiting germination from the seed bank. Seasonal differences in the timing of water-level declines are important, especially in the Great Lakes, where peak water levels occur in the summer and lows occur in the winter (the reverse of the changes in most inland wetlands). An early summer peak and the subsequent beginning of water-level decline allow more plants to grow from the seed bank than a later peak. Water-level declines in winter can result in ice-induced sediment erosion. Consistent annual fluctuations during the growing season favor the species that are most competitive under those conditions, while variable summer water levels produce changing environmental conditions and result in variability in the vegetation (Wilcox, Thompson, et al. 2007).

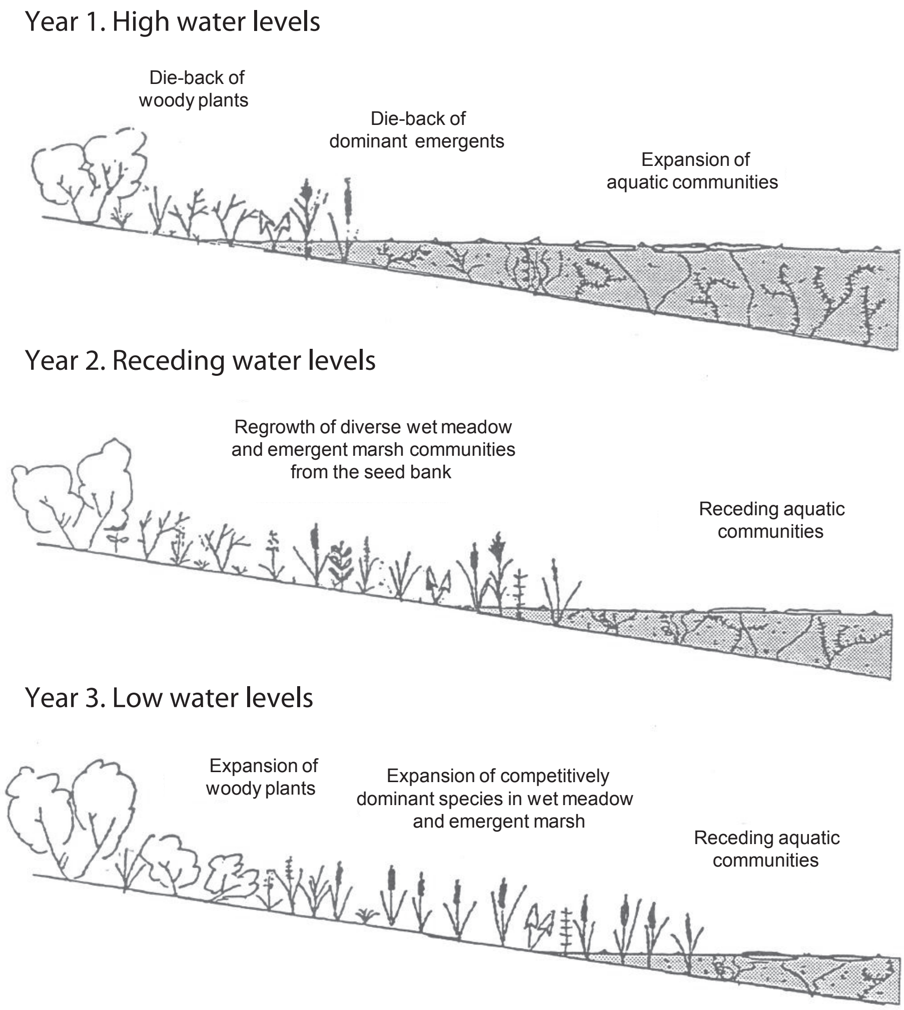


FIG. 13.6. Simplified diagram of the effects of water-level fluctuations on Great Lakes coastal wetland plant communities. (From Maynard and Wilcox 1997.)

