The Relationship Between Anthropogenic Disturbance and the Distribution of a Nonindigenous Species, *Echinogammarus ischnus* Stebbing, 1898 (Amphipoda: Gammaridae), at Great Lakes Coastal Margins

By

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ABSTRACT

Invasive species are becoming increasingly common components of Great Lakes zoobenthic communities. Elton (1958) proposed that biotic resistance against exotic species establishment is greater in intact communities than in those disturbed by human activities. However, Baltz and Moyle (1993) suggested that if abiotic conditions are appropriate, invasion is likely, regardless of the biota already present.

I tested these hypotheses by investigating the distribution of *Echinogammarus ischnus* Stebbing, 1898, an exotic amphipod, at U. S. Great Lakes coastal margin sites influenced by varying degrees of anthropogenic stress. Thirty-nine sites supporting *Gammarus fasciatus* Say, 1818, a common amphipod with habitat preferences similar to *Echinogammarus ischnus,* were evaluated (out of a total of 74 sites sampled across the entire U. S. Great Lakes coastline). A highly significant association was detected between *Echinogammarus ischnus* and *Gammarus fasciatus* (Yates corrected $\chi^2 = 7.94$, d. f. = 1, $p < 0.020$, n = 74), consistent with the expectations of Baltz and Moyle's hypothesis.

Principal components analysis identified 7 independent classes of stressors, each made up of intercorrelated groups of over 200 environmental variables. The presence/absence of *Echinogammarus ischnus* was ordinated across ranges of each of 6 different stressor variables that explained most of the variance of Great Lakes' stressor variables: overall nutrient input, total N + P load, areas of agricultural land, human population density, overall pollution loading, and relative maximum stressor score. Runs tests and logistic regression analyses were used to determine randomness of *Echinogammarus ischnus'* occurrence at these sites ordinated from low to high stress. None of the analyses showed a significant association between the presence of *Echinogammarus ischnus* and the amount of stress.

Across the five Great Lakes, *Echinogammarus ischnus* was found only in association with *Dreissena* spp, suggesting that dreissenids may regulate

Echinogammarus ischnus' distribution at the landscape scale and may be an important predictor of *Echinogammarus ischnus'* ultimate distribution. *Echinogammarus ischnus'* successful establishment in the Great Lakes appears to be a consequence of the prior establishment of *Dreissena polymorpha* Pallas, 1771, demonstrating "invasional meltdown" (synergistic facilitation among introduced species resulting in an accelerated accumulation of introduced species and effects) (Simberloff and Von Holle, 1999). Interactions among *Echinogammarus ischnus*, *Dreissena polymorpha*, and the round goby *Neogobius melanostomus* Pallas, 1811 suggest that the sequence of introductions is an important factor in invasion facilitation.

For Alda,
Mom, and Dad

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INTRODUCTION

GENERAL INTRODUCTION

The objective of my research is to elucidate the factors that regulate the distribution of nonindigenous species of the Great Lakes, using the nonindigenous amphipod, *Echinogammarus ischnus*, as a case study. A brief introduction to invasion biology is given in this section, as well as the possible role of disturbance in invasion processes. Two hypotheses proposed by Elton (1958) and Baltz and Moyle (1993) to explain invasion processes using disturbance as a mechanism for nonindigenous species establishment are tested in this project (see Study Objectives).

The Great Lakes collectively cover 24.5 million ha and are the largest freshwater system in the world. They carry more shipping than any other freshwater system on Earth, and their shores have seen some of the continent's heaviest industrial and agricultural development while the lakes support a set of fisheries worth $4 billion annually (Bright, 1998). A growing number of fish, mollusks, plants, plankton, and assorted other organisms have entered the system either as a result of human planning and intensive management (e.g. coho salmon, *Oncorhynchus kisutch*) or unintentional introductions (e.g. sea lamprey, *Petromyzon marinus*). At least 162 nonindigenous organisms have established themselves in the Great Lakes or on their shoreline (Ricciardi, 2001; Grigorovich *et al.*, 2003), and the current rate of invasion is estimated at ~2 species per year (Grigorovich *et al.*, 2003). The movement of organisms beyond their natural range can have consequences that are ecologically or even economically devastating. However, most nonindigenous species never establish self-sustaining populations. It has been reported that generally ~10% of species that invade new habitats establish successfully worldwide (Williamson and Fitter, 1996). Ecologists have attempted to understand why some nonindigenous species are so successful at invading while others are unsuccessful (Mooney and Drake, 1986; Drake *et al.*, 1989), so they often examine the interaction between the nonindigenous species and its new habitat. Many have tried to

understand the attributes of habitats that make them vulnerable to invasion (Elton, 1958; Drake *et al.*, 1989; Lodge, 1993). The presence of particular environmental stressors may play a role in the success of nonindigenous species because disturbed communities are thought to be especially vulnerable to invasion (Elton, 1958; Hobbs, 1989).

INVASION BIOLOGY

Model for Biological Invasions

Invasion biology is based on a common conceptual model in which the invasion process is depicted as having three basic phases: arrival, establishment, and integration (Vermeij, 1996). In this project, I focused on the establishment phase. Establishment is said to have occurred when a nonindigenous population persists by means of local reproduction and recruitment (Vermeij, 1996). Each newly arriving species meets with what Elton (1958) termed 'biotic resistance' to its establishment, which is considered by Moyle and Light (1996) to consist of three interactive elements: biotic, demographic, and environmental resistance. Assembly theory has emphasized the role of biotic resistance (mainly predation and competition) in the success and failure of invasions (Case, 1991). Demographic factors are often listed among traits of successful nonindigenous species. Environmental factors have been found to be the most critical element in determining the outcome of invasions in aquatic systems (Moyle and Light, 1996), although the success or failure of most invasions depends on the interaction of all three elements (Lodge, 1993).

A very real focus of many practical questions regarding the likely establishment success of introduced species in particular places concerns how much of the variance in success rates of introductions is due to biological differences between the introduced species or to differences among the communities that they invade (Case, 1991). Although it is difficult to determine universal attributes of successful invasive species, they generally have characteristics such as high abundance, short generation time, polyphagy, the

ability to occupy a broad diversity of habitats, broad physiological plasticity, and often, high genetic variability (Mills *et al.*, 1994). Common attributes shared by ecosystems that are vulnerable to invasion include climatic match between host and source habitats, early successional state, absence of predators, and low diversity of native species (Lodge, 1993). One of the most frequently cited features of communities thought to be vulnerable to invasion is that they tend to be disturbed (Elton, 1958; Orians, 1986; Hobbs, 1989; Rejmanek, 1989).

Disturbance is widely regarded as a mechanism that permits nonindigenous species to avoid or reduce the intensity of biological resistance usually manifested through interspecific competition or predation in the invaded community. If disturbance is an important determinant of biological invasions, the event must modify species interactions or the nature of the environment in a manner that favours establishment of nonindigenous species. This view is consistent with White and Pickett's (1985) definition of disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." The term, 'stressor', is used here as a reference to anthropogenic activities that cause disturbance. Hence, stressed communities will exhibit shifts in community and population structure (i.e., species numbers, species biomass, species density, species interactions) from direct (impact of a stressor on native species) and indirect (impact of a stressor on native species resources, substrate, physical environment) pressures. A number of established nonindigenous species have been indeterminately linked with disturbance. Purple loosestrife, *Lythrum salicaria*, grows along roadways and ditches, as it is able to thrive in disturbed soils, areas that many other species are unable to tolerate (Rachich and Reader, 1999). Eurasian watermilfoil, *Myriophyllum spicatum*, depends on stem fragmentation for its dispersal. Hence, mechanical clearing of vegetation enhances its dispersal since clearing creates new stem fragments as well as providing new habitat by clearing away other vegetation (Aiken *et al.*, 1979). The round goby, *Neogobius melanostomus*, is tolerant of polluted conditions, so it may be able to establish itself in stressed sites where

native species are less able to survive as well. It may have an advantage over native fishes by being able to occupy both stressed and unstressed sites. However, there are also examples of nonindigenous species that have not been dependent on disturbance for their establishment. Both the sea lamprey, *Petromyzon marinus*, and the fish hook water flea, *Cercopagis pengoi*, entered the Great Lakes after overcoming a dispersal barrier of some form. *Petromyzon marinus* is a marine organism that spawns in freshwater and was given the opportunity to enter the Great Lakes when the Welland and Erie canals were built (Morman *et al.*, 1980; Emery, 1985). *Cercopagis pengoi* is an example of a nonindigenous species that was transported into the Great Lakes by ballast (MacIsaac *et al.*, 1999).

