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HYDROGEOMORPHIC FACTORS AND ECOSYSTEM RESPONSES IN COASTAL WETLANDS OF THE GREAT LAKES

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Abstract: Gauging the impact of manipulative activities, such as rehabilitation or management, on wetlands requires having a notion of the unmanipulated condition as a reference. An understanding of the reference condition requires knowledge of dominant factors influencing ecosystem processes and biological communities. In this paper, we focus on natural physical factors (conditions and processes) that drive coastal wetland ecosystems of the Laurentian Great Lakes. Great Lakes coastal wetlands develop under conditions of large-lake hydrology and disturbance imposed at a hierarchy of spatial and temporal scales and contain biotic communities adapted to unstable and unpredictable conditions. Coastal wetlands are configured along a continuum of hydrogeomorphic types: open coastal wetlands, drowned river mouth and flooded delta wetlands, and protected wetlands, each developing distinct ecosystem properties and biotic communities. Hydrogeomorphic factors associated with the lake and watershed operate at a hierarchy of scales: a) local and short-term (seiches and ice action), b) watershed / lakewide / annual (seasonal water- level change), and c) larger or year-to-year and longer (regional and/or greater than one-year). Other physical factors include the unique water quality features of each lake. The aim of this paper is to provide scientists and managers with a framework for considering regional and site-specific geomorphometry and a hierarchy of physical processes in planning management and conservation projects.

Key Words: coastal wetlands, ecosystem response, geomorphology, Great Lakes, hydrology, ice, reference condition, seiche, water level, water quality

INTRODUCTION

Evaluating the consequences of ecosystem manipulation, from rehabilitation to development, must include an understanding of the local and regional setting and especially those factors that are responsible for the features of an ecosystem. In the case of wetlands, there is a general appreciation for the overriding role of physical and environmental features, especially those related to hydrology, in characterizing many ecosystem functions (Mitsch and Gosselink 1993, Wilcox 1995a). Water storage, flood amelioration, ground-water recharge, and erosion protection are functions or values that are obviously controlled by hydrology (National Research Council 1995). Patterns of biotic succession, biodiversity, condition of fish and wildlife habitat, productivity, and other ecological functions of wetlands are also strongly influenced by hydrology.

Wetland managers can more accurately gauge the impact of manipulative activities if they have a notion of the unmanipulated or "reference" condition. The concept of reference condition as a standard is imbedded in nearly every attempt to assess ecosystem condition (e.g., index of biotic integrity [IBI] (Karr et al. 1986, Karr 1991, Lyons 1992); the hydrogeomorphic method for wetland assessment (HGM) (Smith et al. 1995, Brinson 1996); and others (Loeb and Spacie 1994)) and in developing endpoints for risk assessment (USEPA 1992), although the problem of defining "reference" has led to considerable debate (Hughes 1995). The science of wetland rehabilitation is currently at the stage of attempting to measure the success of efforts (Kusler and Kentula 1990, Kentula et al. 1992, National Academy of Science 1992), and standards or endpoints are needed for comparison (Davis and Simon 1995). Whether or not standards or endpoints are achievable is also subject to debate, yet the importance of having a "reference condition," if not a "pristine condition," as a measure of success is beyond question (Brinson et al. 1994, Davis and Simon 1995, Smith et al. 1995).

Defining the reference condition requires a basic understanding of the factors that influence ecosystem functions and biological communities. Located at the interface between land and water, wetlands are notoriously dynamic in nearly every feature. No two wetlands are alike; wetlands within a region form a continuum of configurations dictated by the relative influences of factors, such as size of a wetland or watershed, variation in and nature of hydrology, geomorphic setting, turnover of biota, and site age. To develop a notion of reference condition from a diverse array of sites drawn from such a continuum, it is necessary to understand the continuum itself and the dominant factors that influence the relative position of individual wetlands along it.

Here, we focus on natural physical factors that influence coastal wetlands of the Laurentian Great Lakes. We wish to provide a review of these in the context of how hydrologic and other physical features of coastal wetlands relate to ecosystem functions. In our opinion, many linkages between physical factors and ecosystem functions of Great Lakes coastal wetlands have not been well-documented. Where available, examples of site-specific interactions between physical factors and ecosystem response will be provided. Additional documentation within and among individual Great Lakes is required before general relationships can be recognized and used in planning and implementation of projects.

For purposes of this review, a definition of coastal wetlands of the Great Lakes is useful. We suggest a modification of Cowardin et al. (1979) that was presented by Keough and Griffin (1994) and similarly modified by McKee et al. (1992): "*lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. Wetlands must have one or more of the following three attributes: 1) at least periodically, the land supports predominantly hydrophytes; 2) the substrate is predominantly undrained hydric soil; and 3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of the year. Wetlands may be considered to extend lakeward to the water depth of two meters, using the historic low and high water levels or the greatest extent of wetland vegetation. Hydrologic connections with one of the Great Lakes may extend upstream along rivers since exchanges caused by seiches and longer-period lake-level fluctuations influence riverine wetlands. Wetlands under substantial hydrologic influence from Great Lakes waters may be considered coastal wetlands.*"

Because there is limited documentation on the physical characteristics and physical and hydrologic processes in coastal wetlands of the Great Lakes, this review cannot be exhaustive. The goal of this review is to provide an organization of our current understanding of the physical factors underlying natural variation in Great Lakes coastal wetland ecosystems in order to assist managers in developing reasonable expectations for their projects.

PHYSICAL FEATURES OF COASTAL WETLANDS

Connection with waters of the Great Lakes is a key feature distinguishing coastal wetlands from other freshwater inland wetlands. Lakes of such large volume and area support internal and surface currents and waves that affect coastal habitats (Bedford 1992). Under natural conditions without human controls, the water level of each of the Great Lakes varies seasonally and yearly due to basin-wide, continental, and global climate patterns. Geologic substrates in the coastal zone also vary within and between individual lake basins, providing site-specific patterns of erosion and deposition of substrates supporting flora and fauna.