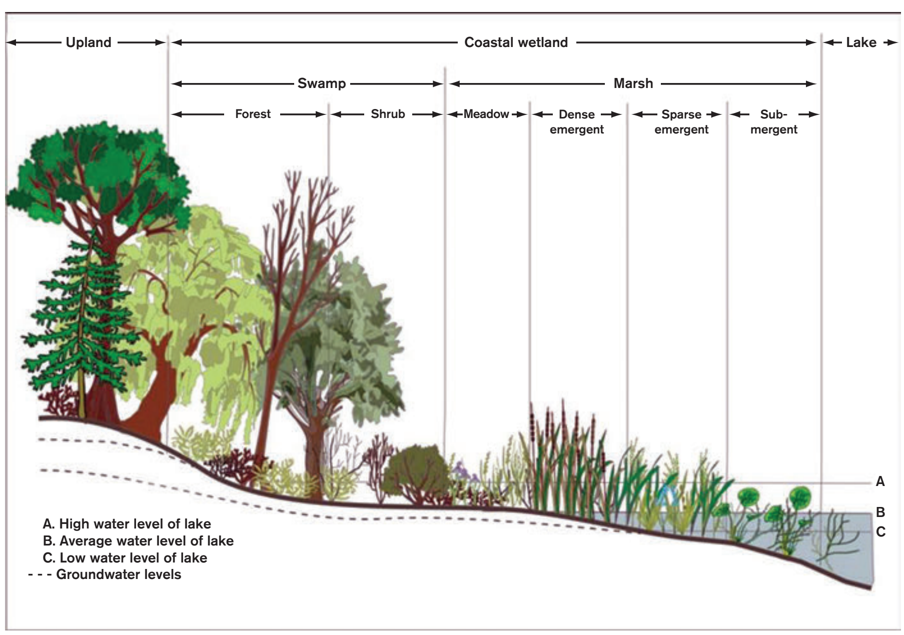


FIG. 13.7. Profile of a typical Great Lakes coastal marsh from lake to upland showing changes in plant communities related to lake-level history. (From Environment Canada 2002.)

Successional processes often occur in plant communities. However, the hydrologic variability of the Great Lakes does not allow succession to proceed for long in most geomorphic settings. The ridge and swale terrains in many large embayments of the Great Lakes contain sequences of wetlands of similar origin but different ages that can be several thousand years old, with older wetlands always farther from the lake. These settings suggest an opportunity for successional processes. Analyses of plant communities across a sequence of wetlands at the south end of Lake Michigan showed an apparent successional pattern from submersed to floating to emergent plants as water depth decreased with wetland age. However, paleoecological analyses showed that the observed vegetation changes were driven largely by disturbances associated with increased human settlement in the area. Climate-induced hydrologic changes were also shown to have greater effects on plant-community change than autogenic, or self-driven, processes (Wilcox and Simonin 1987; Jackson, Futyma, et al. 1988; Wilcox 2004).

Sediment Supply and Transfer

Another key ecological process affecting Great Lakes coastal wetlands is the constant change in the location and movement of sediments. These sediments can form barrier beaches and sand spits that protect wetlands; their erosion can expose wetlands to wave attack. If deposited onto existing wetlands, they can bury wetland plant communities. Coastal processes are greatly affected by lake-level changes, both through net erosion and net deposition of sediments at specific wetland sites and through changes in sediment transport mechanisms. Waves from storms that occur during periods of high lake levels can erode materials not accessible at low stages and increase the load of sediment transported in the littoral drift. At low lake levels, sediments are exposed to transport by wind. These processes also serve to determine and perhaps change the exposure of a wetland to the forces of the open lake (Maynard and Wilcox 1997).

Ice and Storms

Great Lakes wetlands are also affected by ice and storms, both of which are affected by lake-level changes. Ice formed before water levels decline in winter can come to rest on bare sediments and freeze them, thus affecting the survival and dominance of plants at those sites (Renman 1989; Wilcox and Meeker 1991). Frozen sediments can be dislodged and float away with the ice pack in spring (Geis 1985). Large ice packs washing onto the shore during storms can also gouge away sediments. Large waves associated with storms not only erode sediments, but also can physically destroy vegetation in exposed wetlands (Maynard and Wilcox 1997).

Biological Stressors

Natural stressors of Great Lakes wetlands include certain native plants and animals. Invasive emergent plants such as cattails can stress wetlands by forming monotypic stands that greatly reduce wetland diversity. However, the most invasive species are hybrid and narrow-leaf cattail, which may or may not be native. Muskrats can substantially alter wetland habitat by cutting emergent vegetation, such as cattails and bulrushes, for food and shelter. The unvegetated pools around lodges, formed by cutting activity, create open areas within the wetland. When muskrat populations are high, extensive areas of emergent vegetation may be cut. Beavers also use wetlands of the Great Lakes in some locations and have similar habitat-altering effects. Diseases of both plants and animals are natural phenomena that also stress wetland communities (Maynard and Wilcox 1997).

Conservation Concerns

Large areas of Great Lakes wetlands have been converted to other uses, most notably in the lake plains of western Lake Erie and Saginaw Bay, where ditches and dikes were constructed to drain wetlands for agricultural and urban use. Other alterations include filling, excavating, clearing vegetation, and introduction of nutrients and toxic chemicals. Despite stricter regulations, wetlands continue to be lost, degraded, and altered by human activities. Some alterations are temporary; others may be permanent.

Water-Level Regulation

High water levels create problems for lakeshore property owners and industries with structures built in the flood hazard zone. Low water levels create problems for the shipping, hydropower, and recreational boating industries (Gauthier and Donahue 1999). Regulation of water levels on lakes Superior and Ontario at their outlets seeks to reduce the occurrence of both high and low lake levels. Regulation of water levels creates problems for wetlands; it is a human-induced stressor. It reduces the diversity of wetland plant communities and alters habitat values for wetland fauna.

