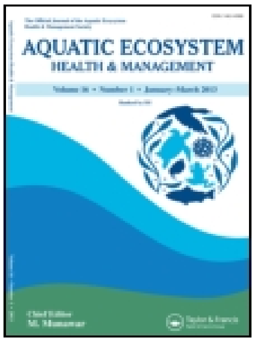

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A review of selected ecosystem services provided by coastal wetlands of the Laurentian Great Lakes

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Significant ecosystem services derive from the coastal wetlands of the Laurentian Great Lakes even though two-thirds of the original coastal wetlands have been lost since European settlement, and the remaining 126,000 ha of U.S. coastal wetlands and ≥70,000 ha of Canadian wetlands are affected by anthropogenic stressors. Published information indicates that wildlife habitat, fisheries support, and water quality improvement are significant ecosystem services provided by Great Lakes coastal wetlands that should be strongly considered during management decision making. 30 species of waterfowl, 155 breeding bird species, and 55 species of reptiles and amphibians are supported by coastal wetland habitats across the Basin. Nearly all sport and commercial Great Lakes fish species use coastal wetlands for life-cycle functions, and Great Lakes food webs are supported by wetland export of young sport and forage fish. Biological responses indicate declines in the wildlife and fishery services with increasing levels of anthropogenic disturbance. Extrapolation from a single well-studied system suggests that, Basin-wide, coastal wetlands may retain nearly 4000 tonnes P and 53,000 tonnes N per year, but additional studies are needed to support these estimates and determine stressor effects. Coastal wetlands appear to retain sediments over long time scales, but may either retain or release sediments during storm events. Extrapolation of carbon sequestration from other wetland types suggests that less than 90 g C yr^{-1} might be retained across the Basin. Wild rice production provides a culturally important ecosystem service, and coastal protection may be locally significant where fringing wetland remain. To support management decisions, quantitative relationships between specific stressors or land use practices and the delivery of ecosystem services are needed, as are ecosystem service indicators to measure those responses.

Keywords: wildlife habitat, fisheries, water quality

Introduction

Analysis of the goods, services, and benefits provided by ecosystems to humans provides an approach for comprehensively evaluating the consequences of management actions to ecosystem function and human welfare. The Millennium Ecosystem Assessment provided a synthesis of the importance of ecosystem services to human well-being at a global scale (Millennium Ecosystem Assessment, 2005). However, for managers to base decisions on the full range of benefits provided

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Table 1. Current estimates for numbers and areas of Great Lakes coastal wetlands in the United States and Canada, by waterbody (based upon Moffett et al. [2006] and Environment Canada [2003]).

	United States		Canada	
Waterbody	Number of GLCWs	Total area, ha	Number of GLCWs	Total area, ha
Lake Superior	299	19,000	24	4,600
Lake Michigan	459	53,800	N/A	N/A
Lake Huron	185	26,400	>145 (estimated)	unknown
Lake Erie	92		33	19,330
Lake St. Clair	7	12,500	6	25,651
Lake Ontario	167	5,700	87	11,096
St. Marys River	71	5,284	184	unknown
St. Clair River	6	153	5	<100
Detroit River	7	156	4	1,136
Niagara River	9	158	4	85
St. Lawrence R.	144	2,876	40	7,018
Total	1446	126,027	>532	>69,016

by ecosystems, a better understanding of services provided at finer (e.g. regional) spatial scales is needed. The Great Lakes are about to experience a wave of management actions, focused on ecosystem restoration and funded by the U.S. Environmental Protection Agency through the Great Lakes Restoration Initiative. An ecosystem services perspective toward restoration of coastal wetlands and other Great Lakes systems would help to quantify the spectrum of benefits from those activities, and would more comprehensively communicate progress to stakeholders. Together with assessments of coastal wetland condition to evaluate progress toward restoration (e.g. SOLEC, 2009), it may contribute toward improving water quality in the Great Lakes as called for in the Great Lakes Water Quality Agreement.

Studies of functional linkages between coastal wetlands of large lakes and offshore waters point to the importance of the land-water interface in regulating chemical, biological, and ecological processes of the lake itself (Wetzel, 1990). Moreover, the importance of coastal wetlands to Great Lakes productivity, nutrient cycling, fisheries, and biodiversity has been shown to be greater than their size alone would indicate (Wetzel, 1992; Brazner et al., 2000; Wei et al., 2004). The ecosystem services that coastal wetlands provide, while recognized, have seldom been analyzed, and a scientific approach toward quantifying those services has not been developed. Toward that objective we present measures that quantify or illustrate the functions that coastal wetlands perform in support of ecosystem services. This review of the principal ecosystem services supplied by Great Lakes coastal wetlands and identification of information needs regarding those services should be particularly useful to ecological assessment and restoration efforts across the Great Lakes Basin, and relevant to economic valuation of Great Lakes coastal wetlands.

