Submerged terra incognita: Lake Michigan's abundant but unknown rocky zones

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Introduction

"It was six men of Indostan
 To learning much inclined,
Who went to see the Elephant
 (Though all of them were blind),
That each by observation
 Might satisfy his mind." (Saxe, 1872)

The Great Lakes are too large to see, hence we are all blind. This is true for many large-scale landforms. In classical terrestrial ecology the example lies in the sand dunes of Indiana and Michigan. For an ecologist in Michigan to assume that dune ecology applies to Illinois and Wisconsin would be myopic since dunes are nearly

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absent along the Illinois and Wisconsin shores. The differences extend well under the water surface, but are not as obvious. In the water we are lucky to see 10 meters in any direction, therefore it is important to remember that Lake Michigan is too big to be seen by bottom grabs, trawls, or SCUBA divers alone. Unfortunately, there has been much more sampling by bottom grabs and trawls on the easily sampled, increasingly barren unconsolidated bottoms, than on the rocks by SCUBA divers. By unbalanced sampling of the "elephant" we prevent complete understanding of the whole.

It has been understood for a long time by lake and marine ecologists that hard-bottom substrates, in contrast to unconsolidated (soft) substrates, are disproportionately important habitats. The productivity of marine hard-bottoms may be much more obvious because of the spectacular organismic abundance and diversity. Despite less diversity, Great Lakes rocky habitat provides stable substrate for an encrusting community and three-dimensional structure for benthic and epibenthic animals. Their importance has been long recognized by fishery scientists, as evidenced by artificial reefs that have been established in many locations, including the Great Lakes (D'Itri, 1985). Despite this apparent importance, these abundant natural habitats scarcely have been studied in Lake Michigan.

There are multiple reasons why rocky habitats have been ignored. Rocky habitats are much more difficult to sample remotely via bottom grabs and nets. In a sense, boulders are the bane of benthologists; Brinkhurst (1974) dedicates his book to those who have pulled an Ekman grab from deep water by hand from a rowboat only to find a rock in the jaws. A more circumspect response would be excitement at the rare chance to study the organisms still attached to the rock. It is also easy to presume that, because the euphotic littoral zone is rather thin, shallow rocky areas are relatively unimportant and that rocky areas deeper than the euphotic zone cannot be very productive. That the new encrusting community, based on the invasive zebra mussel, has in some way depressed the soft-bottom infaunal invertebrate populations in vast areas to a depth up to 70 meters (Nalepa et al., 1998) indicates that the rocky areas are currently extremely important and their prior importance was overlooked.

The evolving influence of modeling efforts and associated efforts to track ecological commodities such as energy and carbon have brought a new focus to the study of the littoral zone. The analysis of publications presented by Vadeboncouer et al. (2002) points out the discrepancy between the large number of studies of pelagic productivity and the paucity of those in the littoral zone. This discrepancy and the evolving demand for data imposed on hard-bottom researchers by modelers highlights another challenge regarding benthic research. Pelagic studies are much easier to perform because the water is filtered in some way and it is convenient to extrapolate findings because it appears to be homogenous to the human observer. Substrate heterogeneity complicates modeling because it is difficult to estimate mean densities or variances and the mean may not be a useful estimator of the expected density (see Elliott, 1971).

Many rocky habitats can only be sampled qualitatively because organisms hide in crevices in bedrock or under boulders that cannot be moved. Yet the importance of rocky habitat is well understood by fishers. When commercial fishers target rock-affiliated fish such as yellow perch (*Perca flavescens*), they preferentially fish the rocky habitat. The consequence of avoiding difficult habitat is that researchers tend to avoid critical habitat. Extrapolating to rocky habitat from more easily sampled habitats is extremely suspect and almost certainly yields great errors, even when generating lists of taxa. For example, Hudson et al. (1998) used rock affiliated fishès as "collecting devices" to survey copepods and increased the Great Lakes species list from 16 to 30 species for cyclopoid copepods and 15 to 34 species for harpacticoid copepods. Because Lake Michigan is a managed system, and because the rocky areas are prime habitat, we are obliged to do our best to understand the dynamics of the hard substrates.

This is, for the most part, an inventory of Lake Michigan's rocky habitats and a review of the natural history of the organisms found there. There are many gaps in the habitat species inventories; the gaps are "invitations" for exploration and study. Indeed, we hope that the map we present will soon be as "quaint" as the maps of the early French explorers. One reviewer of this paper suggested that a more useful format would be a comparison of the rocky benthos before and after the zebra mussel (*Dreissena polymorpha*) invasion. That format is not feasible because such data appear to be nonexistent. We present little with regards to ecological processes because little is known. We have focused our review almost entirely on Lake Michigan's main basin largely because the bays have flora and fauna typical of small lakes. Most of what we present is descriptive or even anecdotal, but this is an attempt to establish a foundation for more extensive study.

Inventory of rocky habitat

The sediments of Lake Michigan can be separated into three major units: lacustrine clays, glacial deposits, and Paleozoic bedrock. Here we focus on the latter two sediment types. Approximately 500 million years ago, sedimentary rocks were deposited in marine water at various times when the sea covered the continent. The rock types are mainly limestones, dolomites, shales, and sandstones. The rocky habitats from bedrock exposed by Pleistocene glaciers include three major Paleozoic formations (Hough, 1958; Lineback et al., 1971; 1974). During the Pleistocene epoch, periods of glaciation are marked by the deposition of till or clay with the apparent complete scouring of older deposits from the lake basins by succeeding glacial stages. To help identify the possible location of rocky habitats in Lake Michigan, we created a map of potential sites from four sources. For the southwestern shoreline, we used maps created for the IL Department of Conservation (Norby and Collinson, 1977; Collinson et al., 1979; Holm et al., 1987; Fucciolo, 1993). For the northwestern shoreline, we used NOAA Great Lakes nautical charts to complete the mapping of reefs, shoals, and rocky outcrops. For northern and northeastern Lake Michigan, Dawson et al. (1997) used commercial catch reports to determine historic lake trout spawning aggregations in Lake Michigan. The spawning sites were most numerous where Silurian Niagaran rocks outcrop along the north and northwest shore and where Devonian rocks outcrop in the northeast areas of Lake Michigan (Fig. 1). Other rocky sites along the Michigan shore were listed in the spawning atlas of Goodyear et al. (1982). For Wisconsin we used the map of Powers and Robertson (1968), along with personal observations by J. Janssen and anecdotal observations by commercial and sport fishers.

The Silurian Niagaran Dolomite formation defines the west boundary of Lake Michigan from Chicago, along the Door peninsula, and extends north to the Straits of Mackinac (see Fig. 8, Hough, 1958). The general bottom contour is determined by the bedrock surface which slants downward so that strata surfaces face toward mid-Michigan, the center of the Michigan Basin (Chrzastowski et at., 1994; Foster and Folger, 1994). What substrate appears at the benthic-water interface is determined by whether the area is presently erosional or depositional, whether there are bedrock outcrops, and whether there are local glacial deposits. The best-studied region is from Illinois to Indiana where the bottom includes bedrock reef outcropping, glacial boulders, cobble, and clay, and recent sand deposits in nearshore areas (Fucciolo, 1993). Most of the Illinois sector is erosional due to the effects of storms. Hough (1935) found the western side of the lake in this area to be complex, characterized by gravel or gravel-veneered till. However, the more detailed mapping reported by Fucciolo (1993), along with personal observations by J. Janssen and M. Berg, indicates that there are up to about 160 bedrock reefs and the area between these reefs is almost entirely cobble to boulder glacial till. Much of the loose rock is limestone/dolomite, probably from the bedrock reefs, but occasional igneous rocks are also found. Near shore the rock tends to be covered by mobile sand; the transition from sand to rock generally occurs at 3-6 m deep. Storm-generated sand movements render the area dynamic with the sand deposits changing position atop the bedrock and loose rock (Shabica and Pranschke, 1994; Foster and Folger, 1994). The thin nature of the sand is evident at jetties where the sand has been eroded at the ends and "downcurrent" (counterclockwise).