Great Lakes coastal wetlands are inherently dynamic (Keddy and Reznicek 1986). The flora and fauna are adapted to the unstable and unpredictable conditions of the coastal zone that impose stressors, such as periodic high and low lake-levels, currents, storms, ice, and sediment erosion and redistribution. In coastal wetlands, the extent of disturbance determines patterns of plant and animal establishment and persistence, ranging from elimination of biota by extreme events to undisturbed ecosystems organized by biotic interactions. In this review, we distinguish natural and human-induced disturbance and will focus on the former. Anthropogenic development and pollution that impose additional perturbations on wetlands are outside the scope of this paper. Rehabilitation activities in the coastal zone are usually aimed at correcting degradation caused by human activity. If the latter is relieved through intervention, one would still expect basin- and site-specific levels of natural variation. Thus, it becomes necessary to recognize and distinguish natural disturbance that causes typical ecosystem variation from anthropogenic disturbance.

The reference condition for coastal wetlands includes a disturbance regime that is imposed at several spatial and temporal scales (Keough 1990). Natural disturbance factors can be organized at scales that are 1) local or short-term (site-specific and/or seasonal), 2) watershed, lake-wide, or annual, and 3) larger or long-term (regional and/or greater than one year). This hierarchy is congruent with the spatial and temporal extent of ecosystem response. Short-term disturbance affects organisms and processes with daily or otherwise short turnover times, while longer-term disturbances affect perennial plant communities, population trends, configuration of wetland landscapes, and geomorphic processes.

At longer temporal scales, the Great Lakes have water-level variation with uneven decadal and epochal cycles forced by climate change at regional, continental, and global scales. Presently, two of the Great Lakes (L. Ontario and L. Superior) have semi-regulated water levels, with reduction of extreme variation at longer time scales. Interannual variation in lake level affects shoreline processes such as fluvial and eolian transport and overwash and greatly alters the extent and composition of wetland vegetation.

Other environmental factors are linked less to particular time scales yet exert influence over wetland biotic assemblages and ecosystem processes. Such factors may be specific to individual lakes or regions within lakes and include general water quality, sediment type and movement, and water temperature.

GEOMORPHIC TYPES OF WETLANDS

Coastal wetlands can be grouped into three broad categories based on physical and hydrologic characteristics: open, drowned river mouth/flooded delta, and protected (Figure 1). A continuum exists between these end members, and from a geohistorical perspective, many coastal wetlands have systematically or episodically migrated between the end members. The end members differ in their geomorphology, sedimentology, and hydraulic and hydrogeologic connection to the lake and fluvial systems draining into the lake. We will briefly and qualitatively describe the physical and hydrologic differences between these wetland categories.

Open Coast Wetlands

Open coast wetlands range in length along the coast from less than a kilometer to tens of kilometers and vary in width from a few to hundreds of meters. Smaller wetlands are commonly confined to embayments into the mainland, while larger open wetlands occupy long stretches of linear shoreline. All typically have a predepositional surface of bedrock or unconsolidated material that gently slopes into the lake. Nearshore bars of sand and gravel may occur within or offshore of the wetland, providing shallow water areas for vegetation establishment and wave attenuation. Most open coast wetlands have inorganic bottom substrate ranging from clay to gravel and even exposed bedrock with minimal overlying organic material.

Open-coast wetlands have a direct surface-water connection to the lake and can be influenced by wave-generated oscillatory, onshore/offshore (storm surge), and longshore currents, by seiche-induced onshore/offshore and longshore (contour) currents, and by ice push (Figure 1a). Although the wave and seiche climate can range from moderate to high, little sediment typically is available for transport and deposition, or sediments are rapidly deposited at the margins of the wetlands as currents are damped by vegetation. The magnitude of the impact of hydraulic processes in open coast wetlands can be enhanced during high lake levels because the increased depth of the water column results in reduced frictional resistance with the bottom. Ground-water flow in open-coast wetlands is also directly influenced by the elevation of the lake. Short-term and long-term lake-level fluctuations may affect the magnitude and direction of ground-water flow. Because these wetland systems overlap the mainland, flow-systems within the wetland can be influenced by both regional and local flow systems of the mainland.

Drowned-River Mouth and Flooded-Delta Wetlands

Drowned-river mouth and flooded-delta wetlands share with open-coast wetlands the feature of having direct surface-water connections with the lake but differ from open wetlands in that they occupy flooded river valleys or cap drowned deltas. Consequently, riverine and delta wetlands are typically oriented near-

