Chapter 9
Invertebrates in Great Lakes Marshes

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Introduction

These habitats form where hydrologic energy sources, such as waves and lake currents, are reduced to the point that macrophytes can establish and persist and where sediment is conducive to macrophyte growth. While marshes form along the shorelines of many large lakes globally, this chapter focuses primarily on marshes of the Laurentian Great Lakes in North America (Fig. 9.1). These are some of the best-studied freshwater coastal wetlands in the world, and much of the research on Great Lakes marsh invertebrate ecology is applicable to other global lakeshore wetlands.

The Laurentian Great Lakes system includes Lakes Superior, Michigan–Huron (hydrologically a single lake), Erie, and Ontario as well as their connecting waterways (Fig. 9.1a). The Great Lakes extend from 41°20′N latitude (the southern shore of Lake Erie) to approximately 49°N latitude (Nipigon Bay on the north shore of Lake Superior), representing approximately 800 km of latitude. The Great Lakes span 1200 km of longitude, from approximately 76°W (eastern Lake Ontario) to 92°W longitude (western Lake Superior). The Great Lakes have over 17,000 km of shoreline, which is greater than the total length of the United States' east and west coasts, combined. This immense freshwater system contains approximately 21 % of the world's surface freshwater supply and 84 % of North America's surface freshwater. Over 2000 coastal wetlands occur along the Great Lakes shoreline (Fig. 9.1b). In this chapter, "lakeshore marsh" refers to a coastal wetland that contains at least some habitat that is dominated by herbaceous vegetation, though these wetlands often contain areas that are dominated by woody vegetation (i.e., swamp) as well.

Lakeshore marshes of the Laurentian Great Lakes are important habitats for fish, amphibians, reptiles, wading birds, and waterfowl (Harris et al. 1983; Jude and Pappas 1992; Prince et al. 1992; Maynard and Wilcox 1997; Weeber and Vallianatos 2000; Uzarski et al. 2005). Invertebrates make up a large component of the diets of these wetland fauna, thus linking algal and detrital energy sources to higher trophic levels. These energy pathways—from primary producers to invertebrate consumers

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to fish and other macrofauna—support important functions of coastal wetlands in the broader lake ecosystem (Brazner et al. 2004; Sierszen et al. 2012a). Therefore, because invertebrates represent key trophic linkages in wetland food webs, environmental drivers of invertebrate community structure have ecosystem-level implications.

Climate and Its Influence on Invertebrate Assemblages

In general, the Great Lakes region has a temperate climate with pronounced seasonality. Three primary factors influence the region's climate: air masses that originate in other areas, the continental location of the basin, and the effect of the Great Lakes themselves. In the summer, conditions in the northern portion of the basin are most influenced by cold dry air from the Canadian northwest while the southern portion of the basin receives warm moist air from the Gulf of Mexico. The balance of these different air masses largely dictates local conditions over relatively short timescales. Average July daytime high temperatures are typically around 25 °C in the northern Great Lakes basin and around 30 °C in the southern portion of the basin. In winter, the region is most frequently influenced by Arctic air from the northwest of the continent. Average January nighttime lows are typically around −15 °C in the northern part of the basin and −5 °C in the south. Great Lakes water temperatures continue to drop throughout the winter. Ice frequently covers all of Lake Erie by late winter. The other lakes rarely are fully ice-covered but coastal ice is common. Because coastal wetlands occur in shallow protected bays and inlets, they are usually ice-covered throughout the winter on all of the Great Lakes. Shifting ice along the coast creates an "ice foot" that redistributes sediment and rhizome mats in coastal wetlands. This physical disturbance is an important driver of spatial heterogeneity in lakeshore marsh vegetation communities, which leads to heterogeneity in the resident invertebrate communities (Burton 1985).

Spring and autumn in the Great Lakes region are characterized by highly variable weather. The lakes are slower to warm than the land in the springtime, which tends to keep coastal areas cool well into the spring. In most years, this delays the leafing and blossoming of plants and protects wetland vegetation from late frosts. The lakes are also slow to cool in the autumn, keeping coastal areas warmer than inland regions of the same latitude. These moderating effects of the lakes on coastal climatic conditions also influence wetland invertebrate phenology and the timing of emergence relative to more inland wetlands.

The temperate climate and strong seasonality of the Great Lakes region have significant implications for invertebrate life histories. Most invertebrates cope with the freezing temperatures and ice cover in winter by entering into a dormant stage in the autumn and reemerging the following spring or summer when conditions are once again favorable. Dormancy may involve either quiescence or diapause. Quiescence is the slowed or completely halted development that results as a direct response to the onset of unfavorable conditions, with development resuming when

Fig. 9.1 (**a**) The Laurentian Great Lakes and the Great Lakes drainage basin. Select coastal cities, political boundaries, major tributaries, and interconnecting channels are also included (*source*: US Army Corps of Engineers, Detroit District). (**b**) Locations and hydrogeomorphic types of Great Lakes coastal wetlands identified by the Great Lakes Coastal Wetlands Consortium

conditions improve. Diapause is an arrested state of development triggered by specific physiological stimuli. Major environmental cues that induce and/or terminate diapause include temperature, photoperiod, moisture, pH, and changes in dissolved oxygen, among others. The ability to overwinter in a dormant stage and then rapidly recolonize habitats when conditions are favorable is a key adaptation for marsh invertebrates in temperate climates, including those in the Great Lakes. Patrick et al. (2014) noted dramatically increasing invertebrate diversity and density from May to August in a Lake Michigan drowned river mouth wetland and attributed this to taxa coming out of resting stages as conditions became increasingly favorable and to the developing aquatic vegetation communities that provide physical habitat for invertebrates.

Strong seasonality in the Great Lakes region also influences the number of generations that invertebrate species can produce in any given year (i.e., voltinism). Many invertebrate taxa inhabiting Great Lakes coastal wetlands are univoltine, emerging as adults to reproduce only once per year, often during the warm summer months. However, many other taxa, especially insects in the order Diptera, are able to reproduce multiple times throughout the growing season (i.e., multivoltine), with the number and timing of generations dictated by local conditions. Kovalenko et al. (2014) compiled voltinism information for 77 insect taxa collected from Great Lakes littoral habitats (including lakeshore marshes) and found that 48 of these were univoltine, with an additional 10 taxa representing combinations of bi-, uni-, semi-, and merovoltinism. These 58 non-multivoltine taxa represented a majority of insect taxa that were evaluated (75 %) and belonged primarily to the orders Odonata, Trichoptera, and Ephemeroptera, along with a few other rarely occurring groups.

Hydrology

One of the greatest effects of climate on lakeshore marshes is its influence on lake water levels. Water levels of the Great Lakes represent a dynamic balance between inputs from tributaries, precipitation, and groundwater versus losses through connecting channels, evaporation, and withdrawal. Humans exert some control over these fluxes, especially through connecting channels with control structures and via withdrawals and diversions (see "Conservation and Management" section below). However, most variability in water levels of the Great Lakes remains the result of factors out of human control. Fluctuations in Great Lakes water levels occur over varying timescales—from hourly to decadal—and cause coastal habitats to flood and dry as water levels rise and fall.

Pronounced intra-annual (i.e., seasonal) water-level fluctuations result from differences in lake inputs and outputs that occur throughout any given year. Water levels in Lake Michigan–Huron, for example, typically reach an annual maximum in August while Lake Superior reaches its maximum in September, after the previous winter's snowmelt and spring rains have had sufficient time to accumulate.

Annual water-level minima generally occur in late winter when evaporation coincides with reduced tributary inputs. Over broader timescales, variation in basin inputs and outputs from 1 year to the next can cause dramatic interannual water-level fluctuations, often on the order of 1–1.5 m over decadal periods (Fig. 9.2).

Water-level fluctuations are a natural part of the Great Lakes ecosystem. Accordingly, plant and animal species inhabiting lakeshore marshes are uniquely adapted to survive and even flourish in habitats with cyclical wetting and drying (Wilcox 1995; Keough et al. 1999; Mayer et al. 2004; Albert et al. 2005; Uzarski et al. 2009). For example, many wetland plants that cannot establish under permanently flooded conditions are able to germinate in seasonally flooded habitats that maintain a non-flooded, aerobic environment during the spring and early summer. Seedlings of many wetland plants can then survive as water levels rise (Gathman et al. 2005), which results in the productive and diverse vegetation assemblages found in lakeshore marshes. These macrophytes, which often exhibit "zonation" in lakeshore marshes due to physical factors (e.g., depth and wave energy), in turn, form the physical habitat template that invertebrate communities assemble within (Burton et al. 2002; Gathman and Burton 2011).

Superimposed on the seasonal and interannual water-level variation are short-term fluctuations caused by wind-driven or atmospheric pressure-induced seiches. Seiche period depends on basin morphology and wind direction but periods from 2 to 10 h are typical. Seiche amplitudes of 10–20 cm are most common across the Great Lakes (Trebitz 2006), though seiches over 1 m are possible and are generally associated with strong storms. Seiche action causes the shallow marsh habitats at the land–water interface, such as meadow marsh, to cyclically flood and drain several times per day. This is especially pronounced in marshes with gently sloping bathymetry, such as those around Saginaw Bay, Lake Huron. Typical bathymetric slope for Saginaw Bay marshes is approximately 0.25 cm per 1.0 m (M.J. Cooper, unpublished data). Thus, a 15 cm seiche, which is common for Saginaw Bay, will cause the water's edge to move 60 m shoreward and lakeward during a single seiche cycle. The unique inter-seiche meadow marsh habitat is home to invertebrate taxa that are adapted to tolerate such dynamic conditions and exploit the detrital food resources commonly available within these habitats (Burton et al. 2002). For example, collector/gatherer and detritivore crustaceans such as *Gammarus*, *Hyalella*, and *Caecidotea* are often found in high densities within seiche-influenced wet meadow zones (Cardinale et al. 1998; Burton et al. 2002).

