Insular lake island biogeography: using lake metrics to predict diversity in littoral zone mollusk communities

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Abstract.   Island biogeography theory can be used to explain patterns of species richness on various types of habitat islands, including freshwater lake systems. Mollusk production in these systems also has been linked to various water-chemistry variables, such as pH, alkalinity, hardness, and specific conductance. We examined how mollusk diversity patterns were related to geographical and limnological factors in insular lakes of the Beaver and Manitou Archipelagos in Lake Michigan (Laurentian Great Lakes), USA. The strongest correlations observed were with shoreline development ($r = 0.80$), specific conductance ($r = 0.87$), and pH ($r = 0.87$). Principal components analysis revealed that isolation by distance and PO_4^{3-} concentration also may have affected species richness and abundance. Shoreline length was a better predictor of species richness than surface area, but both measures of habitat size were unable to account for much of the variation in species richness. The data suggest that shoreline length and development represent available habitat area more accurately than lake area for primarily littoral-dwelling mollusks. The relatively weak correlations observed with lake area and isolation from Lake Michigan suggest that application of island biogeography theory to predict mollusk species richness using only lake surface area and isolation by distance is limited for freshwater mollusks.

Key words: island biogeography, Lake Michigan, Great Lakes islands, Sphaeriidae, Gastropoda, Unionidae.

The traditional use of island biogeography theory (MacArthur and Wilson 1967) is to predict the number of species an ocean island could hold at equilibrium from the size and remoteness of the island. However, a habitat island does not have to be an ocean island, and any isolated habitat surrounded by an uninhabitable zone can be considered a habitat island. Island biogeographical theory has been extended to freshwater lakes (Browne 1981, Jokinen 1987, Carlsson 2001), temporary pools (March and Bass 1995), and forest tree assemblages (Gove et al. 2009). Area and distance effects are important aspects of island biogeography, but they cannot be used alone as precise predictors of diversity (MacArthur and Wilson 1967). This limitation is important when the theory is applied to conservation efforts because neglecting other abiotic and biotic processes could potentially lead to undesirable results. In addition,

conserving species-rich sites will not necessarily result in conservation of global diversity and the perpetuation of rare species (Oertli et al. 2002). In studies of lakes as habitat islands, the island biogeography model and specific abiotic factors have been used separately to predict species richness with mixed success (Lassen 1975, Brönmark 1985, Watters 1992). A combination of these factors may be needed to develop successful predictors of species richness in insular lake systems.

The islands of the Laurentian Great Lakes system are an outstanding natural laboratory for examining recent biogeographic events. The Laurentian Great Lakes were formed ~12,000 y ago when the last Pleistocene glaciers retreated (Colman et al. 1994). This retreat formed several island systems in Lake Michigan, and some of these islands have interior lakes. Water levels in the Great Lakes have fluctuated since their formation because of changes in water courses and isostatic rebound (Baedke and Thompson 2000). This fluctuation has caused inundation of the inland lakes by Lake Michigan waters at various times. The final inundations occurred as recently as

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5000 y ago (Colman et al. 1994). The Beaver and Manitou island archipelagos in Lake Michigan contain 11 of these insular lakes. These lakes are an excellent system for examining ecological and evolutionary processes because they have remained relatively undisturbed and presumably ecologically isolated since their last inundation. Elevation and water-level data can be used to assess invasion and extinction processes in these isolated habitats by determining the relative point in history when they became fully isolated from Lake Michigan waters.

Variation in the physicochemical characteristics of these waters presents an opportunity to examine how these elements affect the diversity and distribution of mollusks in isolated lakes. Several water-chemistry variables, such as pH, alkalinity, hardness, and conductivity, affect mollusk productivity (Kilgour and Mackie 1991, Strayer 2008, Brown and Lydeard 2010). Moreover, biotic factors, such as composition of the fish community, may influence mollusk population dynamics (Brönmark 1994). Investigators have studied the geological, chemical, and biotic factors that influence mollusk diversity, but few have attempted to combine these factors in a single study.

Freshwater mollusks are among the most imperiled taxonomic groups in the world (Christian and Harris 2008). Sixty-eight percent of freshwater mussels from the order Unionoida in North America are considered to be at risk of extinction (Lydeard et al. 2004), and 48% of freshwater gastropod species are at risk or extinct (Christian and Harris 2008). Few studies have been made of the less diverse and ubiquitous Sphaeriidae (fingernail and pea clams), and this lack of study presents a gap in conservation knowledge (Mackie 2007). Understanding the effects of multiple variables on the diversity of an isolated population is valuable when attempting to conserve populations in isolated habitats (Wilcox and Murphy 1985, Shafer 1990).

Four major groups of mollusks are native to the Great Lakes region. Caenogastropoda is the most diverse group of gastropods worldwide, but most of that diversity is achieved in marine systems. Several caenogastropod groups have independently colonized freshwater habitats (Brown and Lydeard 2010). The other clade of gastropods common in the Great Lakes region is the Heterobranchia. These gastropods are common in shallow, ephemeral habitats, and many groups have achieved worldwide distribution. Sphaeriidae and Unionidae are the 2 groups of bivalve mollusks native to the region. Unionidae, the freshwater mussels, reach their peak diversity in North American streams, but many species also commonly inhabit lentic systems. The Sphaeriidae are less studied, but are common in streams, lakes, and wetlands (Mackie 2007).