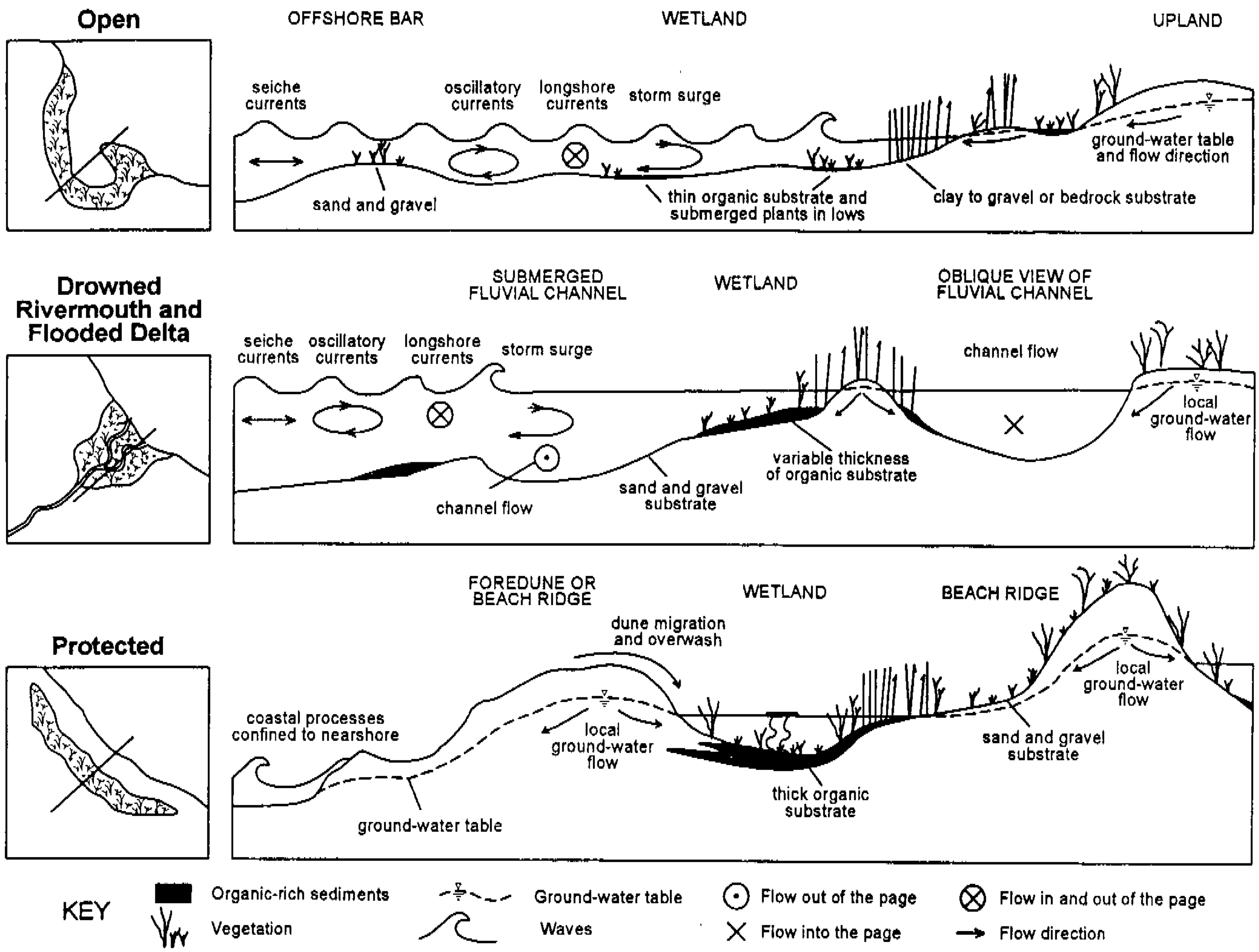


Figure 1. Continuum of basic hydrogeomorphic types of Great Lakes coastal wetlands—open coastal, drowned rivermouth and flooded delta, and protected. Illustrations of various physical and hydrologic processes are shown as general profiles, not-to-scale. Specific sites may show features of more than one type or may alternate between types.

perpendicular to the lakeshore and are constrained in their width and length by the river valley or size of the delta platform. Riverine and delta wetlands are highly variable in thickness and extent of organic substrate and contain a wide variety of inorganic substrate materials.

Drowned-river mouth and flooded-delta wetland systems experience both coastal and riverine physical processes. Lakeward parts of the wetland can be impacted by wave-generated oscillatory, onshore/offshore, and longshore currents, by seiche-induced onshore/offshore and longshore currents, and by ice push (Figure 1b). Landward portions are impacted by fluvial currents as direct channel flow and sheet flood and by ice flow. Fluctuations in lake level enhance or reduce the velocity of the fluvial currents by changing the base level of the river. Ground-water flow in these wetlands can be highly complex, with many local flow systems responding to changes in lake level and fluvial discharge.

Protected Wetlands

In contrast to the open-coast and drowned-river mouth/flooded-delta wetlands, protected wetlands are isolated from most direct hydraulic processes generated by the lake. Protected wetlands commonly occur landward of a sand barrier, such as an attached spit or beach ridge. A requisite for these systems, therefore, is a high rate of sediment supply to the nearshore sand barrier. If the wetland occupies a formerly drowned river mouth that has been closed off by a barrier, the wetland will be oriented approximately perpendicular to the lakeshore. Sites within a strandplain of beach ridges commonly are oriented subparallel to the coastline. Because these wetlands are isolated from hydrau-

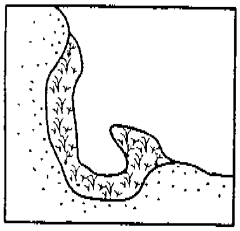
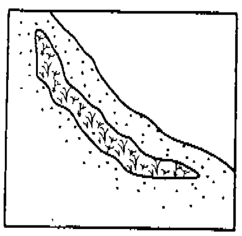
Type	Physical	Hydrologic	Biological	Chemical
Open 	Variable inorganic substrate (clay to gravel). Thin to non-existent organic substrate. Moderate to high wave climate. Low rate of sediment supply. Gentle offshore and underlying-surface slopes. May or may not have offshore bars of sand to gravel.	Direct surface-water connection to lake. Ground-water flow-system directly influenced by elevation of lake.	Plant morphometry adapted to hydraulic stress. Vegetation aligned with shoreline bars and dunes. Vegetation sensitive to wave climate and protective dunes, ridges, bars, and points. Plant species preferring inorganic substrates. Stray lake faunal species. Biota tolerant of ice action.	Strongly influenced by lake-water constituents. Low turbidity. Vegetation may isolate nearshore water from mixing with lake.
Drowned River 	Variable inorganic substrate (clay to gravel). Variable thickness of organic substrate. Low to moderate wave climate. Low to moderate rate of sediment supply from coast and river.	Direct suface-water connection to lake and river. Ground-water flow-system influenced by elevation of lake and fluvial system Many local flow systems. Seiches transmitted upstream.	Plants and animals of riverine, lagoonal, and coastal habitats. Wild rice, mud-flat annuals, and plants preferring organic sediments. Warm-water fish. Biota tolerant of flooding and high turbidity.	Upstream-downstream gradient in water constituents caused by seiche mixing of lake and river water and reversal of currents. Variable turbidity.
Protected 	Uniform inorganic substrate (sand to gravel). Thick organic substrate. High rate of sediment supply to shoreline lakeward of wetland.	May or may not have a surface-water connection to lake. Ground-water flow-system may or may not be influenced by the elevation of the lake. Many local flow systems.	Peatland vegetation is often present in northern areas. Ridges and swales show successional patterns. Warm-water fish in lagoons. Plants preferring organic substrates.	Organic matter may dominate water chemistry if limited riverine inflow. High water temperatures in summer. Ground-water seepage may cause temperature gradients. Low turbidity Ground water may dominate chemistry where inputs are high.