The regular water-mixing action induced by seiche activity also helps to distribute nutrients and other dissolved materials within and among lakeshore wetlands (Trebitz 2006). Large storm-driven seiches, particularly when combined with high-energy waves, can serve as a strong physical disturbance in lakeshore marshes, causing sediment redistribution and even destruction of emergent vegetation, with concomitant impacts on resident invertebrate communities. Large-amplitude seiches can also cause vast areas of some marshes to be flooded at highly irregular intervals, especially in marshes with gently sloping bathymetry such as those on Saginaw Bay and western Lake Erie.

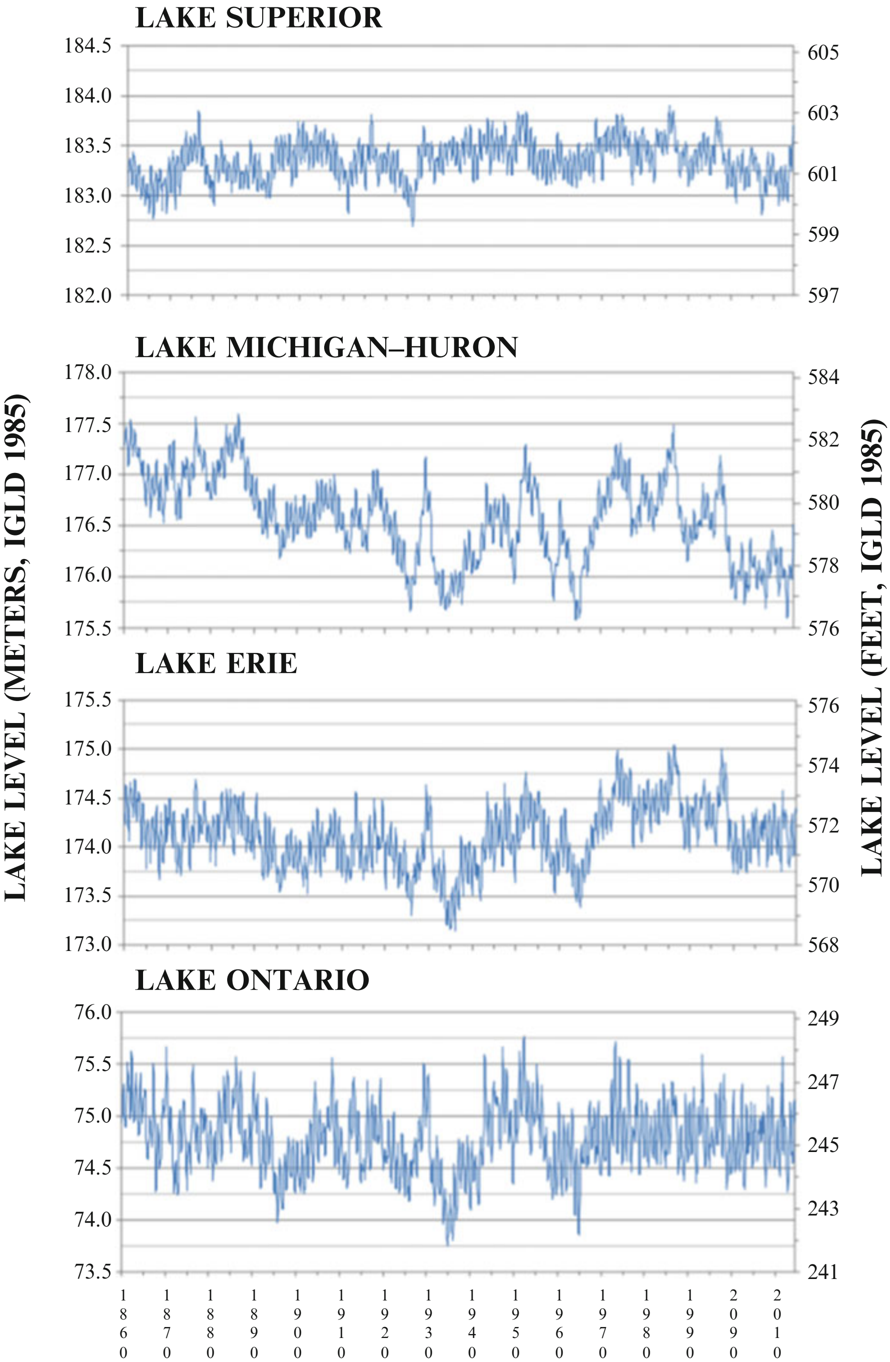

Fig. 9.2 Hydrographs for all five Great Lakes for the period 1860–2013. The figures show the high variability in water levels over the 153 years and the dampening of variability that occurred on Lake Ontario after the Moses–Saunders Power Dam went into operation in 1958. Data were obtained from the National Oceanic and Atmospheric Administration's Center for Operational Oceanographic Products and Services (NOAA CO-OPS; http://www.co-ops.nos.noaa.gov/). Figure courtesy of Douglas A. Wilcox (State University of New York–College at Brockport)

Lakeshore Marsh Hydrogeomorphic Types

In 2002, the Great Lakes Coastal Wetlands Consortium developed a hydrogeomorphic wetland classification system to characterize coastal wetlands of the Laurentian Great Lakes (Albert et al. 2005). The classification system separates wetlands into three broad types—lacustrine, riverine, and barrier-protected—based on geomorphology of the shoreline, primary water source, and hydrologic connectivity to the lake. The scheme includes finer-resolution classification as well and reflects numerous elements of wetland hydrology and geomorphology that collectively influence the structure of floral and faunal communities.

Lacustrine

Lacustrine marshes are adjoined directly to waters of the Great Lakes and are strongly influenced by lake water levels, nearshore currents, and ice scour (Albert et al. 2005). The primary water source for lacustrine marshes is the adjacent lake, though groundwater, tributary streams, and direct precipitation can also contribute to lacustrine marsh hydrology (Fig. 9.3). The main form of water loss is direct outflow to the adjacent lake, though evaporation and evapotranspiration also result in water loss from lacustrine marshes (Fig. 9.3). Geomorphic features along the shoreline such as headlands, embayments, and bathymetry (e.g., sandbars, shallow slope) provide varying degrees of protection from wave energy and coastal currents and allow wetland habitat to develop and persist. Lacustrine marshes can be further subdivided into open and protected embayments, sandspit embayments, and open shoreline wetlands. Invertebrates inhabiting the lakeward margin of lacustrine marshes must be tolerant of wave energy, while those inhabiting wet meadow habitats at the shoreward margin must be tolerant of seiche-induced drying and rewetting cycles.

Riverine

Riverine wetlands occur along the margins of and within tributary streams and rivers and along the margins of large connecting channels between lakes (Albert et al. 2005). Riverine wetlands often occur in deltaic or fluvial habitats at the confluence of rivers and the receiving lake. Water quality, hydraulic processes, and sediment input are controlled in large part by the individual drainages; however, water levels and fluvial processes in these wetlands are directly or indirectly affected by the downstream lake as lake waters flood back into the lower portions of tributary marsh systems. Accordingly, the primary source of water to riverine coastal marshes is direct inputs from tributary streams (Fig. 9.3). The primary

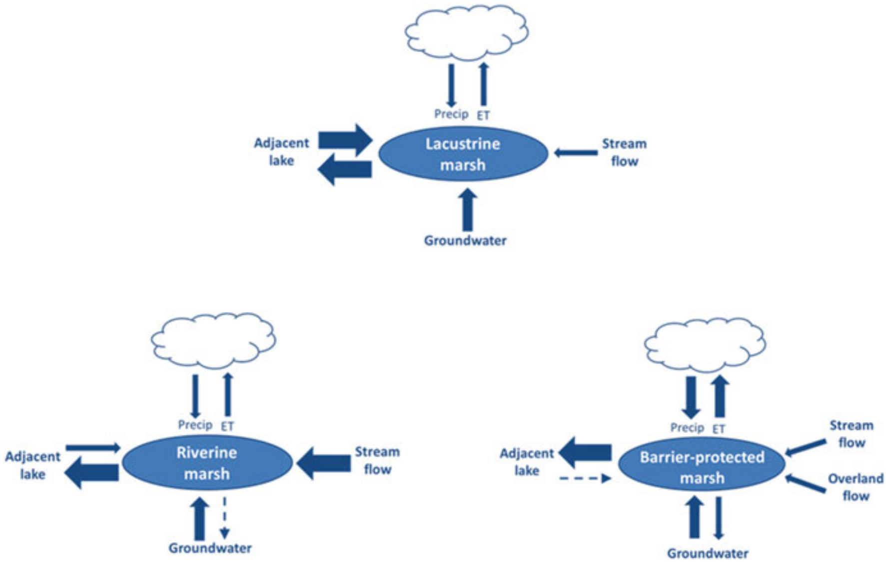

Fig. 9.3 Conceptual models demonstrating the relative magnitudes of water inflows and outflows for the three main hydrogeomorphic types of Great Lakes coastal marshes. *Dashed arrows* represent known but minor flows

outflow is to the receiving lake, though hydrologic inputs and outputs related to atmospheric and groundwater exchange can also occur. Protection from lake waves and coastal currents is provided by sand and gravel bars near river outlets and by channel morphology. Riverine wetlands can be further subdivided into open and barred drowned river mouth wetlands, delta wetlands, and connecting channel wetlands, all of which generally contain herbaceous marsh habitat. Lakeshore riverine wetlands encompass a wide variety of habitat types, from fast-flowing channels to quiet backwater areas with deep organic sediment deposits. Accordingly, a diverse array of invertebrates inhabit these marshes, from rheophilic mayflies in the family Heptageniidae, to sediment-burrowing mayflies in the family Ephemeridae, to grazing snails, shredding and collecting crustaceans (Amphipoda and Asellidae), and surface-dwelling hemipterans in the families Gerridae and Mesoveliidae (Cooper et al. 2007).