The various groups of mollusks in the Great Lakes region exhibit large variation in dispersal ability. In general, mollusks are poor dispersers as adults and rely on passive dispersal mechanisms for transport between watersheds (Brown and Lydeard 2010). Several sphaeriid clams and gastropods have effective passive dispersal mechanisms, resulting in high immigration rates and presence in ephemeral habitats (Burky 1983). These mechanisms include passage on the feathers of waterfowl, attachment to the limbs of insects, and survival of ingestion by waterfowl (Mackie 1979, Burky 1983). The ability to disperse passively via several methods has allowed a cosmopolitan distribution of sphaeriids and pulmonate snails (Russel-Hunter 1983). In contrast, unionid mussels and caenogastropods have relatively poor dispersal mechanisms and lack significant passive dispersal abilities. Unionids depend primarily on host-fish transport of glochidia (Kat 1984), which generally limits their dispersal to within a watershed (Smith 1985). Caenogastropods probably are limited in the habitats they can invade because of their slow-moving adult life stage and absence of significant passive dispersal abilities, whereas dispersal of pulmonates is facilitated by their short life cycles and air-breathing juveniles (Davis 1982).

Our goal was to elucidate which limnological and geographical variables are most important in predicting mollusk diversity in insular lake habitats so that conservation efforts could be focused on the most crucial variables for preserving molluscan diversity. Several geographic variables might be useful predictors of freshwater mollusk diversity in insular lakes. Island biogeography theory predicts a positive relationship between habitat size and species richness and that species richness should be low in extremely isolated island/habitat patches because of low probability of colonization (MacArthur and Wilson 1967). The relatively recent formation of the island systems in Lake Michigan allows examination of spatial (distance from shoreline) and temporal (elevation above lake level) isolation. Surface area and elevation should be strongly correlated with species richness because these variables are good indicators of available mollusk habitat and length of temporal isolation (Carlsson 2001). Carlsson (2001) used elevation successfully as a predictor of mollusk diversity in recently formed insular lake systems.

Methods

Nine (of 11) insular lakes on the Beaver and Manitou Archipelagos of Lake Michigan were sampled (Fig. 1). The lake basins consisted mostly of
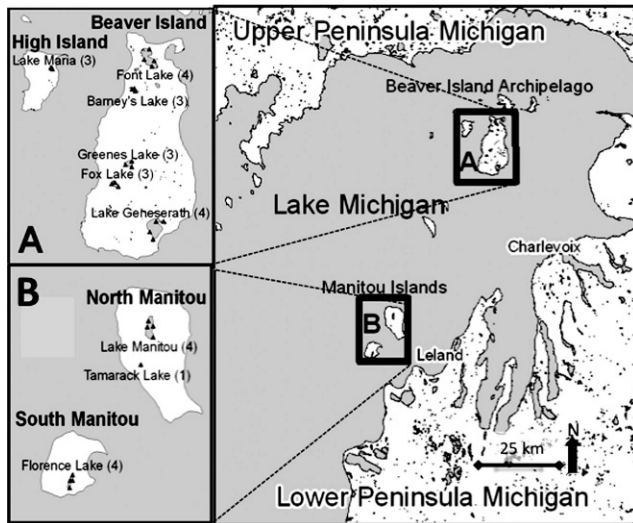
FIG. 1. Map and sampling sites of 9 lakes in the Beaver Archipelago and Manitou Island systems in the Laurentian Great Lakes of North America. Number of replicate samples in each lake is indicated parenthetically.

limestone, dolomite, or sandstone (Hatt et al. 1948). Benthic samples were taken in the littoral zone of each lake with sweep-net sampling procedures modified from the Ontario Benthos Biomonitoring Protocol (Jones et al. 2004). Sampling was conducted along transects in the littoral zone from the shoreline to ~1 m depth. Thirty minutes of active sampling time was allotted for each replicate along these transects, and up to 4 replicates were sampled/lake depending on lake size and shoreline habitat heterogeneity (Fig. 1). All benthic invertebrates were collected, but mollusks were separated for further identification. Samples were preserved in 95% ethanol, and mollusks were identified to species from taxonomic guides (Clarke 1981, Burch and Jung 1992) and an unpublished key for the Sphaeriidae (G. Mackie, University of Guelph) following taxonomy from Turgeon et al. (1998). In addition, targeted, qualitative visual searches were used to establish presence/absence of each unionid mussel species because of their large size and specialized habitat preferences in lakes (Zanatta et al. 2002). Abundances of unionids were calculated from the number of individuals encountered during littoral-zone sampling.

Surface area (A_o), shoreline length (SL), and the minimum distance from the shoreline of the insular lake to the shoreline of Lake Michigan were calculated with the path tool in Google Earth^{TM} (version 4.3 for Mac OS X; http://earth.google.com). Elevation data were obtained from topographic maps and were based on distances above mean Lake Michigan water level. Shoreline development (D_L) was calculated as

$$D_L = \frac{SL}{2\sqrt{A_o \pi}}$$

and was used as a measure of basin shape and index of available littoral habitat (Wetzel 2001).

An Ephemeroptera, Plecoptera, Trichoptera (EPT) index was used as a biological indicator of water quality (Mackie 2001). The index is based on the ratio of relative abundances of the pollution-sensitive groups EPT to the relative abundance of the pollution-tolerant Chironomidae group. For lakes in the Manitou Island system, NH_4^+, PO_4^{3-}, NO_3^-, pH, and specific conductance data (means from ≥4 surface water samples collected in summer 2008 with National Park Service Water Resource Division protocols; Elias et al. 2008) were obtained from the EPA STORET database (USEPA 2010). For lakes in the Beaver Island system, epilimnetic nutrient concentrations and fish taxonomic richness data were obtained through ongoing research at the Central Michigan University Biological Station (T. Clement and B. Murry, Central Michigan University, unpublished data).