Elton's Hypothesis (1958)

Elton (1958) observed that invasions were often human mediated and expanded this view with the concept of 'biotic resistance'. He argued that resistance by established species against nonindigenous species is greater in intact communities than in those disrupted or disturbed by human activities. To determine if biological resistance is a significant factor in invasions of ecosystems, it is necessary to ascertain the importance of disturbance in biological invasions.

Community assembly theory stresses process and history, and seeks explanation for community patterns in the context of dynamic rather than static (equilibrium) community structure. It holds that all present communities were built up by a continuous process of sequential invasions and extinctions over evolutionary time. This places modern invasions (human mediated or natural, long-term expansion and contraction of species' ranges) into the larger context of community development. Consequently, assembly theory studies focus on the interaction between the invader and the target community (Lodge, 1993). A number of generalizations relevant to invasion biology have emerged from work on community assembly (Case, 1991). One such generalization is that invasion success decreases with species richness (Lodge, 1993) and the amount of time

the community has been accumulating species. If this generalization holds for the zoobenthic communities of the Great Lakes, stressed sites (sites with the presence of a stressor) should show evidence of modification of native species interactions (i.e., changes in native species assemblage or native species numbers), thereby decreasing native species richness, resulting in establishment by nonindigenous species. These dynamics would provide support for Elton's (1958) hypothesis.

Baltz and Moyle's Hypothesis (1993)

Assembly theory addresses the biological characteristics of the invading species and of the ecosystems being invaded, on the assumption that competition and predation are the major processes determining the outcome of invasion. From their studies of invading fishes in California streams, Moyle and Light (1996) suggest that if abiotic factors are appropriate for a nonindigenous species, successful invasion by that species is likely, regardless of the biota already present. Where nonindigenous species fail to become established despite repeated invasions, that failure is best attributed to their inability to adapt to abiotic conditions rather than to biological resistance on the part of the recipient community (Baltz and Moyle, 1993). These abiotic conditions may be set by anthropogenic stressors, which will be examined in this project.

BIOLOGY AND ECOLOGY OF STUDY SPECIES

Given that Baltz and Moyle (1993) predicted that invaders establish where abiotic conditions are suitable, areas that meet the habitat requirements of *Echinogammarus ischnus* are therefore potential establishment sites for this invader. Five species from the genus *Gammarus* Fabricius, 1775 have North American ranges that cover the Great Lakes. *Gammarus fasciatus* Say, 1818 shares habitat preferences with *E. ischnus*. The biology and ecology of these similar gammarids are provided here to outline areas of the Great Lakes where *E. ischnus* would be expected to occur according to Baltz and Moyle's hypothesis (1993).

Family Gammaridae

The amphipod family Gammaridae is heterogeneous in composition and diverse in comparison with other families of the suborder Gammaridea. It is the largest and most widespread member of the suborder, represented by about 130 genera and species (Holsinger, 1976). Although the family is found in both marine and freshwater habitats, it is the only group of amphipods that has invaded continental freshwaters on a broad basis (Holsinger, 1976). At least 100 genera occur only in freshwater, and some of these are exclusively subterranean (ca. 25) (Holsinger, 1976).

Holsinger (1976) distinguishes Gammaridae from other families by the following phenotypic characteristics:

> "Body laterally compressed. Antenna 1 usually longer than antenna 2; accessory flagellum of antenna 1 with 2 to 7 small segments. Mandible usually with a palp (present in all North American genera north of Mexico); maxilla 1 with 2-segmented palp. Gnathopods subchelate; pereopods 5, 6, and 7 alike in structure but different in length; pereopod 7 about equal to pereopod 6 in length but often a little longer or a little shorter. Uropod 3 with or without rami, but outer ramus usually present although often

greatly reduced; outer ramus longer than inner ramus when both rami present. Telson entire or variously cleft."

Given their diversity, amphipodologists have proposed groups/phyletic lineages within the family to indicate closely related genera or common clusters (Holsinger, 1976). These may remain informal evolutionary categories rather than being designated families or even subfamilies (Holsinger, 1976).

Three familial groups are recognized in the United States and Canada: *Gammarus*, *Crangonyx* Bate, 1859, and *Allocrangonyx* Schellenberg, 1936 (Holsinger, 1976). The eight genera of North American Gammaridae with freshwater species are arranged within these groups as follows:

Gammarus group – *Gammarus;*

Crangonyx group – *Crangonyx, Synurella, Apocrangonyx, Stygonectes, Stygobromus,* and *Bactrurus*;

Allocrangonyx group – *Allocrangonyx* (Holsinger, 1976).

North American *Gammarus* (s.lat.) species

General Biology and Ecology

Currently, the genus *Gammarus* (s. lat.) is considered to be composed of a number of subgenera and numerous species widely distributed throughout the northern hemisphere (Holsinger, 1976). Species occur in shallow marine, brackish, and freshwater habitats, but most inhabit littoral brackish and freshwater biotopes (Holsinger, 1976). Confusion in taxonomic delineation of species is due to various factors including the presence of sibling species, sympatric ranges, overlapping ecology, and extreme morphological variation. This confusion is especially true among the brackish water forms, but seems less pronounced among the freshwater species of *Gammarus*, which appear more clearly differentiated (Holsinger, 1976). Holsinger (1976) warns that this may be an oversimplification, as freshwater species of *Gammarus* have not been carefully studied in some parts of the world. A revision is desirable and necessary for a complete understanding of the systematics of this complex group (Holsinger, 1976; Bousfield, 1969).

Nine species are recognized from North American freshwaters. A number of other species have been described but are regarded as synonyms (e.g., *Gammarus elki* Reimer, 1969, which is considered a synonym of *G. minus* Say, 1818 by Holsinger (1976). *Gammarus tigrinus* Sexton, 1935 and *G. duebeni* Lilljeborg, 1881 occur in brackish waters of the Atlantic coastal region but are occasionally found in marginal freshwater habitats (Holsinger, 1976).

Gammarus fasciatus Say, 1818

Gammarus fasciatus generally inhabits lakes and slow-moving, often turbid rivers (Bousfield, 1958). Holsinger (1976) reports that this species also occurs in small streams and occasionally in spring runs, especially in the southern part of its range. Populations have been found in rocky substrates with current, often reaching 5, 000 indiv./m^2 on wave washed cobble beaches in western Lake Ontario and the Bay of Quinte (Dermott *et al.*, 1992), and can exceed 20, 000 indiv./m^2 in Lake Erie on the recently created habitat of *Dreissena polymorpha* Pallas, 1771 colonies attached to cobble (Dermott *et al.*, 1993). *Dreissena* spp. benefits some members of the benthic community, such as *Gammarus* spp. and *Echinogammarus ischnus*, in nearshore areas by providing substrate and food in the form of feces and pseudofeces (Vanderploeg *et al.*, 2002). *Gammarus fasciatus* occurs in water bodies that are warm in summer at depths ranging from shoreline to about 12 m (Bousfield, 1958).

Gammarus fasciatus is originally known from the Chesapeake, Delaware, Hudson, and St. Lawrence drainage systems, including the Great Lakes (Bousfield, 1958). The amphipod is widely distributed in the United States and Canada, ranging from the upper Mississippi River drainage eastward throughout the Great Lakes area and south along the Atlantic coastal plain to southern North Carolina (Holsinger, 1976). Studies of *G. fasciatus* populations of Lake Erie showed an increase in 1993 relative to 1979, which was associated with *Dreissena polymorpha* clusters (Dahl *et al.*, 1995). Thus, an increase in *G. fasciatus* abundance may occur with the increasing dispersal of *D. polymorpha*.

Sexually mature males grow up to 14 mm in length whereas sexually mature females grow to be 8 to 12 mm (Holsinger, 1976). Ovigerous females are present from May to September (Bousfield, 1958), although they have been observed from February to April in the more southern parts of its range (Holsinger, 1976). The life span of *G. fasciatus* is less than one year, and two generations occur per year (Bousfield, 1958).

Bousfield (1958) points out that *G. fasciatus* has been confused with *G. tigrinis* and *G. pseudolimnaeus* in the past, and provides a key to distinguish among species. *Gammarus fasciatus* may also be confused with a complex of two to three closely related species that have characters in common with both *G. fasciatus* and *G. tigrinus* in coastal areas extending from South Carolina westward to Louisiana (Holsinger, 1976).