Barrier-Protected

Barrier-protected wetlands form as a result of either coastal or fluvial processes that create barriers that separate wetland habitats from the lake (Albert et al. 2005). Barriers may be active or may be the result of some past process that leaves behind the barrier as a relict coastal feature. These wetlands are completely protected from lake waves and currents but may be connected to the lake by one or more channels through the barrier. Water budgets in barrier-protected lakeshore marshes are highly variable and complex, including inputs from precipitation, groundwater, streams, and surface flow and outputs to the atmosphere via evaporation or evapotranspiration as well as outputs to the adjacent lake through temporary channels or shallow subsurface flow (Fig. 9.3). When connected to the lake, water levels reflect those of the adjacent lake because lake water either flows into the marsh or creates sufficient hydraulic head pressure to keep marsh water at the same elevation as the lake. Channels connecting barrier-protected marshes to the lake may be permanent or ephemeral as coastal sediment transport can intermittently close off connecting channels. Invertebrates inhabiting barrier-protected lakeshore marshes must be tolerant of the dramatically fluctuating hydrology that often occurs in these habitats. Strategies to withstand dry periods, such as diapausing eggs or pupae, or the ability to cyclically colonize ephemeral aquatic habitats are common among taxa found in barrier-protected lakeshore marshes (Burton and Uzarski 2009).

Basic Invertebrate Research in Great Lakes Marshes

Our understanding of Great Lakes marsh invertebrate communities has grown considerably in recent years. For example, the structure of these communities has been related to vegetation zonation (Cardinale et al. 1997; Merritt et al. 2002), fetch and wave exposure (Burton et al. 2002, 2004; Cooper et al. 2014), benthic substrate (MacKenzie et al. 2004; Cooper et al. 2007), water-level fluctuation (Gathman and Burton 2011; Cooper et al. 2014), water quality and surrounding land use (King and Brazner 1999; Schneider and Sager 2007; Cooper et al. 2014; Kovalenko et al. 2014; Schock et al. 2014), invasive plants (Kulesza et al. 2008; Holomuzki and Klarer 2010), and habitat fragmentation (Uzarski et al. 2009; Cooper et al. 2012). These drivers are not mutually exclusive of one another, and invertebrate assemblages are often influenced by several of these variables simultaneously.

Indices of Biotic Integrity

In addition to traditional community assembly research, invertebrate-based Indices of Biotic Integrity (IBIs) have been developed and currently are being used throughout the Great Lakes to assess coastal wetland health (Uzarski et al. 2004). The approach leverages the information contained in invertebrate community structure to detect anthropogenic disturbances that may not be discernible with traditional water quality monitoring (Burton et al. 1999; Uzarski et al. 2004). The applicability and performance of IBI-type assessment tools relies on a thorough understanding of invertebrate community responses to both natural and anthropogenic drivers.

An important step in developing wetland IBIs is to partition variability in community structure that is due to natural factors from variability that is due to human disturbance. For Great Lakes coastal wetlands, this has been achieved by developing IBIs for specific wetland types (e.g., lacustrine, riverine, barrier-protected) and vegetation types within wetlands (Burton et al. 1999; Uzarski et al. 2004). Because vegetation structure tends to correlate with hydrology in Great Lakes coastal wetlands (Albert et al. 2005; Gathman et al. 2005), this approach controls for much of the overriding influence of hydrology and macrohabitat structure on IBI metrics. For example, separate sets of IBI metrics have been developed for bulrush-dominated zones and wet meadow zones in Great Lakes lacustrine wetlands (Burton et al. 1999; Uzarski et al. 2004). Stratifying IBIs by vegetation type also allows the protocols to be used at various Great Lakes water levels because vegetation zones move upslope and downslope as water levels fluctuate. Therefore, invertebrate sampling and subsequent IBI metric calculations can “follow” the vegetation zones over time as they move upslope and downslope.

Invertebrate IBI metric identification has been accomplished by comparing community structure in reference wetlands to community structure in impaired wetlands. Attributes of the community that differ between these disturbance categories then have the potential to become IBI metrics. For example, the relative abundance of sphaeriid clams has been shown to decline with increasing human disturbance in Lake Huron lacustrine wetlands, and accordingly, sphaeriid abundance was incorporated into the IBI for these systems (Uzarski et al. 2004). An alternative approach is to quantify anthropogenic disturbance using a multivariate index and then identify invertebrate community metrics that vary predictably along this disturbance gradient. After candidate metrics are identified, metric scoring schemes must be derived to translate metric values into scores for the final IBI determination. Final IBI results are then derived by summing the component metric scores. While the IBI approach is common in lake and stream monitoring and management, it has been used infrequently in wetlands. However, current broadscale monitoring and use of invertebrate-based IBIs in Great Lakes coastal wetlands have become valuable tools for prioritizing wetland restoration projects and tracking restoration outcomes.

Lakeshore Marsh Taxa

Given the immensity of the Great Lakes system, constructing a truly exhaustive list of taxa would be a difficult undertaking. However, several Great Lakes basin-scale invertebrate sampling efforts have occurred or are currently underway in Great Lakes marshes, and these can be used to create a preliminary inventory of taxa. These efforts were conducted in an ecosystem monitoring context, either to develop or test monitoring protocols, or in fully implemented monitoring programs. The Great Lakes Environmental Indicators (GLEI) project (Niemi et al. 2009) sampled invertebrates at 101 coastal wetlands along the US shoreline of the Great Lakes in 2002 and 2003. This program identified 222 invertebrate taxa—most at the genus level (Kovalenko et al. 2014). The Great Lakes Coastal Wetlands Consortium (GLCWC) sampled invertebrates in 67 coastal wetlands in all five Great Lakes in 2002 (Cooper et al. 2014) and identified 215 taxa, mostly at the genus level. In 2011, the GLCWC, along with several researchers from the GLEI group, and others initiated a monitoring program that included sampling invertebrates in lakeshore marshes across the Great Lakes basin. For this effort, over 100 marshes are being sampled each year in the initial 5-year sampling rotation (2011–2015). This monitoring effort is sponsored by the US EPA for the purpose of supporting wetland restoration, protection, and other management activities. More specifically, data and IBI scores are being used to select wetlands for restoration and to track restoration outcomes. While many studies of invertebrate community structure have occurred in Great Lakes coastal marshes in recent decades, the GLCWC effort is the single largest coordinated effort to occur in these systems. In addition to invertebrates, the monitoring program is collecting data on fish, birds, amphibians, vegetation, and water quality in each marsh.

To collect invertebrates, GLCWC researchers use D-frame dip nets to sweep through the water column and vegetation and then "field pick" organisms from the gathered plant matter and detritus. Samples are returned to the laboratory for identification to lowest operational taxonomic unit (usually genus or species) under magnification.

A number of general characteristics of the invertebrate assemblages inhabiting Great Lakes coastal marshes can be gleaned from this large dataset. First, in the initial 3 years of sampling (2011–2013), in which 319 unique marshes were sampled and >270,000 organisms were collected, 331 genera were identified, along with an additional 102 taxa identified at a coarser resolution (Appendix). Second, similar to the finding of Cooper et al. (2014), a small subset of taxa tend to be numerically dominant in the overall assemblage, with the ten most abundant taxa representing 61 % of the organisms collected (Fig. 9.4). Accordingly, the vast majority of taxa could be considered "rare," resulting in a very hollow species-abundance curve (Fig. 9.4). Third, these data reveal that the majority of observed taxa tend to be cosmopolitan, occurring in more than one Great Lake (Appendix).

Environmental Drivers of Invertebrate Communities

Great Lakes Water Levels

The natural fluctuations in water levels of the Great Lakes have important implications for lakeshore marsh invertebrate communities. Perhaps most importantly, intra-annual low-water periods allow macrophyte seeds to germinate and

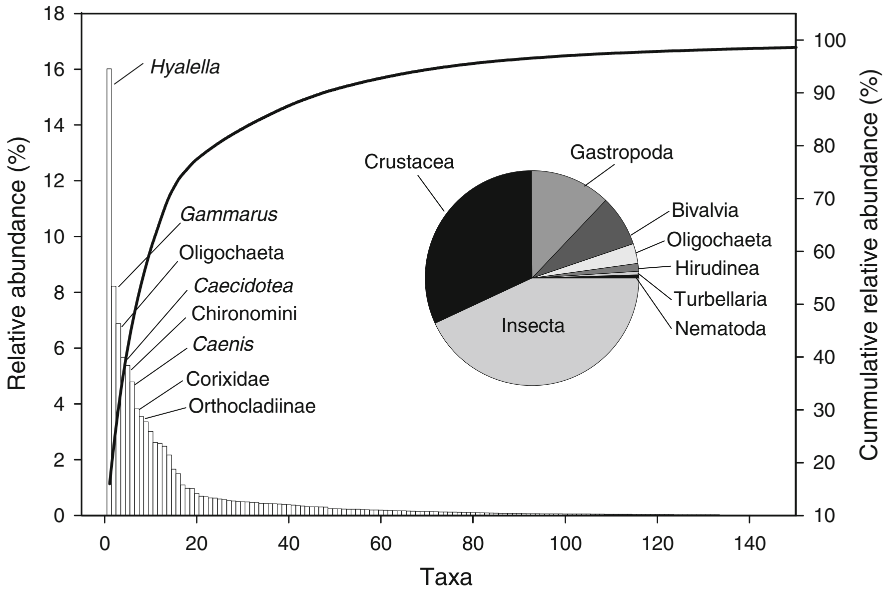

Fig. 9.4 Invertebrate assemblage from 319 Great Lakes marshes sampled by the Great Lakes Coastal Wetlands Consortium from 2011 to 2013. *Vertical bars* represent relative abundances of each taxon from all sites, with the ten most abundant taxa labeled. Only the 135 most abundant taxa (of 433 total taxa collected) are shown on the graph. The *solid line* depicts the asymptotic nature of cumulative relative abundance in the assemblage (right-hand axis). *Pie graph* shows the distribution of invertebrate abundances among major taxonomic groups

seedlings to develop before the wetlands flood again later in the year. Interannual low-water periods (i.e., "low-water years") allow for replenishment of the seedbank. Also during low-water years, the upland portion of meadow marsh is invaded by woody plants, while true marsh (i.e., herbaceous) communities shift lakeward. When water levels rise again, woody species retreat upslope and the emergent marsh and wet meadow communities also move shoreward. Long-term water-level fluctuations, therefore, cause long-term movement and alteration of marsh vegetation zones (Burton 1985; Gathman and Burton 2011). Invertebrate community structure is influenced strongly by structural composition of vegetation (e.g., Voigts 1976; McLaughlin and Harris 1990; Batzer and Resh 1992) as well as sediment characteristics (e.g., Nelson et al. 1990; Cooper et al. 2007). Therefore, maintenance of marsh vegetation structure and sediment characteristics by Great Lakes water levels has a strong influence on invertebrate community structure. Correlations between water levels, marsh vegetation, and invertebrate assemblage structure demonstrate these linkages (Burton et al. 2002; Uzarski et al. 2004; Gathman and Burton 2011).