Pearson correlation analysis and regression analysis (α = 0.05) were used to test for relationships among all biological and physicochemical variables and total mollusk species richness, overall mollusk abundance, species richness of poorly dispersing mollusks (Unionidae and Caenogastropoda), and species richness of passively dispersing mollusks (Sphaeriidae and Pulmonata). Groupings of passive and poor dispersers were based on information published by Brown and Lydeard (2010), Kat (1984), and Mackie (1979).

The entire data set was analyzed using PC-ORD version 4.39 (McCune and Mefford 2011). Principal components analysis (PCA) was used to simplify the data, visualize patterns among all environmental variables (Gotelli and Ellison 2004), and highlight the most important variables determining variance of mollusk abundance by species (relative abundances reflecting abundance/unit sampling effort). The explanatory variables used in the PCA were A_o, SL, D_L, distance to Lake Michigan shoreline, elevation, pH, EPT index, NH_4^+, PO_4^{3-}, and NO_3^- concentrations, specific conductance, fish richness, and presence/absence of a stream outlet to Lake Michigan (Table 1). Cluster analysis based on Ward's linkage and between-clusters sum-of-squares distance was done in SAS (version 9.2; SAS Institute, Cary, North Carolina). Patterns in species abundances were used to group lakes containing similar molluscan communities.

Table 1. Geographical, chemical, limnological, and biological variables used in principal components, cluster, and correlation analyses of mollusk communities from insular lakes of Lake Michigan islands. Data points with an 'x' were unavailable or not calculated. Elevation = elevation above Lake Michigan; distance = nearest distance to Lake Michigan shoreline; stream outlet = the number of current outlet streams to Lake Michigan; EPT = Ephemeroptera, Plecoptera, Trichoptera; A_o = lake area; SL = shoreline length; D_L = shoreline development.

Lake name	Geneserath	Fox	Barney's	Greene's	Maria	Font	Manitou	Florence	Tamarack
A_o (ha)	197.9	30.4	18.2	25.1	4.07	154.6	103.6	31.57	4.22
Elevation (m)	8	44	8.9	41.8	2.8	12	19	4.1	14.2
Distance (km)	0.28	2.67	0.49	1.31	0.28	0.49	2.25	0.5	0.84
SL (m)	8151	2445	2601	2133	920	6380	4887	3080	759
D_L	1.635	1.251	1.720	1.201	1.287	1.448	1.355	1.547	1.043
pH	8.38	6.74	8.88	x	x	8.5	8.13	7.93	x
EPT index	10.09	8.57	0.85	0.16	28	8.91	10.5	0.11	0
Steam outlet	1	0	0	0	0	0	1	0	0
Fish richness	20	7	11	2	x	12	x	x	x
NH_4^+ (µg/L)	42.51	x	0.25	48.78	x	1.22	9.67	32.67	x
NO_3^- (µg/L)	2.87	x	8.2	4.23	x	4.74	6	18.33	x
PO_4^{3-} (µg/L)	0.72	x	8.12	2.89	x	1.95	22.88	19.5	x
Specific conductance (µS/cm)	0.183	0.030	0.200	0.084	x	0.174	0.281	0.116	x

Results

A total of 29 mollusk species was found in the 9 lakes (Appendix). The most common species were *Pisidium nitidum* and *Pisidium casertanum*, which were present in all 9 lakes. In all lakes, unionid populations consisted of many size classes, and several juveniles were collected. Two species, the unionid *Anodontoides ferussacinanus* and the limpet *Ferrissia parallela* were present in only 1 lake. The most species-rich lake was Barney's Lake, which contained 25 of the 29 species collected. Tamarack Lake was the most species poor and contained only 3 members of the genus *Pisidium*. Highest mollusk abundances (modified to reflect catch per unit effort) were observed in Barney's Lake (413 individuals/sample) and Lake Manitou (463 individuals/sample) (Appendix).

The first 3 PCA axes together accounted for 77.6% of the total variation in the relative abundance of mollusk species (Fig. 2A, B). Tamarack, Greene's, Fox, and Florence lakes (group 1) were tightly grouped in all PCA biplots. These lakes had the lowest diversity and abundance of mollusks (Appendix). Barney's, Manitou, and Font lakes (group 2) had high mollusk diversity and abundance and were widely separated from the group-1 lakes on the first 3 PCA axes. Maria and Geneserath Lakes had a moderately diverse molluscan fauna, but lacked the high abundances seen in the group-2 lakes. PCA axis 1 (40.3% of the variation) was negatively correlated with D_L ($r = -0.62$), specific conductance ($r = -0.74$), and pH ($r = -0.59$). The more basic, irregularly shaped lakes grouped on the left and the more acidic, round lakes grouped on the right side of axis 1. The separation of Barney's Lake from the others along axis 1 was caused by its high D_L, low pH, and high specific conductance. PCA axis 2 (22.5% of the variation) was positively correlated with distance to Lake Michigan ($r = 0.60$), total P ($r = 0.67$), and presence of a stream outlet to Lake Michigan ($r = 0.60$). The separation of Lake Manitou from the other lakes along axis 2 was caused by its high P level and long distance from Lake Michigan. PCA axis 3 (14.8% of the variation) was strongly negatively correlated with A_o ($r = -0.75$), SL ($r = -0.71$), and EPT index ($r = -0.68$). The 3 largest lakes (Geneserath, Font, and Manitou) were on the low end of axis 3.