Other species of *Gammarus* occur within the same habitat and range as *G. fasciatus.* The biology and ecology of these are included here as they have likely been found in Great Lakes samples of this study, occupying similar habitat and ranges as *Echinogammarus ischnus*.

Gammarus pseudolimnaeus Bousfield, 1958 n. sp.

This species is widely distributed in the Mississippi drainage basin of east central United States, as well as the southwestern St. Lawrence system, from Texas and Arkansas north to Wisconsin, Ontario, and western Quebec (Bousfield, 1958). *Gammarus pseudolimnaeus* occupies large rivers and lakes and breeds in tributary streams and springs that are cool in summer (Bousfield, 1958). It is common in springs and sometimes in cave streams in eastern Iowa, southwestern Illinois, east-central Missouri, and northern Arkansas (Holsinger, 1976). In the more northern part of its range, especially in the Great Lakes region, it is often found in streams (Holsinger, 1976). Bousfield (1958) suggests that it is probably seasonally migratory. This amphipod is frequently associated with *G. fasciatus* and *Crangonyx pseudogracilis* (Crangonyctidae) Bousfield, 1958 in rivers and lakes, and with *Hyalella azteca* (Hyalellidae) Saussure, 1858, and *Crangonyx* Bate, 1859 spp. in streams (Bousfield, 1958).

Sexually mature males reach a length of 17 mm, whereas sexually mature females reach 14 mm but may become mature at only 6 mm (Holsinger, 1958). Ovigerous females appear mainly from April to July (Bousfield, 1958), although they have been collected during every season of the year, implying that breeding is continuous throughout the year (Holsinger, 1976). The life span of *G. pseudolimnaeus* is approximately 16 months (Bousfield, 1958).

This species has previously been confused with *G. lacustris, G. limnaeus, G. minus,* and *G. fasciatus* (Bousfield, 1958).

Gammarus lacustris lacustris G. O. Sars, 1864

This species is found in cold lakes, tundra ponds, sloughs, and their outflows (Bousfield, 1958). The distribution of *G. lacustris lacustris* spans from Baffin Island and the Hudson Bay drainage basin, west to the Yukon and Alaska, and south through the Midwest and the Rocky Mountains to New Mexico and California (Bousfield, 1958). It is also located in northwestern Europe (Holsinger, 1976). Ovigerous females develop in late spring and early summer. The life cycle of *G. lacustris lacustris* has a duration of about 15 months (Bousfield, 1958).

Gammarus lacustris limnaeus S. I. Smith, 1874

Bousfield (1958) describes *G. lacustris limnaeus* as being authentically only from the St. Lawrence drainage basin, from western Ontario to eastern Quebec and Newfoundland. It occurs in large lakes (Superior, Huron, Michigan), and smaller lakes (Nipigon, Nipissing, Simcoe) and their outflows, as well as in marshes, swamps, swamp streams and springs that are cool to cold in summer (Bousfield, 1958). It is often found under stones, among algae, bottom detritus and weeds (Bousfield, 1958). This species is found from the shoreline to more than 18 m in depth (Bousfield, 1958). Ovigerous females appear from April to August (Bousfield, 1958). This species completes its life cycle in approximately 15 months (Bousfield, 1958).

Holsinger (1976) examined specimens of *Gammarus lacustris* s. lat. from localities in the northern and western United States, Canada, and Alaska and

found it difficult to differentiate between *G. lacustris lacustris* and *G. lacustris limnaeus*, as diagnostic features were highly variable and without regional consistency. With the exception of disjunct populations in Oklahoma, the range of *Gammarus lacustris* s. lat. appears to be continuous across Canada and the United States (Holsinger, 1976). Separation into allopatric populations seems unlikely (Holsinger, 1976). Holsinger (1976) suggests that genetic studies be performed to distinguish the two subspecies.

***Gammarus lacustris* s. lat.**

Gammarus lacustris s. lat. is widely distributed with localities found throughout most of the western United States (particularly in the cold alpine lakes of the Rocky Mountain region), across the northern part of the United States, including the Great Lakes area, throughout most of Canada and Alaska, north to the Arctic circle and latitude 70 degrees in some areas (Holsinger, 1976). The species is also found in northwestern Europe and disjunct populations occur in central Oklahoma (Holsinger, 1976). This species occupies a variety of cold-water habitats, including lakes, tundra ponds, streams, sloughs, swamps, and springs (Holsinger, 1976). Sexually mature males range in size from 14 to 18 mm and occasionally reach 22 mm (Holsinger, 1976). Sexually mature females reach 14 mm and rarely up to 18 mm (Holsinger, 1976). Ovigerous females occur from March to September but their occurrence probably varies with several factors including latitude and water temperature (Holsinger, 1976).

Echinogammarus ischnus Stebbing, 1898

General Biology and Ecology

Studies of *Echinogammarus ischnus* (syn. *Chaetogammarus ischnus*) in Europe have revealed the variable life history of the amphipod. In its native range of the Dnieper River Delta in the Ukraine, *E. ischnus* reproduction takes place from mid-April until October but ceases from November to March (Konopacka and Jesionowska, 1995). However, in native tributaries of the Don River in Russia, where the water temperature has a limited annual range, *E. ischnus*

breeds throughout the year. In addition, Konopacka and Jesionowska's (1995) study of a thermally polluted lake in Poland found breeding to begin in February and to peak in June when 98% of females are ovigerous. During July, most females lacked eggs, but a second session of reproduction occurred in early fall before ceasing in November. Breeding seems to be flexible and dependent on water temperature.

Echinogammarus ischnus is primarily a euryhaline, riverine species that prefers large, slow-moving water with stony substrates (Jazdewski, 1980) but also occurs in the open Black Sea (Jazdewski, 1980). However, it has been found in a eutrophic freshwater lake (Kohn and Waterstraat, 1990) predominantly in mussel clumps.

In its native habitat, *E. ischnus* is considered part of the lithophilic community of large rivers, where *Dreissena* clumps may be a coincidence of habitat preference for cobble by both species (Dermott *et al.,* 1998). Kohn and Waterstraat (1990) found that *E. ischnus* was scarce outside *Dreissena* clumps, but did not indicate how common other hard substrates were in the German lake.

In Europe, *E. ischnus* is present mainly on stone or gravel substrates along the shallow margins of lakes and large rivers (Neseman *et al.*, 1995; Van Der Velde *et al.*, 1999), and greatest densities are often found in shallow water (< 2 m) within dreissenid druses (Kohn and Waterstraat, 1990).

Kohn and Waterstraat (1990) reported that three Ponto-Caspian species, *Dreissena polymorpha* Pallas, 1771, *Corophium curvispinum* Sars, 1895, and *Echinogammarus ischnus*, were closely associated when in druses. The druses ranged in size from 2 to 5 cm (mean length of the mussel 7.72+-4.56 mm, ranging from 1.0 up to 28.5 mm). Approximately 10 *Corophium* and up to 40 *Echinogammarus* occupied each cluster. Investigation of the druses led to the conclusion that *Echinogammarus ischnus* occurs in high frequency in shallow water, especially where *Dreissena*-clumps occur at depths of 0 to 2 m. *Corophium curvispinum* can be expected to become common in Great Lakes druses.

The range extension of *Echinogammarus ischnus* in Europe demonstrates that the amphipod has the ability to disperse effectively along natural and man-made watercourses (Jadzewski, 1980). As a result, Witt *et al.* (1997) predicted that further colonization of the Great Lakes basin by similar means will be rapid.

The rapid spread of *E. ischnus* through the canal systems in Europe (Jazdzewski, 1980), and its spread from the west end of Lake Erie to the east end in just two years (Dermott *et al.*, 1998) suggests that this species is very active in the water column. Vertical migrations in the water column have been documented (Dediu, 1980), and *E. ischnus* has been collected in vertical net tows taken at night at 45-m depth off Muskegon in Lake Michigan (Pothoven, 2001). Pelagic individuals in shallow water can be swept to deeper regions by nearshore-offshore bottom currents that can occur in the southern basin of Lake Michigan (Meyers and Eadie, 1993). Nalepa *et al.* (2001) found six individuals in a ponar replicate at a 45-m depth site off St. Joseph and suggest that *E. ischnus* is capable of colonizing substrates in deeper regions. However, the occurrence of *E. ischnus* unassociated with *Dreissena* spp. is unusual (Nalepa *et al.*, 2001).