Great Lakes coastal wetland inventory

Because the provision of ecosystem services by Great Lakes coastal wetlands (GLCWs) depends upon the amount and distribution of the wetlands, we present estimates of the numbers and areas of GLCWs, by waterbody (Table 1; based upon Environment Canada (2003) and Moffett et al. (2006)). GLCWs are wetlands that have substantial hydrologic influence from Great Lakes waters, and are considered to extend lakeward to the greatest extent of wetland vegetation and landward to the extent that water level is influenced by lake level (Keough et al., 1999). Uncertainty in wetland numbers and areas exists, especially in remote regions on the Canadian side that have not been fully inventoried (Environment Canada, 2003). Basin-wide, as much as two-thirds of the original coastal wetlands present prior to European settlement have been lost (Hecnar, 2004). Coastal wetlands develop

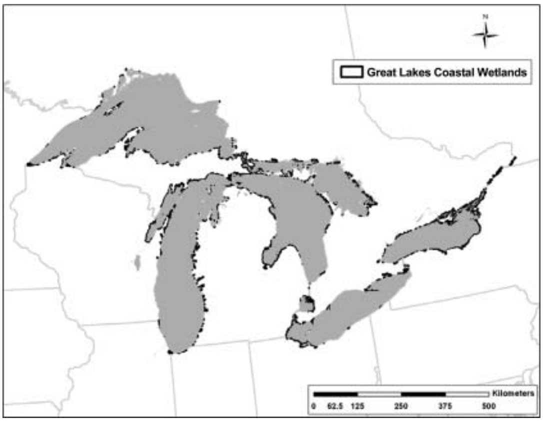

Figure 1. Distribution of present-day coastal wetlands across the Laurentian Great Lakes and connecting channels (from Great Lakes Coastal Wetland Consortium, available at http://www.glc.org/wetlands/inventory.html).

only in sheltered or low-energy environments; therefore, coastal wetlands and the services they provide are not evenly distributed (Figure 1). For example, the rocky north shore of Lake Superior and the bluffs along the western shore of Lake Michigan, southeastern Lake Huron, and southern Lake Erie have few sheltered areas and, therefore, few coastal wetlands.

Ecosystem services

Whereas the Millenium Ecosystem Assessment (MEA, 2005) took a broad view of ecosystem services as all the benefits provided by ecological systems, a more constrained definition of "final" ecosystem services has been proposed by economists as "those components that are directly enjoyed, consumed, or used to yield human wellbeing" (Boyd and Banzhaff, 2007). Final ecosystem services are those which can be valuated, using monetary or non-market values. Predicted effects of different management scenarios on services and their sum values then become a basis for making management decisions (Farber et al., 2006; Jenkins et al., 2010). As with other commodities, the value of ecosystem services is determined through considerations of both supply and demand, which requires economic analysis. The objective of this review is to examine the supply side of the relationship, which is in the realm of ecological study.

Final ecosystem service measures are rare relative to ecological data. Because the supply of services by ecosystems is governed by the physical and functional attributes of those systems (MEA, 2005), measures of ecosystem properties may be useful as service indicators. Further, the functions that support ecosystem services are more difficult to measure than are structural attributes (e.g. abundance, biomass, or concentration). Therefore, most ecological data available to evaluate ecosystem services are structural measurements. In this review we present the best measures or indicators of ecosystem services available in the literature, as well as effects of anthropogenic stressors on those measures. To predict ecosystem service responses to management actions, stressor-response functions between manageable anthropogenic stressors (e.g. eutrophication, contaminant levels) and ecological endpoints that govern or indicate the provision of services are needed (Wainger and Boyd, 2009). Where information exists, we refer to stressor-response relationships that may be useful for those analyses.

Coastal wetlands provide a variety of services linked to their ecological function (Table 2; Mitsch and Gosselink, 2000a; MEA, 2005). Wetlands also provide humans with recreational opportunities that are indirectly linked to these ecological services and functions, and which we will not address. We do touch upon biological diversity, which is not itself a service, but it is recognized to be closely linked to ecosystem health and services, and therefore relevant to ecosystem service assessments (MEA, 2005). We cite numbers of species (fish, birds, reptiles, and amphibians) found in GLCWs, both as a reflection of biodiversity and because we consider the use of GLCWs by fish and wildlife to be direct evidence and measures of fisheries support and wildlife habitat services. Although quantitative relationships between the characteristics of biological communities and the services they provide have not been established, we believe that the responses of biota to anthropogenic stress indicate potential effects on ecosystem services.

Wildlife habitat ecosystem service

Birds

In a thorough review of the use of GLCWs by waterfowl, Prince et al. (1992) concluded that Great Lakes coastal wetlands are regionally important to waterfowl production, with more than 30 species of waterfowl using Great Lakes coastal zones during breeding, migration, or wintering. Swans (Cygnini),

Table 2. Summary of services provided by Great Lakes coastal wetlands, with current or potential indicators, estimated importance of GLCWs in provision of services, and present level of available information.

Ecosystem Service Endpoints/Indicators	Importance	Information
Wildlife Habitat		
birds: presence/absence, habitat	high	high
amphibians & reptiles: presence/absence, habitat	high	moderate
mammals (muskrats): presence/absence	limited	limited
Fisheries Support		
fish: presence/absence, habitat	very high	high
Water Quality Improvement		
nutrient retention: indicators lacking	high but variable	locally high
sediment retention: indicators lacking	variable	limited
Plant Crops		
wild rice: presence/absence, area	localized/rare	limited
Climate Regulation		
carbon sequestration: indicators lacking	unknown	lacking
Coastal Protection		
lacustrine wetland extent	localized	limited

Geese (Anserini), Dabbling Ducks (Anatini), Perching Ducks (Cairinini), Diving Ducks (Aythyini), Sea Ducks (Mergini), and Stiff-tailed Ducks (Oxyurini) all breed in coastal wetlands. GLCWs supported an estimated total of 26,450 breeding pairs of Dabbling Ducks, the most common ducks using coastal wetlands. The greatest use of GLCWs by waterfowl is during migration in the spring and, especially, the fall. For example, annual migratory waterfowl use in Lake St. Clair coastal wetlands in the 1970s totaled over 12 million use-days, of which nearly 10 million days were during autumn.