Ferrissia parallela had the only negative score on the 1st eigenvector (data not shown). This species occurred only in Greene's Lake and was the only limpet found in any lake. No clear patterns were observed in the subsequent eigenvectors, and separation of related or co-occurring species was common, e.g., *P. casertanum* and *P. nitidum* were separated from *P. rotundatum* and *P. variabile*, and the unionids *Pyganodon* spp. *(grandis + lacustris)* were separated from *Lampsilis siliquoidea*.

Lakes clustered into 2 distinct groups based on species abundances (Fig. 3). These groups showed strong similarities with the patterns described by the PCA. Barney's, Font, and Manitou lakes were separated from the other 6 lakes, and Fox, Tamarack, Greene's, and Florence Lakes grouped within this cluster of 6 lakes, a pattern that suggests these 4 lakes have similar mollusk community composition.
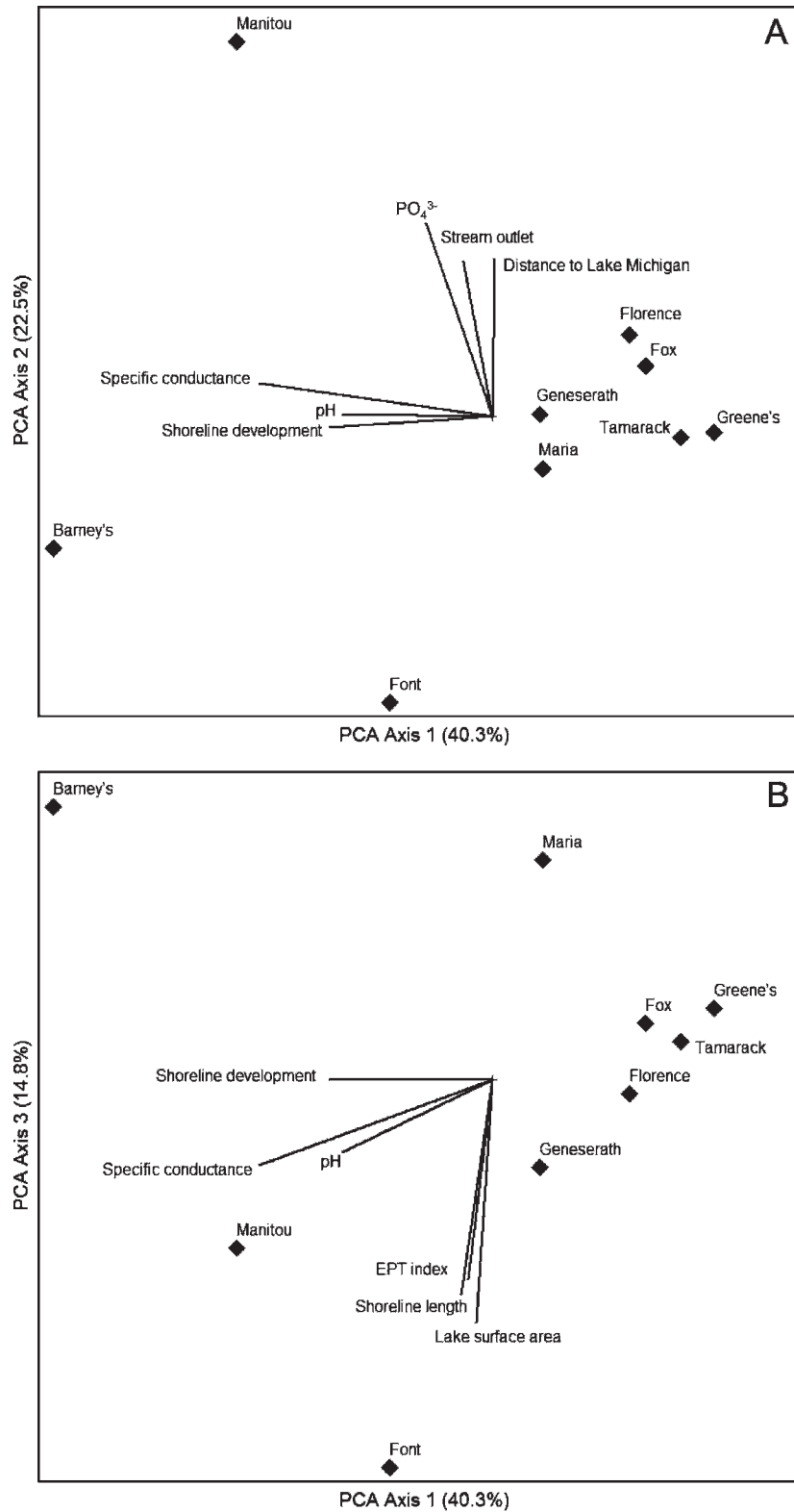
FIG. 2. Principal components analysis (PCA) ordinations for mollusk species abundance in 9 insular lakes of the Beaver Archipelago and Manitou Island systems. A.—PCA Axis 1 vs 2. B.—Axis 1 vs 3. Vectors represent correlations of geographic, physicochemical variables, and bioindicators to mollusk species abundance. Vector length indicates the strength of the correlation of the factor with the PCA axes. EPT = Ephemeroptera, Plecoptera, Trichoptera.
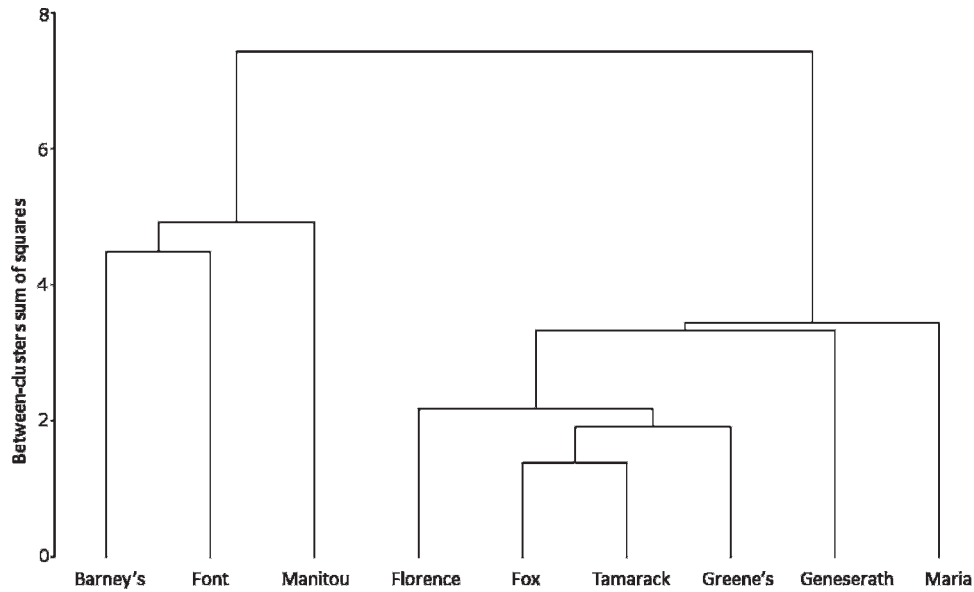
FIG. 3.   Cluster diagram based on mollusk species abundances in 9 insular lakes of the Beaver Archipelago and Manitou Island systems. Clustering was done based on Ward's method for linkage and between-clusters sum-of-squares distance measure.