Studies have shown *E. ischnus* specimens to belong to 2 or 3 size classes suggesting that the amphipod produces 2 to 3 generations per year (Kohn and Waterstraat, 1990). Females usually carry less than 20 eggs or embryos (Kohn and Waterstraat, 1990). Amongst other food, the species preys on ostracods, which occur in large numbers in *Dreissena*-clumps (Kohn and Waterstraat, 1990).

Native Ranges

Echinogammarus ischnus is originally known from the Dnieper River Delta in the Ukraine, north of the Black Sea (Jazdewski, 1980). The amphipod migrated to Europe from the Dnieper River via the Pripet-Bug canal system, which connects to the Vistula River in Poland (Konopacka and Jesionowska, 1995). It is present in the middle Danube (Musko, 1994) and in the Ems River and Wser-Elbe canal in Germany. It has recently been discovered in the lower

Rhine in the Netherlands (Van den Brink *et al.*, 1993). Its dispersal through Europe shows that the amphipod moves easily through man-made canals.

Kohn and Waterstraat (1990) observed that *E. ischnus* is closely associated with *Dreissena*-clumps and proposed that the two Ponto-Caspian species immigrated together, along with *Corophium.* The extinction of *E. ischnus* populations due to pollution or changes in ion composition of the water has been given as a possible explanation for the occurrence of isolated populations of the Ponto-Caspian trio.

Great Lakes Ranges

Witt *et al.* (1997) reported the presence of a breeding population of *E. ischnus* in 1995 at a Detroit River site, the first account of the nonindigenous amphipod in the Great Lakes basin. However, van Overdijk *et al.* (2002) analyzed archived samples and found E. ischnus in Lake Erie samples from 1994 and possibly as early as 1993 (although specimens were not detected in samples collected by Dahl *et al.* in 1993 (1995)). The Detroit River population was found to occupy a habitat typical of *Gammarus fasciatus*, suggesting the possibility of competitive displacement of the native species. By 1996, *E. ischnus* was widely distributed from southern Lake Huron downstream to the mouth of the Niagara River (Dermott *et al.*, 1998). *Echinogammarus ischnus* has been reported from the nearshore rocky areas of the northern to southern ends of Lake Michigan (Vanderploeg *et al.*, 2002) and from Thunder Bay, Ontario in silty-sand substrate in littoral waters (Grigorovich *et al.*, in review).

Dermott *et al.* (1998) found *E. ischnus* to be the only amphipod in samples collected in 1996 from Lake Huron, and the St. Clair River-western Lake Erie corridor, in close proximity to the location of its first discovery. These sites had rocky substrates with moderate current in the rivers, or rubble substrates on wave washed beaches.

Echinogammarus ischnus became the dominant amphipod in the Niagara River vicinity within a single year, and the proportion of *E. ischnus* increased while *Gammarus fasciatus* decreased over a 2 year study period (1996-1997) in

Port Weller, Lake Ontario, suggesting the displacement of *G. fasciatus* (Dermott, *et al.*, 1998). Densities were greatest among mussel colonies near Gibraltar Island, on wave washed cobble on Pelee Island, western Lake Erie, and on cobble fill in the Welland Canal (Dermott *et al.*, 1998). *Echinogammarus ischnus* was the sole amphipod collected in rocky habitats sampled along the eastern shoreline of Lake Michigan (Nalepa *et al.*, 2001). Although information on the amphipod taxa in these areas prior to the sampling conducted is sparse, *Gammarus* is a common component of the fauna found within rocky, breakwall habitats in the Great Lakes (Manny *et al.*, 1985), while *Hyalella* is commonly found in nearshore cobble areas (Winnell and Jude, 1987). Dermott *et al.*, (1998) found *E. ischnus* to be frequently present on cement slabs used for shoreline protection on the wave-washed beaches in Lake St. Clair and Lake Erie, and speculated that the slabs are the only hard substrate present at these locations. Sites in Lake St. Clair and Erie with dense submerged vegetation or quiet, turbid water generally had low densities or *E. ischnus*.

Echinogammarus ischnus was found in Great Lakes locales similar to its European habitats, being most abundant around concrete slabs, cobble, and within *Dreissena* colonies in shallow water (< 3 m) in the Detroit River, Lake Erie, and Lake Ontario (Witt *et al.*, 1997; Dermott *et al.*, 1998; Stewart *et al.*, 1998a). *Echinogammarus ischnus* was only present in close association with *Dreissena* clusters in shallow, soft-substrate sites in Lake Erie (Bially and MacIsaac, 2000). In contrast, Nalepa *et al.* (2001) found *E. ischnus* to be unassociated with *Dreissena* in some deepwater, soft-bottom habitats, a new habitat for the species in the Great Lakes. *Echinogammarus ischnus* has, however, been found at depths of 300 m on mud substrates in the Caspian Sea (Birshtein and Romanova, 1968; Kasymov, 1994).

Dermott *et al.* (1998) proposed that strong eastward longshore currents in Lake Erie and Lake Ontario (Simons 1976; Csanady and Scott, 1974) swept amphipods along the shore (Barton and Hynes, 1978), explaining the rapid expansion of *E. ischnus'* distribution downstream to Lake Ontario. They predicted that *E. ischnus* would quickly move downstream in the St. Lawrence River to its

estuary, and enter the Mississippi River and Hudson River basins via the interconnecting canals. They also speculated that *E. ischnus* must have been in the western approaches to Lake Erie during 1994, one generation prior to its presence being reported at two separate locations in 1995. This indicates that *E. ischnus* was able to migrate from the west to the east end of Lake Erie in 2 years, the same rate taken by *Dreissena*, which has a planktonic larval stage (1987-1989, O'Neill and Dextrase, 1994).

Echinogammarus ischnus may not become abundant in the offshore region of Lake Michigan (> 30 m depth), as this species has a preference for hard substrates over the soft sediment (Birshtein and Romanova, 1968) that is dominant in offshore regions (Nalepa *et al.*, 2001). However, a possible increase in *E. ischnus* populations may occur in deep water given its close association with *Dreissena* and the expansion of the bivalve's range to depths below 30 m. Recent *D. polymorpha* populations in Lake Michigan were expanding most rapidly at depths between 30 and 50 m, but were generally not abundant at depths > 50 m (Fleischer *et al.*, 2001). Conversely, *Dreissena bugensis* Andrusov, 1897 will likely occur at depths > 50 m, and replace *D. polymorpha* at the 30 to 50 m zone as has been the case in Lake Ontario (Mills *et al.*, 1999).

Many recent Great Lakes invaders such as *Dreissena* spp., *Petromyzon marinus* (the sea lamprey), *Neogobius* spp. (round goby and tubenose goby), and *Echinogammarus* are euryhaline, which is explained by the fact that most ocean-going vessels load ballast in estuarine settings. Witt *et al.* (1997) noted that both *Echinogammarus* and *Neogobius* lack both a pelagic stage and parthenogenic reproduction, two traits that facilitate ballast water transfer and subsequent colonization. They suggested that these species may represent a new wave of colonizations of the Great Lakes by sexually reproducing organisms that lack planktonic stages, as a result of an increase in permeability of the Great Lakes communities to invading organisms.

Interspecific Competition

The amphipod, *Gammarus fasciatus*, has been a major component of the Great Lakes littoral benthic community (Barton and Hynes, 1978; Dermott *et al.*, 1993; Stewart and Haynes, 1994). Specifically, in the lower Great Lakes, *G. fasciatus* constitutes more biomass than any other littoral benthic invertebrate, with the exception of *Dreissena* and possibly crayfish (Stewart and Haynes, 1994). This amphipod is prominent in the diets of numerous fish species, such as yellow perch (*Perca flavescens*) and whitefish (*Coregonus* sp.) (Price, 1963). A possible consequence of the *Dreissena* invasion is the increase in abundance of *G. fasciatus* (Griffiths, 1993; Stewart and Haynes, 1994), which represents one of the most important components of littoral food webs in the Great Lakes, as well as a major link in the contaminant pathway in the Great Lakes (Bruner *et al.*, 1994).