Lakeshore marsh invertebrate communities appear to also be influenced directly by water levels. Cooper et al. (2014) evaluated a 1997–2012 time series of invertebrate community data from bulrush (*Schoenoplectus* spp.)-dominated habitats at three representative Saginaw Bay wetlands. Their analysis revealed substantial shifts in community structure throughout the period, especially from 2001 through 2004. This period followed a 1 m decline in Lake Huron water levels that occurred between 1997 and 2000. For example, from 2002 to 2004, gastropod relative abundance increased dramatically at all three wetlands, and at one wetland, gastropods increased from just 3 % of the community in 2002 to approximately half of the community in 2004. Over about the same period, insects—especially chironomids—declined substantially at all three wetlands. This decline was particularly evident at one wetland, where chironomids fell from roughly half to just 10 % of the community between 2002 and 2004. Crustaceans declined at all three wetlands beginning in 1999, reaching minima in 2002–2004. Coarse-level community metrics (e.g., % insects, % crustaceans, % gastropods, etc.) correlated with the prior year's water level suggesting a lagged response of communities to the water level decline. Burton et al. (2004) and Uzarski et al. (2004) noted that marsh invertebrate communities in Lake Huron changed surprisingly little during the 1998–2000 water level decline. This observation is consistent with the conclusion of Cooper et al. (2014) that the response to water level was delayed by one to several years following the major decline.

Gathman and Burton (2011) reported changes in invertebrate community structure in a Lake Huron marsh for a 3-year period in which water levels increased approximately 30 cm from year 1 (1996) to year 2 (1997) and then declined again in year 3 (1998). Sampling occurred at fixed stations along transects perpendicular to the shoreline. Multivariate analyses indicated that during the high-water period, assemblages became more homogenized (e.g., wet meadow assemblages resembled emergent marsh assemblages). This was driven by increased dominance by a subset of taxa throughout the marsh, especially *Caecidotea*, Chironomidae, Caenidae, and Amphipoda. Gathman and Burton (2011) also identified four categories of responses to water levels: (1) high-elevation specialists, which were generally restricted to the upper portion of the marsh regardless of the water level; (2) rapid, reversing taxa, which rapidly occupied the wet meadow under high-water conditions, but then retreated back to lower positions as water declined in year 3; (3) time-lagged responders, which expanded upslope as water levels rose, but in a time-lagged nature; and (4) low-elevation specialists, which always remained most common in the emergent marsh, showing little indication of upslope spread with rising water levels. Consistent with Cooper et al. (2014), Gathman and Burton (2011) demonstrate the profound influence of water levels on lakeshore marsh invertebrate communities and provide a framework for evaluating taxonomic responses to interannual water-level fluctuations.

Hydraulic Energy

An important driver of invertebrate community structure in lakeshore marshes is hydraulic energy and its influence on chemical, physical, and biological conditions. Wave energy affects shoreline vegetation by uprooting seedlings, damaging mature plants, and eroding fine sediments around roots and rhizomes (Keddy 1982; Riis and Hawes 2003). Accordingly, plant biomass and wave energy are negatively correlated along most vegetated shorelines, and a threshold exists where rooted vegetation can no longer persist (Keddy 1982; Azza et al. 2007). Effects of wave energy on sediment conditions are complex in lakeshore marshes since the plants themselves attenuate wave energy and affect sedimentation rates (Cooper et al. 2012). In general, however, increased wave energy results in increased particle size and decreased sediment organic content (Keddy 1982; Cooper et al. 2012), which influences basic biogeochemical conditions, including community metabolism (Cooper et al. 2013). Not surprisingly, therefore, exposure to wave and current energy influences faunal community structure in lakeshore marshes, especially for invertebrate communities (Burton et al. 2004; Cooper et al. 2014).

Cooper et al. (2014) analyzed invertebrate data from 67 lakeshore marshes from across the Great Lakes and found that fetch (i.e., potential wave energy) was one of the most important drivers of community structure among 16 candidate variables. The relationship between fetch and community structure was evident in whole-assemblage analyses, though a subset of taxa appeared to drive the observed gradients. For example, Oligochaeta and *Bezzia* were among the dominant taxa in the wave-exposed marshes of Saginaw Bay, while *Gammarus* and *Caecidotea* (both crustaceans) were much less abundant in Saginaw Bay compared to low-fetch marshes such as drowned river mouths of eastern Lake Michigan and protected embayments of northern Lake Huron. These results are largely consistent with Burton et al. (2004) who found that a majority of invertebrate taxa were generalists, occurring in wetlands across varying degrees of exposure, yet subsets of taxa were associated with either low-fetch or high-fetch marshes. Burton et al. (2004) reported higher densities of *Gammarus*, *Crangonyx*, *Caecidotea*, Chironomini, and Tanytarsini in low-fetch wetlands and higher densities of *Sigara*, *Trichocorixa*, Oligochaeta, and *Bezzia* in high-fetch wetlands, which partially overlaps with findings of Cooper et al. (2014).

Specific mechanisms linking wave exposure and invertebrate community structure are unclear; however, a combination of physical disturbance of organisms, the influence of wave energy on sediment organic matter, and the effect of wave-induced turbidity on visual predators are likely all important (Metzler and Sager 1986; Burton et al. 2004; Schneider and Sager 2007). Cooper et al. (2006, 2007) noted that sediment organic content was the best predictor of invertebrate community structure in drowned river mouth wetlands of eastern Lake Michigan. Similarly, MacKenzie et al. (2004) found that in the Peshtigo River wetland, a riverine wetland on the western shore of Lake Michigan, abundances of several invertebrate taxa varied predictably along gradients of sediment organic matter from the river channel into wetland vegetation. Taken collectively, these findings suggest that interactions between wave exposure or other hydraulic forces, sediment organic content, and turbidity are important in structuring invertebrate communities along gradients of hydrologic energy in lakeshore marshes.

Vegetation Zonation

Macrophytes comprise much of the physical habitat that invertebrate communities assemble within. Therefore, differences in vegetation, either different component species or different plant morphotypes, can influence invertebrate community structure. While few studies have investigated the influence of vegetation on invertebrate community structure directly, available evidence suggests that vegetation zonation plays a role in structuring these communities. Burton et al. (1999) suggested that stratifying invertebrate-based indices of biotic integrity by vegetation type would improve the performance of the index. This was later confirmed by Uzarski et al. (2004) who found that stratification by vegetation zone was indeed necessary to account for variation in habitat structure and to allow the index to be used at varying water levels as vegetation zones move upslope and downslope. However, given that vegetation communities are influenced by nearshore hydraulic forces (e.g., wave energy) and Great Lakes water levels, it has been difficult to partition these interacting drivers of invertebrate community structure. For example, Gathman and Burton (2011) found that invertebrate community composition was influenced more by flooding conditions than by vegetation, though vegetation structure is also influenced by flooding regime. Additional experimental research is needed to partition these influences, especially in regard to the effects of nonnative vegetation (e.g., *Phragmites australis* and *Typha* X *glauca*) on invertebrate communities.

Conservation and Management

Lakeshore marshes provide critical habitat for many species of birds, mammals, reptiles, and amphibians (Austen et al. 1994; Hecnar 2004; Hanowski et al. 2007; Wieten et al. 2012). These wetlands also provide essential spawning and nursery areas for many fish species of ecological and economic importance (Chubb and Liston 1986; Klarer and Millie 1992; Uzarski et al. 2005). Additionally, lakeshore marshes trap, process, and remove nutrients from Great Lakes nearshore waters, and their effects on drainage patterns can help recharge groundwater supplies (Burton 1985; Heath 1992). These functions reinforce the notion that conservation and restoration of lakeshore marshes are vital elements of long-term management of the Great Lakes (Sierszen et al. 2012b). Unfortunately, approximately half of the coastal wetland area that was present before European settlement has been converted to other land uses, especially in the lake plains of western Lake Erie and Saginaw Bay where large tracks of wetland were ditched and drained for agriculture and urban development. The majority of remaining wetlands are affected to varying degrees by numerous anthropogenic disturbances.

Water-Level Regulation

Outflow regulation of Lakes Superior and Ontario has altered water-level dynamics within these lakes. On Lake Ontario, sustained deviations from the overall mean water level are noticeably infrequent after the Moses–Saunders Power Dam began its operation in 1958 (Fig. 9.4). The range of fluctuations was approximately 2 m prior to regulation, but this has been reduced to approximately 1 m since regulation began. As a result, cattail (*Typha* spp.) stands spread dramatically in Lake Ontario's marshes, often replacing other more diverse habitat types such as sedge/grass meadow marsh (Wilcox et al. 2008). Invertebrates and other fauna that utilize the dynamic meadow marsh were undoubtedly affected by this change in hydrology and vegetation. Regulation of Lake Superior, which began in the early 1920s, had less of an effect on water levels and Lake Superior reached a near-record high in 1986 and a near-record low in 2007. However, regulation of Lake Superior outflow does dampen seasonal and interannual variability somewhat, with consequences to wetland habitat structure and resident fauna (Ciborowski et al. 2008). Given the importance of natural water-level fluctuations for maintenance of marsh vegetation community structure, it is critical that water-level management policies incorporate natural variation to the greatest extent possible (Ciborowski et al. 2008).