Water levels on Lake Superior have been regulated for much of the 20th century. The range of fluctuations and the cyclic nature of high and low lake levels have not been altered substantially (Wilcox and Meeker 1995; Wilcox, Thompson, et al. 2007), although periods of low lake levels seem to have been eliminated (Fig. 13.2). Over 275 plant taxa were recorded in a sampling of 18 wetlands along the U.S. shoreline, and 78% of them were obligate or facultative wetland species (Wilcox, Meeker, et al. 1992). Most upland plant species were found at elevations that had not been flooded for four or more years. These invading upland plants composed about one-third of the total number of taxa at those elevations, and many of them were found only at a certain elevation with a specific water-level history. Vegetation mapping from aerial photographs showed the most prevalent vegetation types in the Lake Superior wetlands to be those dominated by submersed aquatic vegetation that had not been affected by low lake levels or shrubs that had not been affected by extremely high lake levels. Both vegetation types were present in all sites and averaged about 25% of the cover. Vegetation types dominated by cattails (or other taxa plus cattails) occurred in about half the sites but averaged only about 6% of the cover. Across all sites, 27 different vegetation types were mapped.

Water levels on Lake Ontario have been regulated since the St. Lawrence Seaway began operation. Prior to regulation, the range of fluctuations during the 20th century was about 2 m. Following initiation of regulation, the range was reduced slightly during the period between 1960 and 1976, but low water-supply conditions in the mid-1960s and high supplies in the mid-1970s maintained much of the range. Regulation reduced the range to about 1.3 m in the years following 1973 (Wilcox, Thompson, et al. 2007) (Fig. 13.2). The lack of alternating flooded and dewatered conditions at the upper and lower edges of the wetlands, especially the lack of low lake levels, resulted in establishment of extensive stands of cattail at the expense of other plant community types, especially the sedge/grass community (Wilcox, Kowalski, et al. 2008). In a preliminary study of the effects of regulation on Lake Ontario wetlands (Wilcox, Meeker, et al. 1992), more than 250 taxa were recorded in sampling of 17 wetlands along the U.S. shoreline; however, only 58% were obligate or facultative wetland plants. Most of the upland species were found at elevations that had not been flooded for 15 to 38 years, and they composed over half of the total number of taxa at those elevations. Of the 54 taxa found only at the elevation not flooded for 38 years, 45 were upland plants, again demonstrating the role of water-level history as a critical plant habitat characteristic in the coastal zone of the Great Lakes.

An extensive follow-up study of Lake Ontario water-level regulation at 32 U.S. and Canadian wetlands tied plant community type to lake-level history and lake-level regulation (Wilcox, Ingram, et al. 2005; Wilcox, Kowalski, et al. 2008; Wilcox and Xie 2007, 2008). Portions of wetlands at elevations that had not been flooded for 5 or more years were dominated by sedges and grasses, with shrubs invading. Elevations that had not been dewatered for 4–38 years were dominated by cattails. The intervening elevations that were intermittently flooded and dewatered over a 5-year span contained a combination of sedges, grasses, cattails, and other emergent species. Plant communities that had not been dewatered in the growing season for many years were dominated by floating and submersed species.

Photointerpretation studies used photographs from the 16 sites in the U.S. (4 each from drowned river mouth, barrier beach, open embayment, and protected embayment wetlands) and spanned a period from the 1950s to 2001 at roughly decadal intervals (Wilcox, Kowalski, et al. 2008). Sedge/grass meadow was the most prominent vegetation type in most wetlands in the late 1950s, when water levels had declined following high lake levels in the early 1950s (Fig. 13.2). Sedge/grass meadow marsh increased at some sites in the mid-1960s in response to low lake levels and decreased at all sites in the late 1970s following a period of high lake levels. Cattail increased at nearly all sites, except wave-exposed open embayments, in the 1970s. Sedge/grass meadow continued to decrease and cattail to increase at most sites during sustained higher lake levels through the 1980s, 1990s, and into 2001 (Fig. 13.2). Site-by-site analyses showed that most vegetation changes could be correlated with lake-level changes and with life-history strategies and physiological tolerances to water depth of prominent taxa. Much of the cattail invasion, largely by hybrid cattail, was landward into meadow marsh. Lesser expansion toward open water included both narrow-leaf and hybrid cattail. The results suggested that canopy-dominating, moisture-requiring cattail was able to invade meadow marsh at higher elevations because sustained higher lake levels following regulation allowed it to survive and overtake sedges and grasses that can tolerate periods of drier soil conditions.

In addition to having adverse effects on wetland plant communities, reduction of water-level fluctuations can affect wetland animal communities. High water levels (i.e., levels above the historical long-term mean) increase fish access to spawning and nursery habitat in emergent vegetation, and flooded detrital plant materials are also colonized by invertebrates that are fed upon by fish and waterfowl. Structural complexity of vegetation resulting from water-level fluctuations creates more diverse habitat for a variety of waterbirds. Although low water levels can jeopardize fish spawning and reduce waterfowl nesting areas, they provide the opportunity for regeneration of the plant communities that are the foundation of the habitat.