The replacement of amphipods by a related nonindigenous species has been documented in Europe (Pinkster *et al.*, 1977), and Witt *et al.* (1997) suggested the possibility of similar competitive displacement of *G. fasciatus* by *E. ischnus* in the Detroit River. The replacement of *G. fasciatus* may not change the organization of littoral food webs in the Great Lakes but may change transfer efficiencies if the two species are not physiologically equivalent (Dermott *et al.*, 1998). However, Nalepa *et al.* (2001) predicted that the expansion of *E. ischnus* and *Dreissena bugensis* over wide areas will have implications for the Lake Michigan food web. Studies have predicted (Witt *et al.*, 1997) or demonstrated (Dermott *et al.*, 1998; Stewart *et al.*, 1998a; Burkart, 1999) replacement of *G. fasciatus* by *E. ischnus* on *Dreissena* substrata. The ongoing replacement of *G. fasciatus* by *E. ischnus* in the Great Lakes may be related to the stronger affinity of the latter for substrata fouled by *Dreissena*, a genus with which it co-evolved. *Dreissena bugensis* may potentially aid in expanding the depth range of *E. ischnus* and consequently, *E. ischnus* may become a food item for many fish species. It has been intentionally introduced into some Russian water bodies, presumably as a diet item for forage fish (Olenin and Leppakoski, 1999), and it has been found in the stomachs of yellow perch and whitefish collected at a

depth of 20 m in Lake Michigan (Pothoven, 2001). *Dreissena bugensis* will likely cause other changes to the offshore food web and inadvertently magnify the impacts of *E. ischnus* expansion. van Overdijk *et al.* (2003) showed that the density of *G. fasciatus* in western Lake Erie was lower than the density ($33.2/cm^2$) reported by Stewart *et al.* (1998b) in August after the *Dreissena* invasion. The density of *E. ischnus* was almost always higher than that of *G. fasciatus* in the field survey, except during 1994.

Dermott *et al.* (1998) juxtaposed the rarity of *G. fasciatus* and frequency of *E. ischnus* on rocky habitats, particularly where currents were moderate, such as in the St. Clair, Detroit, and Niagara rivers. They predicted that *G. fasciatus* would be replaced by *E. ischnus* on wave washed cobble beaches, rubble armored shorelines, and breakwalls, and especially on the rocky substrates in the interconnecting rivers and larger tributaries of the Great Lakes. Nalepa *et al.*, (2001) reported the absence of *Gammarus* and *Hyalella* and the sole presence of *E. ischnus* along the eastern shoreline of Lake Michigan, supporting the prediction of competitive displacement by *E. ischnus* of other amphipod taxa in rocky habitats (Dermott *et al.*, 1998). *Echinogammarus ischnus* may have a competitive advantage over *G. fasciatus* on hard substrates, as it is able to gain upright support with its uropods and antenna, making it agile and capable of walking across firm surfaces (Dermott *et al.*, 1998). *Gammarus* and *Hyalella* were found at shallow water sites in the Straits of Mackinac without *E. ischnus*. Substrates at these sites were variable and consisted of medium to coarse sand (gravel), silt, and submerged vegetation. Such substrates may be more suitable for *Gammarus* and *Hyalella* than to *E. ischnus* as suggested by Dermott *et al.* (1998). *Gammarus fasciatus* is a generalist and well adapted to habitats with dense submergent vegetation or quiet turbid areas, so is expected to continue to dominate these habitats (Dermott *et al.*, 1998), although fish predation may determine relative dominance in rocky areas (Vanderploeg *et al.*, 2002). Alternatively, *E. ischnus* may not have yet colonized these substrates in the northern portion of the lake. Research on the mechanisms of competition

between the two amphipods on rocky substrates where *G. fasciatus* is still common is required (Dermott *et al.*, 1998).

Conversely, *G. fasciatus* is well equipped to cling to vegetation (Clemens, 1949), and appears to be able to compete with *E. ischnus* in these habitats, such as the turbid Canard River, Ontario, and areas with abundant submergent aquatic vegetation (e.g., Thames River mouth and Mitchell Bay, Lake St. Clair). Griffiths (1993) found that *G. fasciatus* densities increased in Lake St. Clair following the increased abundance of aquatic plants.

Fecundity and generation time do not give *E. ischnus* a competitive advantage over *G. fasciatus* (Dermott *et al.*, 1998). *Echinogammarus ischnus* has a lower fecundity and evolved in a region with many more amphipod species, making it more of specialist on rocky habitats compared with the generalist *G. fasciatus* (Dermott *et al.*, 1998). Dermott *et al.* (1998) found that where both species were present, competition reduced the frequency of immature *G. fasciatus* in the population as compared to sites where *E. ischnus* was not common. They also found *G. fasciatus* females grew larger and produced more eggs than *E. ischnus*. However, *E. ischnus* apparently begins reproducing at a slightly smaller size (4.8 mm) as compared to *G. fasciatus* (5.2 mm). Differences in density were unrelated to body size, as mean body length of *E. ischnus* (6.5cm) and *G. fasciatus* (6.2 cm) did not differ statistically (van Overdijk *et al.*, 2003). Mature *E. ischnus* are at least as large as mature *G. fasciatus*, and appear more active and aggressive (van Overdijk *et al.*, 2003). Thus, behavioural differences may accentuate, or be the source of habitat preferences.

It is unknown whether replacement of *G. fasciatus* by *E. ischnus* will be permanent and is occurring via exploitative competition for habitat, interference competition, or some other mechanism. Comparative studies of *G. fasciatus* and *E. ischnus* on substrate preferences, growth efficiencies, production rate, as well as contaminant transfer, are required to determine if *E. ischnus* will take over the role currently occupied by *G. fasciatus* (Dermott *et al.*, 1998). Although *E. ischnus* is well established in most of the Great Lakes, its impact on the

ecosystem of the lakes may be minor, and certainly less dramatic than that of *Dreissena* (Dermott *et al.*, 1998).

van Overdijk *et al.*, (2003) compared microhabitat selection of *E. ischnus* and *G. fasciatus* in field and laboratory studies. Lake Erie surveys conducted between 1995 and 1998 and laboratory studies revealed that *E. ischnus* preferred *Dreissena*-encrusted rocks more than *Cladophora*-encrusted rocks, while *G. fasciatus* used both substrata. *Echinogammarus ischnus* abundance was usually higher than that of *G. fasciatus*, was lowest at nearshore locations, and was highest on *Dreissena* substrata. The overall pattern that emerged was of progressive dominance of the amphipod community by *E. ischnus* at the expense of *G. fasciatus*. The species exhibited an inverse pattern at low density, with one species always present at low density whenever the other was present at high density. The maximum density of *E. ischnus* during 1995 was $4.4/cm^2$, on a *Dreissena*-encrusted rock without *G. fasciatus*. Conversely, field colonization experiments showed a positive correlation between *E. ischnus* and *G. fasciatus* densities when overall amphipod density was low. Laboratory experiments and field colonisation studies failed to show evidence consistent with interspecific competition, while long-term census data at Middle Sister Island provides weak evidence in support of it (van Overdijk *et al.*, 2003).

STUDY DESIGN AND SITES

Study Objectives

My project focused specifically on the distribution of the nonindigenous amphipod, *Echinogammarus ischnus*, to elucidate factors that control its establishment at particular locations. My goals were to evaluate two contrasting hypotheses purported to explain the distribution of invading species :

1) the hypothesis proposed by Elton (1958) that biotic resistance against exotic species establishment is greater in intact communities than in those disturbed by human activities; and
2) an alternate hypothesis proposed by Baltz and Moyle (1993) that biotic resistance is unimportant - if abiotic conditions are appropriate for a nonindigenous species, invasion is likely, regardless of the biota already present.

The hypotheses were evaluated by examining a subset of zoobenthic samples collected at 74 locations across the U.S. Great Lakes coastline. Sample sites were predetermined as part of the Great Lakes Environmental Indicators project (see 'Site Selection' below). Evidence that *E. ischnus* is strictly located at sites that are influenced by relatively high disturbance would give support for Elton's (1958) hypothesis. This disturbance was characterized by stressors (see 'Introduction') in this study. Alternatively, distribution of *E. ischnus* at sites providing suitable habitat, regardless of the impact of stressors, would provide support for Baltz and Moyle's (1993) hypothesis. These sites were characterized by those that supported *Gammarus fasciatus*, a common amphipod with habitat preferences similar to *E. ischnus*. Results that are consistent with Elton's hypothesis may indicate that the number of invaders occurring at a site may be a good indicator of stress, so there is the potential to use nonindigenous species as an environmental indicator. The results of my investigation will be useful in understanding and predicting the location and dispersal of invaders.

Great Lakes Environmental Indicators Project Overview

The main objective of the "Great Lakes Environmental Indicators" (GLEI) project is to develop environmental indicators that measure and monitor the condition, integrity, and long-term sustainability of the Great Lakes (Johnson *et al.*, 2000). Two types of indicators are being developed: 1) ecological (state) indicators that directly indicate the condition of the coastal margin ecosystems from several scales, the broad landscape scale to the local scale, and 2) stressor (pressure) indicators that provide information on the anthropogenic factors suspected to influence the ecological condition (Johnson *et al.*, 2000). Collaborators will be testing indicators to link stressors with environmental responses (Johnson *et al.*, 2000). The resulting suite of indicators can be used to develop management strategies for the Great Lakes (Johnson *et al.*, 2000).