Figure 2. Examples of basic physical, hydrologic, biological, and chemical features of three hydrogeomorphic types of coastal wetlands of the Great Lakes. Lists re not intended to be exhaustive and were drawn from the general literature and the authors' knowledge and experience.

lic stress, thick organic sediments can overlie a fairly uniform inorganic substrate, typically of sand or sandy gravel.

Protected wetlands may or may not have a surface-water connection to the lake. Some protected wetlands have a fluvial channel to the lake if the wetland was formally a drowned-river mouth wetland or if the wetland contains a large prism of surface water that exits or enters during seiches. Although isolated from direct currents caused by waves and seiches, dunes may migrate from the sand barrier landward into the wetland or overwash may enter the wetland by overtopping the barrier during storms. Both mechanisms can cause interfingering of sands and gravels with the organic substrate along the lakeward margin of the wetland. Ground-water flow systems connecting the wetland to regional aquifers are influenced by the presence or absence of permanent or temporary fluvial connections to the lake and by flow systems established in the mainland and in the barrier (Figure 1c). For example, beach ridges commonly occupy embayments that can focus ground-water flow into the strandplain (Cherkauer and McKereghan 1991). Ground-water focusing creates a regional flow-through system that can keep the water table elevated above and, for the most part, isolated from the lake. Regardless of the regional flow-system, a protected wetland can have many smaller local flow-systems between the wetland, the sand barrier(s), and surrounding drainages.

Ecosystem Properties

The continuum of physical properties of open coast, drowned river mouth, and protected coastal wetlands extends to and drives the features of ecosystems (Figure 2). Thus far, investigations of links between physical features and biotic and environmental functions of wetlands have been site-specific. Consequently, comparisons within and among different geomorphic types of wetlands can only be inferred. It is incumbent on

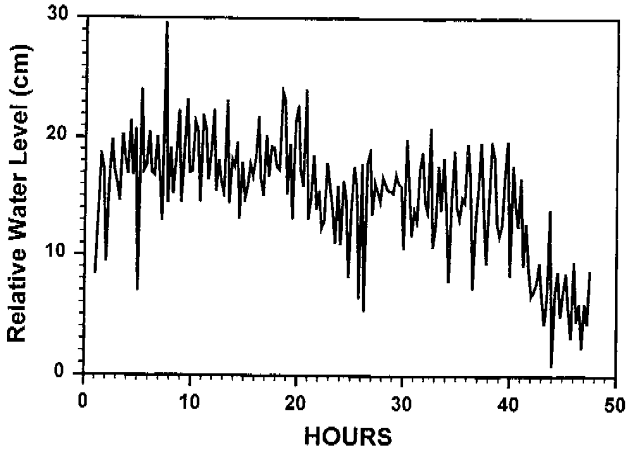


Figure 3. Example of seiche-driven water-level change in the Mink River Estuary of northern Lake Michigan. Series represents data collected over the 48-hour period from May 9, 1986 at 1800h to May 11, 1996 at 1800h.

each study or management task to include a thorough understanding of the geomorphic type and hydrogeomorphic setting before approaching an assessment of the impacts of rehabilitation or management actions. In the next section, we discuss some of the links between ecosystem functions and physical forcing factors that can occur to varying degree in each wetland type.

ECOSYSTEM RESPONSES TO HYDROGEOMORPHIC FACTORS

Responses to Local/Short-Term Factors

Seiches. Seiches are short-term water-level oscillations that are characteristic of large lakes and functionally analogous to tides (Herdendorf 1990) (Figure 3). Seiches not only change the water level within a wetland over a short cycle (hours), but they also move material up and down and back and forth. In the shallow waters of coastal wetlands, the extent of seiche oscillations relative to the total water column can be significant. The amplitude of seiche-driven, water-level change in coastal wetlands is closely related to the occurrence of storm fronts that progress across lake basins. The seiche period and amplitude at a given site depend on the site location relative to the null oscillation point for each of several seiche modes (Bedford 1992). In basins as large as any of the Great Lakes, seiches occur continuously at predictable periods during the ice-free season because the time between forcing events is shorter than the time required for oscillations to die away (Mortimer and Fee 1976, Bedford 1992).

Water-level oscillations driven by seiches can be measured over long distances in Great Lakes tributaries (Jordan et al. 1981, Duluth Harbor, Lake Superior; Keough 1986, Mink River, Lake Michigan; Meeker 1996, Kakagon Sloughs, Lake Superior). Schroeder and Collier (1966) and Brant and Herdendorf (1972) reported on the ingress of lake water into coastal wetlands. Reversing currents have been reported for sites on Lake Erie (Bedford et al. 1983, Dereki and Quinn 1990). Typically, one observes a gradient in specific conductance as discharging river water or ground-water mixes with inflowing lake water (Keough 1986). Dissolved and suspended material in the littoral zone oscillates in resonance with the lake seiche cycles. Bedford (1992) reported on seiche-driven, bidirectional sediment-flux recorded in sites between the Sandusky River, Sandusky Bay, and Lake Erie. Keough (1990) reported that water temperature, dissolved nutrients, and chlorophyll-*a* demonstrated periodicity within the Mink River wetland coherent with the seiche periods of Lake Michigan. An increase in dissolved nutrients at the wetland/lake interface was hypothesized to be caused by upwelling of lower lake strata. Sager et al. (1985) concluded that nutrients in the seiche zone are transformed. They found net retention of particulate organic nitrogen and a net release of ammonia and nitrogen oxides from Peter's Marsh, except in spring when there was net retention of the latter. The marsh transformed incoming total phosphorus and particulate organic carbon and exported inorganic phosphorus and dissolved inorganic carbon. The southern portion of Green Bay is hypereutrophic, so it may be an imperfect model for seiche-induced nutrient dynamics in other less-eutrophic portions of the Great Lakes. As Burton (1985) pointed out, with only a handful of site-specific studies, we cannot yet generalize about the role of seiches in nutrient dynamics.