Mollusk abundance was correlated only with specific conductance ($r = 0.83$, $p = 0.02$).

Mollusk species richness was strongly related to pH (Fig. 4A), specific conductance (Fig. 4B), and D_L (Fig. 4C) and weakly related to SL (Fig. 4D). Species richness of passively dispersing mollusks was positively related to pH (Fig. 5A), specific conductance (Fig. 5B), and D_L (Fig. 5C). Species richness of poorly dispersing mollusks was positively related to pH (Fig. 5A), specific conductance (Fig. 5B), D_L (Fig. 5C), and both direct measures of habitat size, A_o (Fig. 5D) and SL (Fig. 5E).

Discussion

Species–area relationships

SL and D_L were better predictors than A_o of mollusk abundance and diversity, although even these measures of habitat size left a large portion of the variation unexplained. Other investigators have suggested that the relationship between species richness/diversity and island/habitat area is weaker for benthic invertebrates than for terrestrial organisms (Oertli et al. 2002). However, A_o probably is an inappropriate measure of available habitat for littoral invertebrates. SL is a better measurement than A_o of available littoral habitat area, and high D_L values indicate diverse and productive littoral communities (Wetzel 2001). Thus, use of SL and D_L as measures of available mollusk habitat would help improve the utility of island biogeography theory as a predictor of diversity of littoral communities.

The small range of lake sizes in our study may account for the weak relationship between A_o and mollusk species richness. In similar studies of zooplankton, a relationship between lake size and richness was not detected until lakes spanning 3 to 4 orders of magnitude in area were examined (Karatayev et al. 2005), and the strength of the relationship increased as the range of lake size increased. Karatayev et al. (2005) also noted a difference in species–area curves for pelagic and littoral zooplankton species, a result suggesting that A_o probably influences littoral and pelagic species in different ways. Dodson (1992) and Shurin et al. (2000) also found that A_o and zooplankton richness were correlated only across a large range of lake sizes.

Species–area relationships for gastropods are similar to those of zooplankton. Gastropod species richness was correlated with pond area in a group of Swiss ponds that ranged in surface area from 6 to ~100,000 m^2 (Oertli et al. 2002) and in a group of Finnish ponds that spanned 3 orders of magnitude in area (Carlsson 2001). However, in both studies, the positive relationship accounted for only a small percentage of the variation in the data, results suggesting that lake area has only a mild effect on gastropod diversity at small scales. Differences in water chemistry variables, such as pH and specific conductance, and biotic factors probably account for a large component of this variation.