In 40 coastal wet meadows along northern Lake Huron, Riffell et al. (2001) identified 53 bird species, of which 26 nested there. The probability of occurrence of nine species (Swamp Sparrow *Melospiza georgiana*, American Bittern *Botaurus lentiginosus*, Virginia Rail *Rallus limnicola*, Sora *Porzana carolina*, Mallard *Anas platyrhynchos*, Eastern Kingbird *Tyrannus tyrannus*, Sedge Wren *Cistothorus palustris*, Red-winged Blackbird *Agelaius phoeniceus*, and American Goldfinch *Carduelis tristis*) increased with wetland or habitat patch area. Species richness and composition of breeding bird communities vary across the Basin and according to wetland characteristics. Species richness and abundance increased with wetland habitat complexity (Riffell et al., 2003). In western Lake Huron, 80 bird species use protected coastal wetlands (Burton and Uzarski, 2009), and 63 species used Saginaw Bay wetlands for feeding or breeding (Prince and Burton, 1996). Among 215 coastal wetlands across the U.S. portion of the Great Lakes Basin, there were 155 species of breeding birds (Howe et al., 2007); bird community composition differed geographically and by wetland geomorphic type (Hanowski et al., 2007). The proportion of wetland-obligate birds declined with the proportion of developed land within 1 km of wetlands. In a comprehensive inventory of the Fish Creek wetland complex on Chequamegon Bay on Lake Superior, 226 bird species (including 23 species of waterfowl) used the wetland, 109 of which for breeding (Pratt, 1981). Among 6 different coastal wetlands also along the south shore of Lake Superior, 112 bird species were identified, and individual systems held from 32 to 72 species (Elias and Meeker, 1999).

Organohalide contaminants are the most well documented anthropogenic stressors on bird populations in the Great Lakes. Chemical contamination in GLCWs has been much less thoroughly investigated than in the Great Lakes themselves, but comparable contaminant concentrations in Snapping Turtle and Herring Gull eggs suggest that wetlands and open-water habitats have similar contaminant levels (Bishop and Gendron, 1998). The widespread application of DDT for mosquito control in the 1940s and 1950s led to food web biomagnification of its biodegradation product, DDE, whose powerful endocrine disrupting properties led to reproductive failure and population declines in fish-eating birds. Many bird populations recovered after

DDT was banned in the early 1970s, but residual contamination may still suppress reproduction in some areas (Bowerman et al., 1995). Organohalides such as PCBs, dioxins, and furans continue to have detrimental effects on Great Lakes bird populations (Grasman et al., 1998). Following the bird reproductive failures from DDT, attempts to balance the desirable and undesirable effects of pesticides through new formulations were a precursor to the ecosystem services approach of accounting the positive and negative effects of management actions.

The diversity of coastal wetland wildlife habitat, which is primarily provided by wetland vegetation, is maintained by water-level changes at a variety of temporal scales (Keough et al., 1999; Wilcox, 2004; Wilcox and Nichols, 2008). Regulation of the water levels of Lake Ontario has reduced annual water level fluctuations from 2 meters, prior to regulation, to 0.9 m (Maynard and Wilcox, 1997), causing marked changes in vegetation structure (Wilcox and Meeker, 1995) that may have led to declines in wetland birds at a regional scale (Steen et al., 2006; Timmermans et al., 2008). Vegetation structure and anthropogenic disturbance influence the presence (Peterson and Niemi, 2007) and abundance (Miller et al., 2007) of bird species in GLCWs, through declines in disturbance-intolerant species and increases in tolerant species. For tolerant species such as Red-winged Blackbirds *Agelaius phoeniceus*, landscape disturbance suppressed nesting success through increasing the accessibility of nests to predators (Grandmaison and Niemi, 2007).

The systematic responses of biological communities to disturbance have been used as indicators of system condition. A breeding bird Index of Biological Integrity (IBI) captured responses to disturbance, but its performance was affected by water level (Crewe and Timmermans, 2005). Using a landscape-scale stressor characterization of wetland condition, Howe et al. (2007) developed functions describing the probability of occurrence of 23 individual bird species in GLCWs of varying condition. Such relationships could be applied toward management in an ecosystem service framework by relating the probability of occurrence of desirable wildlife to underlying manageable stressors such as nutrient enrichment or landscape practices.

Amphibians and reptiles

Approximately 33 species of amphibians occur across the U.S. portion of the Great Lakes Basin, and because the Basin contains the northerly range limit for approximately half of those species, richness declines with increasing latitude. Lake Erie hosts 28 species, Ontario 22, Michigan 21, Huron 17, and Superior 17 species (Hecnar, 2004), suggesting that indicators based upon amphibian richness should be Lake-specific. Amphibian diversity is enhanced by wetland habitat complexity and presence of adjacent riparian forests (Hecnar, 2004). In a single Lake Superior wetland, Pratt (1981) listed 11 frog species, 1 toad, 6 salamander, 4 turtle, and 6 snake species. Richness in protected coastal wetlands in western Lake Huron (Burton and Uzarski, 2009) was estimated to exceed 20 species each of amphibians and reptiles.