Anthropogenic Nutrient Pollution

Human-derived nitrogen (N) and phosphorus (P) enter aquatic ecosystems from point and nonpoint sources. Runoff from agricultural and urban landscapes is a common source of these nutrients to streams, lakes, and wetlands. Anthropogenic nutrients can impact lakeshore wetlands in dramatic ways, particularly by stimulating excessive primary production (i.e., eutrophication). This production can be in the form of phytoplankton or macrophytes, which can subsequently alter organic matter dynamics as the plants or algae senesce. Organic detritus can be a food resource for invertebrates but excessive organic matter accumulation can cause hypoxic or even anoxic conditions. Thus, nutrient loading has the potential to dramatically alter both the physical habitat and chemical conditions in lakeshore marshes, which can then impact invertebrate communities.

In lakeshore marshes, the response of invertebrates to anthropogenic nutrient loading is perhaps most apparent in relationships between surrounding land use and community structure. Cooper et al. (2014) found that while invertebrate community structure responded most strongly to hydrologic factors (e.g., wave energy, water levels), watershed percent agriculture was also highly correlated with community structure across the Great Lakes basin. These results suggest that at the Great Lakes basin-scale, invertebrate communities respond to the suite of impacts brought about by agricultural runoff, including nutrient loading. Marshes of Saginaw Bay and western Lake Erie, in particular, receive considerable nutrient loads from surrounding agricultural lands (Danz et al. 2007; Dolan and Chapra 2012; He et al. 2013). Others have reported similar relationships between watershed agriculture and coastal wetland invertebrates. For example, Burton et al. (1999) and Uzarski et al. (2004) identified coastal wetland invertebrate community shifts that correlated with surrounding land use in Lake Huron, including Saginaw Bay. Schneider and Sager (2007) reported that agriculturally derived nutrient and sediment loading to Green Bay (Lake Michigan) determined trophic state and light attenuation in Green Bay's coastal wetlands. They further proposed that these variables drove epiphytic invertebrate community structure by influencing food resources. Given the apparent impacts associated with nutrient-laden runoff on lakeshore marsh invertebrates, restoration and protection efforts should identify and ameliorate sources of nutrient pollution when designing projects and programs.

Invasive Species

One of the most serious threats to the biotic integrity of lakeshore marshes is the establishment and spread of nonnative organisms. Pathways of introduction include intentional release, the live bait trade, aquarium trade, ballast water of ships, escape from cultivation, and migration along human corridors such as highways and railroads where natural barriers would have existed otherwise. Because macrophytes form the physical habitat and influence organic matter dynamics in lakeshore marshes, nonnative plant invasions can be particularly detrimental to invertebrates. Examples of invasive macrophytes that dominate in marshes throughout the Great Lakes include submersed aquatic species such as Eurasian water milfoil (*Myriophyllum spicatum*), curly leaf pondweed (*Potamogeton crispus*), and slender naiad (*Najas minor*) and emergent plants such as purple loosestrife (*Lythrum salicaria*), reed canary grass (*Phalaris arundinacea*), and common reed (*Phragmites australis*). It is likely that many invasions around the Great Lakes would not have been successful in healthy marsh ecosystems. However, prior physical habitat disturbances, alteration of natural water-level regimes, and anthropogenic nutrient loading can facilitate the establishment and spread of nonnative plants.

Attempts to control invasive vegetation, especially common reed, often include glyphosate herbicides such as Roundup (Monsanto Corporation) or Glypro (Dow AgroSciences). Effects of these herbicides on non-macrophyte aquatic organisms are not straightforward. Some reports suggest that glyphosate is not harmful to aquatic invertebrates, fish, or algae (USDA 1997; Kulesza et al. 2008) while others show variable toxicity to these taxa (Chen et al. 2004; Relyea 2005). As the use of glyphosate herbicides to treat common reed and other invasive plants continues to increase in lakeshore marshes, additional research on the short- and long-term impacts to nontarget organisms is needed.

Direct impacts of invasive vegetation on invertebrates in lakeshore marshes are equally complex. For example, the extremely high density and biomass of common reed can reduce available nutrients and light and the accumulation of reed detritus can affect system hydrology, can cause sediment anoxia and phytotoxin buildup (e.g., hydrogen sulfide, acetic acid), and can kill the roots of native plants (Armstrong et al. 1996). These effects on native plant communities presumably would impact invertebrate communities as well (Schultz and Dibble 2012). However, Kulesza et al. (2008) and Holomuzki and Klarer (2010) found that *Phragmites* invasion did not adversely affect macroinvertebrate community density and diversity in Lake Erie marshes. Additional factors such as stand age, ambient water quality, and plant community composition prior to invasion likely all influence the degree of impact that nonnative vegetation has on macroinvertebrates.

Nonnative invertebrate species that are now commonly observed in Great Lakes marshes include zebra and quagga mussels (*Dreissena* spp.), rusty crayfish (*Orconectes rusticus*), faucet snails (*Bithynia tentaculata*), Chinese mystery snail (*Cipangopaludina chinensis*), and the amphipod, *Echinogammarus ischnus*. Zebra and quagga mussels are particularly detrimental to native unionids because they colonize unionid shells and outcompete them for food resources (Zanatta et al. 2002, 2015). Additional nonnative species are likely also common in Great Lakes marshes but cryptic identity at the species level impedes detection. Broadscale monitoring and archival of invertebrate collections is an invaluable tool for identifying and tracking range expansions of invertebrate invaders (Peters et al. 2014).

Lakeshore Marsh Restoration

A number of large lakeshore marsh restoration projects have been initiated in the Great Lakes (e.g., Sensiba Wildlife Area in western Green Bay, Cat Island Ecosystem in southern Green Bay, Erie Marsh Preserve in western Lake Erie, Braddock Bay in southern Lake Ontario). Many smaller-scale restoration efforts have also occurred or are planned throughout the basin, often focused on controlling invasive vegetation or reconnecting marsh habitats to the Great Lakes after previous activities such as diking or coastal development has isolated marsh fragments. Significant investment of public and private funds for both large- and small-scale marsh restoration has been made in the region because long-term benefits provided by healthy marshes are believed to outweigh short-term restoration costs.

Effective restoration planning and evaluation require monitoring, and invertebrates can provide important ecological information for this purpose. In Great Lakes marshes, an unprecedented basin-scale ecosystem monitoring program, which includes sampling invertebrates, fish, vegetation, birds, and amphibians, began in 2011 with approximately 1000 marshes scheduled for sampling in the first 5-year rotation. The primary goal of the program is to generate data to prioritize wetland restoration projects and track restoration outcomes. This innovative and strategic approach is being led by the US Environmental Protection Agency with a consortium of wetland researchers who utilize Indices of Biotic Integrity (IBI) and other similar measures to estimate conditions within each wetland. Habitats are targeted for restoration or protection based on the monitoring data. Restoration outcomes are then evaluated over the long term by resampling the restored habitats in subsequent years. A secondary goal of the monitoring program, therefore, is to support adaptive management of restoration techniques as post-restoration monitoring reveals successful and unsuccessful approaches as the biotic communities respond to the restoration activities.

Summary and Conclusions

Lakeshore marshes in the Great Lakes provide habitat for a vast array of invertebrate taxa (well over 400 genera; see "Appendix"). The marshes themselves represent incredible variability in terms of climate, geomorphic types, dominant vegetation, and nutrient conditions. Despite the large number of taxa observed in these habitats, a small subset of taxa tend to be numerically dominant in the overall assemblage, with the ten most abundant taxa representing over 60 % of the organisms collected in basin-scale monitoring programs. Accordingly, most taxa could be considered "rare," resulting in a very hollow species-abundance curve. Invertebrate community structure is driven by a combination of both natural and anthropogenic factors. Important natural drivers include hydrology (e.g., lake water levels), hydraulic forces (e.g., wave energy), and vegetation zonation. Important anthropogenic factors include water quality (e.g., nutrient runoff) and invasive vegetation. Therefore, reducing anthropogenic nutrient loading and controlling the spread of invasive species are important conservation practices. While these marsh-scale impacts warrant attention by managers and policy-makers, the most significant insult to lakeshore marsh invertebrates is the loss of habitat. Approximately half of the original marsh area along the Great Lakes coast has been lost to human development, with even greater losses in some areas. Therefore, restoring severely degraded and previously destroyed marshes and protecting existing intact marshes are key strategies to ensuring the integrity of the Great Lakes coastal ecosystem. Invertebrates inhabiting these critical habitats represent an important nexus as they link primary productivity to higher trophic levels (e.g., fish and waterfowl), facilitate the cycling of wetland nutrients, and provide wetland managers with vital information on ecosystem health.