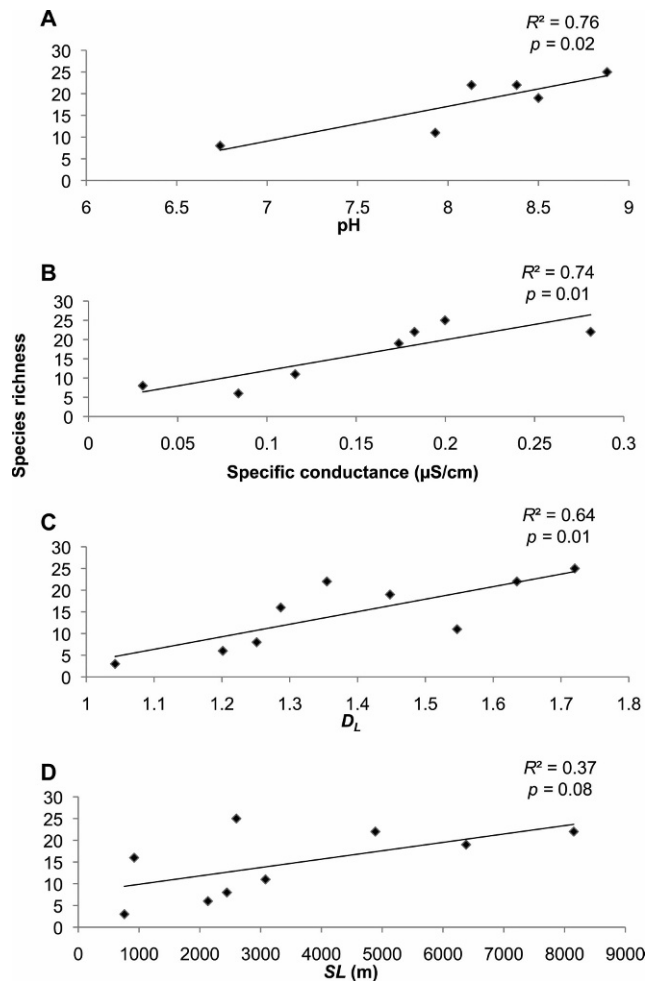Mollusk species richness was highly variable among small lakes (<20 ha) in southwestern Finland

FIG. 4.   Regressions for total mollusk species richness vs pH (A), specific conductance (B), shoreline development (D_L) (C), and shoreline length (SL) (D) for insular lakes of the Beaver Archipelago and Manitou Island systems. Specific conductance and pH values were unavailable for Tamarack and Maria.

(Carlsson 2001) and New England (USA) (Jokinen 1987). Environmental factors might have a stronger effect on mollusk distribution and species composition in small than in large habitats. If smaller lakes in the system had low habitat heterogeneity or were physicochemically homogeneous, each lake might support a different complement of species depending on local conditions. Thus, smaller lakes would have high among-lake variation in mollusk abundance and diversity. For example, Barney's and Greene's lakes had similar small A_o and SL, but very different species compositions. These 2 lakes also differed greatly in acidity and dissolved nutrient concentrations, and species diversity was much greater in more basic, nutrient-rich Barney's Lake than in Greene's Lake. In contrast, if larger lakes in the system had greater

habitat heterogeneity and more diverse within-lake physicochemical conditions than the smaller lakes, then larger lakes should have supported mollusk assemblages representative of the regional species pool and, therefore, more similar among lakes. The smaller number of transects sampled in the 6 smaller lakes also might have contributed to the high among-lake variance.

The 3 largest (100+ ha) lakes in our study had similar species richness (19–22 species). These lakes also contained the only extant populations of unionid mussels in the region. Size classes indicated healthy, reproducing populations in the 3 lakes, and several juvenile unionids were found, so it is unlikely that these lakes contained only relict populations. Several unionid shells were found in very small (4.1 ha) Lake Maria, but no living unionids were collected. Lake Maria is not currently hydrologically connected to Lake Michigan, but it is the least isolated lake in terms of distance to the Lake Michigan shoreline and elevation. A relatively recent connection to Lake Michigan probably would have allowed colonization of Lake Maria by unionid mussels, but the lake might not have been large enough to sustain a population.

Effects of lake isolation and mollusk dispersal ability

Two of the 3 lakes with unionid populations (Geneserath and Manitou lakes) had stream outlets to Lake Michigan. Unionid distributions are limited by the movement of their host fishes (Kat 1984). Thus, host fish movement has important implications for the mussel assemblage in an aquatic system. A connection to Lake Michigan through the stream outlet potentially would allow dispersal and gene flow among Lake Michigan and the insular lakes. The stream outlet from Lake Manitou is intermittent but might permit movement of some fish during higher flows (S. Yancho, Sleeping Bear Dunes National Lakeshore, National Park Service, personal communication). In contrast, Font Lake does not have an outlet, and the populations of mussels in the lake presumably have remained completely isolated from Lake Michigan populations since Lake Michigan water levels stabilized several thousand years ago. Data related to the presence of possible host fishes for unionid glochidia were not available for Lake Maria. These data might give more insight into the recent extirpation of this lake's unionid population.