Bedrock outcrops occur in a variety of locations in the southern basin, particularly along the western side, where glaciation left an escarpment (Wickham et al., 1978). In Illinois the Silurian/Devonian escarpment is evident from an estimated 160 bedrock reefs that have been mapped (Fucciolo, 1993). These range greatly in

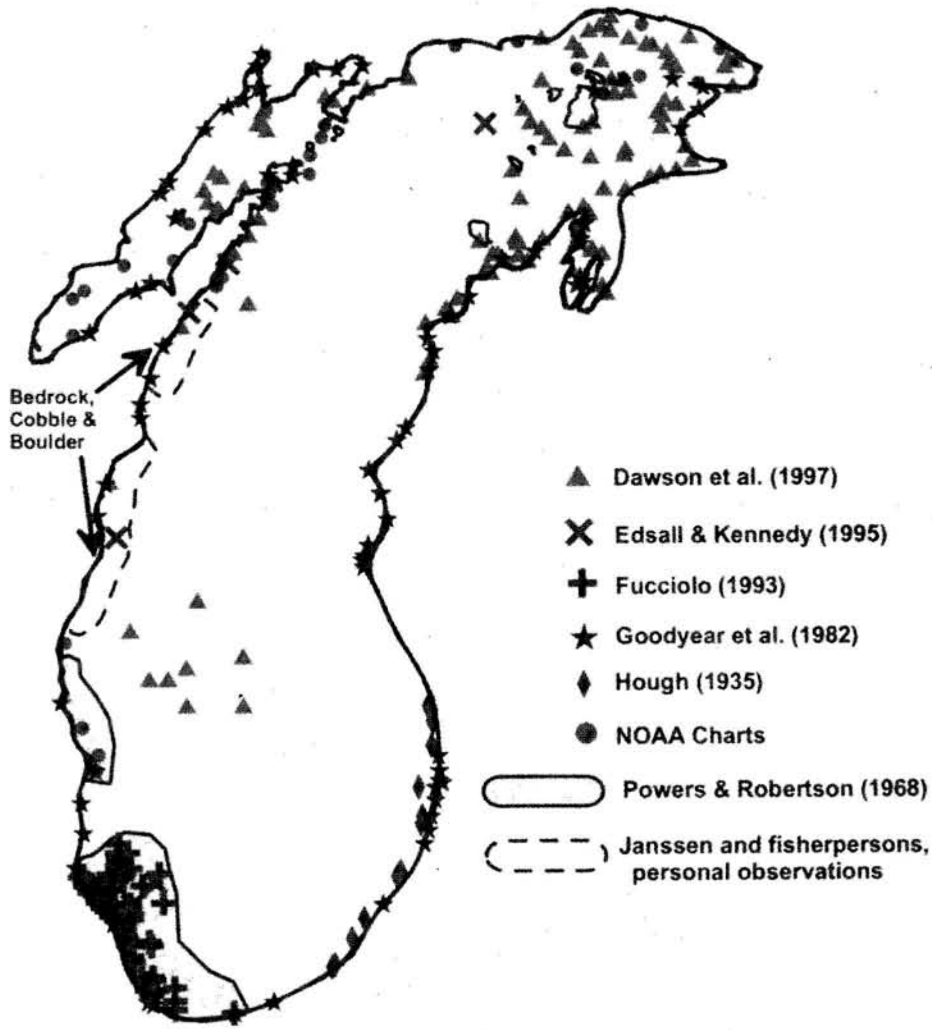

Fig. 1. Rocky habitats of Lake Michigan were obtained from geographical locations (Dawson et al., 1997; Edsall and Kennedy, 1995), maps (Fucciolo, 1993; Hough, 1935; Goodyear et al., 1982; Powers and Robertson, 1968), and NOAA charts.

size. Some of the larger reefs such as Julian's Reef and Wilmette reef have been mapped using sidescan and ROV's. The area between the shallower reefs is filled with glacial boulders, cobble, and gravel (Foster and Folger, 1994). Most likely the southwestern area has bedrock near the lake bed bottom and the bedrock reefs are found in areas where particularly hard rock was not eroded by glaciation.

Bedrock outcrops and other rocky areas are relatively rare on the eastern side of Lake Michigan, but some are shown in Fig. 1. A continuous band of sand

Fig. 2a. The Silurian dolomite reef is located near New Buffalo, MI. The photograph was taken prior the invasion of dreissenids.

Fig. 2b. The boulders are encrusted with the mussel, *Dreissena polymorpha*. The attached algae is *Cladophora*.

occurs along the shore from Gary, IN to Muskegon, WI (Cote, 1967). Further from shore, i.e. at depths greater than 20 m, discontinuous bands of sand/silt are found. A pre-dreissenid mussel photograph of a reef near New Buffalo, MI, is shown in Fig. 2a. In contrast, most rocky substrates are now covered with dreissenids as illustrated by a photograph from boulders located near Highland Park, IL (Fig. 2b). Dreissenids have invaded even the Mid-Lake Reef complex. In 2001 occasional zebra mussels were found (< 1 per rock) but by 2002 the more cold-tolerant quagga mussel (*D. bugensis*) was very abundant (dozens to hundreds estimated per rock).

The Silurian reefs and bedrock continue into Wisconsin with shoreline outcroppings at Racine, Harrington Beach, Sheboygan, Kewaunee, and especially along the Door Peninsula, where the Silurian escarpment is very evident. These have been poorly mapped (Fig. 1), but most of the area between Milwaukee and Two Rivers is treacherous to trawlers. Some reefs that are used by lake trout for spawning were identified by Dawson et al. (1997) and additional shoals, reefs, or rocky locations were indicated on NOAA navigation charts. Between Waukegan and Racine the lake floor is unconsolidated. Sand dominates and rock is apparently scarce.

The Bois Blanc formation (dolomite, limestone) extends along the south shore of the Straits of Mackinac through Waugoshance Point and to the rocky area around Grays Reef, Hog Island, Beaver Island, Trout Island, High Island, and Gull Island. Bedrock does not often outcrop in this area. During a survey of rocky outcroppings using SCUBA (Somers 1968), only two bedrock outcrops were found near Hog Island and Ile aux Galet Reefs. All other locations proved to be deposits of large boulders, consolidated clay till, and unconsolidated sediments. Rocks in this cluster were subjected to slumping and irregular fracturing following dissolution of underlying late Silurian salt beds (Landes et al., 1945). The process of brecciation followed by re-cementing results in a more resistant structure, which may account for the preservation of reefs despite repeated glacial scouring.

The Traverse Group formation (limestone) forms the east shore of Lake Michigan from Little Traverse Bay southwestward through Petoskey, Charlevoix, and the headlands of Grand Traverse Bay. The formation underlies the shore as far southwest as Frankfort, Michigan. Hough (1958) suggests that it projects as a ridge across Lake Michigan on a line from Frankfort, MI, to Port Washington, WI. A small patch of Devonian rocks is present north of Port Washington and another is found north of Milwaukee.

The Mid-Lake Reef complex rises from deep water (about 100 m) to as shallow as about 40 meters approximately in between Milwaukee and Muskegon. The geologic structures are cuestas, which have gentle slopes on one side of the peak, and steep drop-offs on the other. The drop-off at one cuesta was estimated to be 35 ° by Somers (1968). Our observations (2002-2004) at three sites near to Somer's indicates diverse drop-off geology. One site had a "staircase" of strata, with each stratum being about 1 m thick. Two other sites had a rock "cap" with vertical walls leading to a talus slope. At one site the cap was 3-4 m thick while at the second the cap was about 1 m. The rock is presumably resistant Silurian/Devonian bedrock. Rock fragments sometimes contain crinoid stem segments. ROV reconnaissance by Edsall and Kennedy (1995) at the shallowest of the reefs shows that the bedrock is fully exposed in some areas and covered by boulders and cobbles elsewhere. Sand covers some areas and ripple marks on the sand indicates that it is dynamic and shifts frequently (J. Janssen, personal observations using

ROV). In that the Mid-Lake Reef Complex was exposed for several thousand years when Lake Michigan's depth was about 100 m shallower (Chrzastowski and Thompson, 1994) the present reef morphology is probably a result of both glaciation and terrestrial weathering.

In our review of rocky habitats, it became apparent that there are no standard procedures for mapping. Early studies of Lake Michigan sediments relied on gravity cores (Hough, 1958; Gross et al., 1970) but this method did not provide information on bedrock outcropping or other hard substrates. Somers (1968) used SCUBA and a deep diving submersible to locate and observe bedrock exposures and to correctly identify the composition of suspected bedrock exposures within the Bois Blanc formation. Based on these studies, Somers found a great variation of sediment types within a given area. He determined that sampling and mapping of sediment distribution from cores would be of little validity in this area. Lineback et al. (1971;1974) used high-resolution seismic profiles and gravity cores to map the sediments in southern Lake Michigan. They found that physically hard bottoms have high acoustic impedance and their records show powerful returns and multiple reflections from the highly reflective sediment-water interface. The seismic records in their study show that lake clays, glacial drift, and bedrock can be distinguished by geophysical means.

Foster and Folger (1994) used side scan sonar, Van Veen grab samples, or SCUBA observations to create a more detailed distribution and boundaries between different sediment types. Analyses of side scan and sediment samples revealed a relationship between backscatter strength and sediment texture. Sediments with strong acoustic returns were often covered by boulders, cobbles, gravel, coarse sand, or silt/clay till. The details of the sediments could only be verified in areas where side scan data overlapped with direct observations.