Ice. Few studies have examined the effects of ice on biological communities in the coastal zone of the Great Lakes. Reports by Geis (1979, 1985) and Duffy and Batterson (1987) are the only published work that we have found. Geis (1985) described ice formation along the shorelines of Lake Ontario and the St. Lawrence River. Wetland habitats are affected where the entire water column freezes and wetland sediments are incorporated in the ice. Water level in early winter determines how deeply ice formation penetrates into the sediment. Under shallow or exposed conditions, freezing into the sediments can be deep. If the spring water-level increase occurs before the thaw of frozen sediment, lifting and transport of sediment, plant roots, and rhizomes can be extensive (Kautsky 1987). During years of high lake level, extensive movement of frozen sediment can occur in mid-winter. Spring movement of grounded ice can result in erosion of the wetland edge, the extent of which is determined by local factors, including slope of the sediment surface, morphometry and fetch of the shoreline, and the above- and below-ground winter structure of the shoreline vegetation.

Ice jams occur in constricted channels, such as the St. Clair River between Lake Huron and Lake St. Clair (Herdendorf and Raphael 1985). Wind forcing in late winter results in ice accumulation in the channel, raising the water level in Lake Huron and lowering the level in Lake St. Clair. Subsequently, when the ice jam breaks, shoreline and coastal wetland erosion results from the release of water and eroded material. Herdendorf and Raphael (1985) attributed the delta wetlands of Lake St. Clair to the extreme flow events following ice jams. Sediments in the St. Clair delta are sandy, indicating deposition resulting from events of high discharge.

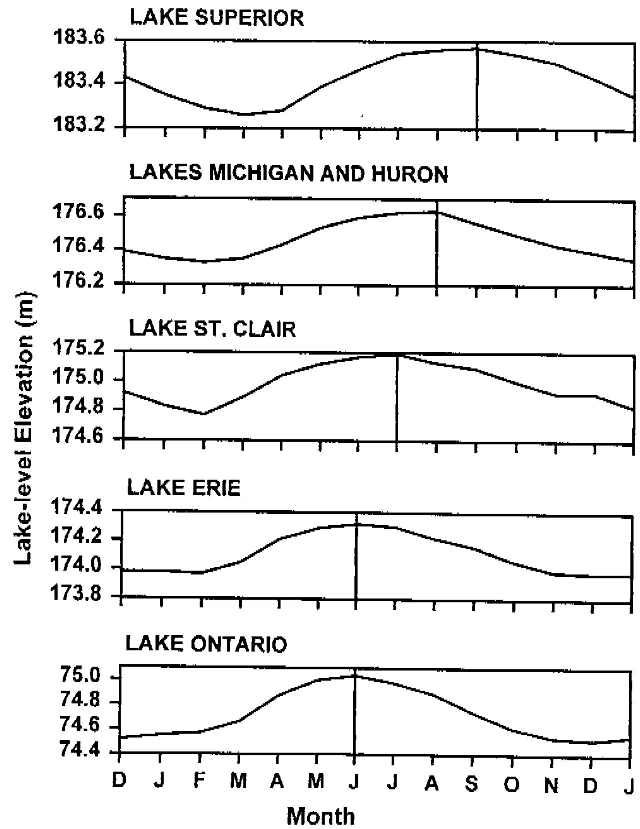


Figure 4. Patterns of average water level in the Great Lakes. Reference lines showing the month of highest average water level are included. Data are from 1918–1994 records provided by the U. S. Army Corps of Engineers, Detroit District (USACOE 1995).

Responses to Watershed/Lakewide/Seasonal Scales

The water level of the Great Lakes is typically lowest in winter and highest in mid-summer (USACOE 1995)(Figure 4). This pattern is distinct from other inland wetlands that typically show highest water-levels in spring with decreases through the growing season. Little research has addressed the linkages between this seasonal pattern and ecosystem processes in coastal wetlands. Emergent vegetation in the flooded lakeward zone must respond to rising, not falling, water level during the growing season. Flooding is a well-known stressor to wetland vascular plants (Koslowski 1984, Hale and Orcutt 1987, Mendelssohn and Burdick 1988, McKee and Mendelssohn 1989). Flooding results in reduction of available oxygen and production of toxic byproducts in the root zone of wetland sediments. The lakeward zone of emergent vegetation is composed of species adapted to flooding stress. Adaptations include well-developed aerenchyma tissue to transport oxygen from emergent leaves and stems to roots (e.g., *Scirpus* sp., *Eleocharis* sp., *Typha* sp., *Sparganium eurycarpum* Engelm. Ex Gray); basal meristems that produce stem tissue continuously, allowing plants to become taller as the water level rises (Keough 1987, 1990) (e.g., *Scirpus* sp., *Eleocharis* sp., *Typha* sp., *Sparganium* sp.); perennial tussock life forms in which rhizomes and roots develop on top of earlier structures, maintaining the active root zone near the water surface (e.g., *Carex stricta* Lam); simple photosynthetic culms that present a flexible narrow profile to wave action (*e.g., Scirpus* sp., *Eleocharis* sp., *Equisetum* sp.); rhizomes with fibrous roots to anchor plants in strong currents and waves (e.g., *Scirpus* sp.); and life histories with a succession of forms to take advantage of changing hydrologic conditions. An example of the latter is wild rice (*Zizania palustris* L.), which germinates on mud flats and in shallow water but assumes a succession of aquatic, floating-leaf, and emergent forms suited to rising water-levels (Meeker 1993). Meeker (1996) found that the different life-stages of wild rice variously enhance sediment deposition in rivers, to the advantage of growth in plants of the population.

The suite of species in the Great Lakes region adapted to such conditions is somewhat limited. Plant diversity is greatest in the gently-sloping upper-wetland zone that is subject to intermediate disturbance (Keough, personal observation; Keddy and Reznicek 1985). This zone experiences moderate water-level variation within and between years and less extreme storm and ice effects than lakeward vegetation zones.