Shoreline Modification

A common response to the threat of flooding and erosion along the shoreline of the Great Lakes is to construct revetments or breakwalls along the shore, which can affect wetlands. By reducing erosion, these structures also reduce the supply of sediments that naturally nourishes the shoreline and replaces eroded sediments. Barrier-beach wetlands may thus lose the protection of a barrier beach. Hard shoreline structures also shift wave energy farther downshore and may locally accelerate erosion of beaches and wetlands elsewhere. When revetments are constructed along the gently sloping shore of a wetland, a "backstopping" effect can result. Wave energy can scour sediments from in front of the revetment, leaving an abrupt boundary between upland and deep water and no migrating, sloping shoreline with the required water depths for various wetland plant communities (Maynard and Wilcox 1997). In response to low lake levels, common actions that modify the shoreline include dredging of marinas and recreational boating access channels (Uzarski, Burton, et al. 2009).

Dike Construction

Although diking of wetlands is considered a solution to management problems when protection from water-level change and wave action is required, dikes also create problems for wetlands along the Great Lakes shoreline (Wilcox and Whillans 1999). Isolation from lake waters and the surrounding landscape results in elimination or reduction of many of the values of wetlands, including flood conveyance, sediment control, and improvement of water quality. Habitat for waterfowl and certain other animals may be improved by diking, but shorebirds and many less common plants and animals lose the habitat provided by a continually changing boundary between land and water. In addition, fish and invertebrates not capable of overland travel do not have access to diked marshes and lose valuable habitat. Fish larvae pumped into diked wetlands during filling operations cannot leave and are thus lost to the lake population. Trapped common carp remain in diked wetlands through adulthood and cause management problems by uprooting vegetation and increasing turbidity (Maynard and Wilcox 1997).

Road Construction

Coastal wetlands of the Great Lakes occupy the shoreline, which also serves as a transportation corridor connecting coastal cities and providing access for owners of private land along the coast. Roadways following the shoreline and crossing wetlands serve as stressors on wetlands (Maynard and Wilcox

1997). A substantial percentage of the drowned river mouth wetlands on all the lakes are crossed by roadways, which alter natural hydrology. The often broad, multichanneled river is constricted to pass under a narrow bridge placed along a roadbed causeway, partially damming the river and wetland. Floodwaters slowed by the causeway dam and narrowed outlet deposit excessive sediments in the wetlands and raise the elevation of the substrate. This allows invasion of plant species that would otherwise not tolerate the hydrologic regime of the wetland. Water-level changes due to seiches are also dampened by the reduced connection with the lake. Barrier beaches are commonly used for roadbeds, with similar hydrologic impacts to wetlands behind them and added alteration of the coastal processes that create and maintain them. In addition, roadways can contaminate wetlands with by-products of combustion and with road salt in winter.

Other Physical Alterations

Large-scale physical alteration and destruction have been the greatest sources of wetland loss in the Great Lakes. While the conversion of wetlands to agricultural, urban, and industrial uses has decreased, it has not ended. Filling of nearshore lake waters for urban development continues at a decreased rate. Dredging and channelizing for boat harbors continue in many river mouths, representing a loss of significant wetland habitat (Limno-Tech 1993). Development of shoreline for recreation and residential uses continues seemingly unchecked, and likely affects adjacent wetlands. Dams constructed on tributary rivers trap sediment that may be necessary to maintain wetlands at the river mouth. Conversely, deforestation for agriculture and timber production has increased sediment loading in other streams and rivers flowing into wetlands, adding pollutants, reducing photosynthesis, reducing dissolved oxygen concentrations, and affecting the survival rates of invertebrate and fish eggs. Increased turbidity caused by sediments in suspension may also seriously interfere with the food-finding activities of many valuable predator fish. Water temperatures can increase as a result of removal of shade from streamside vegetation. The narrow temperature requirements of many fish are relatively well documented. Increased temperature fluctuations have restricted the habitat of fish species (Dodge and Kavetsky 1995; Maynard and Wilcox 1997).