The GLEI project will assess 7 different groups of response variables as potential indicators of environmental stress: birds, wetland emergent vegetation, amphibians, fishes, zoobenthos, diatoms, and water quality characteristics. Researchers at the University of Windsor and the University of Minnesota, Duluth simultaneiously sampled fish and zoobenthos as potential indicators.

Site and Stressor Assessment

Geomorphic Types

The first step in the site/stressor assessment process involved classifying the distribution of geomorphic types among the coastline segments because the distribution of biota differs among habitats, geology and land morphology independently of any response to anthropogenic stressors. Waterbodies at the coastal margins of the U. S. Great Lakes were classified on the basis of hydrogeomorphologic connections with the lake (as per Keough *et al.*, 1999) based on geographic information systems (GIS) data sources, aerial photograph surveys, established databases, and field measurements by GLEI collaborators from the Natural Resources Research Institute and the University of Minnesota, Duluth. Five different classes of aquatic ecosystem type were identified .Non-wetland areas were identified as being either high-energy shoreline (HE), or low

energy shoreline/embayments (EB). Wetland types, defined by Minc (1998), were aggregated into three functional groupings: coastal marshes (CW) (i.e. open shorelines, unrestricted bays, shallow sloping beaches); river-influenced wetlands (RW) (i.e. river deltas, restricted riverine, and lake connected inland types); and protected wetlands (PW) (i.e., barrier beach systems) (Johnson *et al.*, 2000).

Environmental Characterization

Data quantifying pressure and state indicators were obtained from existing GIS data sources, established databases, and field measurements (primarily comprising a pilot study conducted in 2001) by GLEI collaborators (Johnson *et al.*, 2000). These data were used to identify potential sources of stressors such as contaminants, sediments, nutrients, structures that alter hydrology and geomorphology, etc., and to derive independent variables that will be used to link stressors to response variables (state indicators) (Johnson *et al.*, 2000).

Measurements of local environmental conditions were made at each sample location at the time that fish and zoobenthos were collected. A suite of measurements was collected that characterized the local habitat (water depth, slope, sediment texture, sediment organic matter content, sediment odour, and macrophyte diversity and density) and water characteristics (temperature, dissolved oxygen, pH, conductivity, turbidity) (Johnson *et al.*, 2000). Specific environmental variable conditions will be correlated to stressed and unstressed sites.

Stressor Data Compilation

For each ecosystem type, sites were located and sampled that cover a range of stressor levels, from relatively unimpacted to quite disturbed. Various human activities, such as agriculture, energy production, mining, recreation, silviculture, transportation, and urbanization have an impact on various processes such as habitat alteration, chemical disturbance, biotic processes,

physical processes, and hydrologic disturbance, and can apply stress to systems.

GLEI collaborators examined a total of 229 stressor variables that affected segment-sheds from 19 data sources. These data sources consisted of the following: agricultural fertilizer and herbicide use; runoff from agricultural land (erosion, pesticides, and nitrogen); distance to nearest AOC (Areas of Concern); National Atmospheric Deposition Program (NADP) (collection and analysis of precipitation for hydrogen, sulphate, nitrate, ammonium, chloride, and base cations); population density; land use by cropland type; amount of erosion from agricultural land; fertilizer use on agricultural land; confined animal facility waste treatment; shoreline alteration; general land use; N, P runoff potential; National Pollutant Discharge Elimination System categories (permit issuance to companies for wastewater discharge into rivers); urbanization amount/rate; wetland types, hydric soils, and erosion; road area (total length and density for freeways, highways, local roads, and trails); soil properties; toxic release inventory points; wetland amount. GLEI collaborators will ultimately use multimetric and multivariate approaches to generate ecologically relevant suites of indicators that had the greatest discriminatory power to distinguish degraded systems from least-impaired systems.

Site Selection

Existing GIS data sources, established databases, and field measurements by GLEI collaborators were used to delineate the shoreline segments and their watersheds. Geographic Information System analysis was used to identify second order and higher order streams in order to divide the coastline into segments. Segment boundaries were situated were situated midway between adjacent steams so that each segment contained only one second-order or higher stream that flowed into the lake. In order to associate these coastal segments with land-based environmental factors that may possibly be affecting them, digital elevation models (DEMs) were employed to delineate the runoff areas (i.e. watersheds) for each segment. For each shoreline

segments, elevation data was use to delineate the areas that flow into each of these segments, using the watershed analysis tools available in ArcInfo. Areas such as islands and connecting channels were not included in delineation of segment-sheds. A total of 762 segment-sheds encompassing the entire U. S. Great Lakes coast were identified through this process.

A major aim was to select a suite of sites for each project subcomponent so that samples would be spread across the environmental variables (gradients of degree of anthropogenic stress) to the highest degree possible. In addition, it was necessary to allow for maximum overlap of sites among project subcomponents (i.e. maximum overlap of bird subcomponent sites with contaminant subcomponent sites, etc.). Coastal locations on islands, connecting channels and Lake St. Clair were excluded from the suite of potential locations.

Data selection

Having defined segment-sheds, stressors that influence each segment-shed were then identified (Niemi *et al.*, 2002). Fourteen stressor variables of the original set of 229 were excluded from further analysis because either there were missing data or because most (>90%) of the values were zeroes. This process resulted in a data matrix consisting of 173 columns (stressor variables) and 762 rows (segment-sheds). To reduce the influence of outliers and to improve the distributional characteristics for each variable, one of three transformations were applied. Data that were proportions were subject to the arcsin(square root) transformation. Where arcsin(sqrt) did not seem appropriate (e.g., for variables that were ranks), square root transformations were used. All other variables were transformed by first adding 1.0 and then calculating the natural logarithm.

Principal Components Analysis Methodology

Niemi *et al.* (2002) performed principal components analysis on the stressor-segment shed matrix to reduce the information contained in the large set of stressor variables to a smaller number of statistically independent, interpretable stressor gradients for the entire Great Lakes coastal region.

Through an iterative approach of calculating and interpreting a small number of exploratory PCAs, GLEI collaborators were able to derive one index (values scaled along a PCA axis) that summarized the stressor gradients in the dataset. Criteria for an adequate PCA ordination were that 1) stressor gradients could be interpreted from the first few principal components of the analysis; 2) the principal component scores of the segment-sheds were evenly distributed across the length of the gradients (i.e., there were no groups of extreme outliers or large groups of tightly packed segment-sheds), and 3) a large amount of variance was explained by the *n* principal components of interest (Niemi *et al.*, 2002).

The entire set of observational units (e.g., single wetlands) was not known prior to site selection. Segment-sheds were used as surrogates for observational units and were across environmental gradients. It was assumed that observational units contained within a segment-shed would have a profile of environmental characteristics similar to that of the entire segment-shed.

Environmental variables were categorized according to their influence. Some of the categories contain known stressors, while others represented sources of environmental variation that influence potential indicators but are not intrinsically stressors (e.g., soil type). The categories are: agricultural/chemical, atmospheric deposition, land cover, point source, human population/development, shoreline, and soils. Principal components analysis was used to reduce the number of variables in these 7 categories, and the principal component scores were standardized and rescaled.

The site-selection procedure consists of environmental stratification followed by random evaluation of sites from the strata. Three environmental strata were used (Ecological Provinces, geomorphic units, and clusters).

The first strata included Ecological Provinces classified by Keys *et al.* (1995). Two ecological provinces border on the Great Lakes: 212 Laurentian Mixed Forest, and 222 Eastern Broadleaf Forest.

The second strata level consisted of the 5 geomorphic units (coastal wetland, protected wetland, river-influenced wetland, high-energy shoreline, and embayments). Segment sheds were examined to identify the geomorphic types

that each contained. The goal for the fish and invertebrate subproject was to select approximately 20 locations of each geomorphic type from among the segment sheds within each ecological province such that the 20 locations were evenly spaced across the range of the stressor gradients (20 sites x 5 geomorphic types x 2 provinces = 200 sites total). All segment sheds (N) within one ecological province (A) that contained a particular geomorphic type (e.g., protected wetlands) were determined. An Nx7 matrix was assembled where each row was a segment shed (n) in province A. The column entries were the PCA scores for segment shed n for each of the 7 classes of stressors.