Anuran species occurrence responds to habitat variables at multiple spatial scales (Price et al., 2007). Because anurans require both terrestrial and aquatic habitats during their life cycles, their distribution is influenced by both landscape-scale and local habitat features (Price et al., 2007). Across the Basin, amphibian species richness responded negatively to human development within 5000 meters of wetlands (Brazner et al., 2007). Although no amphibian species are known to have been extirpated across the Great Lakes Basin, about two-thirds of species have conservation concerns somewhere in the Basin. Habitat loss has been reported for 60% of species, pollution for 43%; over-harvesting for 14%, and disease for 6% (Hecnar, 2004). Turtle assemblages had greatest species richness at intermediate levels of wetland condition, and road density shifted turtle sex ratios due to road mortality of females (DeCatanzaro and Chow-Fraser, 2010). Organic contaminant concentrations influenced Snapping Turtle hatching success and hatchling deformities in Lake Ontario coastal wetlands (Bishop et al., 1991).

Price et al. (2007), in an approach similar to that of Howe et al. (2007), derived functions describing the probability of occurrence of anuran species in GLCWs of varying condition. Those relationships may also be useful to relate the occurrence of desirable amphibian wildlife to stressor regimes in an ecosystem services context.

Mammals

Many species of mammals are associated with coastal wetlands; for example, Pratt (1981) listed 51 species that used one coastal wetland on Lake Superior. However, most mammals are not obligate wetland species, instead using them periodically for feeding or cover. In contrast, Muskrats *Ondatra zibethicus*, one of the most economically important furbearers in the United States, are almost completely dependent upon wetlands. Muskrat abundance is controlled by water depth, water quality, and vegetation type and abundance (Mortsch, 1998). Because water level governs vegetation type, water level disturbance is extremely influential on Muskrat populations. Sufficient water depth is necessary for maintenance of open water below ice in the winter and access to food sources, and the seasonal timing of low water levels can control Muskrat reproductive success (Mortsch, 1998). For other mammal species commonly associated with GLCWs, little has been published on abundance patterns across the Basin or responses to stressors.

Information needs for wildlife

Indicators of wildlife-related ecosystem services are needed. Although wildlife-based indicators of system condition have been developed, it is not known whether they are reliable indicators of wildlife ecosystem services. Further, whereas species presence or probability of occurrence may serve well as indicators, assessment of physical habitat for wildlife might be less time-consuming than wildlife surveys. Most wetland habitat indicators (Thoma, 2006; Johnston et al., 2007) have measured the responses of habitat to anthropogenic stressors, and may not reflect the support of biota. The development of wetland habitat-wildlife relationships would help establish integrated wildlife assessments using habitat characteristics.

Fishery support ecosystem service

We define fishery support services as the ecological functions in GLCWs that foster the production of fish for commercial harvest or recreational angling. Fish also influence services through nutrient cycling and food web structure (Holmlund and Hammer, 1999), but we consider those roles to be distinct from fishery support. A direct indicator of fishery support by wetlands is the presence of fish species. Coastal wetlands support both wetland-resident species and Great Lakes residents subsidized by wetland production. From 75 to 90% of Great Lakes fish species use coastal wetlands for part of their life cycle, including at least 21 sport and commercially important species such as Northern Pike *Esox lucius*, Walleye *Sander vitreus*, Muskellunge *Esox masquinongy*, and Largemouth Bass *Micropterus salmoides* (Jude and Pappas, 1992; Brazner et al., 2000). Coastal wetlands provide essential nursery habitat for both wetland-resident and migratory lake fishes. The well-studied Fish Creek wetland on Chequamegon Bay of Lake Superior is used by 50 species of fish; 37 for spawning, 12 for migration, and 49 as a nursery area. The wetland provides a nursery for nearly every species of fish found in 3440-km^2 Chequamegon Bay. A 1980 mark-recapture study concluded that Fish Creek wetland supported a spawning population of Northern Pike in excess of 1200 adults (Pratt, 1981). Additionally, GLCWs support important forage species for coastal and nearshore food webs (Jude and Pappas, 1992; Wei et al., 2004).

Studies of the interactions of wetlands and adjacent Great Lake have demonstrated the role of wetlands in support of lake fisheries. Using entrainment of juvenile fishes in industrial cooling water intakes to infer production from adjacent wetlands, coastal and inland marshes in the State of Michigan were estimated to produce 494 and 151 fingerlings ha^{-1} yr^{-1} of Walleye and Northern Pike, respectively (Jaworski and Raphael, 1978). Brazner et al. (2001) found a large net export of individuals from a Lake Superior coastal wetland, reflecting the important function of wetlands as nurseries for sport and forage fishes; more than 40,000 young-of-year (YOY) Yellow Perch, >600 YOY Northern Pike, >8,000 yearling Emerald Shiner *Notropis atherinoides*, and >500 YOY Brown Bullhead *Ameiurus nebulosis* emigrated from the wetland to the adjacent lake in one season. A study comparing the size structure of fish entering and exiting a gated marsh quantified growth from foraging in the wetland (Herdendorf, 1987). Quantification of fisheries support services provided by coastal wetlands to nearshore fisheries (e.g. using commercial landings; Krantzberg and de Boer, 2006) is difficult because of the coarse spatial scale of fisheries data and the physical separation of nearshore fisheries from wetlands. Modern approaches using chemical signatures retained in fish tissues to trace past habitat use are being used to address this issue. Otolith analyses have been used to identify the natal coastal wetlands of fishes caught in coastal waters (Brazner et al., 2004), and quantifications of the nutritional contributions of wetland and lake habitats using stable isotope techniques indicate strong interactions between nearshore and wetland habitats through foraging activities of adult fish (Sierszen, unpubl.).