Sphaeriid clams and pulmonate gastropods were the most common groups of mollusks observed. The passive dispersal ability of these groups may have contributed to increased immigration rates and their cosmopolitan distribution (Burky 1983, Brown 2007).
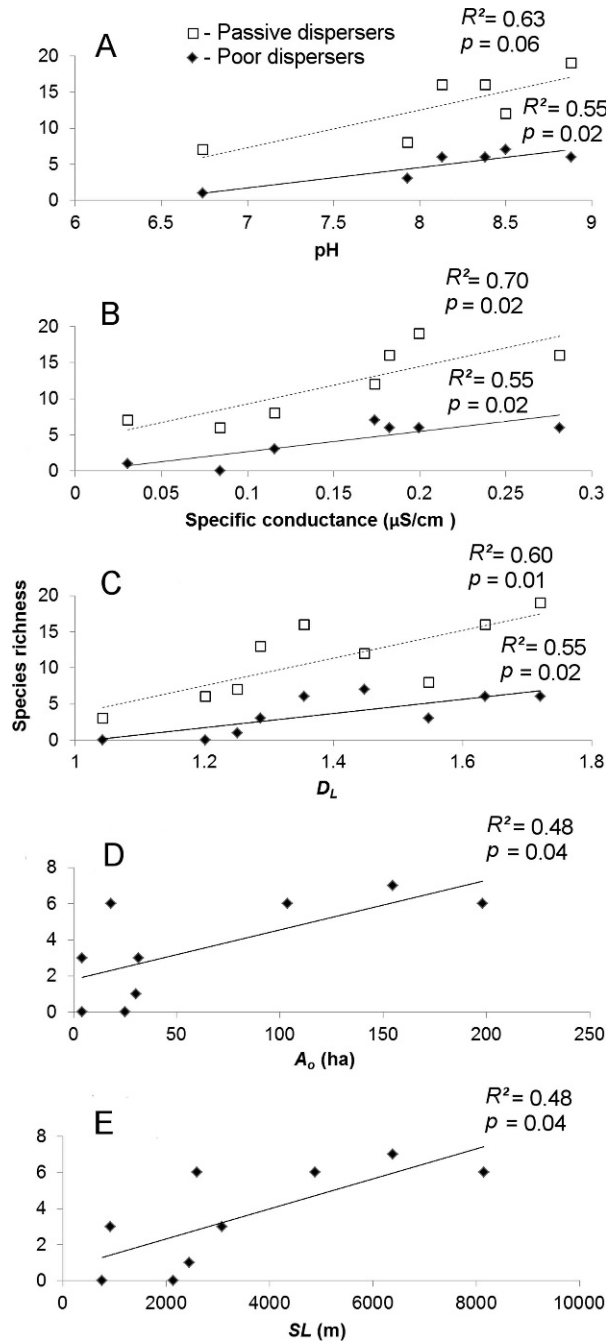
FIG. 5. Regressions for species richness of passively dispersing (Pulmonata and Sphaeriidae) and poorly dispersing (Caenogastropoda and Unionidae) mollusks vs pH (A), specific conductance (B), shoreline development (D_L) (C), lake surface area (A_o) (D), and shoreline length (SL) (E) for insular lakes of the Beaver Archipelago and Manitou Island systems. Specific conductance and pH values were unavailable for Tamarack and Maria.

Sphaeriid clams from the genus *Pisidium* had the most widespread distribution of the groups sampled. Five of the 9 lakes contained all 4 species encountered, and 2 species (*P. casertanum* and *P. nitidum*) were present in all 9 lakes. This distribution pattern is indicative of the wide range of habitat tolerances

of sphaeriids and their ability to disperse passively on birds and insects (Rees 1965). In addition, several species of sphaeriids can survive ingestion by fish (Brown 2007). Some valve snails (Caenogastropoda: Valvatidae) also can survive ingestion by fishes. Thus, colonization of insular lakes by valve snails

might be enhanced in lakes connected to Lake Michigan via a stream outlet.

Species richness of poorly dispersing mollusks was strongly related to both direct measures of habitat size (A_o and SL) and to D_L, an indirect measure of habitat size. In contrast, species richness of passively dispersing mollusks was related only to D_L. Colonization rate is expected to increase with habitat size simply because probability of encountering an island increases with habitat size (MacArthur and Wilson 1967). However, dispersal mechanisms also influence colonization in island systems (Rundle et al. 2002). The efficiency of passive dispersal mechanisms may have negated the influence of habitat size on colonization by pulmonates and sphaeriids. In contrast, poorly dispersing mollusks lack dispersal mechanisms that would increase the likelihood of encountering small habitats. Thus, these taxa should exhibit classic species–area relationships. For example, zooplankton species richness was not correlated with lake size, whereas species richness of the benthos was higher in large than in small lakes (Karatayev et al. 2005). The authors concluded that the difference in passive dispersal ability of zooplankton (high) and benthos (low) might explain the difference between the groups in the effect of habitat size on species richness.

Patterns of species richness also are expected to be influenced by the degree of spatial or temporal isolation of habitat islands (MacArthur and Wilson 1967). Isolation by distance appears to be unimportant to patterns of mollusk diversity in these insular lakes. Differences in isolation by distance were relatively small (≤ 2.7 km) among lakes. This distance is negligible for the waterfowl that could be facilitating much of the dispersal between Lake Michigan and individual lakes. Duration of isolation from Lake Michigan also does not appear to have affected mollusk species composition in the insular lakes. The decline in Lake Michigan water levels after the last glacial retreat isolated the lakes at different times (Colman et al. 1994). Lakes at higher elevations (perched lakes) or with greater distances from Lake Michigan probably have been isolated longer than those at lower elevations. Nevertheless, the relatively small differences in degree of spatial and temporal isolation coupled with relatively good dispersal abilities in some of the common mollusk groups probably account for the absence of isolation effects.

Other factors affecting mollusk distributions

Mollusk species richness and abundances are affected by several physicochemical and biotic factors. In our study, pH was highly correlated with total species richness and poor disperser richness. pH has not been identified as a powerful predictor of mollusk diversity in other studies, but Økland (1990) found that pH did influence mollusk richness in soft-water lakes. In our study, all measures of mollusk richness and abundance were correlated with specific conductance, which can reflect Ca^{2+} concentrations (Gorham et al. 1983; Ca^{2+} not analyzed in our study). Dussart (1976) found that mollusk abundance was highest in hardwater lakes, but the relationship was often driven by large numbers of a single species. Diversity was less affected by water hardness, although assemblages in very soft waters were much less diverse than those in water of medium-to-high hardness. Ca^{2+} affected mollusk population density more than species richness in a group of lakes (6.4–~400 ha) in eastern France (Mouthon 1992), and gastropod diversity and abundance were positively correlated with Ca^{2+} concentration in a group of English lakes (Savage and Gazey 1987). Gastropod species richness and abundance were positively correlated with hardness in 1500 lakes across Norway, but the relationship was stronger for richness than abundance (Økland 1990). Other factors that can influence mollusk species richness include % organic matter (Savage and Gazey 1987) and macrophyte diversity (Brönmark 1985). In our study, species richness was not correlated with PO_4^{3-} ($r = 0.03$), but PO_4^{3-} was strongly associated with PCA axis 2 and may be of secondary importance.