Appendix

Invertebrate taxa collected as part of the Great Lakes Coastal Wetlands Consortium basin-wide monitoring program (2011–2013). Wetlands were located on Lake Erie (LE), Lake Huron (LH), Lake Michigan (LM), Lake Ontario (LO), and Lake Superior (LS)

Phylum Class **Order** Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Cnidaria						
Hydrozoa		X	X	X	X	X
Anthoathecatae		X	X	X	X	X
Hydridae	*Hydra*	X	X	X	X	X
Nematoda		X	X	X	X	X
Nematomorpha		X	X		X	
Platyhelminthes						
Turbellaria		X	X	X	X	X
Annelida						
Clitellata[a]		X	X	X	X	X
Hirudinea		X	X	X	X	X
Euhirudinea[b]		X	X	X	X	X
Arhynchobdellida		X	X	X	X	X
Erpobdellidae		X	X	X	X	X
	Erpobdella	X	X	X	X	
	Mooreobdella	X	X	X	X	X
Rhynchobdellida		X	X	X	X	X
Glossiphoniidae		X	X	X	X	X
	Batracobdella		X	X	X	X
	Desserobdella	X	X		X	X
	Gloiobdella	X	X			
	Glossiphonia	X	X		X	X
	Helobdella	X	X	X	X	X
	Marvinmeyeria		X			
	Placobdella	X	X	X	X	X
	Theromyzon	X	X		X	
Piscicolidae		X	X			X
	Myzobdella					X
Oligochaeta		X	X	X	X	X
Haplotaxida			X	X	X	X
Naididae			X	X	X	X
Tubificidae			X	X		
Lumbriculida					X	
Polychaeta[a]					X	X
Canalipalpata					X	
Sabellidae	*Manayunkia*				X	
Mollusca						
Bivalvia		X	X	X	X	X
Unionoida		X	X			
Veneroida		X	X	X	X	X

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Dreissenidae	*Dreissena*	X	X	X	X	X
Sphaeriidae		X	X	X	X	X
	Musculium	X	X	X	X	X
	Pisidium	X	X	X	X	X
	Sphaerium	X	X		X	X
Gastropoda		X	X	X	X	X
Architaenioglossa		X	X	X	X	X
Viviparidae		X	X	X	X	X
	Campeloma		X	X	X	
	Cipangopaludina	X	X	X		X
	Viviparus	X	X	X		X
Basommatophora		X	X	X	X	X
Ancylidae	*Ancylini*	X	X	X	X	X
	Ferrissia		X	X	X	X
	Laevapex	X	X	X	X	X
Lymnaeidae		X	X	X	X	X
	Acella		X		X	
	Bulimnaea		X			X
	Fossaria	X	X	X	X	X
	Lymnaea	X	X	X	X	X
	Lymnaea		X		X	X
	Pseudosuccinea	X	X	X	X	X
	Stagnicola	X	X	X	X	X
Physidae		X	X	X	X	X
	Aplexa		X	X	X	
	Physa	X	X	X	X	X
Planorbidae		X	X	X	X	X
	Armiger		X	X	X	
	Gyraulus	X	X	X	X	X
	Helisoma	X	X	X	X	X
	Menetus		X	X	X	X
	Planorbella	X	X	X	X	X
	Planorbula	X	X	X	X	X
	Promenetus	X	X	X	X	X
Heterostropha		X	X	X	X	X
Valvatidae	*Valvata*	X	X	X	X	X
Mesogastropoda			X	X	X	X
Pomatiopsidae	*Pomatiopsis*		X	X	X	X
Neotaenioglossa						
Bithyniidae		X	X	X	X	X
	Bithynia tentaculata	X	X	X	X	X

(continued)

(continued)

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Hydrobiidae		X	X	X	X	X
	Amnicola	X	X	X	X	X
Pleuroceridae		X	X	X	X	X
	Elimia			X	X	
	Goniobasis	X	X		X	
	Pleurocera	X	X	X	X	X
Stylommatophora		X	X	X	X	X
Succineidae	*Succinea*	X	X	X	X	X
Arthropoda						
Arachnida		X	X	X	X	X
Acari[c]		X	X	X	X	X
Malacostraca		X	X	X	X	X
Decapoda		X	X	X	X	X
Cambaridae		X	X	X	X	X
	Cambarus		X	X	X	X
	Orconectes	X	X	X	X	X
Palaemonidae	*Palaemonetes*	X	X	X	X	X
Amphipoda		X	X	X	X	X
Crangonyctidae	*Crangonyx*	X	X	X	X	X
Gammaridae		X	X	X	X	X
	Echinogammarus	X	X	X	X	X
	Gammarus	X	X	X	X	X
Dogielinotidae	*Hyalella azteca*	X	X	X	X	X
Isopoda		X	X	X	X	X
Asellidae		X	X	X	X	X
	Caecidotea	X	X	X	X	X
	Lirceus	X	X	X	X	X
Entognatha		X	X	X	X	X
Collembola		X	X	X	X	X
Isotomidae			X	X	X	
Poduridae	*Podura*		X	X		
Insecta		X	X	X	X	X
Ephemeroptera		X	X	X	X	X
Ameletidae	*Ameletus*		X			
Baetidae		X	X	X	X	X
	Acentrella		X			
	Acerpenna	X				
	Baetis		X	X		X
	Callibaetis	X	X	X	X	X
	Centroptilum	X	X	X	X	X
	Cloeon	X	X	X	X	X
	Procloeon		X	X	X	X
	Pseudocloeon	X		X		

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Baetiscidae	*Baetisca*		X		X	X
Caenidae		X	X	X	X	X
	Brachycerus	X	X	X	X	X
	Caenis	X	X	X	X	X
Ephemerellidae		X	X	X	X	X
	Attenella		X			
	Drunella			X		
	Eurylophella		X	X	X	X
	Serratella		X			
	Timpanoga		X			
Ephemeridae		X	X	X	X	X
	Ephemera	X	X	X	X	X
	Hexagenia	X	X	X	X	X
Heptageniidae		X	X	X	X	X
	Macdunnoa		X			
	Stenacron		X			X
	Stenonema		X	X	X	X
Isonychiidae	*Isonychia*		X			
Leptohyphidae	*Tricorythodes*		X		X	X
Leptophlebiidae			X	X		
	Choroterpes			X		
	Leptophlebia		X			
Metretopodidae	*Siphloplecton*					X
Neoephemeridae	*Neoephemera*			X		
Tricorythidae					X	
Odonata		X	X	X	X	X
Anisoptera[d]		X	X	X	X	X
Aeshnidae		X	X	X	X	X
	Aeshna	X	X	X	X	X
	Anax	X	X	X	X	X
	Basiaeschna		X	X		X
	Boyeria		X	X	X	X
Corduliidae		X	X	X	X	X
	Cordulia		X	X	X	X
	Dorocordulia		X	X	X	X
	Epitheca	X	X	X	X	X
	Neurocordulia		X	X		X
	Somatochlora		X	X	X	X

(continued)

(continued)

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Gomphidae		X	X	X	X	X
	Arigomphus	X			X	
	Dromogomphus			X		
	Gomphus		X	X	X	X
	Hagenius		X			X
	Stylurus					X
Libellulidae		X	X	X	X	X
	Celithemis		X		X	X
	Erythemis	X	X	X	X	X
	Ladona		X			X
	Leucorrhinia	X	X	X	X	X
	Libellula	X	X	X	X	X
	Miathyria		X		X	
	Pantala		X		X	X
	Perithemis	X			X	
	Plathemis		X	X	X	
	Tramea	X	X	X	X	X
Macromiidae			X	X	X	X
	Macromia		X	X		
	Didymops		X		X	X
Zygoptera[d]		X	X	X	X	X
Calopterygidae	*Calopteryx*		X			
Coenagrionidae		X	X	X	X	X
	Amphiagrion		X			
	Argia		X		X	
	Chromagrion		X		X	X
	Coenagrion		X	X	X	
	Enallagma	X	X	X	X	X
	Ischnura	X	X	X	X	X
	Nehalennia	X	X	X		X
Lestidae	*Lestes*	X	X	X	X	X
Plecoptera		X			X	X
Chloroperlidae						X
Perlidae		X			X	
	Neoperla				X	
	Perlesta	X				
Hemiptera		X	X	X	X	X
Belostomatidae		X	X	X	X	X
	Belostoma	X	X	X	X	X
	Lethocerus			X		X

Phylum Class **Order** Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Corixidae		X	X	X	X	X
	Callicorixa		X	X	X	X
	Corisella	X	X	X		X
	Dasycorixa				X	
	Hesperocorixa	X	X	X	X	X
	Neocorixa		X	X	X	
	Palmacorixa	X	X	X	X	X
	Sigara	X	X	X	X	X
	Trichocorixa	X	X	X	X	X
Gerridae		X	X	X	X	X
	Aquarius	X		X		X
	Gerris	X	X	X	X	X
	Limnoporus	X	X	X	X	X
	Metrobates		X		X	X
	Rheumatobates		X	X	X	X
	Trepobates	X	X	X	X	X
Hebridae		X	X	X	X	X
	Hebrus	X	X	X	X	X
	Lipogomphus	X	X	X	X	
	Merragata	X	X	X	X	X
Hydrometridae	*Hydrometra*	X	X	X	X	X
Macroveliidae			X			X
	Macrovelia	X	X			
Mesoveliidae	*Mesovelia*	X	X	X	X	X
Naucoridae	*Pelocoris*	X	X	X	X	
Nepidae	*Ranatra*	X	X	X	X	X
Notonectidae		X	X	X	X	X
	Buenoa	X	X	X	X	X
	Notonecta	X	X	X	X	X
Pleidae	*Neoplea*	X	X	X	X	X
Veliidae		X	X	X	X	X
	Microvelia	X	X	X	X	X
	Steinovelia	X				
Saldidae	*Pentacora*		X			
	Rupisalda		X			
Coleoptera		X	X	X	X	X
Anthicidae		X	X			
Chrysomelidae		X	X	X	X	X
	Donaciinae		X			
Curculionidae		X	X	X	X	X
	Bagous		X		X	
	Lixellus		X			

(continued)

(continued)