The timing of highest water level in the annual cycle varies among the lakes. Water levels of lakes Ontario and Erie typically are highest in mid-June, lakes Michigan, Huron and St. Clair in July, and Lake Superior in early autumn (Figure 4). In a study of unregulated and regulated large inland lakes in northern Minnesota, Wilcox and Meeker (1991) reported that both increases and decreases in amplitude of water-level variation led to reduced plant diversity. Lyon et al. (1986) found, in wetlands of the Straits of Mackinac (Lake Michigan), density of emergent macrophytes to be greatest where the duration of flooding was variable and less than 100% of the growing season, coinciding with higher levels of soil nutrients. Krieger (1992) suggested that seasonal or other short-term dewatering of sediments imposes stress on the infauna and selects for invertebrate assemblages that are physiologically or behaviorally adapted to flooding/dewatering cycles.

Responses to Long-term Factors

Year-to-Year Water-Level Variation. Physical factors operative at scales greater than one year exert the most dramatic effects on community structure. Year-to-year changes in Great Lakes water-levels have served to remove stands of wetland vegetation during high water periods and stimulate succession. At temporal scales between one year and decades, variation in water level is on the order of meters. Such increases and decreases in water level cause wetland habitat to change position up- and down-slope; seldom are entire communities removed completely (Harris et al. 1981, Burton 1985, Kelley et al. 1985, Herdendorf and Raphael 1986, Keough 1986, 1990, Williams and Lyon 1991). Planck (1993) summarized the results of the Levels Reference Study of the International Joint Commission (IJC) conducted by the IJC Natural Resources Task Group. Analysis of reference sites showed that changing water levels sustain wetland diversity and that reduction in year-to-year lake-level variation through regulation leads to loss of wetland extent, diversity and resilience to environmental disturbance. Clonal expansion of outlier plants and germination from the seed bank allow communities to persist, albeit forming more narrow zones upslope during high water periods or successional communities downslope during low water periods (Keddy and Reznicek 1986). Siegley et al. (1988) examined the seed bank of a Lake Erie wetland that had been dewatered after submergence for over three decades. They concluded that duration of a high or low water period (one vs. multiple years) and the wetland surface topography determine the size and structure of the reconfigured wetland ecosystem.

Lakes with fully-regulated water-level (such as Lake Ontario) no longer exert such unpredictable stimulation on coastal wetlands. Wilcox et al. (1993) documented the effect of stable lake-level on wetland plant communities of Lake Ontario, compared to the somewhat more dynamic conditions of Lake Superior. Unpredictable year-to-year changes in water level typically result in greater diversity within and among habitats (Wilcox and Meeker, 1991, Wilcox 1993, Wilcox

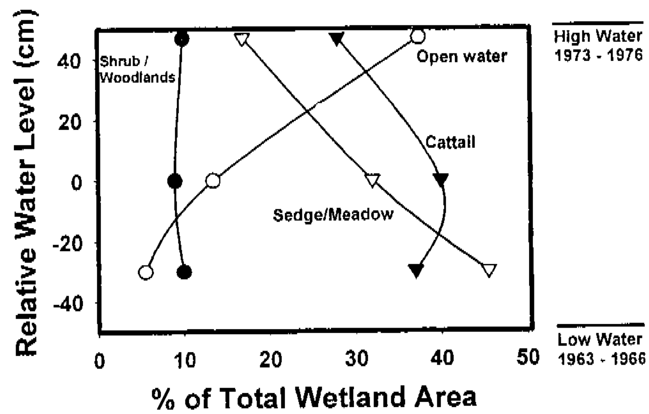


Figure 5. Response of wetland vegetation communities of lower Dickinson Island (Lake St. Clair) to lake level. This series was developed from wetland maps from 1949 (average lake level), 1964 (low lake level), and 1975 (high lake level). Modified from Edsall (1988) and Williamson (1979).

et al. 1993), while stable water-levels tend to encourage dominance by woody species and other highly competitive species, such as cattail (*Typha* sp.), reed canary grass (*Phalaris arundinacea* L.), various shrubs (*Salix* sp., *Alnus* sp.), and exotic nuisance species (e.g., purple loosestrife [*Lythrum salicaria* L.]).

Keddy and Reznicek (1986) provided a model to describe the relationship between frequency of flooding and zonation of wetland plant communities based on the water-level history of Lake Erie. At elevations below a minimum annual water-level, submersed aquatic vegetation dominates, and above a long-term maximum water-level, shrub and forest vegetation prevail. Marsh and wet meadow communities are found at intermediate elevations where flooding is too frequent to allow establishment of trees and shrubs but insufficient to eliminate perennial emergent communities. Edsall et al. (1988, derived from Williamson 1979) also provided a model of the response of each of four major wetland habitat types on Dickinson Island (Lake St. Clair) to variation in water level from 1949 to 1975 (Figure 5). There, responses by submersed aquatic vegetation and sedge meadow were antithetical. Cattail communities occupied greatest area during a period of intermediate water level, while woody communities occupied elevations that were unaffected by high water.

Sediment Transport. Sediment supply and transport associated with coastal wetlands are linked to long-term lake-level patterns, determining the configuration of barrier beaches and sand spits that protect wetlands. Erosion of barrier beaches can expose wetlands to wave attack and allow overwash to extend into the wetland. If deposited onto existing wetlands, transported sediments can bury plant communities and effectively set the stage for secondary succession. Moreover, washover fans can create relief within the wetland basin, providing new habitats. The influence of sediment overwash on habitat diversity has not been examined for Great Lakes wetlands.

Lake-level variation at longer time scales affects coastal processes such as net erosion and net deposition of sediments at specific wetland sites through shifts in sediment transport mechanisms (Wilcox 1995b). During periods of high lake-level, storm-induced waves erode wetland substrate and introduce inorganic sediment in upper reaches that would not be accessible during low water stages. At low lake-levels, sediments are exposed to transport by wind, forming and extending barrier beaches by deposition of littoral drift.