Edsall et al. (1995) used side scan sonar, SCUBA, and an ROV to map potential spawning sites for lake trout at seven sites in Lake Michigan. In another study, Edsall et al. (1995) used similar habitat mapping techniques to assess the potential for natural reproduction by stocked lake trout on the reef. In a more recent study, Barnes et al. (2003) used LIDAR in northern Lake Michigan to make detailed seafloor and lakebed maps in areas too shallow for practical use of sonar systems. In the most recent mapping, data were obtained from five reef sites and two coastal sites. In addition to water depths, the LIDAR data will be used to extract the reflectivity (albedo) of the lake floor. The albedo may provide information on the lakebed geological composition.

Multi-beam sonar, bottom classification system, and video are being used in southern Lake Michigan (Lozano et al., 2002) to map the distribution of dreissenids on different sediment types. The segment of coastline in their study included a variety of habitats, i.e. areas of sand, silt, and rock, with and without dreissenids including rocky habitats. Multibeam/sidescan sonar operates by transmitting sound waves to surrounding water (and lake bottom) and then analyzing characteristics of returning sound waves reflected from objects in the water or on the bottom. The Questor Tangent Sediment Classification Systems (QTC) was also used to map the sediments. Seabed classification is the organization of lakebeds into discrete units based on a characteristic acoustic response. The backscatter is influenced by features of the lakebed and immediate subsurface. The QTC approach involves digital signal processing of the first returning echo. Video from SCUBA or sediment grab samples was used to validate acoustic maps. Lakebed characteristics are influenced by sedimentary properties (grain size), lakebed roughness (sedimentary bedforms and bedrock features), and organisms living on the lake floor (Hamilton et al., 1999).

The data produced by the bottom classification system reflect changes in the lake floor immediately below the boat. The multibeam data were used to fill in gaps in coverage. The strength of the sidescan response is controlled by the bottom type, surface roughness, and shape of the lake floor. We obtained quantitative information on the shape of the lake floor (in addition to its depth), from the high-resolution bathymetry. Given this information, a qualitative interpretation of the sidescan data was made in terms of substrate type. The combined sidescan and bathymetric information was used to fill in areas between the boat tracks in a controlled, meaningful fashion. Preliminary results suggest that zebra mussel populations on the lake bottom reflect sound in a unique way and produce a distinct "signature" that will allow researchers to distinguish bottom types with and without dreissenids.

Biota

Periphyton

The structure and composition of epilithic algal communities in Lake Michigan have not been extensively studied, however Blum (1982) presented a detailed description of the seasonal dynamics of epilithic algae in a variety of habitats with hard substrates including harbors, breakwalls, shoreline areas, and offshore sites. In general, species richness increases with depth (Blum, 1977). Despite the general paucity of benthic algal research on hard substrates in Lake Michigan, the few studies that have mentioned benthic algae have noted that the predominant filamentous alga is *Cladophora glomerata* (Blum, 1982; Rutecki et al., 1985). *Cladophora* is particularly conspicuous and has been seen as a nuisance by humans for many decades, especially when it washes up on beaches in large quantities, apparently in response to nutrient enrichment and resuspension following storms (Herbst, 1969). *Cladophora* attaches to rocks, although this is not always apparent because sand and silt can collect around rocks and obscure the attachment site. *Cladophora* also attaches directly to zebra mussels and, where the filaments are thick and long, pulling on the alga pulls off many of the mussels. When *Cladophora* washes onto beaches, it often has zebra mussel shells beneath it and stranded crustaceans crawling on the surface attracting gulls and shorebirds. *Cladophora* has been favored by the zebra mussel invasion; how that has impacted other rock-associated algae has yet to be documented. However, it is very likely that many filamentous alga species have been extirpated. Although *Cladophora* and other filamentous species are known to serve as substrates for many other algal taxa, especially diatoms (Lowe et al., 1982), it is not clear how these epiphytes have responded to changes in the filamentous algal assemblage.

The invasion of dreissenids into Lake Michigan has impacted the algal community in perhaps many ways that are still unexplored. It is yet unknown how the following types of filamentous algae have/will respond, therefore, they are described with pre-invasion characteristics. The invasive red alga *Bangia atropurporea* attached to rocks in the splash zone and in very shallow water (Lin and Blum, 1977; Blum, 1982). A brown alga, *Sphacelaria lacustris*, occurred in deeper water (Schloesser and Blum, 1980), in the shadow of the rocks. *Spirogyra* and *Mougeotia* were occasionally seen in sufficient abundance to be a nuisance for a SCUBA diver, but appeared to entangle among the rocks rather than anchor there. *Chara* could be found among the rocks and also on soft sediments.

Diatoms are often indicated as being a major component of the epilithic flora on hard substrates in Lake Michigan (Rutecki et al., 1985; Zenchak, 1993). Diatoms encrusted the rocks in Illinois and Wisconsin at 6 + meters prior to the zebra mussel invasion. With increased water clarity subsequent to the zebra mussel invasion, this has been replaced by thick *Cladophora* growth.

Although few studies have attempted to examine epilithic algal community structure, some insight into community composition can be inferred from laboratory studies that used algae-colonized rocks collected from the lake. In a laboratory study Zenchak (1993) used an algal slurry derived from rocks collected in 5-6 m of water along the Chicago shoreline as a source of algal colonists, examining the effects of crayfish grazing on benthic algal community dynamics. Although this study was conducted in the laboratory with a relative dominance of algal taxa probably not naturally occurring in the lake, the species composition likely reflects what is found in the lake and can be instructive in discerning algal species richness. A total of 90 species/varieties (39 genera) of algae were reported with diatoms accounting for 64% (58 species/varieties and 22 genera) of total algal species richness (Zenchak, 1993). The major diatom taxa were *Achnanthes linearis*, *A. minutissima*, *Amphora perpusilla*, *Fragilaria crotonensis*, *F. pinnata*, *Navicula radiosa*, *Navicula* spp, *Nitzschia dissipita*, *N. microcephala*, *N. fonticola*, *N. palea*, *Nitzschia* spp, and *Synedra* spp. Non-diatom taxa accounted for 36% (32 species/varieties and 17 genera) of benthic algal species and were dominated by *Chroococcus* spp., *Lyngbya limnetica*, *Oscillatoria limnetica*, *Phormidium tenue*, and *Scenedesmus* spp. Rutecki et al. (1985) also reported that diatoms dominated the taxa on artificial reefs in southeastern Lake Michigan. They found a total of 62 benthic algal taxa with diatoms comprising 81% (50 taxa), green algae 16% (10 taxa), and blue-greens 3% (2 taxa) of epilithic algae species richness. All the above-mentioned studies were conducted prior to the invasion of zebra mussels, although the data from Zenchak (1993) were collected < 2 months after the first zebra mussel sighting in western Lake Michigan (J. Janssen, pers. obs.). Given the critical role that many of these primary producers fill in the transfer of energy resources in rocky nearshore areas, our lack of understanding as to how benthic algae have responded to zebra mussels and other invaders has inhibited our ability to accurately predict the broad ramifications of these perturbations to Lake Michigan food webs.

Benthic invertebrates

Benthic invertebrates in rocky habitats of Lake Michigan, and the Great Lakes in general, have been historically understudied compared to those associated with unconsolidated substrates such as sand or silt (Eggleton, 1936; Winnell and Jude, 1987; Fullerton et al., 1998; Nalepa et al., 1998). More recently, our understanding of rock-associated benthic invertebrate communities has advanced as a result of the increased number of studies focusing on the invasion of exotic species such as the zebra mussel, quagga mussel, round goby (*Neogobius melanostomus*), and the gammarid amphipod *Echinogammarus ischnus* (Jude et al., 1992; Jude and DeBoe, 1996; Dermott et al., 1998; Stewart et al., 1998; González and Downing, 1999; Kuhns and Berg, 1999; Djuricich and Janssen, 2001; Jude, 2001; Nalepa et al., 2001).

Taxonomic composition of invertebrates on rock substrates in Lake Michigan can be very diverse, but typically is dominated by amphipods, isopods, oligochaetes, and chironomids, accounting for 83% of organisms collected (Janssen and Quinn, 1985; Winnell and Jude, 1987). Additional invertebrate groups commonly collected on rock substrates, but not necessarily locally abundant, include mayflies, caddisflies, crayfish, and snails.