Water Quality

Pollutants, turbidity, and increased water temperatures, along with increased nutrient concentrations, can decrease wetland water quality. Wetlands may be stressed by enrichment of nutrients from agricultural runoff (Trebitz, Brazner, et al. 2007) and also from residential runoff and sewage discharges. Wetland and aquatic plants can obtain nutrients from both sediments and the water column; the predominant source of nutrient uptake is generally species specific. Therefore, the trophic status of the water in a wetland has obvious importance in determining productivity and species composition (Wisheu, Keddy, et al. 1990). Plant communities in nutrient-enriched wetlands may differ from those in other areas. The growth of some plant species is enhanced by nutrient enrichment; other plants, adapted to low-nutrient environments, can be displaced by species better adapted to greater nutrient concentrations. In addition, nutrient enrichment may cause excessive algal blooms that can reduce light available to macrophytes for photosynthesis. Excessive growth of macrophytes or algae can also result in depletion of dissolved oxygen when these plants die and decay; this is especially critical in shallow basins with little mixing, such as barrier-beach wetlands (Maynard and Wilcox 1997). Oxygen depletion can also be caused by discharge of organic wastes into wetlands.

Toxic chemicals can also stress wetland biological systems, especially animal communities. Through the processes of biomagnification and bioaccumulation, the impact of toxic chemicals has been greatest on animal species at the top of the food web, such as predatory birds, fish, and mammals (Wren 1991; Hoffman, Smith, et al. 1993). The highest concentrations of these chemicals have been observed in top predators in nutrient-poor systems with reduced overall productivity and few prey species. Because these systems are simple, the potential for biomagnifaction is greater. Animal health and reproduction can also be affected by contaminants. Contaminated sediments may be toxic to fish eggs. Thinning of eggshells and deformities are well documented among fish-eating birds of the Great Lakes (Hoffman, Smith, et al. 1993). Although levels of banned DDT, PCBs, and their metabolites will likely continue to decline, the effect of the continuing discharge of other persistent toxic chemicals on the quality of the chemical regime of habitats is not well understood.

Long-term effects of toxic chemicals on plants and herbivores are also not well understood. Herbicides (e.g., Atrazine) from cropland may be interfering with aquatic plant growth. Herbicides are present in the wetlands and bays of Lake Erie at levels high enough to alter planktonic species composition and inhibit photosynthesis of algal and rooted plant communities (Dodge and Kavetsky 1995). Increased salinity caused by road salt runoff can alter algal and macrophyte communities of wetlands, as well as animal communities.

Other water-quality alterations that can stress wetlands are temperature and turbidity (Trebitz, Brazner, et al. 2007). Temperature differs most between protected wetlands (e.g., behind barrier beaches) and those with greater mixing of lake water. Water temperature may affect the length of the growing season and thus productivity. In some cases, such as shallow barrier-beach wetlands with dark sediments, extremely high water temperatures may inhibit plant growth, exceed the tolerance limit of invertebrates and fish, and result in oxygen depletion. In wetlands with a strong discharge of groundwater, low water temperatures may limit productivity and species tolerance. High turbidity reduces the availability of light to submersed plants and can limit growth. It can also limit feeding activity by sight-feeding fish such as northern pike. Turbidity can be affected by the source of water, the type of sediment, exposure to wave attack that suspends sediments by mixing, and biological action, such as feeding activity by common carp.

Nonindigenous Species

The most serious biological stressors affecting wetlands of the Great Lakes are species not native to the area and aggressive species of uncertain origin that compete with native biota. Methods of introduction include intentional release, deposition of ship ballast, escape from cultivated or cultured populations, and migration along travel routes such as railroads, highways, and canals (which may also overcome natural physical barriers to aquatic travel). In many cases, introductions may not be successful in a healthy ecosystem. However, given the means and extent of wetland alteration in the Great Lakes, habitats and food webs have been sufficiently disturbed to allow many introduced species to thrive (Maynard and Wilcox 1997).

As many as 180 nonindigenous aquatic organisms have been documented in the Great Lakes (Mills, Leach, et al. 1993; Ricciardi 2001, 2006); many of them do not occur in wetlands or do not cause identifiable problems, but several do cause or have the potential to cause considerable problems. Examples of such plants include submersed aquatics such as Eurasian watermilfoil, curlyleaf pondweed *(Potamogeton crispus),* slender naiad *(Najas minor),* and common waterweed; floating European frogbit; and emergents such as purple loosestrife *(Lythrum salicaria),* reed canarygrass, flowering rush, and common reed (Trebitz and Taylor 2007). Although biological controls may be reducing purple loosestrife locally, common reed has been highly invasive in recent years and is difficult and costly to control.

Animal invaders that may affect Great Lakes wetlands include zebra and quagga mussels (*Dreissena* spp.), rusty crayfish *(Orconectes rusticus),* and common carp. The latter fish species has been shown to affect wetlands by reducing the diversity and biomass of macrophytes (King and Hunt 1967; Crivelli 1983). Changes in macrophyte communities may also contribute to reduced abundance of emergent insects in wetlands where common carp are abundant (McLaughlin and Harris 1990). Although common carp have been found to dominate larval fish samples from some Great Lakes marshes (Chubb and Liston 1986; Johnson 1989; Petering and Johnson 1991) and are often very abundant as adults, they cause the greatest problems in diked marshes, where they remain in residence year-round and are in greater abundance than in lake-connected wetlands (Johnson 1989). Common carp begin to enter wetlands as early in the year as February; their numbers are greatly reduced by the end of summer, and nearly all carp have returned to the lake by autumn. Common carp may cause problems in degraded coastal wetlands, but they seem to have little effect on healthy marshes. Management becomes a major concern when wetlands are diked, common carp larvae enter through screens or via pumping operations, and adult fish have no means of returning to the lake.