The final strata was created from groups of sites (clusters) that had similar environmental (i.e., stressor) profiles. This was done using cluster analysis. K-means cluster analysis was performed on the Nx7 matrix to generate 10 groups of segment sheds. The segment sheds within a group were subject to similar types of stress. However, each group differed from the others in degree of stress.

With this method, the number of clusters thought to be appropriate could be specified *a priori*, and scores for the number of PCs thought to be useful could be determined. Once the clusters were created, *n* segment-sheds within each cluster were randomly selected (*n* depends on the number of study sites needed for each subcomponent). By sampling at least one site from each cluster, the main environmental gradients influencing Great Lakes coastal margin ecosystems were integrated.

Each indicator subcomponent (i.e. diatom group, vegetation group, bird group, etc.) evaluated the segment-sheds in random order within clusters to assess whether the segment could theoretically be sampled (e.g. site accessibility). After a suite of segment sheds had been provisionally selected, their PCA scores were plotted along particular gradients of interest to see whether these gradients were adequately covered. In cases where they were not, additional segment sheds were purposely selected to fill gaps along these gradients.

The fish and invertebrate subproject created 20 clusters for each geomorphic type (10 for each ecological province); site selection was done

independently for each type. One primary site and two backup sites were identified in each cluster for each geomorphic type. However, this was not always possible. A segment shed could be rejected due to there being no wetlands of sufficient size (4 ha or larger), no vegetation within the waterbody (riverine, coastal, and protected wetlands), or because of accessibility or safety issues. A total of 120 sites were identified for sampling in 2002, of which 74 were actually sampled.

Sites were evaluated in random order from strata so that bias would be minimized. The design is set up so that samples are distributed across both stressor gradients and gradients of ecological condition. This allows detection of variables that discriminate sites along the condition gradient (indicators) and to characterize relationships with stressors so that sources of ecosystem stress can be identified.

METHODS AND MATERIALS

Sample Collection

Sampling within each coastal ecosystem followed a transect approach. Preliminary synoptic surveying of a site (based on aerial photography and field observations) identified the two most dominant shoreline zones by shoreline length (vegetation communities; non-vegetated high energy shoreline; non-vegetated low energy beaches). The relative frequency of the various shoreline habitat types was determined using aerial photographs and GIS coverages for each site sampled. Two transects were delineated extending from each of the two most common inshore habitat types. Benthic samples were then collected at four topographic contour points along each transect at discrete depths, corresponding to the emergent macrophyte zone (20-50 cm deep), submergent macrophyte zone (typically 50-75 cm deep), 5-m depth, and 10-m depth zones (Johnson *et al.*, 2000). Only 3 locations were sampled along a transect (emergent zone, submergent zone, deepest point) if the open water was less than 5 m deep, as was often the case for embayments, river-influenced wetlands, and protected wetlands. A maximum of 24 points was sampled at each site.

A combination of sampling methods was employed to capture the greatest amount of zoobenthic diversity, while minimizing processing costs. Thirty-second sweep net samples were taken in combination with 10-cm deep, 5-cm diameter cores in the emergent and submergent habitats; cores and ponar grabs were employed in the soft sediments of 5-m and deeper habitats (Johnson *et al.*, 2000). Two Petite Ponar grabs were collected at the 5- and 10-m depth contours as located by an echosounder. A 10-cm deep, 5-cm diameter core sample was taken from each of 2 other Petite Ponar samples. Where the substrate of emergent and submergent zone locations was too rocky to permit use of cores, rocks equivalent in size to a Ponar grab were scraped to remove all adhering organic material and invertebrates. All samples were preserved in 2.5:1 v/v ethanol:formalin solution diluted 1:1 with lake water.

Sample processing and sorting

In the laboratory, one sample of each duplicate from each zone of each transect was randomly selected and sorted. The remaining sample was kept in reserve. Benthic samples were rinsed through a series of nested sieves (4 mm, 1 mm, 0.5 mm, 0.25 mm) following the procedures of Ciborowski (1991). Individual size fractions were subsampled as necessary to generate at least 100 animals per fraction such that the total sorting time spent per sample did not exceed 3 h. Specimens were sorted and identified to the genus level where practicable using a dissecting microscope, and fixed in 70% ethanol. Amphipods were identified to the genus level using the key of Covich and Thorp (2001). Identification of species of *Gammarus* was performed using keys written by Holsinger (1976) and Bousfield (1958). *Echinogammarus ischnus* specimens were identified using the description outlined by Witt *et al.* (1997).

Table 1 lists the samples processed for the 74 sites used in this study. Sites at which samples contained no *Gammarus fasciatus* were deemed to be unsuitable habitat for gammarids and were not used in further analyses. The presence (1) or absence (0) of *Echinogammarus ischnus* was evaluated for all sites sampled and compared with the distribution of *G. fasciatus*. Sites where other amphipods, such as *Hyalella azteca* and *Diporeia* spp., were detected in samples were not considered to exemplify habitat suitable for *Echinogammarus*, because these amphipods do not share habitat requirements (see Biology and Ecology of Study Species section).

Different geomorphic types situated in a segment shed were regarded as discrete sites. For example, Toledo Beach (Lake Erie) contained both a protected wetland and high-energy shoreline so these different geomorphic types were treated as 2 separate sites.

Table 1: All sites and samples used for determination of *Gammarus fasciatus* and *Echinogammarus ischnus* presence (1) and absence (0) (n = 74).

Segment Number	Site Name	Site Type	Lake	*Gammarus* presence	*Echinogammarus* presence	Number of Samples
5	NSU 2b Houvland B (Swamp Lake)	HE	Superior	0	0	1
8	NSU 2a Houvland A (Paradise Beach)	HE	Superior	0	0	1
27	NSU 6b Little Marias B (Caribou River)	HE	Superior	0	0	1
28	NSU 6a Little Marias A (Manitou River)	HE	Superior	0	0	1
42	Two Harbors	HE	Superior	0	0	1
51	Duluth	HE	Superior	0	0	1
55	Fond du Lac	RW	Superior	1	0	5
59	Dwight's Point	RW	Superior	1	0	9
63	Allouez Bay	RW	Superior	0	0	1
63	Allouez Bay	EB	Superior	1	0	12
68	Middle River	RW	Superior	0	0	1
76	SSU 24 Brule River (Smith Creek)	HE	Superior	0	0	1
180	Agate Harbour	HE	Superior	0	0	1
183	SSU 4 Bete Grise	HE	Superior	1	0	2
192	Baraga	PW	Superior	1	0	1
200	Peterson Creek	PW	Superior	1	0	4
203	SSU 14 Big Bay (Conway Bay)	HE	Superior	0	0	1
213	Laughing Whitefish River	HE	Superior	0	0	1
213	Laughing Whitefish River	RW	Superior	0	0	7
215	Au Train	RW	Superior	1	0	12
229	NGL 49 Tahquamenon River	RW	Superior	1	0	11
247	McKay Creek	CW	Huron	1	0	2
247	NGL 53 McKay Creek	RW	Huron	1	0	1
248	Pine River 1	CW	Huron	0	0	1
248	Pine River	EB	Huron	1	0	1
257	Hog Island Creek	HE	Michigan	0	0	1

275	Ogantz River	CW	Michigan	0	0	1
277	NGL 67 Whitefish River	RW	Michigan	1	0	1
281	Ford River	RW	Michigan	0	0	1
289	Menominee River	HE	Michigan	1	0	6
291	Peshtigo River	RW	Michigan	1	0	4
294	Otonto River	CW	Michigan	0	0	1
299	Little Suamico River	RW	Michigan	0	0	1
300	Little Tait Point	CW	Michigan	0	0	1
302	Suamico River	PW	Michigan	0	0	1
303	Green Bay Shores	CW	Michigan	1	1	1
310	NGL 69 Sugar Creek	HE	Michigan	1	0	3
321	Kewaunee River	RW	Michigan	0	0	1
325	West Twin River	HE	Michigan	1	0	2
359	Trail Creek	HE	Michigan	0	0	1
361	Galien River	RW	Michigan	1	0	2
372	Kalamazoo River	RW	Michigan	0	0	5
374	Port Sheldon	HE	Michigan	0	0	3
378	Mona Lake	RW	Michigan	1	0	8
388	Lincoln Lake	HE	Michigan	1	0	1
389	Big Sable	RW	Michigan	1	0	14
393	Arcadia Lake	RW	Michigan	1	0	15
407	Crossvillage	CW	Michigan	1	0	7
417	Rogers City	EB	Huron	1	0	1
419	Presque Isle Harbour	EB	Huron	0	0	3
422	Thunder Bay River	RW	Huron	1	0	7
425	Butternut Creek	HE	Huron	0	0	1
442	Great Lakes Marina	CW	Huron	1	0	9
446	Cooper Drain	CW	Huron	0	0	1
447	Pinconning	CW	Huron	0	0	3
448	Johnson Drain	CW	Huron	1	0	5
453	Saginaw River	CW	Huron	1	1	8
458	Shebeon Creek	CW	Huron	1	0	4
470	Willow Creek	HE	Huron	1	1	2
486	Purdy Bay	CW	Huron	0	0	2
578	Toledo Beach	HE	Erie	1	1	12
578	Toledo Beach	PW	Erie	0	0	4
585	Maumee River	EB	Erie	1	0	8
590	Toussaint River	RW	Erie	1	0	6
593	Little Muddy Creek	PW	Erie	1	0	4
602	Little Pickerel Creek	PW	Erie	0	0	8
606	Plum Brook	CW	Erie	0	0	1