Although a variety of factors, including water chemistry and fish predation, can be expected to influence benthic invertebrate species composition, the strong similarity in invertebrate communities among rocky habitats across broad geographic areas suggests that differences in the physical environment, such as water temperature, wave activity, and substrate configuration play a more important role (Winnell and Jude, 1987). As a result, rocky habitats in areas with <10 m of water are characterized by an invertebrate taxonomic composition that is highly represented by organisms commonly found in lotic environments (Barton and Hynes, 1978; Lauritsen and White, 1981; Winnell and Jude, 1987; Kuhns and Berg, 1999). Similar observations have been made for the benthic fauna in western Lake Erie (Shelford and Boesel, 1942). For example, the benthic fauna on rocks located at depths of 5-7 m along the Illinois shoreline in southwestern and western Lake Michigan is represented by a diverse assemblage of aquatic insects including *Hydropsyche, Agraylea, Polycentropus, Setodes, Ceraclea* and *Oecetis* (Trichoptera), *Epeorus*, *Stenonema* and *Stenacron* (Ephemeroptera), *Optioservus* (Coleoptera), and *Krenopelopia, Chaetocladius, Cricotopus/Orthocladius, Thienemanniella, Stilocladius, Paratanytarsus*, and *Rheotanytarsus* (Diptera). Although these taxa are not found exclusively in lotic systems, their presence on rock substrates in Lake Michigan suggests that substrate type and wave action in these areas provide conditions similar to erosional areas in lotic systems.

Although the physical environment clearly plays a major role in invertebrate species composition on rock substrates, the establishment and interactive effects of invasive species have dramatically altered benthic invertebrate community composition and energy flow. Prior to the zebra mussel invasion there was sparse encrusting fauna, consisting of bryozoans and sponges. One of these, *Lophopodella carteri*, persists and may impede zebra mussel settlement (Lauer et al., 1999). The presence of *Dreissena* spp. increases substrate complexity, water clarity, and the deposition of particulate organic matter in the form of fecal and pseudofecal deposition (Stewart and Haynes, 1994; Lowe and Pillsbury, 1995; Botts et al., 1996; González and Downing, 1999; Vanderploeg et al., 2002). These changes provide additional refugia, colonizable surface area, and food resources for benthic invertebrates resulting in an overall positive effect on non-mussel invertebrate densities, biomass, and diversity (Stewart and Haynes, 1994; Stewart et al., 1998; Kuhns and Berg, 1999). Kuhns and Berg (1999) reported significantly higher densities of amphipods, hydroptilid caddisflies, isopods, and chironomids on hard substrates colonized by zebra mussels than on uncolonized substrates in southwestern Lake Michigan. These trends are consistent with those reported from Lake Erie (Dermott et al., 1993; González and Downing, 1999), Lake St. Clair (Griffiths, 1993), and Lake Ontario (Stewart and Haynes, 1994). Although the above-mentioned mechanisms individually may account for these changes, it is likely that multiple mechanisms are acting in concert (e.g., increased number of interstices, increased benthic algal biomass, and/or increases in benthic particulate organic matter) to enhance rock-associated benthic invertebrate populations.

The presence of the exotic, molluscivorous round goby has been shown to have a negative indirect effect on benthic invertebrates in rocky habitats via disruption of zebra mussel colonies and via direct predation on colony-associated invertebrates. Djuricich and Janssen (2001) found that in the presence of round goby predation, the size structure of zebra mussel populations shifted to larger-sized individuals that were typically larger than the size preferred by round gobies. A likely explanation for this shift in zebra mussel size-structure is that round gobies preferentially prey on smaller-sized individuals. When round goby predation was absent, however, the size of individual zebra mussels was within the range preferred by round gobies. This alteration in the size of zebra mussels comprising a colony, and the effect of colony disturbance, has important implications for the size, abundance, and stability of interstices that serve as refugia for colony-associated invertebrates.

In addition to indirect effects of round gobies on rock-dwelling invertebrates, round gobies may affect invertebrate populations by direct predation. In southern Lake Michigan the diet of round gobies < 75 mm is comprised of primarily soft-bodied benthic invertebrates such as amphipods (56% of diet by numbers), isopods (16%), and chironomids (15%) (M. Berg, unpubl. data). Larger round gobies, however, feed primarily on zebra mussels (74% of diet by numbers). Round gobies can reduce non-mussel invertebrate densities on hard substrates by as much as 44% compared to substrates where round gobies are excluded (Kuhns and Berg, 1999). The presence of zebra mussels, however, can offset some of the negative effects of round gobies on non-mussel benthic invertebrates. In the presence of round gobies, substrates with low and high zebra mussel densities have higher colony-associated invertebrate biomass (non-mussel) than when zebra mussels are absent (Kuhns and Berg, 1999).

Amphipods, primarily *Gammarus* spp., often represent a major invertebrate component on rocky substrates in Lake Michigan (Janssen and Quinn, 1985; M. Berg, unpubl. data). *Gammarus* abundance responded positively to the establishment of zebra mussel populations because of increased habitat heterogeneity and/or food resources (Stewart and Haynes, 1994; Stewart et al., 1998; González and Downing, 1999; Kuhns and Berg, 1999). With the introduction and spread of the exotic amphipod *Echinogammarus ischnus*, however, the taxonomic composition of amphipod assemblages has been substantially altered (Nalepa et al., 2001). *Gammarus*, primarily *G. fasciatus* (itself invasive), was the numerically dominant amphipod on rock substrates in western Lake Michigan in 1995 comprising as much as 90% of amphipod taxa. In summer 2001, the abundance of *Gammarus* declined precipitously and was concomitant with an increase in *E. ischnus*, which accounted for the majority of amphipod taxa collected. The presence of *E. ischnus* also has been reported from rock and other hard substrates in southern and eastern Lake Michigan (Nalepa et al., 2001); the replacement of *G. fasciatus* by *E. ischnus* has been reported to be widespread in other areas of the Great Lakes (Dermott et al., 1998). Although the ecological implications of this replacement are still unclear, it is likely to be minor because of the ecological similarity between the two species (Dermott et al., 1998).

An often overlooked component of the benthos on hard substrates is freshwater sponges. Sponge populations increased dramatically in the mid 1990s, presumably the result of increased water clarity following the invasion by zebra mussels (M. Berg and J. Janssen, pers. obs.). Concomitant with this increase was an increase in the presence of the spongillafly, *Climacia* (Sisyridae) (M. Berg and J. Janssen, pers. obs.). This effect persisted for several years after which sponge populations appeared to stabilize or slightly decline (M. Berg and J. Janssen, pers. obs.). Although more commonly found on vertical than horizontal surfaces, Lauer et al. (2001) reported that *Spongilla lacustris*, *Eunapius fragilis*, and *Ephydatia muelleri* in southern Lake Michigan harbors could cover up to 13% of the available surface area on revetment walls, stone rip-rap, and wood pier posts with sponge density increasing as the angle of substrate orientation changed from horizontal to vertical. On more submerged structures, such as the hull of a permanently moored ship, sponge density increased with increasing depth and was greater at 2- and 3-m depths than at 1-m (Lauer and Spacie, 1996). The presence of freshwater sponges also has implications for zebra mussels. Epizoic growth of sponges on zebra mussels has negative implications for zebra mussels by impacting growth and survivability (Ricciardi et al., 1995; Lauer and Spacie, 2000).

The hydroid *Cordylophora caspia* (= *lacustris*?) has received little attention from researchers in Lake Michigan although it is relatively common at depths < 10 m where it occurs on rocks, live and dead zebra mussel shells, submersed wood, and on the underside of docks. The species designation of *Cordylophora* in the Great Lakes is somewhat confusing as *C. lacustris* is sometimes considered a junior synonym of *C. caspia*. In general, freshwater *Cordylophora* are usually referred to as *C. lacustris*, however most reports from the Great Lakes refer to *C. caspia*, a brackish species originating in the Black and Caspian seas. Because the genus is euryhaline and exhibits high phenotypic plasticity, it is difficult to ascertain whether these are two distinct species. Ongoing DNA analyses and cross-breeding experiments should help to clarify this situation (N. Folino-Rorem, Wheaton College, Wheaton, IL, pers. comm.). Little is known of the diet of *C. caspia* in Lake Michigan, however N. Folino-Rorem (pers. comm.) has documented the ingestion of a variety of benthic and planktonic invertebrates such as chironomids, annelids, calanoid and harpacticoid copepods, and cladocerans. In addition, *C. caspia* also may feed on zebra mussel veligers as evidenced by their ingestion of *Corbicula* veligers in the Des Plaines River (N. Folino-Rorem, pers. comm.).

Historically, crayfish species composition in rocky habitats of Lake Michigan has been dominated by *Orconectes virilis* and *O. propinquus* (Quinn and Janssen, 1989). *Orconectes virilis* was likely the first crayfish to invade Lake Michigan after the last glaciation (Capelli and Munjal, 1982) and *O. propinquus* was reported to be widespread in the Lake Michigan drainage by 1930 (Creaser, 1932). More recently, the introduction and establishment of the congeneric rusty crayfish (*O.*

rusticus) has resulted in a decline in *O. virilis* and *O. propinquus* abundance on rocks in nearshore areas (< 7 m) (M. Berg, pers. obs.). These observations, however, were based on external morphological characteristics that are easily observed by divers using SCUBA. A more rigorous genetic analysis showed a high degree of hybridization in specimens collected in southern Lake Michigan and that the majority of individuals identified as *O. rusticus* on the basis of morphological characters, were actually hybrids of *O. rusticus* and *O. propinquus* (Perry et al., 2002).