Rarely occurring species were not restricted to lakes with high mollusk species richness. Greene's Lake, one of the smallest and most species-poor lakes, contained the only species and population of freshwater limpet (*F. parallela*) found. Greene's Lake was unique among the lakes sampled because it was surrounded by wetlands. Freshwater limpets are common in wetland habitats (Burch and Jung 1992). Unionid mussels were found only in the 3 largest lakes (in surface area). The restriction of unionid mussels to larger lakes and the extirpation of the unionid population in Lake Maria suggest that these species may need resources provided only by larger lakes to maintain viable populations. This variation in the distribution of rare species highlights the importance of conserving all types of lake habitats and not just those that best match some predetermined set of characteristics associated with high mollusk species richness or abundance. For example, a small lake with suitable physical and chemical conditions (high shoreline development, specific conductance, and pH) might appear to be best suited for conservation of mollusks. Barney's Lake is relatively small and contained 25 of the 29 species total. However, the lake contained none of the rare species or unionid mussels. Thus, when conservation of rare species is important, assignment of higher priority on any particular lake system based only on physicochemical factors might be inappropriate.

Additional research should be conducted on similar systems in the Great Lakes and other freshwater systems to expand our knowledge and understanding of mollusk distribution patterns. The insular lakes in our study had similar (and low) degrees of spatial and temporal isolation. Examination of similar variables in other mainland and island systems in the Great Lakes watershed or other regions would shed additional light on the effects of isolation on patterns of mollusk distribution and richness.

Our study revealed some of the pitfalls of using only traditional island biogeography variables (habitat size and isolation) when attempting to predict species richness. More appropriate measures of available habitat, i.e., amount of littoral habitat in the case of freshwater mollusks, should be considered. Moreover, isolation and habitat size may have vastly differing effects on immigration rates within a group of species depending on dispersal abilities. Thus, geographic metrics most appropriate to the taxa under study and key abiotic factors will be needed to predict species richness patterns in insular lakes. More than 30,000 islands exist in the Great Lakes system, and many have insular lakes (Ewert et al. 2004). Thus, the opportunity for future study is large.

Acknowledgements

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APPENDIX. Species abundance (mean abundance/30 min of sampling) for 9 insular lakes on the Beaver Archipelago and Manitou Islands.

Species	Geneserath	Fox	Barney's	Greene's	Maria	Font	Manitou	Florence	Tamarack
Passive dispersers ($n = 20$)									
Sphaeriidae ($n = 8$)									
Musculium securis	1	0	15	0	25	20	14	0	0
Musculium transversum	0	4	32	0	78	8	3	0	0
Pisidium casertanum	1	26	68	8	61	52	104	19	7
Pisidium nitidum	1	158	77	13	1	44	255	108	5
Pisidium rotundatum	2	2	84	0	0	86	77	51	0
Pisidium variabile	15	0	39	8	5	92	15	9	8
Sphaerium rhomboideum	1	0	18	0	6	29	2	0	0
Sphaerium simile	1	0	24	0	3	63	0	0	0
Pulmonata ($n = 12$)									
Ferrissia parallela	0	0	0	1	0	0	0	0	0
Fossaria exigua	4	0	47	0	6	0	10	0	0
Fossaria obrussa	6	0	55	1	28	0	3	0	0
Gyraulus parvus	0	1	39	0	18	57	181	23	0
Helisoma anceps	6	0	25	0	0	30	34	1	0
Lymnaea stagnalis apressa	0	0	8	0	0	0	25	0	0
Physa sayi	15	0	6	0	0	0	17	9	0
Physa integra	15	0	23	0	5	0	9	0	0
Planorbella campanulata	3	2	24	0	0	5	29	4	0
Planorbella trivolvis	14	29	45	0	0	15	61	0	0
Stagnicola emarginatus	5	0	25	1	1	14	0	0	0
Stagnicola elodes	7	0	69	0	3	0	0	0	0
Poor dispersers ($n = 9$)									
Caenogastropoda ($n = 6$)									
Amnicola limosa	46	0	30	0	6	11	75	10	0
Amnicola walkeri	0	0	10	0	0	10	54	88	0
Campeloma decisum	25	1	20	0	0	16	0	0	0
Elimia livescens	295	0	385	0	0	0	846	0	0
Pyrgulopsis lacustris	1	0	2	0	14	0	37	1	0
Valvata sincera	0	0	69	0	23	52	1	0	0
Unionidae ($n = 3$)									
Anodontoides ferussacinanus	0	0	0	0	0	1	0	0	0
Lampsilis siliquoidea	3	0	0	0	0	3	0	0	0
Pyganodon spp.	4	0	0	0	0	2	6	0	0
Species richness	22	8	25	6	16	19	22	11	3
Number of mollusks	471	223	1239	32	283	610	1858	323	20
Mollusk abundance (no./30 min effort)	117	74	413	11	94	152	463	81	20