Wrack—shoreline accumulations of dead vegetation by wind and currents—is a variation of sediment transport. Where the source of biomass is high and in situations where material can be focused by strong directional winds or currents, detritus can build up to many decimeters thickness and, in severe storms, can be deposited far into upper wetland reaches. Wrack can effectively smother existing vegetation and become a site for secondary succession. Thick deposits of organic debris have a rough surface, good moisture-holding capacity, and ample nutrients from decomposing vegetation, making them excellent sites for seed trapping, germination, and seedling establishment. While the influence of wrack on biodiversity has been reported for marine coastal ecosystems (Bertness and Ellison 1987, Bertness 1992, Guntenspergen et al. 1995), the role of wrack in Great Lakes coastal wetlands has received scant attention.

Effects on Ecosystems. Major changes in habitat extent and structure affect the fauna that use them. Wetlands that expand and contract in response to lake-level change provide unpredictable extent, spatial structure, and juxtaposition of habitat for organisms. Although several studies (O'Gorman 1983, Chubb and Liston 1986, Brazner and Magnuson 1994, Brazner 1997, Brazner and Beals 1997) have described fish communities of coastal habitats, to our knowledge no studies have attempted to document the relationship between fish use of wetlands and environmental and habitat variation associated with short- or long-term water-level change. Liston and Chubb (1985) suggested that high water level in spring provides a greater amount of warm, shallow water and improved habitat for spawning and development of young-of-the-year fish. In Pentwater Marsh (Lake Michigan), they found larval fish abundance and diversity increased as annual lake level increased, especially minnows, black crappie (*Pomoxis nigromaculatus* Les.), and largemouth bass (*Micropterus salmoides* Lace.) (Chubb and Liston 1986). Kallemeyn (1987) reported that year-class strength of walleye (*Stizostedion vitreum* Mitch.) and yellow perch (*Perca flavescens* Mitch.) are positively correlated with high water level during their respective spawning periods, a response associated with flooded wetland vegetation. Long-term lake-level variation results in littoral habitats with diverse structure, attracting a diverse fish community (Jude and Pappas 1992, Brazner and Beals 1997). Wetlands provide a variety of densities and life forms of plants and other surfaces for periphyton and invertebrate prey for fish. Liston and McNabb (1986) found increased areal production by periphyton associated with increasing water depth in the St. Marys River and attributed this to increased surface area of emergent macrophyte hosts. Sediment fertility, texture, and organic content are additional factors determining the composition and biomass of infauna (Cole and Weigmann 1985, Reynoldson 1995). Long-term changes in water level with attendant seiche and storm effects lead to variation in vegetation structure and sediment texture, benefitting benthic invertebrate communities and vertebrate consumers.

Habitat structure is also one of the most important factors determining use by waterbirds (see reviews by McNicholl 1985 and Prince et al. 1992). Suitability of nesting habitat for many waterbirds of the Great Lakes is enhanced by disturbance that reduces density of wetland vegetation. Openings, if colonized by submersed vegetation, are ideally suited to waterfowl (Bookhout et al. 1989). Prince et al. (1992) point out that low water periods generate conditions that are temporarily less suitable for waterfowl, since wet meadow habitats usually replace marsh vegetation. They concluded that "short-term water-level fluctuations about the long-term mean create the best hydrological regime for maintenance of productive wetland ecosystems beneficial to waterfowl." However, long-term changes in lake level make coastal wetland habitats unpredictable as sites for breeding waterfowl (Prince et al. 1992), affecting nest sites, food availability, and vulnerability to predation. Courtenay and Blokpoel (1983) concluded that stabilization of water level of the lower Great Lakes had led to encroachment of vegetation over traditional nesting sites for common terns (*Sterna hirundo* Linn.), leading to relocation by some colonies. Harris et al. (1983) found that bird diversity in Green Bay coastal wetlands is directly correlated with diversity of cover types and amount of edge. Year-to-year change in water level alters the availability of feeding pools in beaches for shorebirds (Bradstreet et al. 1977).

Long-Term (>Decade) Variation. Temporal scales greater than decadal have profound effects on watersheds, as well as coastal wetlands. The most dramatic

Table 1. General chemical constituents (mean (+/− 1 SD)) of offshore waters of the Great Lakes. Samples collected during cruises by the U. S. Environmental Protection Agency in Spring, 1992. From unpublished information provided by U. S. E. P. A. Great Lakes National Program Office, Chicago, IL, USA.

Constituent	Ontario	Erie	Huron	Michigan	Superior
Number of samples	N = 8	N = 6	N = 10	N = 22	N = 13
Alkalinity	95.32	88.93	79.64	110.11	42.34
mg L^{-1} $CaCO_3$	(0.57)	(4.27)	(0.43)	(0.85)	(0.54)
Conductivity	313.21	264.97	210.73	287.34	97.28
μS cm^{-1}	(1.58)	(26.68)	(1.15)	(1.70)	(0.91)
Turbidity	0.38	6.24	0.70	0.44	0.41
Formazin units	(0.17)	(4.13)	(0.36)	(0.20)	(0.64)
Dissolved Organic Carbon	1592.88	27.21	1177.04	1400.51	1120.00
μg L^{-1}	(140.24)	(22.42)	(74.70)	(94.46)	(170.05)
Dissolved SiO_2	0.25	0.93	0.73	0.61	1.21
mg L^{-1}	(0.05)	(0.46)	(0.02)	(0.08)	(0.02)
Dissolved NO_3	362.01	2.85	325.14	281.87	335.72
μg L^{-1}	(9.72)	(2.52)	(10.22)	(16.67)	(7.60)
Dissolved Reactive Phosphorus	2.55	10.81	0.13	0.73	0.27
μg L^{-1}	(0.97)	(5.91)	(0.23)	(0.66)	(0.23)
Total Phosphorus	6.71	20.20	3.38	3.83	1.86
μg L^{-1}	(0.46)	(3.29)	(0.51)	(0.51)	(0.74)
Dissolved SO_4	27.31	1.00	16.57	21.98	2.85
mg L^{-1}	(0.52)	(0.0)	(0.67)	(0.84)	(0.17)