Fishes

Fishes collected from rocky habitat vary in their specificity to that habitat. Pelagic species are likely to be transients, but could aggregate for feeding on emerging insects or for spawning. Truly benthic species are likely to specialize on either rocky or soft bottoms because of feeding adaptations and cryptic coloration. The array of more common fishes is discussed beginning with those most characteristic of rocky substrate and concluding with transients.

Fishes strongly associated with rocks

Sculpins: Mottled sculpin (*Cottus bairdi*), slimy sculpin (*Cottus cognatus*). Sculpins of the genus *Cottus* are probably the most specialized fishes for rocky habitat. As with the invertebrates, these have most certainly invaded Lake Michigan from stream glacial refugia, hence also present as stream fauna. Mottled sculpin hide beneath rocks during the day and forage on invertebrates at night (Hoekstra and Janssen, 1985). Slimy sculpins are abundant on soft bottoms and little is known about them on rocky substrate. At Wilmette Reef (Illinois), one of the Silurian fossil coral reefs, the summit is in the epilimnion (minimum depth about 8 m) and its slope passes through the summer thermocline to a depth of about 20 m. There is a transition from mottled sculpins to slimy sculpins along the slope with both species beneath rocks by day. At the Midlake Reef Complex, ROV dives indicate that slimy sculpins predominate on the plateaus, but occasionally deepwater sculpins (*Myoxocephalus thompsoni*) are seen (J. Janssen, unpublished data). Presumably the relative abundance of deepwater sculpins increases down the slopes. Slimy sculpins are frequently fully exposed perhaps because they are feeding on *Mysis* that have descended onto the reef from the previous night's vertical migration.

Mottled sculpins are very patchy in their abundance. The patchiness is due to the patchiness of rocks with suitable cavities. While most of Illinois water from about 6 to 20 meters has rocky substrate, there are long stretches where the rock is imbedded, hence without cavities. These areas are devoid of mottled sculpins. The fish will hide in cracks within the bedrock of the Paleozoic reefs, however. Janssen and Quinn (1985) reported average densities of approximately 0.16 m^{-2}

for age 1+ mottled sculpins in rocky areas of Illinois, with a variance much greater than the mean, indicating patchy distribution. Young of the year (late summer) were also patchy with a mean of about 0.8 m^{-2} and also a much larger variance. A similar density of mottled sculpin (adults + YOY) was reported by Janssen and Jude (2001) for Calumet Harbor prior to their extirpation as a consequence of invasion by round gobies. Biga et al. (1998) found larger mottled sculpins in rubble vs. gravel rock piles that had been set experimentally. The rock piles, which were about 0.75 m in diameter and 0.25 m high, had 1-2 mottled sculpins each for a local density greater than 1 m^{-2}, considerably more than those found in Janssen and Quinn's (1985) surveys. Based on this comparison, it is likely that mottled sculpin density is determined by density of suitable shelters, hence indirectly by predation on individuals that fail to find shelter.

Mottled sculpins make their nests in cavities of rocks, which are defended by the males. Janssen and Jude (2001) provided evidence that nesting interference by the round goby, which is also a cavity nester, may be responsible for local extirpations of mottled sculpin.

Slimy sculpin males are in their dark spawning coloration by late April at the Mid-Lake Reef Complex so are presumably spawning beneath rocks there (depths 40 – 60 meters, J. Janssen unpubl. ROV observations).

Round gobies: Round gobies are strongly associated with rocks. Their successful invasion has probably been enhanced by their specializations for feeding on molluscs, particularly zebra mussels. Molariform pharyngeal teeth (Ghedotti et al., 1995) allow them to crush bivalve shells and they are unusual in that they are able to spin somewhat in order to break byssal threads (Djuricich and Janssen, 2001).

Round gobies nest in cavities defended by males (see review by Corkum et al., 1998). For rocks on soft substrate the round goby can excavate a burrow.

Fishes with a preference for rocks

Yellow perch: Wells (1977) argued that yellow perch became abundant on soft bottoms only when rocky areas were saturated. His observations were made prior to the zebra mussel invasion. Wells cited unpublished gill net data from 1974, after the great reduction in emerald shiner abundance, which showed that yellow perch were considerably more abundant at a rocky habitat near Saugatauk compared to adjacent soft bottoms. We accessed those unpublished data (USGS Great Lakes Science Center) and found a statistically significant greater abundance on rocks vs. adjacent soft bottoms ($P < 0.025$, 7df, paired t-test with the pairs being paired multigrade gill nets with one set per habitat type). The nets were set for 1-2 nights from May to Sept 1974. The overall relative abundance of yellow perch on rocks vs. soft bottoms was about 3.6.

Wells (1980) reported that yellow perch from the rocky habitat had fuller stomachs than those from soft bottom habitats. Diets from the rocky bottoms consisted mainly of crayfish and fish. For Illinois rocky bottoms Janssen and Quinn (1985), Abrant (1988), and Quinn and Janssen (1989) found primarily crayfish (*Orconectes propinquus* and *O. virilis*) and mottled sculpins in yellow perch stomachs from rocky habitat. In contrast, *Diporeia* and fish were found in yellow perch from soft bottoms by Wells in 1980. The most common fish in the diet reported by Wells (1980) were sculpins and alewives. Abrant (1988) found YOY yellow perch to be a substantial component of the diet in September.

The preference for rocky habitat apparently begins during the yellow perch's first summer. Janssen and Luebke (2004) found that about 80% of the young-of-the-year fish were captured on rocky habitat in August and September with equal sampling effort, with gill nets, on both types of habitat. The fish fed primarily on rock associated fauna such as *Gammarus* and isopods. However, in contrast to Well's (1977) study, the work on juveniles occurred after the zebra mussel invasion and (apparent) consequent loss of *Diporeia* from many areas of Lake Michigan (Nalepa et al., 1998). There may have been less preference for rocky habitat prior to the *Diporeia* decline.

We expect that the preference for rocky habitat is based primarily on food abundance. Wells (1977) noted that when the emerald shiner (*Notropis atherinoides*) was abundant this important forage fish congregated around breakwalls with the result that yellow perch also congregated there. Hence the preference by yellow perch for rocks in deeper water may have been a consequence of the negative impact of alewives (*Alosa pseudoharengus*) on emerald shiners. Because breakwalls are man-made, the presumed yellow perch-emerald shiner interaction may have been anthropogenic. Evidence that the preference for rocks is advantageous and typical of Great Lakes yellow perch comes from Lake Ontario where Danehy et al. (1991) found faster growth for yellow perch from hard bottom habitats.

With the loss of benthic invertebrates, especially *Diporeia*, from many soft bottoms and the increased abundance of many benthic invertebrates on rocky habitats, presumably due to zebra mussel effects, the relative value of rocky habitats for yellow perch has probably increased dramatically. The relative abundance of yellow perch on rocky versus soft bottoms has probably also increased. This has an important impact on assessments, for example, the annual assessments by trawl taken by USGS occur on the trawlable soft bottoms. Sites on the western side of the basin were chosen because the other sites were too rocky (Wells and Edsall, USGS, Ann Arbor, Michigan, personal communications). Such trawling has probably been adequate for assessing non-benthivorous species, but Wells (1977) warned that it was likely inadequate for yellow perch. Wells argued that yellow perch were probably not detectable in high numbers on soft bottoms until the preferred rocky habitat had been "filled". A consequence would be a highly non-linear relationship between trawl-based assessments and actual yellow perch abundance. Hence the great variation in yellow perch abundance estimates, based on trawls, with a coefficient of variation of 131% (Krause et al., 2002) means that assessment has very poor precision due to sample variation and poor accuracy due to sampling on less preferred habitat. Sampling by gill nets and traps on rocky habitat would probably also produced great variation due to schooling behavior and variability in habitat quality, but may reveal that the abundance of yellow perch is much less variable on the preferred rocky habitat than on soft substrates.

Dorr (1982) and Robillard and Marsden (2001) reported preferential spawning by yellow perch on rocky habitat. Eggs are deposited in late May through June and the eggs are encased in a gelatinous mass that is repulsive to predators. For example, round gobies spit them out (J. Janssen, pers. obs.) Dorr (1982) dyed egg masses on sand and rock and found that the egg masses on sand drifted out of the study area overnight while those on rocks remained in position. It is likely that storm-generated currents and surge would move or destroy egg masses among the rocks. The bias toward egg deposition on rocks may be a consequence of relatively higher prey abundance in rocky areas.