Climate Change

Great Lakes water levels typically increase during cool climatic periods and decrease during warm periods (Baedke and Thompson 2000) (Fig. 13.3). The expected linear response of plant communities in the short term is a reduction in emergent species in years when water levels are high and a resurgence of emergents from the seed bank when water levels are lower and expose underlying sediments (Keddy and Reznicek 1986). Over longer time periods, ranging from decades to centuries to millennia, the expected linear response is also deeper open water with few emergent species during cool, wet climate phases and shallow marsh with shoreline and mudflat species during warm, dry phases (Singer, Jackson, et al. 1996). Prolonged warm, dry phases with greater primary production by emergent species may accelerate basin infilling in protected areas not subject to wave attack (Wilcox, Shedlock, et al. 1986; Wilcox and Simonin 1987). Successional processes may accompany shallowing of the basins, leading to further vegetation changes that include the invasion of shrubs and trees, although the return of high water can reset the successional stage (van der Valk 1981; Jackson, Futyma, et al. 1988; Wilcox 2004).

Work in chronosequences of wetlands occurring in ridge and swale terrains of lakes Michigan and Superior, however, suggests that groundwater may mediate effects of climate and successional processes on plant communities in some wetlands. During warm climate phases, plant communities with sufficient groundwater supplies may be resistant to climate-related water-level reductions that drive vegetation change. Over prolonged periods with no climate-driven flooding to reset the successional stage, plant communities may develop with greater fidelity to groundwater influences than to assumed successional processes (Burkett, Wilcox, et al. 2005).

Conclusions

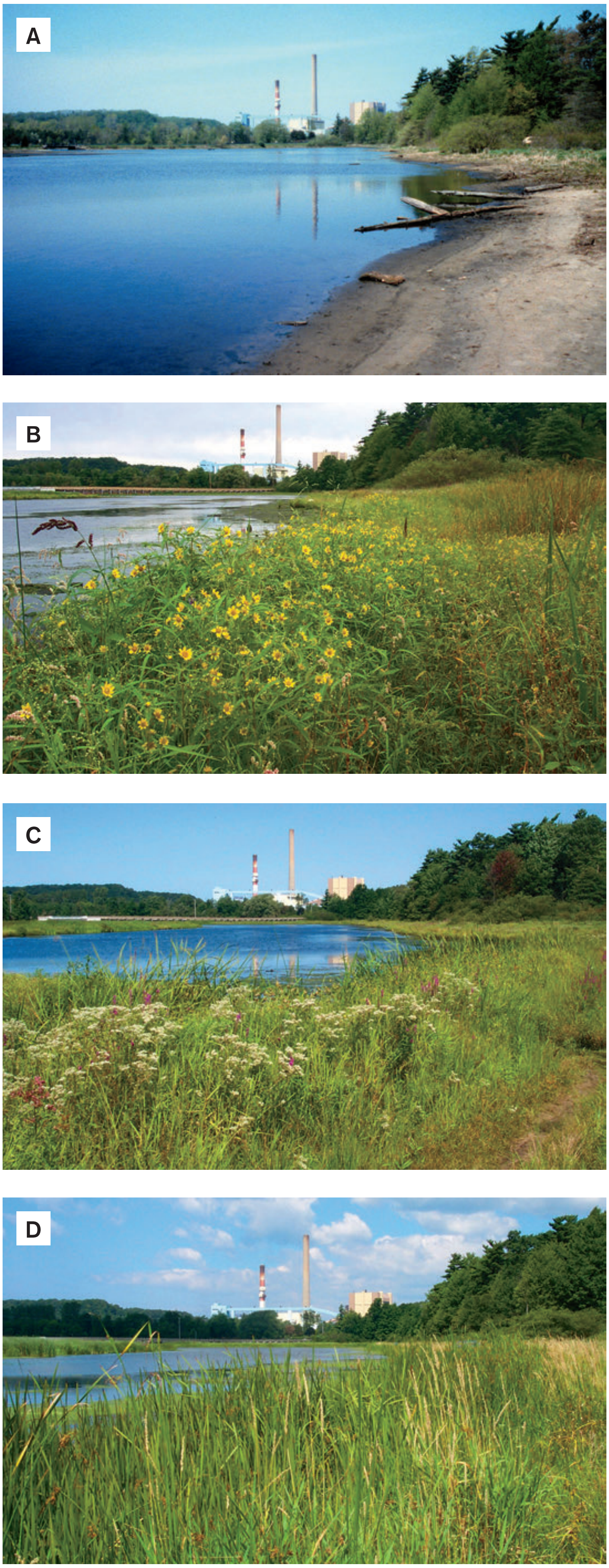
The large expanse of the Great Lakes Basin encompasses a broad geographic range with concomitant variability in underlying geology. Together, these factors result in considerable differences among wetlands across the basin. However, the lakes share many similarities in hydrology that affect wetlands, with peak annual water levels in summer and lows in winter. Prior to regulation of lakes Superior and Ontario, all lakes experienced wide fluctuations in water levels at decadal to millennial intervals in response to climatic changes. Coastal processes are also important to wetlands across all the Great Lakes; wetlands occur in similar geomorphic settings that provide varying degrees of protection from wave energy.