Quantity and quality of wetland habitat determine the value of wetlands for fishes. In general, larger wetlands with greater shoreline complexity and habitat diversity host a greater variety, abundance and biomass of fish (Hansson et al., 2005; Jacobus and Webb, 2005). A broad body of literature (reviewed in Smokorowski and Pratt, 2007) bolstered by specific studies in GLCWs (Brazner and Beals, 1997; Uzarski et al., 2005; Trebitz et al., 2009) establishes that wetland/littoral fish composition, diversity, and abundance (and therefore fisheries services) are strongly tied to the habitat provided by aquatic vegetation. Stressors that degrade the extent, zonation, and structural complexity of aquatic vegetation therefore can negatively impact fish composition (Jude et al., 2005). These include vegetation removal by beach grooming and channel dredging (Uzarski et al., 2009), suppression of water-level fluctuations that maintain coastal wetland vegetation diversity (Johnson et al., 1997; Bouvier et al., 2009; Wilcox and Xie, 2008), loading of nutrients and sediments that degrades vegetated habitat by decreasing water clarity and fostering dominance by plant species with poor habitat value (Lougheed et al., 2001; Frieswyk et al., 2007; Trebitz and Taylor, 2007), land-cover changes that lead to greater flood peaks and sedimentation (Fitzpatrick et al., 1999), and the foraging activity of Common Carp which can uproot submersed vegetation and resuspend sediments (Chow-Fraser, 1999). Carp- and wind-driven sediment resuspension may also cause reintroduction of nutrients stored in sediments. Besides fish composition changes mediated through vegetation structure changes, stressors may also directly foster shifts towards less desirable turbidity-tolerant species (Uzarski et al., 2005; Seilheimer and Chow-Fraser, 2007; Trebitz et al., 2009). Fisheries services may also decline with eutrophication simply because algal blooms and reduced water clarity make people less inclined to participate in recreational angling, regardless of direct effects on fish (Krantzberg and de Boer, 2006).

Invasive species continue to alter the ecology of the Great Lakes and cause significant economic damage to commercial and recreational fisheries (Mills et al., 1994; Pimentel et al., 2005). The Round Goby *Neogobius melanostomus* threatens Smallmouth Bass *Micropterus dolomieu* through nest predation and higher energetic costs of nest guarding (Steinhart et al., 2004, 2005). Declines in native fishes have occurred because the Round Goby outcompetes the native Mottled Sculpin *Cottus bairdi* (Janssen and Jude, 2001) and Logperch *Percina caprodes* (Balshine et al., 2005). Food web studies of Ruffe *Gymnocephalus cernuus* and White Perch *Morone americana* in coastal wetlands have shown that they have similar food web niches to native Yellow Perch and thus have the potential to negatively affect Yellow Perch populations (Sierszen et al., 1996), although changes in fish communities have not yet been linked to Ruffe (Bronte et al., 1998). Invasive macrophytes such as *Phragmites australis* and *Typha x glauca* develop dense stands and suppress habitat structural diversity (Frieswyk and Zedler, 2007; Tulbure et al., 2007).

Information needs for fisheries

A stronger understanding of the relationships among stressors, wetland habitat, and fisheries is necessary for management, restoration, and ecosystem service analyses. Because many fishes that use GLCWs move among wetland and nearshore habitats, estimates of fisheries support would be improved by understanding the influence of habitat spatial relationships, quantifying contributions of different habitats through tagging studies or analyses of chemical biomarkers (e.g. tissue and otolith analyses; Brazner et al. [2000, 2004]; stable isotope analyses; Hoffman et al. [2010]), and understanding responses of habitat to watershed disturbance and resulting stressors (e.g. nutrient and sediment loading). Robust relationships between habitat attributes and fishery support would suggest habitat-based service indicators. As with the wildlife habitat ecosystem service, fisheries services may be more efficiently indicated through habitat evaluation than by sampling the biota, to avoid problems associated with gear selectivity and seasonal fish availability. Finally, stressor-response relationships that predict the effects of management actions on fisheries services are needed. Probabilistic approaches as applied by Howe et al. (2007) and Price et al. (2007), or habitat occupancy modeling (Bayley and Peterson, 2001), could relate probability of species occurrence to wetland condition, habitat, and stressors.

Water quality improvement ecosystem service

Phosphorus and nitrogen retention

Nutrient retention by wetlands has been identified as a significant ecosystem service because it decreases nutrient loads to nearshore zones, where nutrient enrichment is an ongoing concern (Mitsch and Gosselink, 2000b; Zedler and Kercher, 2005). Rates of nutrient cycling, production and removal are higher in wetlands relative to other ecosystem types (Schlesinger, 1997; Mitsch and Gosselink, 2000a). Phosphorus (P) has been the primary nutrient of concern for freshwater systems, but nitrogen (N) enrichment can also stimulate algal production (Hecky et al., 1993; North et al., 2007).