Burbot (*Lota lota*): Edsall et al. (1993) found burbot at Julian's Reef, a deep reef off Illinois in the fall. They also occur in aggregations in the fall at the Midlake Reef Complex in at least 40-50 m of water (J. Janssen, unpubl. data). They consume at least some lake trout eggs and we suspect that they spawn on these reefs. Their pelagic larvae are frequently collected (Nash and Geffen, 1991). J. Janssen (unpubl. data) has collected young of the year in the fall at Green Bay in shallow water under rocks.

Longnose dace (*Rhinichthys cataractae*): Longnose dace are found on both rock and sand, but they seem to be especially abundant on rocks. When there is surf they can be seen moving above and between the rocks in schools. In streams these fish are generally found in fast riffles (Becker, 1983), so they are well adapted for surge zones. They become scarce in deeper water and only occasional large ones are found at about 6 m depth. Documentation of their diet and spawning in Lake Michigan is unknown to us.

Fishes that spawn on rocky substrate

Lake trout (*Salvelinus namaycush*): Atypical for salmonines, most lake trout populations spawn in lakes. No redd is constructed and the eggs are deposited among loose rock with an apparent preference for a slope (Marsden et al., 1995). Some egg deposition was recorded by Marsden (1994) at various reefs in Illinois and Wisconsin. The commercial fishers interviewed by Coberly and Horrall (1980) reported spawning on clay and "honeycomb" limestone. In that there were no direct observations, we suspect this conclusion is based on material pulled up by anchor or tangled in nets. Descriptions of some of the rocky reefs, including maps, may be found in Edsall et al. (1989; 1992; 1993; 1995; Edsall and Kennedy, 1995).

Johnny darter (*Etheostoma nigrum*). The johnny darter is found primarily on sand adjacent to the rocky areas (J. Janssen, pers. obs.). They nest in cavities among the rocks with a single layer of eggs defended by the male. Nesting occurs in June. (J. Janssen, unpubl data).

Transient fishes

Some lacustrine fishes characteristic of rocky habitat are mostly restricted to bays. Most notably smallmouth bass and rock bass are absent from exposed shallow sites, except for some that stray from the shelters of bays and harbors during the summer. Why these fishes are constrained is not certain. Strong currents and cold upwellings in Lake Michigan probably limit spawning success. However, both species are found in streams and smallmouth bass are often found in fairly fast streams.

With increasing benthic production in the rocky areas, pelagic fishes may more frequently assemble over rocks, especially for feeding. It is not unusual to see alewives (*Alosa pseudoharengus*) and small salmonids feeding on emerging mayflies and midges. Janssen and Luebke (2004) found that young-of-the-year alewives were preferentially caught over rocky habitat compared to sand. They suggested that the fish may be attracted to midge emergences. Even prior to the zebra mussel invasion midge pupae were common in the diet of alewives (Morsell and Norden, 1968; Wells, 1980). With apparent decreases in the abundance of nearshore zooplankton (Dettmers et al., 2003), it is likely that insects emerging from rocky habitat, with its increased productivity, will become increasingly important in the food chain.

Amphibians

Mudpuppies (*Necturus maculosus*) are occasionally encountered in rocky areas, as far as approximately 15 km offshore in Illinois (Wilmette Reef, J. Janssen pers. obs.). They nest in July under large flat rocks with their eggs glued to the underside of the rock. They may be most abundant on bedrock reefs as they are most frequently encountered there, but they are too sparse to estimate densities.

Impacts of zebra mussels on benthic-pelagic interactions

The invasion of zebra mussels has dramatically altered the interaction of rocky habitat and the water column because of transfer from the phytoplankton to the zooplankton (Ackerman et al., 2001). The diatoms that Rutecki et al. (1985) recorded as settled on rocky substrate probably no longer do so, but are cleared from the water before settling by the zebra mussels.

Especially since the invasion by dreissenids, a clear understanding of benthic-pelagic interactions requires reasonable knowledge of dreissenid distribution and abundance. Fleischer et al. (2001) reported on the "lake-wide" distribution of dreissenids based on bottom trawling at long-established fish survey sites at depths greater than 9 meters. These sites were originally established to avoid rocky areas that tore up trawls (Wells and Edsall, USGS, Pers. Comm.). While we find it interesting and important that dreissenids are on such unconsolidated substrate, the sampling was clearly biased away from the prime rocky habitat that is so abundant on the west side. Fleischer et al. (2001) concluded that zebra mussels are most abundant in the northern and eastern parts of Lake Michigan. Meanwhile, the extensive rocky habitat on the west side of the lake, the prime habitat for zebra mussels, has been ignored.

The interaction between phytoplankton and zebra mussels is likely to be complex because of upwelling that carries the phytoplankton-rich thermocline along with greater nutrients into brighter sunlight (Schelske et al., 1971). Such upwellings are especially frequent on the west side of Lake Michigan (Bowers, 1980), which is also the rockier side of the lake. Each surge of upwelled water bathes the zebra mussels with a fresh supply of phytoplankton that are actively photosynthesizing. When this water, now partially stripped of phytoplankton, is displaced downward, less phytoplankton is available for animals such as *Diporeia*, which feeds heavily on settled diatoms. Historically, *Diporeia* densities have been greatest near the base of the average thermocline (Mozley and Howmiller, 1977) i.e. at the deep chlorphyll maximum. A possible means by which zebra mussels can impact *Diporeia* and other benthic invertebrates at depths as great as 70 meters is via the upwell/downwell movement of phytoplankton.

The task of integrating the ecology of rocky habitats with that of the unconsolidated bottoms and pelagia will probably always be hampered by the difficulty and heterogeneity of the rocky habitat. To ignore the habitat will result in errors in our assessment of how the whole ecosystem operates and it is entirely possible that we will never have good estimates of even the abundance of important organisms such as the dreisennids. But it is essential that the difficult not be ignored because it is inconvenient.

Summary

There is an unfortunate mismatch in the study of the benthic biota in Lake Michigan's main basin. The relatively homogenous habitat of unconsolidated bottoms is easily sampled, but, particularly in the photic zone, too unstable to support much primary production and too homogenous to support much diversity. These "soft bottoms" are easily and more commonly studied because they are readily sampled remotely

by bottom grab. The rocky habitats, the predominant habitat on the west side, are much more difficult to study, with most work conducted using SCUBA. Hence little work has been done on this biota. The introduction of zebra mussels and quagga mussels has made it apparent that the rocky habitats have always been important, and are becoming increasingly important as the invasive mussels transfer pelagic energy to the bottom and increase benthic primary production. The benthic primary producers have changed in productivity, abundance, and probably species composition, but the details of the change have scarcely been reported. The crustacean and insect invertebrate community is largely a stream fauna, presumably because only they survive the strong currents generated during storms. The main-basin fish community has little diversity compared to bays and surrounding inland lakes. The forage fishes most intimately associated with rocks are longnose dace, mottled sculpins, and slimy sculpins, otherwise abundant mainly in streams. The primary non-transient piscivore is the yellow perch. Smallmouth bass and rock bass, usually associated with rocks in inland lakes, are mostly absent. With the increase in benthic-pelagic coupling mediated by zebra mussels and quagga mussels, the impact of the rocky areas that harbor these suspension feeders has dramatically increased, but the details are yet to be discovered.

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References

Abrant, R.J., 1988. Feeding periodicity of yellow perch, *Perca flavescens* (Mitchill), in southwestern Lake Michigan. M.S. thesis, Loyola University, 28pp.

Ackerman, J.D., Loewen, M.R., Hamblin, P.F., 2001. Bentho-pelagic coupling over a zebra mussel reef in western Lake Erie. Limnol. Oceanogr. 46, 892-904.

Barnes, P., Fleischer, G., Gardner, J.V., Lee, K., 2002. Bathymetry and selected perspective views of 6 reefs and coastal areas in Northern Lake Michigan. USGS Open-File Report OF03-120. <http://walrus.wr.usgs.gov/reports/ofr03-120.html>

Barton, D.R., Hynes, H.B.N., 1978. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. J. Great Lakes Res. 4, 27-45.