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Curculionoidea			X			
Dytiscidae		X	X	X	X	X
	Acilius		X	X	X	X
	Agabetes	X	X		X	
	Agabus	X	X	X	X	X
	Celina	X	X	X	X	X
	Colymbetes				X	
	Copelatus	X	X	X	X	
	Coptotomus		X		X	X
	Desmopachria	X	X	X	X	X
	Dytiscus		X	X	X	X
	Graphoderus					X
	Hydaticus	X	X	X	X	X
	Hydroporinae	X	X	X	X	X
	Hydroporus	X	X	X	X	X
	Hydrovatus	X	X	X	X	X
	Hygrotus	X	X	X	X	X
	Ilybius	X	X	X	X	X
	Laccophilus	X	X	X	X	X
	Liodessus	X	X	X	X	X
	Matus	X	X		X	X
	Nebrioporus					X
	Neoporus		X	X	X	X
	Neoscutopterus		X			
	Oreodytes		X		X	
	Rhantus	X				X
	Sanfilippodytes		X			
	Uvarus	X		X		X
Elmidae		X	X	X	X	X
	Dubiraphia	X	X		X	X
	Macronychus				X	X
	Optioservus			X	X	X
	Ordobrevia		X			
	Promoresia				X	
	Stenelmis			X	X	X
Georyssidae	*Georyssus*		X			X
Gyrinidae		X	X	X	X	X
	Dineutus	X	X	X	X	X
	Gyretes			X		X
	Gyrinus	X	X	X	X	X

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Haliplidae		X	X	X	X	X
	Haliplus	X	X	X	X	X
	Peltodytes	X	X	X	X	X
Helophoridae	*Helophorus*	X	X	X	X	X
Hydraenidae	*Hydraena*	X	X			X
Hydrochidae	*Hydrochus*	X	X		X	X
Hydrophilidae		X	X	X	X	X
	Anacaena	X	X		X	X
	Berosus	X	X	X	X	X
	Crenitis	X	X	X		X
	Cymbiodyta	X				X
	Enochrus	X	X	X	X	X
	Helochares					X
	Helocombus		X			X
	Hydrobius	X	X	X	X	X
	Hydrochara		X		X	
	Hydrophilus		X	X	X	
	Laccobius	X	X	X		X
	Paracymus	X	X	X	X	X
	Sperchopsis		X			
	Sphaeridiinae	X	X			X
	Tropisternus	X	X	X	X	X
Lampyridae		X	X		X	X
Noteridae	*Hydrocanthus*	X	X	X	X	X
Ptilodactylidae			X	X	X	
	Anchytarsus		X	X		
Scirtidae		X	X	X	X	X
	Cyphon		X	X		
	Elodes					X
	Prionocyphon		X	X		
	Sarabandus		X			
	Scirtes		X			X
Staphylinidae			X	X	X	X
Staphylinoidea[c]			X			X
Neuroptera		X	X	X	X	X
Sisyridae						X
Corydalidae		X	X	X	X	
	Chauliodes	X	X	X	X	
	Nigronia		X			
Sialidae	*Sialis*	X	X	X	X	X

(continued)

(continued)

Phylum Class **Order** Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Trichoptera		X	X	X	X	X
Apataniidae	*Apatania*					X
Brachycentridae	*Brachycentrus*	X	X			
Dipseudopsidae	*Phylocentropus*		X	X		X
Helicopsychidae	*Helicopsyche*	X	X	X	X	X
Hydropsychidae	*Arctopsychinae*			X		
Hydroptilidae		X	X	X	X	X
	Agraylea	X	X	X	X	X
	Hydroptila	X	X	X	X	X
	Neotrichia		X			
	Ochrotrichia	X	X	X	X	
	Orthotrichia	X	X	X	X	X
	Oxyethira	X	X	X	X	X
Lepidostomatidae	*Lepidostoma*		X			X
Leptoceridae		X	X	X	X	X
	Ceraclea	X	X	X	X	X
	Leptocerus	X	X	X	X	X
	Mystacides	X	X	X	X	X
	Nectopsyche	X	X	X	X	X
	Oecetis	X	X	X	X	X
	Setodes	X	X			
	Triaenodes	X	X	X	X	X
	Ylodes		X		X	
Limnephilidae		X	X	X	X	X
	Glyphopsyche		X			X
	Limnephilus		X	X	X	X
	Nemotaulius	X				
	Onocosmoecus				X	
	Psychoglypha		X			
Molannidae			X	X		X
	Molanna		X	X		X
Phryganeidae			X	X	X	X
	Agrypnia					X
	Banksiola		X			X
	Fabria			X		X
	Phryganea		X	X	X	X
Polycentropodidae		X	X	X	X	X
	Cernotina		X	X	X	X
	Neureclipsis	X	X	X		X
	Nyctiophylax					X
	Polycentropus		X	X	X	X

Phylum Class **Order** Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Lepidoptera		X	X	X	X	X
Crambidae		X	X	X	X	X
	Acentria	X	X	X	X	X
	Nymphuliella					X
	Nymphulini				X	
	Petrophila		X			
	Synclita		X	X		X
Noctuidae			X	X		X
	Bellura			X		X
Pyralidae			X	X	X	X
Diptera		X	X	X	X	X
Athericidae	*Atherix*				X	
Ceratopogonidae		X	X	X	X	X
	Leptoconops		X			
	Alluaudomyia		X	X		X
	Atrichopogon		X	X	X	X
	Bezzia	X	X	X	X	X
	Ceratopogon	X	X	X	X	
	Culicoides	X	X	X	X	X
	Dasyhelea			X		X
	Mallochohelea					X
	Palpomyia		X			
	Probezzia	X	X	X	X	X
	Serromyia		X		X	X
	Sphaeromias			X	X	X
	Stilobezzia	X			X	
Chaoboridae		X	X		X	X
	Chaoborus		X			
	Eucorethra		X			
Chironomidae		X	X	X	X	X
	Chironominae	X	X	X	X	X
	Chironomini	X	X	X	X	X
	Tanytarsini	X	X	X	X	X
	Pseudochironomini	X	X	X	X	X
	Orthocladiinae	X	X	X	X	X
	Podonominae	X	X	X	X	X
	Prodiamesinae				X	
	Tanypodinae	X	X	X	X	X
	Coelotanypodini		X			
	Pentaneurini		X	X		
	Tanypodini					X

(continued)

(continued)

Phylum						
Class						
Order						
Family	Subfamily, tribe, *genus*, *species*	LE	LH	LM	LO	LS
Culicidae		X	X	X	X	X
	Aedes/Ochlerotatus		X			
	Anopheles	X	X	X	X	X
	Culex	X	X		X	
Dixidae			X			X
	Dixella	X	X	X		X
Dolichopodidae		X	X			X
Empididae		X	X	X	X	X
	Hemerodromia			X	X	X
Ephydridae		X	X	X	X	X
	Ephydra		X			
Phoridae						X
Psychodidae		X	X	X		
	Maruina			X		
	Pericoma		X			
Ptychopteridae			X		X	X
	Bittacomorpha					X
	Ptychoptera		X		X	
Sarcophagidae		X				
Sciomyzidae		X	X	X	X	X
Stratiomyidae		X	X	X	X	X
	Caloparyphus		X			
	Myxosargus	X				
	Odontomyia		X	X	X	
	Hedriodiscus	X	X	X	X	X
	Stratiomys		X		X	
Tabanidae		X	X	X	X	X
	Chrysops	X	X	X	X	X
	Tabanus	X				
Tipulidae		X	X	X	X	X
	Antocha		X			X
	Dicranota			X		
	Erioptera		X			
	Helius	X	X		X	X
	Hexatoma				X	
	Limnophila	X				
	Pilaria		X			
	Prionocera		X			
	Tipula	X	X			X
	Ormosia	X			X	X

[a]Subphylum
[b]Infraclass
[c]Subclass
[d]Suborder

References

Albert DA, Wilcox DA, Ingram JW, Thompson TA (2005) Hydrogeomorphic classification for Great Lakes coastal wetlands. J Gt Lakes Res 31:126–146

Armstrong J, Afreen-Zobayed F, Armstrong W (1996) *Phragmites* die-back: sulphide- and acetic acid-induced bud and root death, lignifications, and blockages with aeration and vascular systems. New Phytol 134:601–614

Austen DJ, Bayley PB, Menzel BW (1994) Importance of the guild concept to fisheries research management. Fisheries 19:12–20

Azza N, van de Koppel J, Denny P, Kansiime F (2007) Shoreline vegetation distribution in relation to wave exposure and bay characteristics in a tropical great lake, Lake Victoria. Trop Ecol 23:353–360

Batzer DP, Resh VH (1992) Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. Wetlands 12:1–7

Brazner JC, Campana SE, Tanner DK (2004) Habitat fingerprints for Lake Superior coastal wetlands derived from elemental analysis of yellow perch otoliths. Trans Am Fish Soc 133:692–704

Burton TM (1985) The effects of water level fluctuations on Great Lakes coastal marshes. In: Prince HH, D'Itri FM (eds) Coastal wetlands: proceedings of the first great lakes coastal wetlands colloquium. Lewis, Chelsea, pp 3–13

Burton TM, Uzarski DG (2009) Biodiversity in protected coastal wetlands along the west coast of Lake Huron. Aquat Ecosys Health Manage 12:63–76

Burton TM, Uzarski DG et al (1999) Development of a preliminary invertebrate index of biotic integrity for Lake Huron coastal wetlands. Wetlands 19:869–882

Burton TM, Stricker CA, Uzarski DG (2002) Effects of plant community composition and exposure to wave action on invertebrate habitat use of Lake Huron coastal wetlands. Lakes Reserv Res Manage 7:255–269

Burton TM, Uzarski DG, Genet JA (2004) Invertebrate habitat use in relation to fetch and plant zonation in northern Lake Huron coastal wetlands. Aquat Ecosys Health Manage 7:249–267

Cardinale BJ, Burton TM, Brady VJ (1997) The community dynamics of epiphytic midge larvae across the pelagic-littoral interface: do animals respond to changes in the abiotic environment? Can J Fish Aquat Sci 54:2314–2322

Cardinale B, Brady V, Burton T (1998) Changes in the abundance and diversity of coastal wetland fauna from the open water/macrophyte edge towards shore. Wetl Ecol Manag 6:59–68

Chen CY, Hathaway KM, Folt CL (2004) Multiple stress effects of Vision herbicide, pH, and food on zooplankton and larval amphibian species from forest wetlands. Environ Toxicol Chem 23:823–831