Wetland plant communities have many similarities among lakes, but differing geology and resultant differences in water chemistry sometimes cause stark differences in wetland type. Climatic differences related to latitude add to plant community variability. Animal communities respond both to habitat variability associated with vegetation and to physical habitat characteristics related to geology, water chemistry, and latitude-driven temperature ranges. As with plants, however, many features of animal communities are similar across lakes.

Although Great Lakes wetlands can be affected at the local level by numerous natural stressors, their broader ecological processes are driven by water-level change. Human disturbance can affect Great Lakes wetlands at the local level; however, alteration of natural water-level fluctuations through regulation affects all wetlands on a regulated lake. The relation between ecological processes and lake-level variability often overrides other processes affecting Great Lakes wetlands.

Periodic high lake levels kill invading trees, shrubs, and large, canopy-dominating emergent plants. Succeeding low lake levels expose the sediment and stimulate germination of a variety of species from the seed bank, thus increasing diversity. The open canopy provides the opportunity for these plants to grow, reproduce, and replenish the seed bank. Trees, shrubs, and canopy-dominating emergent plants also recolonize the wetland, but the next cycle of high lake levels begins the process again. Habitat diversity for many animal species is also maintained by this process. As demonstrated in Figure 13.8, lake-level variability provides periodic wetland restoration.

When water levels are regulated and the range and periodicity of fluctuations are altered, wetlands lose diversity. Invasion of Lake Ontario wetlands by cattail is a classic example (see Figure 13.9), but similar problems have been noted in regulated lakes elsewhere. The case for natural lake-level variability and wetlands must be made in relation to other interests. Although hydropower industries tend to seek full water-storage capacity



A. Drowned river-mouth wetland in Pigeon River near Port Sheldon, Michigan; photo taken in spring 1999 after Lake Michigan water levels had dropped more than 0.5 m from the previous year. Note the lack of emergent vegetation along the shore.

B. Same wetland in late summer 2000; photo shows mostly annual emergent plants along the shore that grew from the seed bank.

C. Same wetland in 2001; photo shows perennial emergent plants displacing annuals along the shore.

D. Same wetland in 2003; photo shows a shift in vegetation to a different perennial plant community.

FIGURE 13.8. Some species are particularly well suited to recolonizing exposed areas during low-water phases, and several emergents may coexist there because of their diverse responses to natural disturbance.