Becker, G.C., 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin.
Biga, H., Janssen, J., Marsden, J.E., 1998. Effect of substrate size on lake trout egg predation by mottled sculpin. J. Great Lakes Res. 24, 464-473.
Blum, J.L., 1977. Algal zonation in Lake Michigan. J. Phycol. 13 (Suppl.), Abstract 27.
Blum, J.L., 1982. Colonization and growth of attached algae at the Lake Michigan water line. J. Great Lakes Res. 8, 10-15.
Botts, P.S., Patterson, B.A., Schloesser, D.W., 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? J. N. Am. Benth. Soc. 15, 179-184.
Bowers, J.A., 1980. Effects of thermocline displacement upon subsurface chlorophyll maxima in Lake Michigan. J. Great Lakes Res. 6, 367-370.
Brinkhurst, R., 1974. The benthos of lakes. McMillan Press, London
Capelli, G.M., Munjal, B.L., 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus Orconectes. J. Crust. Biol. 2, 486-492.
Chrzastowski, M.J., Thompson, T.A., 1994. Late Wisconsonian and Holocene geologic history of the Illinois-Indiana coast of Lake Michigan. J. Great Lakes Res. 20, 9-26.
Chrzastowski, M.J., Thompson, T.A., Trask, C.B., 1994. Coastal geomorphology and littoral cell divisions along the Illinois-Indiana coast of Lake Michigan. J. Great Lakes Res. 20, 27-43.
Coberly, C.E., Horrall, R.M., 1980. Fish spawning grounds in Wisconsin waters of Lake Michigan. University of Wisconsin Marine Studies Center and Sea Grant Institute.
Collinson, C., Norby, R.D., Hansel, A.K., 1979. Continued evaluation of Silurian reefs in Lake Michigan as potential breeding sites for lake trout. Illinois Coastal Manage. Program.
Corkum, L.D., McInnis, A.J., Wickett, R.G., 1998. Reproductive habits of round gobies. Great Lakes Research Review 3, 13-20.
Cote, W.E., 1967. Grain size analysis of sediments, southeastern Lake Michigan. M.S. thesis, University of Illinois, 85pp.
Creaser, E.P., 1932. The decapod Crustacea of Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 27, 321-338.
Danehy, R.J., Ringler, N.H., Gannon, J.E., 1991. Influence of nearshore structure on growth and diets of yellow perch (*Perca flavescens*) and white perch (*Morone americana*) in Mexico Bay, Lake Ontario. J. Great Lakes Res. 17, 183-193.
Dawson, K.A., Eshenroder, R.L., Holey, M.E., Ward, C., 1997. Quantification of historic lake trout (*Salvelinus namaycush*) spawning aggregations in Lake Michigan. Can. J. Fish. Aqua. Sci. 54, 2290-2302.
Dermott, R., Mitchell, J., Murray, I., Fear, E., 1993. Biomass and production of zebra mussels (*Dreissena polymorpha*) in shallow waters of northeastern Lake Erie. In: T.F. Nalepa, D.W. Schloesser (Eds.), Zebra mussels: biology, impacts, and control, pp. 399-413. Lewis Publishers, Ann Arbor, MI.
Dermott, R., Witt, J., Um, Y.M., González, M., 1998. Distribution of the Ponto-Caspian amphipod Echinogammarus ischnus in the Great Lakes and replacement of native Gammarus fasciatus. J. Great Lakes Res. 24, 442-452.
Dettmers, J., Raffenberg, M.J., Weis, A.K., 2003. Exploring zooplankton changes in Lake Michigan: implications for yellow perch recruitment. J. Great Lakes Res. 29, 355-364.
D'Itri, F.M., 1985. Artificial Reefs: Marine and Freshwater Applications. Lewis Publishers, Chelsea, Michigan.
Djuricich, P., Janssen, J., 2001. Impact of round goby predation on zebra mussel size distribution at Calumet Harbor, Lake Michigan. J. Great Lakes Res. 27, 312-318.
Dorr, J.A., 1982. Substrate and other environmental factors in reproduction of the yellow perch (*Perca flavescens*). Ph.D. dissertation, University of Michigan, 292 pp.
Edsall, T.A., Kennedy, G.W., 1995. Availability of lake trout reproductive habitat in Lake Michigan. J. Great Lakes Res. 21, 290-301

Edsall, T.A., Poe, T.P., Nester, R.T., Brown, C.L., 1989. Side-scan sonar mapping of lake trout spawning habitat in northern Lake Michigan. N. Am. J. Fish. Manage. 9, 269-279.

Edsall, T.A., Brown, C.L., Kennedy, G.W., French, J.R.P., III, 1992. Surficial substrates and bathymetry of five lake trout spawning reefs in nearshore waters of the Great Lakes. Great Lakes Fisheries Commission Technical Report 58, Ann Arbor, Michigan.

Edsall, T.A., Kennedy, G.W., Horns, W.H., 1993. Distribution, abundance, and resting microhabitat of burbot on Julian's Reef, southwestern Lake Michigan. Trans. Am. Fish. Soc. 122, 560-574.

Edsall, T.A., Holey, M.E., Manny, B.A., Kennedy, G.W., 1995. An evaluation of lake trout reproductive habitat on Clay Banks Reef, northwestern Lake Michigan. J. Great Lakes Res. 21(Supplement 1), 418-432.

Eggleton, F.E., 1936. The deep-water bottom fauna of Lake Michigan. Papers of the Michigan Academy of Science, Arts and Letters 21, 599-612.

Elliott, J.M., 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association Scientific Publication No. 25.

Fleischer, G.W., DeSorcie, T.J., Holuszko, J.D., 2001. Lake-wide distribution of *Dreissena* in Lake Michigan, 1999. J. Great Lakes Res. 27, 252-257.

Foster, D.S., Folger, D.W., 1994. The geologic framework of southern Lake Michigan. J. Great Lakes Res. 20, 44-60.

Fucciolo C.S., 1993. Littoral Zone Habitat Classification and Mapping of Illinois Lake Michigan Coastal Areas; Bathymetry and Distribution of Bottom Materials. Illinois Geological Survey Publ. OFS 1993-7.

Fullerton, A.H., Lamberti, G.A., Lodge, D.M., Berg, M.B., 1998. Prey preferences of Eurasian ruffe and yellow perch: comparison of laboratory results with composition of Great Lakes benthos. J. Great Lakes Res. 24, 319-328.

Ghedotti, M.J., Smihula, J.C., Smith, G.R., 1995. Zebra mussel predation by round gobies in the laboratory. J. Great Lakes Res. 21, 665-669.

González, M.J., Downing, A., 1999. Mechanisms underlying amphipod responses to zebra mussel (Dreissena polymorpha) invasion and implications for fish-amphipod interactions. Can. J. Fish. Aqua. Sci. 56, 679-685.

Goodyear, C.S., Edsall, T.A., Ormsby Dempsey, D.M., Moss, G.D., Polanks, P.E., 1982. Atlas of the spawning and nursery areas of Great Lakes fishes, 14 vols. U.S. Fish and Wildlife Service, Washington, DC, FWS/OBS-82/52.

Griffiths, R.W., 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. In: T.F. Nalepa, D.W. Schloesser (Eds.), Zebra mussels: biology, impacts, and control, pp. 415-437. Lewis Publishers, Ann Arbor, MI.

Gross, D.L., Lineback, J.A., White, W.A., Ayer, N.J., Collinson, C., Leland, H.V., 1970. Preliminary stratigraphy of unconsolidated sediments from the southwestern part of Lake Michigan. Illinois State Geological Survey Environmental Geology Note 30.

Hamilton, L.J., Mulhearn, P.J., Poeckert, R., 1999. Comparison of RoxAnn and QTC VIEW acoustic bottom classification system performance for the Cairns area, Great Barrier Reef, Australia. Continental Shelf Research 16, 1577-1597

Herbst, R.P., 1969. Ecological factors and the distribution of *Cladophora glomerulata* in the Great Lakes. Amer. Midl. Nat. 82, 90-98.

Hoekstra, D., Janssen, J., 1985. Non-visual feeding behaviour of mottled sculpin, *Cottus bairdi* in Lake Michigan. Envir. Biol. Fishes. 12, 111-117.

Holm, N.P., Norby, R.D., Smith, L.R., Collinson, C., 1987. The role of Silurian bedrock reefs in the Lake Michigan lake trout fishery. Federal Aid Report Number F-54-R.

Hough, J.L., 1935. The bottom deposits of southern Lake Michigan. J. Sedimentary Petrology 5, 57-80.

Hough, J.L., 1958. Geology of the Great Lakes. University of Illinois Press, Urbana, IL.

Hudson, P.L., Reid, W.J., Lesko, L.T., Selgeby, J.H., 1998. Cyclopoid and harpacticoid copepods of the Laurentian Great Lakes. Ohio Biol. Surv. Bull New Series 12(2), 50.

Janssen, J., Jude, D.J., 2001. Recruitment failure of mottled sculpin (*Cottus bairdi*) in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby (*Neogobius melanostomus*). J. Great Lakes Res. 27, 319-328.

Janssen, J., Luebke, M., 2004. Preference for rocky habitat by young-of-the-year yellow perch and alewives. J. Great Lakes Res. 30, 93-99.

Janssen, J., Quinn, J., 1985. Biota of the naturally rocky area of southwestern Lake Michigan with emphasis on potential fish prey. In: F.M. D'Itri (Ed.), Artificial Reefs: Marine and Freshwater Applications, pp. 431-442. Lewis Publishers, Chelsea, Michigan.