evidence of coastal adjustment to long-term water-level change can be seen in the many sites of coastal ridges and swales that can be found throughout the Great Lakes (Thompson and Baedke 1995). Sites such as the Ridges Sanctuary (Door County, Wisconsin), Indiana Dunes National Lakeshore (Indiana), Point Pelee State Park (Ontario), Bark Bay (Bayfield County, Wisconsin), the Manistique and Thompson Embayment (Upper Peninsula, Michigan) and Wilderness State Park (Northern Lower Peninsula, Michigan), were formed during the late-Holocene. Beach ridges within these strandplains formed as shoreline responses to quasi-periodic fluctuations in lake level about every 30 years. The ridges and accompanying swales have been elevated above the current lake by isostatic rebound or removed from the coastal system with continued shoreline progradation (Thompson 1992, Thompson and Baedke 1995, 1997). Moist forest communities have developed on older ridges, with wetlands of various types in the swales (Wilcox and Simonin 1987). The rate of succession and community type is determined by local conditions, including regional climate, sediment texture and organic deposition, elevation and topography (Wilcox 1995a), and human settlement and development within the region (Jackson et al 1988, Singer et al. 1996). Kormondy (1969) described the vegetation in a succession of beach swales formed by the Presque Isle spit (Lake Erie). Across the sequence of ridges and swales, vegetation, sediment organic content, and features of community metabolism formed a successional sequence related to site-age, with the youngest sites near Lake Erie and older sites landward. Wilcox and Simonin (1987) described the chronosequence of dune ponds near the south shore of Lake Michigan. Differences in vegetation across the sequence were associated with water depth and development of organic sediment (both functions of site history) and long-term variation in ground-water levels.

Other Site-Specific Physical Factors

An awareness of factors intrinsic to each of the Great Lakes is needed in considering the consequences of activities aimed at wetland rehabilitation. Oriented as they are between the granitic-based boreal ecosystem of northern North America and the sedimentary bedrock and glacial deposits of the midwestern U. S., the Great Lakes encompass a wide range of environments for wetland development (Smith et al. 1991). Lake Superior is less alkaline and less saline (lower specific conductance) than the others, while Lake Erie has most available phosphorus and highest turbidity (Table 1). The trophic status of water and sediments in a wetland has importance in determining productivity and plant species composition. Thus, plant communities in nutrient-enriched wetlands typically differ from sites that are nutrient-limited. Plant communities in wetlands receiving highly alkaline water from ground-water discharge, such as along the Bruce Peninsula (Lake Huron/Georgian Bay) (Cowell and Ford 1980), would be expected to differ from sites on Lake Superior that do not have sources of alkaline water.

Temperature and turbidity are additional water quality factors affecting wetland plant and animal assemblages. Temperature differences are expected between protected sites and those with direct lake contact, affecting length of the growing season, productivity, and phenological cues for individual species. Where shallow water overlies organic sediments, extremely high water temperatures may limit the presence or growth of some organisms. Some native species are adapted to such conditions; warm waters overlying soft sediments in a wetland embayment on Lake Erie have been shown to protect unionid clams from infestation by zebra mussels by eliciting burrowing behavior (Nichols and Wilcox 1997). Conversely, discharges of cold ground-water may limit establishment and growth or organisms. High turbidity reduces the availability of light to submersed macrophytes and epilithic and periphytic algae, thus limiting productivity by those groups and the habitat and resources they provide to other trophic groups (Brazner and Beals 1997). Turbidity in coastal wetlands is influenced by the source of water, productivity, type of sediment, exposure to wave and wind mixing, and activity by animals, such as fish, feeding waterfowl, and other vertebrates.

Local shoreline features, such as orientation to fetch, direction and extent of littoral currents, watershed drainage patterns, proximity to and extent of urban development, and nature of local sediments, contribute to the response of a wetland ecosystem to rehabilitation and management. Distinct plant species assemblages can be expected in wetlands of differing substrates. Organic, sandy, silt-clay, or rock-dominated substrates result in differential nutrient and moisture availability (Mitsch and Gosselink 1986); substrates are influenced by local surficial deposits and extent of transport mechanisms of suspended materials. Sediments of wetlands associated with rivers are often dominated by the materials in the watershed, which can vary considerably within short distances. Wetlands within barrier beaches are protected from wave attack and typically accumulate thick deposits of organic sediments. Wetlands of open shorelines are usually dominated by sand and subject to the dynamic cycle of deposition and erosion.

SUMMARY

Our goal has been to provide an overview of the physical features of Great Lakes coastal wetlands and to highlight interactions between them and ecosystem processes. This effort has been limited, in some respects, by a general lack of process-oriented research. We have attempted to glean available documented examples, but most study results have been site-specific.

We have presented a framework for organizing coastal wetlands of the Great Lakes for purposes of considering the dominant physical features. Site-specific geomorphology interacts with hydrology at a hierarchy of scales to shape the structure and functioning of each wetland ecosystem. We have provided an overview of some of the available evidence that plant and animal communities and ecosystem processes are influenced by geomorphology and hydrology. The scale of ecosystem response is determined by turnover time by each species and process.

Anthropogenic perturbation regimes are superimposed on the hierarchy of natural variation. Distinguishing between the effects of these two remains a challenge. However, a working knowledge of natural physical and biological variation will improve attempts to address anthropogenic degradation and remediation. In our opinion, current understanding of the relationships between community and ecosystem processes and the natural physical variation and disturbance regime in Great Lakes coastal ecosystems is limited. We have a better understanding of biological and physical linkages at higher order (greater than one year) scales than at lower scales. Feedback between ecosystem processes and physical factors has received limited attention for Great Lakes coastal wetlands. Lack of documentation will be particularly challenging for projects that address issues involving communities of species with short turnover that respond to lower order variation.

Plans for wetland restoration must, necessarily, consider this hierarchy of natural factors on a site-specific basis. We need to recognize that the distinct features of each individual lake, the portion of coastal zone of the lake, site history, and regional variation are important for placing a site within the continua of physical disturbance scales and ecosystem responses to natural disturbance. Such placement is critical to project success. References for interpreting the success of a project are most appropriate if they are chosen from sites in similar physical settings and in similar positions along the continuum of natural variation and disturbance.

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