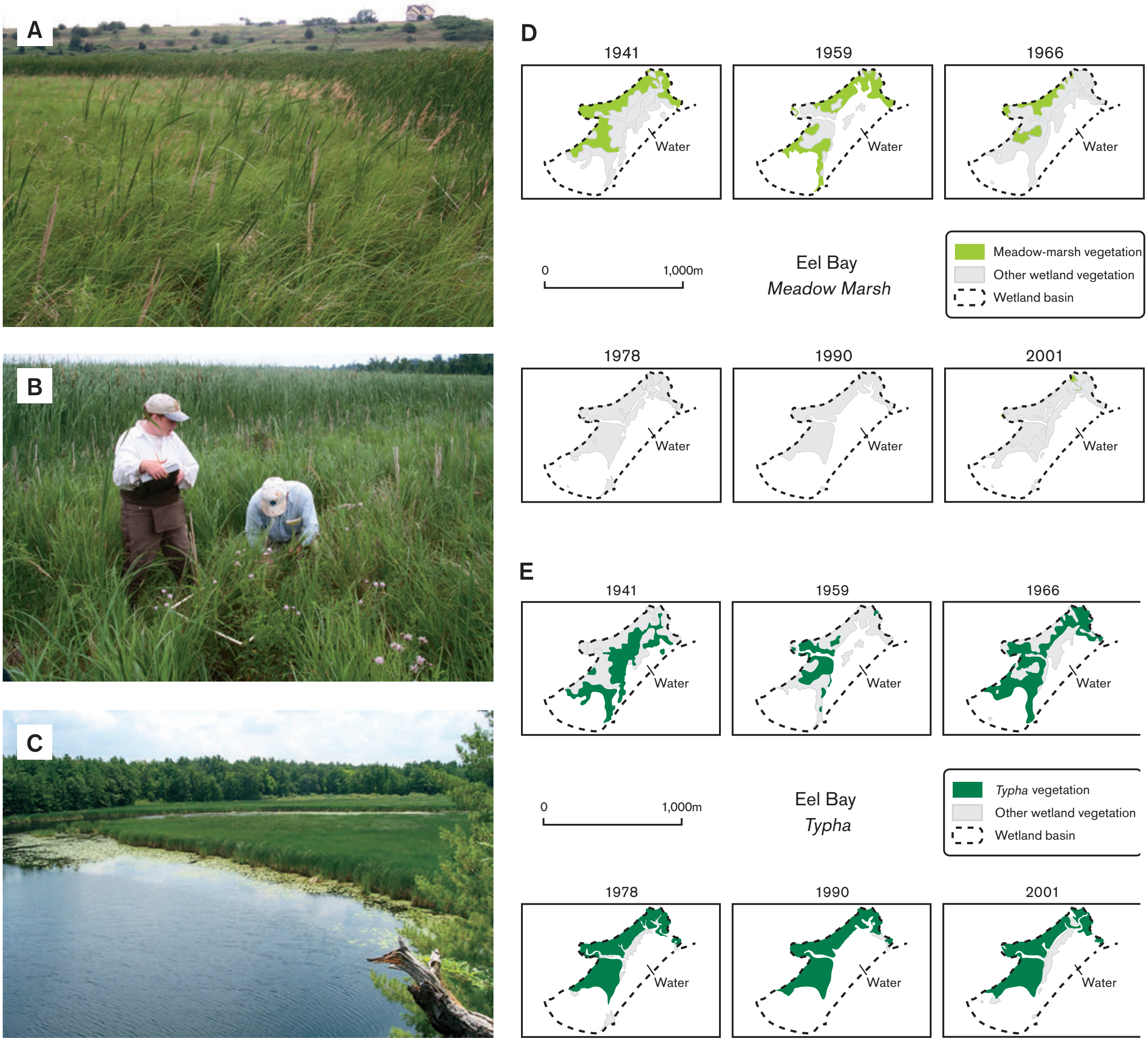


FIG. 13.9. The different plant communities that develop in a Great Lakes wetland shift from one location to another in response to changes in water depth. Illustrations redrawn by Chris Hall.

A. Meadow-marsh vegetation in a Lake Ontario wetland with invading cattails.

B. Scientists sampling vegetation in the narrow band of remaining meadow marsh in a Lake Ontario wetland.

C. Cattail domination of a Lake Ontario wetland extending from near shore to deeper water, with abrupt transition of floating and submersed plant communities.

D. Vegetation maps from Eel Bay near Alexandria Bay, New York, derived from analyses of aerial photographs taken before regulation of Lake Ontario water levels (1960) and continuing through 2001. The loss of meadow-marsh vegetation following regulation is highlighted.

E. Vegetation maps from Eel Bay highlighting the increase in cattail *(Typha)*-dominated plant communities following regulation of lake levels.

to maximize potential electricity generation, they would benefit in years with low water supplies by allowing more water to pass through the turbines instead of holding it back to create unnaturally high lake levels. The resultant lower lake levels would mimic natural conditions. Shoreline property owners tend to prefer average lake levels in all years in an effort to reduce erosion during high-water years. However, all storms then hit the shoreline at the same elevation, and erosion is accelerated. Periodic low lake levels would expose sand that could rebuild protective beaches and dunes through aeolian processes, but some shoreline property owners oppose low lake levels because they allow regeneration of wetland plants from the seed bank (Uzarski, Burton, et al. 2009).

Recreational boaters and marinas tend to prefer higher lake levels to avoid damage to boats from underwater structures, as well as high levels that extend longer into autumn to increase the length of the boating season. Those who use their boats for fishing, as well as the marinas and lakeshore communities that rely on the recreational fishing industry, could receive benefits from wetland habitat enhanced by periodic low lake levels—the foundation for the food web supporting target fish species. Environmental advocates (for wetlands in particular) seek regulation plans that allow both periodic high and low lake levels at the proper frequency to drive ecological processes. The best answer for all interests is rather straightforward: a regulation plan promoting lake levels that mimic natural amplitudes and frequencies as closely as possible while protecting all interests from damages incurred by extremely high or low lake levels.

In common with wetlands found in other geographic settings, conservation of wetlands of the Great Lakes requires protection from a variety of human disturbances at the local and landscape levels. Indeed, physical, chemical, and biological alterations have already degraded nearly all Great Lakes wetlands to varying degrees. However, the high-energy coastal setting of Great Lakes wetlands sets them apart from most inland wetlands. Conservation of Great Lakes wetlands requires maintenance of natural lake-level variability coupled with maintenance of natural shoreline processes that determine the geomorphic settings where wetlands can persist.

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