Jude, D.J., 2001. Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. *Dreissena!* (digest of the ANS Clearinghouse) 11, 1-14.

Jude, D.J., DeBoe, S.F., 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. Can. J. Fish. Aquat. Sci. 53 (supplement 1), 136-141.

Jude, D.J., Reider, R.H., Smith, G.R., 1992. Establishment of the Gobiidae in the Great Lakes basin. Can. J. Fish. Aquat. Sci. 49, 416-421.

Krause, A.E., Hayes, D.B., Bence, J.R., Madenjian, C.P., Stedman, R.M., 2002. Measurement error associated with surveys of fish abundance in Lake Michigan. J. Great Lakes Res. 28, 44-51.

Kuhns, L.A., Berg, M.B., 1999. Benthic invertebrate community responses to round goby (Neogobius melanostomus) and zebra mussel (Dreissena polymorpha) invasion in southern Lake Michigan. J. Great Lakes Res. 25, 910-917.

Landes, K.K., Ehlers, G.M., Stanley, G.M., 1945. Geology of the Mackinac Straits region. Michigan Geology and Biology Survey Pub. 67.

Lauer, T.E., Spacie, A., 1996. New records of freshwater sponges (Porifera) for Southern Lake Michigan. J. Great Lakes Res. 22, 77-82.

Lauer, T.E., Spacie, A., 2000. The effects of sponge (Porifera) biofouling on zebra mussel (Dreissena polymorpha) fitness: Reduction of glycogen, tissue loss, and mortality. J. Freshwater Ecology 15, 83-92.

Lauer, T.E., Barnes, D.K., Ricciardi, A., Spacie, A., 1999. Evidence of recruitment inhibition of zebra mussels (Dreissena polymorpha) by a freshwater bryozoan (Lophopodella carteri). J. N. Am. Benth. Soc. 18, 406-413.

Lauer, T.E., Spacie, A., Barnes, D.K., 2001. The distribution and habitat preferences of freshwater sponges (Porifera) in four southern Lake Michigan harbors. American Midland Naturalist 146, 243-253.

Lauritsen, D.D., White, D.S., 1981. Comparative studies of the zoobenthos of a natural and man-made rocky habitat on the eastern shore of Lake Michigan. Special Report No. 74 of the Great Lakes Research Division.

Lin, C.K., Blum, J.L., 1977. *Bangia*: a recent invader of the St. Lawrence Great Lakes. J. Phycol. 13 (Suppl). Abstract 51.

Lineback, J.A., Gross, D.L., Meyer, R.P., Unger, W.L., 1971. High resolution seismic profiles and gravity cores of sediments in southern Lake Michigan. Environmental Geology Notes Number 47. Illinois State Geological Survey.

Lineback, J.A., Gross, D.L., Meyer, R.P., 1974. Glacial tills under Lake Michigan. Environmental Geology Notes Number 69. Illinois State Geological Survey.

Lowe, R.L., Pillsbury, R.W., 1995. Shifts in benthic algal community structure and function following the appearance of zebra mussels (Dreissena polymorpha) in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21, 558-566.

Lowe, R.L., Rosen, B.H., Kingston, J.C., 1982. A comparison of epiphytes on *Bangia atropurpurea*

(Rhodophyta) and *Cladophora glomerata* (Chlorophyta) from northern Lake Michigan. J. Great Lakes Res. 8, 164-168.

Lozano, S.J., Blouin, M., Wattrus, N., 2002. Characterization of coastal Great Lakes benthic habitat. Symposium on the Effects of Fishing Activities on Benthic Habitats: Linking Geology, Biology, Socioeconomics, and Management. November 12-14, 2002. Tampa, FL

Marsden, J.E., 1994. Spawning by stocked lake trout on shallow, near-shore reefs in southwestern Lake Michigan. J. Great Lakes Res. 20, 377-384.

Marsden, J.E., Perkins, D.L., Krueger, C.C., 1995. Recognition of spawning areas by lake trout: deposition and survival of eggs on small, man-made rock piles. J. Great Lakes Res. 21, 330-336.

Morsell, J.W., Norden, C.R., 1968. Food habits of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Proc. Conf. Great Lakes Res. 11, 96-102.

Mozley, S.C., Howmiller, R.P., 1977. Environmental status of the Lake Michigan Region. Vol. 6. Zoobenthos of Lake Michigan. Argonne National Laboratory, Argonne, IL.

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., Lozano, S.J., 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980-1993. Can. J. Fish. Aquatic Sci. 55, 2402-2413.

Nalepa, T.F., Schloesser, D.W., Pothoven, S.A., Hondorp, D.W., Fanslow, D.L., Tuchman, M.L., Fleischer, G.W., 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. J. Great Lakes Res. 27, 384-391.

Nash, R.D.M., Geffen, A.J., 1991. Spatial and temporal changes in the offshore larval fish assemblage in southeastern Lake Michigan. J. Great Lakes Res. 17, 25-32.

Norby, R.D., Collinson, C., 1977. A preliminary evaluation of Lake Michigan "reefs" in Illinois as potential breeding sites for indigenous fish species, pp. 1-20. In: Third Year Work Product, Coast Geological Studies, Illinois Coastal Zone Manage. Program.

Perry, W.L., Lodge, D.M., Feder, J.L., 2002. Importance of hybridization between indigenous and nonindigenous freshwater species: an overlooked threat to North American biodiversity. Syst. Biol. 51, 255-275.

Powers, C.F., Robertson, A., 1968. Subdivisions of the benthic environment of the upper Great Lakes, with emphasis on Lake Michigan. J. Fish. Res. Board Can. 25, 1181-1197.

Quinn, J.P., Janssen, J., 1989. Crayfish competition in southwestern Lake Michigan: a predator mediated bottleneck. J. Freshwater Ecol. 5, 75-85.

Robillard, S.R., Marsden, J.E., 2001. Spawning substrate preferences of yellow perch along a sand-cobble shoreline in southwestern Lake Michigan. N. Am. J. Fish. Manage. 21, 208-215.

Rutecki, T.L., Dorr, J.A., III, Jude, D.J., 1985. Preliminary analysis of colonization and succession of selected algae, invertebrates, and fish on two artificial reefs in inshore southeastern Lake Michigan. In: F.M. D'Itri (Ed.), Artificial Reefs: Marine and Freshwater Applications, pp. 459-489. Lewis Publishers, Chelsea, Michigan.

Saxe, J.G., 1872. The blind men and the elephant. In: Fables and Legends of Many Countries. J. R. Osgood Publisher, Boston, Massachusetts.

Schelske, C.L., Stoermer, E.P., Feldt, L.H., 1971. Nutrients, phytoplankton productivity and species composition as influenced by upwelling in Lake Michigan. Proc. 14th Conf. Great Lakes Res. 102-113.

Schloesser, R.E., Blum, J.L., 1980. *Sphacelaria lacustirs* sp. Nov., a freshwater brown alga from Lake Michigan. J. Phycol. 16, 201-207.

Shabica, C., Pranschke, F., 1994. Survey of littoral sand deposits along the Illinois and Indiana shores of Lake Michigan. J. Great Lakes Res. 20, 61-72.

Shelford, V.E., Boesel, M.W., 1942. Bottom animal communities of the island area of Western Lake Erie in the summer of 1937. Ohio J. Sci. 42, 179-190.

Somers, L.H., Josephson, P.D., 1968. Bottom sediments of southwestern Lake Michigan. Proc. 11th Conf. Great Lakes Res. Internat. Assoc. Great Lakes Res. 245-252.

Stewart, T.W., Haynes, J.M., 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. J. Great Lakes Res. 20, 479-493.

Stewart, T.W., Miner, J.G., Lowe, R.L., 1998. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. J. Great Lakes Res. 24, 868-879.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59, 1209-1228.

Vadeboncouer, Y., Vander Zanden, M.J., Lodge, D.M., 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience 52, 44-54.

Wells, L., 1977. Changes in yellow perch (*Perca flavescens*) populations in Lake Michigan, 1954-1975. J. Fish. Res. Board Can. 34, 1821-1829.

Wells, L., 1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan. Technical paper 98, U.S. Fish and Wildlife Service. Ann Arbor, MI 48107.

Wickham, J.T., Gross, D.I., Lineback, J.A., Thomas, R.L., 1978. Late Quarternary sediments of Lake Michigan. Illinois Geological Survey Environmental Geology Notes 13, 1-26.

Winnell, M.H., Jude, D.J., 1987. Benthic community structure and composition among rocky habitats in the Great Lakes and Keuka Lake, New York. J. Great Lakes Res. 13, 3-17.

Zenchak, K.A., 1993. The effects of crayfish grazing on benthic algal community dynamics in southwestern Lake Michigan. M.S. Thesis, Loyola University-Chicago.

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