Coastal wetlands may provide significant water quality improvement services to the Laurentian Great Lakes through P removal from tributary waters. The primary mechanism of P removal in GLCWs is sedimentation and burial of particulate forms, including organic matter (Mitsch and Reeder, 1992). Studies of nutrient dynamics in Old Woman Creek wetland on Lake Erie report net P retention (Klarer and Millie, 1989; Mitsch and Reeder, 1992; Krieger, 2003). Annual P budgets during a drought year (Mitsch and Reeder, 1992) and during years with average precipitation (Krieger, 2003) showed estimates of total phosphorus (TP) retention percentages to be similar among years (33–36% of imported TP), whereas areal rates of TP retention were higher in years with average precipitation (3.32 g m^{-2} yr^{-1}, calculated from Krieger, 2003) than in the drought year (0.2 g m^{-2} yr^{-1}). Retention of soluble reactive phosphorus (SRP) in Old Woman Creek wetland was more variable than TP and ranged from 21–80%. In the coastal wetland at the Quanicassee River on Saginaw Bay, Lake Huron, there was lower net annual retention of TP (2.5%) but a rate (0.53 g m^{-2} yr^{-1}) within the range of values for Old Woman Creek (Wang and Mitsch, 1998). Areal retention rates for these wetlands are within the range of values reported for other freshwater wetlands (Johnston, 1991). In Lost Creek wetland on Lake Superior under flow regimes ranging from spring snow melt to fall baseflow, net TP retention ranged from 4–24%, and again SRP dynamics were more variable than TP dynamics. Ratios in SRP concentration between inflowing and outflowing waters suggested that Lost Creek can function as a SRP sink at times (up to 76% retention of SRP), and a SRP source at other times, likely due to mineralization of organic P (Morrice et al., 2004).

The value of GLCWs as P sinks depends on their ability to store P for long time periods, but the time scales of P storage are unknown. P stored in wetland sediments that are stable under average flow conditions may be mobilized during a flood, resulting in the transport of several years of accumulated P to nearshore waters. Because much of the storage and export of P is particle-associated, studies of coastal wetland sediment dynamics during extreme flow events (Wilson et al., 2005) would provide insight into the time scales of P retention.

Studies comparing N concentrations in inflowing and outflowing waters demonstrated that coastal wetlands can be important in reducing N flowing from watersheds to the Great Lakes, but did not identify the biogeochemical processes responsible for N retention. As with P, N associated with particulate organic matter can be stored in wetland sediments. N, however, can also be removed from the biologically available pool by denitrification, or added through N fixation. Denitrification can be a significant sink for nitrogen in GLCWs (Tomaszek et al., 1997; McCarthy et al., 2007). Nutrient budgets derived from data for Old Woman Creek wetland (Krieger, 2003) indicate removal of 18% of imported dissolved inorganic nitrogen (DIN) and 15% of total nitrogen (TN), corresponding to areal rates of retention of 45 g DIN-N m^{-2} yr^{-1} and 41 g TN-N m^{-2} yr^{-1}. DIN was strongly retained in Lost Creek wetland (11–94%; Morrice et al., 2004). N-limiting conditions are conducive to biological uptake of imported inorganic N and suggest that assimilation and burial may be important routes of N retention, whereas investigations in Old Woman Creek illustrate the importance of denitrification (Tomaszek et al., 1997; McCarthy et al., 2007).

Estimates suggest that the mass of nutrients retained by U.S. GLCWs is significant and approaches the mass of N and P flowing out of the Great Lakes via the St. Lawrence River. In other words, coastal wetlands may cut the amount of nutrient export by half. We provide a first-order approximation of basin-wide nutrient removal by GLCWs by applying areal rates of nutrient retention or biogeochemical process from site-specific studies to the total area of coastal wetlands in the Great Lakes Basin (Table 3). However, this approach assumes that all coastal wetlands have rates of nutrient retention similar to Old Woman Creek even though it is understood that GLCWs vary in factors that may organize nutrient retention, including biogeography, morphology and hydrology (Keough et al., 1999). A more refined approach to evaluating nutrient removal by GLCWs would account for those factors that result in significant differences among systems.

Sediment retention

Available studies suggest that water quality improvement through sediment retention by GLCWs can vary among systems and events, and that net retention and export may be time-scale dependent. Sediment retention by GLCWs has been recognized as contributing to water quality improvement (Klarer and Millie, 1989; Mitch and Gosselink, 2000a; Mitch and Reeder, 1992). However, the persistence of GLCWs requires that sediment also be exported (Wilson et al., 2005). Accordingly, estimates of sediment retention efficiencies in GLCWs have been highly variable. Three wetlands along the sandy eastern shore of Lake Michigan appeared to retain little of their suspended solid loads, based upon radioisotope analyses of sediment accretion rates in cores (Kadlec and Robbins, 1985). Load-based analyses in Old Woman Creek wetland found net export (11.5% above imports) of total suspended solids (TSS) over a one-year period, and storm event-related dynamics to vary from 60% TSS retention to 224% export (Krieger, 2003). An elegant radionuclide tracer analysis revealed that Old Woman Creek wetland retained 47% of incoming sediment between 1987 and 1997, with a sedimentation rate ranging from 0.4–1.0 cm yr^{-1} (Wilson et al., 2005). In one storm event the wetland retained 13% of incoming TSS, but resuspension and removal of previously-deposited sediment resulted in a net loss during the event (Wilson et al., 2005).