Chubb SL, Liston CR (1986) Density and distribution of larval fishes in Pentwater Marsh, a coastal wetland on Lake Michigan. J Gt Lakes Res 12:332–343

Ciborowski JJH, Niemi GJ et al (2008) Ecosystem effects of water level changes in the upper great lakes. International Joint Commission Document

Cooper MJ, Uzarski DG, Burton TM, Rediske RR (2006) Macroinvertebrate community composition relative to chemical/physical variables, land use and cover, and vegetation types within a Lake Michigan drowned river mouth wetland. Aquat Ecosys Health Manage 9:463–479

Cooper MJ, Uzarski DG, Burton TM (2007) Macroinvertebrate community composition in relation to anthropogenic disturbance, vegetation, and organic sediment depth in four Lake Michigan drowned river-mouth wetlands. Wetlands 27:894–903

Cooper MJ, Gyekis KF, Uzarski DG (2012) Edge effects on abiotic conditions, zooplankton, macroinvertebrates, and larval fishes in Great Lakes fringing marshes. J Gt Lakes Res 38:142–151

Cooper MJ, Steinman AD, Uzarski DG (2013) Influence of geomorphic setting on the metabolism of Lake Huron fringing wetlands. Limnol Oceanogr 58:452–464

Cooper MJ, Lamberti GA, Uzarski DG (2014) Spatial and temporal trends in invertebrate communities of Great Lakes coastal wetlands, with emphasis on Saginaw Bay of Lake Huron. J Gt Lakes Res 40(Suppl 1):168–182

Danz NP, Niemi GJ et al (2007) Integrated gradients of anthropogenic stress in the U.S. Great Lakes basin. Environ Manage 39:631–647

Dolan DM, Chapra SC (2012) Great Lakes total phosphorus revisited: 1. Loading analysis and update (1994–2008). J Gt Lakes Res 38:730–740

Gathman JP, Burton TM (2011) A Great Lakes coastal wetland invertebrate community gradient: relative influence of flooding regime and vegetation zonation. Wetlands 31:329–341

Gathman JP, Albert DA, Burton TM (2005) Rapid plant community response to a water level peak in northern Lake Huron coastal wetlands. J Gt Lakes Res 31:160–170

Hanowski J, Danz N et al (2007) Consideration of geography and wetland geomorphic type in the development of Great Lakes coastal wetland bird indicators. Ecohealth 4:194–205

Harris HJ, Milligan MS, Fewless GA (1983) Diversity: quantification and ecological evaluation in freshwater marshes. Bio Conserv 27:99–110

He C, DeMarchi C, Tao W, Johengen TH (2013) Modeling distribution of point and nonpoint sources pollution loadings in the Saginaw Bay watersheds, Michigan. Geospat Tools Urb Water Resour 7:97–113

Heath RT (1992) Nutrient dynamics in Great Lakes coastal wetlands: future directions. J Gt Lakes Res 18(4):590–602

Hecnar SJ (2004) Great Lakes wetlands as amphibian habitats: a review. Aquat Ecosys Health Manage 7:289–303

Holomuzki JR, Klarer DM (2010) Invasive reed effects on benthic community structure in Lake Erie coastal marshes. Wetl Ecol Manag 18:219–231

Jude DJ, Pappas J (1992) Fish utilization of Great Lakes coastal wetlands. J Gt Lakes Res 18:651–672

Keddy PA (1982) Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate, particle size, and shoreline plants in Axe Lake, Ontario. Aquat Bot 14:41–58

Keough JR, Thompson TA, Guntenspergen GR, Wilcox DA (1999) Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. Wetlands 19:821–834

King RS, Brazner JC (1999) Coastal wetland insect communities along a trophic gradient in Green Bay, Lake Michigan. Wetlands 19:426–437

Klarer DM, Millie DF (1992) Aquatic macrophytes and algae at Old Woman Creek estuary and other Great Lakes coastal wetlands. J Gt Lakes Res 18:622–633

Kovalenko KE, Brady JV et al (2014) Congruence of community thresholds in response to anthropogenic stress in Great Lakes coastal wetlands. Freshw Sci 33:958–971

Kulesza AE, Holomuzki JR, Klarer DM (2008) Benthic community structure in stands of *Typha angustifolia* and herbicide-treated and untreated *Phragmites australis*. Wetlands 28:40–56

MacKenzie RA, Kaster JL, Klump JV (2004) The ecological patterns of benthic invertebrates in a Great Lakes coastal wetland. J Gt Lakes Res 30:58–69

Mayer T, Edsall T, Munawar M (2004) Factors affecting the evolution of coastal wetlands of the Laurentian Great Lakes: an overview. Aquat Ecosys Health Manage 7:171–178

Maynard L, Wilcox DA (1997) Coastal wetlands of the Great Lakes. State of the Lakes Ecosystem Conference 1996. Environment Canada and US EPA Report, 905-R-97-015b

McLaughlin DB, Harris HJ (1990) Aquatic insect emergence in two Great Lakes marshes. Wetl Ecol Manag 1:111–121

Merritt RW, Benbow ME, Hudson PL (2002) Wetland macroinvertebrates of Prentiss Bay, Lake Huron, Michigan: diversity and functional group composition. Gt Lakes Entomol 35:149–160

Metzler G, Sager PE (1986) A preliminary study of the macrobenthos of wave-swept and protected sites on the Lake Michigan shoreline at Toft Point Natural Area, Wisconsin. Trans Wis Acad Sci Arts Lett 74:126–132

Nelson JW, Kadlec JA, Murkin HR (1990) Responses by macroinvertebrates to cattail litter quality and timing of litter submergence in a northern prairie marsh. Wetlands 10:47–60

Niemi GJ, Brady VJ et al (2009) Development of ecological indicators for the U.S. Great Lakes coastal region: a summary of applications in Lake Huron. Aquat Ecosys Health Manage 12:77–89

Patrick CJ, Cooper MJ, Uzarski DG (2014) Dispersal mode and ability affect the spatial turnover of a wetland invertebrate metacommunity. Wetlands 34:1133–1143

Peters JA, Cooper MJ et al (2014) Historical changes and current status of crayfish diversity and distribution in the Laurentian Great Lakes. J Gt Lakes Res 40:35–46

Prince HH, Padding PI, Knapton RW (1992) Waterfowl use of the Laurentian Great Lakes. J Gt Lakes Res 18:673–699

Relyea RA (2005) The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. Ecol Appl 15:618–627

Riis T, Hawes I (2003) Effect of wave exposure on vegetation abundance, richness and depth distribution of shallow water plants in a New Zealand lake. Freshw Biol 48:75–87

Schneider P, Sager PE (2007) Structure and ordination of epiphytic invertebrate communities of four coastal wetlands in Green Bay, Lake Michigan. J Gt Lakes Res 33:342–357

Schock NT, Murry BA, Uzarski DG (2014) Impacts of agricultural drainage outlets on Great Lakes coastal wetlands. Wetlands 34:297–307

Schultz R, Dibble E (2012) Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: the role of invasive plant traits. Hydrobiologia 684:1–14

Sierszen ME, Brazner JC et al (2012a) Watershed and lake influences on the energetic base of coastal wetland food webs across the Great Lakes Basin. J Gt Lakes Res 38:418–428

Sierszen ME, Morrice JA, Trebitz AS, Hoffman JC (2012b) A review of selected ecosystem services provided by coastal wetlands of the Laurentian Great Lakes. Aquat Ecosys Health Manage 15:92–106

Trebitz AS (2006) Characterizing seiche and tide-driven daily water level fluctuations affecting coastal ecosystems of the Great Lakes. J Gt Lakes Res 32:102–116

USDA (1997) Glyphosate: herbicide information profile. US Forest Service, Pacific Northwest Region

Uzarski DG, Burton TM, Genet JA (2004) Validation and performance of an invertebrate index of biotic integrity for Lakes Huron and Michigan fringing wetlands during a period of lake level decline. Aquat Ecosys Health Manage 7:269–288

Uzarski DG, Burton TM et al (2005) Fish habitat use within and across wetland classes in coastal wetlands of the five Great Lakes: development of a fish-based index of biotic integrity. J Gt Lakes Res 31:171–187

Uzarski DG, Burton TM, Kolar RE, Cooper MJ (2009) The ecological impacts of fragmentation and vegetation removal in Lake Huron's coastal wetlands. Aqu Ecos Health and Manage 12:45–62

Voigts DK (1976) Aquatic invertebrate abundance in relation to changing marsh vegetation. Am Midl Nat 95:313–322

Weeber RC, Vallianatos M (2000) The Marsh Monitoring Program 1995–1999: monitoring Great Lakes wetlands and their amphibian and bird inhabitants. Bird Studies Canada, Port Rowan, ON

Wieten AC, Cooper MJ, Parker AD, Uzarski DG (2012) Great Lakes coastal wetland habitat use by seven turtle species: influences of wetland type, vegetation, and abiotic conditions. Wetl Ecol Manag 20:47–58

Wilcox DA (1995) Wetland and aquatic macrophytes as indicators of anthropogenic hydrologic disturbance. Nat Areas J 15:240–248

Wilcox DA, Kowalski KP et al (2008) Cattail invasion of sedge/grass meadows and regulation of Lake Ontario water levels: photointerpretation analysis of sixteen wetlands over five decades. J Gt Lakes Res 34:301–323

Zanatta DT, Mackie GL, Metcalfe-Smith JL, Woolnough DA (2002) A refuge for native freshwater mussels (Bivalvia: Unionidae) from impacts of the exotic Zebra Mussel (*Dreissena polymorpha*) in Lake St. Clair. J Gt Lakes Res 28:479–489

Zanatta DT, Bossenbroek JM et al (2015) Distribution of native mussel (Unionidae) assemblages in coastal areas of Lake Erie, Lake St. Clair, and connecting channels, twenty-five years after a dreissenid invasion. NE Natur 22:223–235