Information needs for water quality

Functional relationships between water quality improvement services and the natural and anthropogenic factors that govern them are lacking for GLCWs, and the uncertainty associated with estimating services based on data from few “representative” wetlands is large. For example, nutrient retention is strongly affected by hydraulic residence time, and watershed disturbance that alters hydrology and decreases residence time may have deleterious effects on the water quality service. Increases in nutrient loading may result in increased mass of nutrients retained, but it is not known whether nutrient retention efficiency is maintained across nutrient loading conditions. Watershed disturbance also causes increased sediment loads to streams and receiving waters, and effects on the amount and efficiency of sediment retention by GLCWs must be quantified. Because watershed disturbance can generate a syndrome of interrelated nutrient, sediment, and hydrologic effects, elucidating stressor effects on the water quality service will be both challenging and interesting.

The Laurentian Great Lakes Basin includes geographic regions that differ in climatic and geologic characteristics that may influence rates of nutrient and sediment retention (Omernick and Gallant, 1988; Keys et al., 1995). For example, water temperature, which controls rates of biogeochemical processes that are responsible for nutrient retention, differed significantly between wetlands of the two ecoprovinces representing the upper and lower Great Lakes (Trebitz et al., 2007). Old Woman Creek is located near the southern extent of the Great Lakes where water temperatures are warmer and conducive to higher rates of assimilation, mineralization and dentitrification than in northern wetlands. Biogeochemical process rates also vary with nutrient substrate concentrations. Within the Great

Table 3. Basin-wide annual estimates of total phosphorus (TP) and total nitrogen (TN) retention by coastal wetlands along the U.S. shore of the Great Lakes, excluding rivers and connecting channels. Annual retention was calculated by multiplying areal rates of DIN retention measured at Old Woman Creek (Krieger, 2003) by the total wetland area for each lake.

Waterbody	Wetland Area (ha)	TP Retention (tonnes P yr^{-1})	TN Retention (tonnes N yr^{-1})
Lake Superior	19000	637	7885
Lake Michigan	53800	1802	22327
Lake Huron	26400	884	10956
Lake Erie	12500	419	5188
Lake Ontario	5700	191	2365
Total	117400	3933	48721
Export via St. Lawrence R.[a]		5055	59900

[a]Export from Great Lakes is the annual load in the St. Lawrence River at Cornwall, Ontario (Aulenbach, 2006). Nitrogen load for the St. Lawrence River is NO_2+NO_3; TN data not available.

Lakes Basin, natural background nutrient concentrations can vary with parent geology, and phosphorus export can be higher in watersheds with sedimentary geology than in those on Precambrian granite (Dillon and Kirchner, 1975). Similarly, sediment imports and exports may vary with geology. Comparisons of nutrient retention in GLCWs from different biogegraphic regions are needed to evaluate the potential role of geography as a classification factor.

Morphology is considered to be a primary factor determining structure and function of wetlands (Brinson, 1996), and GLCWs are morphologically diverse systems (Albert et al., 2005). Depth, surface area, and shoreline complexity have been shown to influence nutrient retention in constructed wetlands, where large, shallow, and morphologically complex wetlands were most efficient at retaining N and small, deep wetlands most efficiently retained P (Hansson et al., 2005). The influence of morphology on nutrient or sediment retention in GLCWs has not been evaluated, and the only wetlands studied (Old Woman Creek, Quinicasse River, and Lost Creek) are all classified as riverine; no published measures of retention in lacustrine and barrier-protected classes are available. Nutrient retention also appears to differ among morphologically different areas within GLCWs (Johnston et al., 2001; Morrice et al., 2009), suggesting that morphological variability within as well as among wetlands must be considered.

Hydraulic residence time regulates nutrient retention in aquatic ecosystems including streams (Stream Solute Workshop, 1990; Valett et al., 1997), lakes (Vollenweider, 1976), and estuaries (Dettman, 2001). Coastal wetlands are hydrologically complex, with ranges in the strength of hydrologic connections to watershed and lake resulting in significant variability in hydraulic residence time (Trebitz et al., 2002). At Lost Creek wetland, retention was related to hydraulic residence time for N but not P (Morrice et al., 2004). Krieger (2003) found that proportions of imported N and P retained by Old Woman Creek during short residence time flood events were not different from retention under average flow conditions. It is difficult to evaluate the influence of residence time on nutrient retention in GLCWs from just three systems, especially since Old Woman Creek, Lost Creek, and Quinicasse River wetlands are hydrologically similar and represent a narrow range of the hydrologic variability among all GLCWs (Morrice, unpubl.).

Plant crops ecosystem service

Crop services reported for wetlands include food, fiber, hay, peat, timber, firewood, and horticultural stock (Mitsch and Gosselink, 2000a). The only significant crop currently harvested from Great Lakes coastal wetlands is Wild Rice *Zizania palustris*, a wetland obligate species. While Wild Rice does support a modest subsistence and commercial harvest, its greater importance lies in the cultural and spiritual value it holds for Native American tribes in the Great Lakes region (Vennum, 1988; Meeker, 1993; MN DNR, 2008). Thus, in addition to a commercial value, Wild Rice has a substantial cultural value which is unlikely to scale directly with more easily established market values or yields.

Wild Rice is a cold-water annual that occurs only in the northern Great Lakes (Lake Superior and the northern portions of Lakes Michigan and Huron; Pillsbury and McGuire, 2009) and more often in inland water bodies (Sundance, 2007; Drewes, 2008; Pillsbury and McGuire, 2009). A synoptic survey of GLCW vegetation (Trebitz, unpubl.) found Wild Rice in only a few coastal wetlands within the species' range on the U.S. side, and in significant quantities in even fewer. Detailed information on Wild Rice ecology is available for one large wetland complex on Lake Superior, the Kakagon Slough (Meeker, 1993). This wetland complex lies entirely within the tribal lands of the Bad River band of the Lake Superior Chippewa, and harvest levels are not published.

Because Wild Rice develops from seeds each year rather than forming a perennial root system, young shoots are susceptible to uprooting and do not have the energy reserves to withstand shading. Wild Rice also requires permanent inundation. Threats to Wild Rice include reductions in water clarity associated with eutrophication or sediment loading, invasive plant species, and water level controls that reduce the water-level variability to which it is adapted. Seed germination requires a 3–4 month dormancy period in near-freezing water temperatures, and the range of Wild Rice is likely to contract northward under global climate change (MN DNR, 2008). Regionally, the number of water bodies supporting Wild Rice and the quantity of the harvest has been declining for several decades (Drewes, 2008; MN DNR, 2008) and even small levels of agriculture and residential development in the watershed may be detrimental to Wild Rice populations (Pillsbury and McGuire, 2009).

Information needs for plant crops

With the exception of one study on Wild Rice in Kakagon Slough (Meeker, 1993, 1996) most published information on Wild Rice pertains to inland water bodies. The number of GLCWs supporting Wild Rice appears to be small. Because of the very limited extent of Wild Rice in coastal wetlands, we do not consider the plant crop ecosystem service to be a major function of these systems and do not identify this service as a research priority for GLCWs.

Climate regulation

Carbon sequestration

We found no publications providing estimates of carbon sequestration for GLCWs. However, if carbon accumulation rates for coastal wetlands are bounded by rates published for northern peatlands in the conterminous U.S. (0.71 mg C $ha^{-1}yr^{-1}$) and those for freshwater mineral-soil wetlands (0.17 mg C $ha^{-1}yr^{-1}$; Bridgham et al., 2006), total C accumulation by U.S. GLCWs may lie between 21.5 and 89.5 g C yr^{-1} (using wetland areas from Table 1). As a consequence of the low rates of C sequestration for freshwater wetlands compared to those for estuaries (2.13 mg C ha^{-1} yr^{-1}; Bridgham et al., 2006) and the small current area of GLCWs, the C sequestration estimated for GLCWs is a tiny proportion of the total for wetlands in the conterminous U.S. (estimated at 10.3 Tg yr^{-1}; Bridgham et al., 2006). If these estimates are accurate, carbon sequestration may not be a major ecosystem service provided by GLCWs, but given the considerable uncertainty in these estimates, C sequestration should be further evaluated.

Coastal protection

We found a single study of wave attenuation through GLCW macrophytes that suggests a significant coastal protection service for lacustrine (fringing) wetlands (Silander and Hall, 1997). Plant type did not significantly influence the wave attenuation characteristics of the wetland. Typical wave transmission coefficients of 0.8 to 0.6 were obtained for plant beds 10 to 20 m in width, respectively. Thus, a stand of wetland plants 20 m wide would attenuate waves by 40%. Lacustrine wetlands are naturally rare in Lake Superior and much reduced in the lower Lakes, although some significant systems remain at Saginaw Bay on Lake Huron, Grand Traverse Bay and Bay de Noc on Lake Michigan, Lake St. Clair, Long Point Bay on Lake Erie, and Black River Bay and the Bay of Quinte on Lake Ontario.

Conclusions and Management Implications

Great Lakes coastal wetlands provide an array of ecosystem services that should be considered during management and policy formulation. There is strong evidence that GLCWs provide extensive wildlife habitat, fishery support, and water quality improvement ecosystem services. Management decisions would be informed by development of quantitative stressor-response relationships between specific stressors or land use practices and the delivery of ecosystem services. Wildlife and fish, and by extension the ecosystem services associated with them, exhibit strong relationships with wetland condition and are therefore susceptible to anthropogenic stressors. The influence of natural factors and anthropogenic stressors on nutrient and sediment retention must also be better understood. There is almost no existing information about coastal protection and carbon sequestration for Great Lakes wetlands. Coastal protection may be locally significant where extensive fringing coastal wetlands persist; the effects of anthropogenic stressors other than reduction in wetland extent are not known for this service. GLCWs may not contribute significantly toward carbon sequestration at the continental scale, although only cursory estimates are available. The plant crop service is most strongly represented by Wild Rice harvest, which has strong cultural importance among native Americans, but very few GLCWs support Wild Rice.

Research needs also include the development of ecosystem service indicators to efficiently gauge the effects of management actions. Because the functions responsible for ecosystem services are often difficult or expensive to measure, monitoring and assessment of services would be facilitated by more easily-measured structural system attributes. Currently, best available indicators for wildlife and fish may be based upon presence/absence, but because both wildlife and fish respond strongly to habitat quality (particularly vegetation type and abundance), habitat assessments may be more efficient at evaluating fish and wildlife services than sampling organisms once strong habitat-service relationships are developed. For water quality improvement and carbon sequestration, research is needed to determine even the basic factors (e.g. hydraulic residence time, sedimentation) upon which to base indicators.

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