636	EOL 79 Milestone Marker	HE	Erie	1	1	5
645	Walnut Creek	HE	Erie	0	0	1
653	EOL 74 Slippery Rock Creek	HE	Erie	0	0	2
658	EOL 73 Cattaraugus Creek	HE	Erie	1	1	6
746	Henderson Bay	EB	Ontario	1	1	5
747	Muskalonge Creek	CW	Ontario	1	1	4

Statistical Analyses

Runs tests were performed on data from sites containing *G. fasciatus* arranged along each of 6 stressor variables to test Elton's hypothesis. The runs test evaluates the randomness of a sequence of dichotomized events (presence of *E. ischnus* (n_1), absence of *E. ischnus* (n_2)) to see whether the observed number of runs is significantly different from the expected value. The 6 stressor variables were: human population density stress, N and P load stress, agricultural stress, population density stress, overall pollution loading stress, and relative maximum principal component score (the greatest principal component score of all stressor variables for a particular site site). Sites supporting *E. ischnus* were assigned a value of 1, whereas sites from which no *E. ischnus* were collected received a value of 0. These site values were plotted against the principal components scores each of the 6 stressor variables. If Elton's hypothesis holds for the Great Lakes sites, one would expect to observe only 2 runs in a scatterplot pattern that resembles Figure 1. Those sites with a low score of the stressor in question would not be expected to contain *E. ischnus* since the required decrease in species richness for invader establishment due to the impact of the stressor would not have occurred at these unstressed sites. Alternatively, sites with higher scores of the stressor would be expected to support *E. ischnus* if the disruption to system processes by that stressor resulted in a lowering of species richness or a reduction in predation. If Elton's hypothesis holds, one would expect the number of runs to be 2 ($p < 0.009$ for $n= 39$). A Bonferroni corrected p-value of 0.0083 was used to adjust the study-wide Type I error to 0.05.

Simple logistic regression models were fitted to scatterplots to refine runs test analyses of the relationship between presence/absence of *E. ischnus* and each independent variable (stressor). A logistic regression curve can fitted to the scatterplot data, from which the critical/threshold stressor score at which *E. ischnus* occurs can theoretically be determined when H_0 is rejected by the runs test. This would imply that *E. ischnus* is more likely to occur above a particular intensity of stress. In that event, logistic regression was to be used to determine

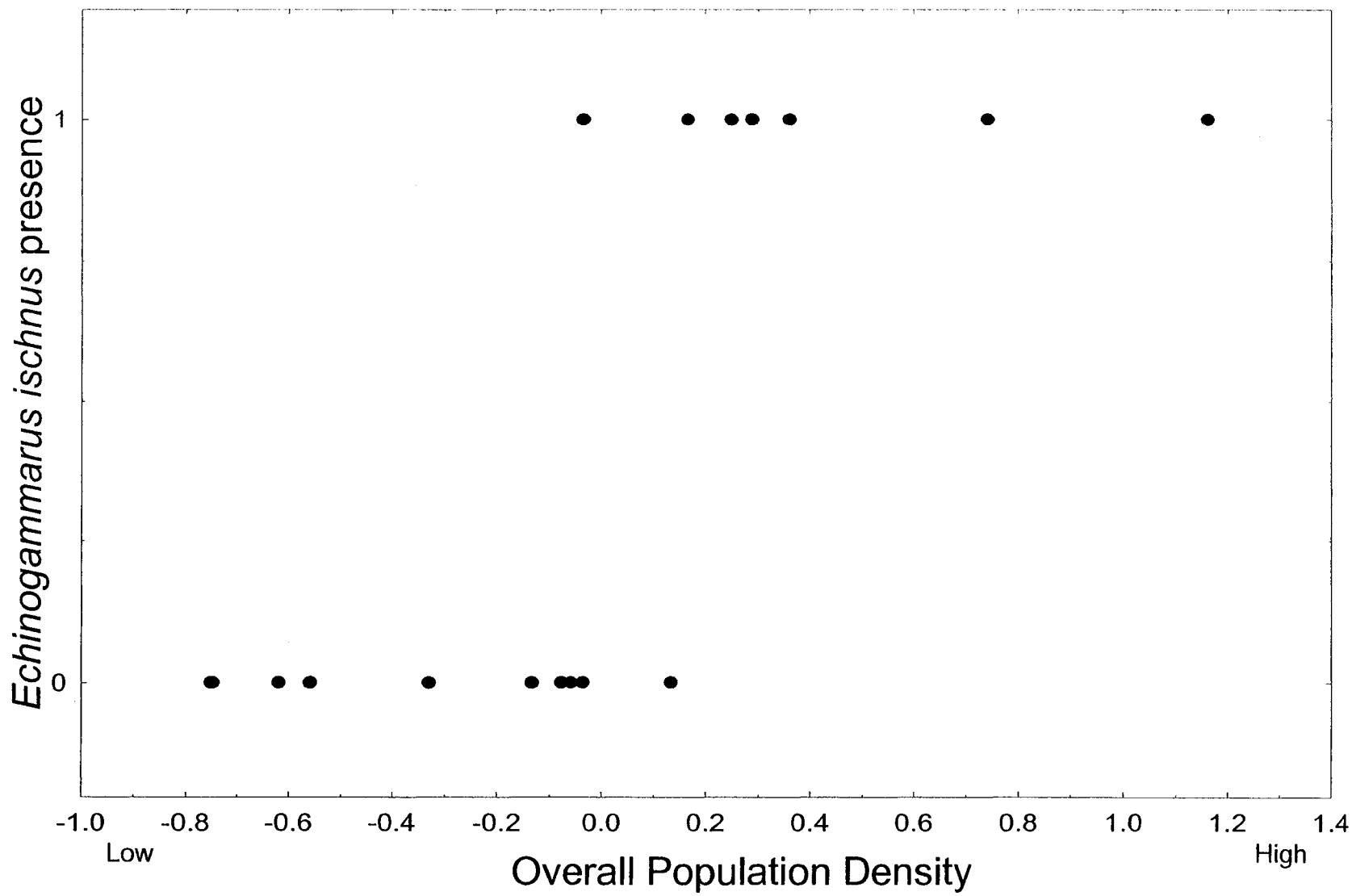

Figure 1: Hypothetical scatterplot of *Echinogammarus ischnus* presence/absence at sites influenced by varying degrees of overall population density, as predicted by Elton's hypothesis.

the threshold stressor score at which *E. ischnus* is more than 50% likely to occur. It is at this point that the stressor purportedly affects the species richness of the system and consequently facilitates establishment of the invader. This value can be determined for each of the 6 stressor variables being examined.

Odds ratios are given in logistic regression analyses of this study. The odds ratio is computed as the ratio of the product of the correctly classified cases over the product of the incorrectly classified cases. Odds ratios that are greater than 1.0 indicate that the classification is better than one would expect by pure chance. However, these are *post-hoc* classifications, because the parameters were computed to maximize the probability of observed data. Thus, the predictive capabilities of models generated in the logistic regressions of this study would be weaker when applied to classify new (future) observations.

The presence of *E. ischnus* was compared with that of native gammarids, using frequency analyses (Yates corrected chi-square on presence/absence data) to investigate Baltz and Moyle's hypothesis (1993) of invader establishment at sites with suitable habitat. A significant relationship between occurrence of *G. fasciatus* and *E. ischnus* at the same sites would indicate that the amphipods share habitat preferences. A nonsignificant Chi-square outcome would imply that habitat matching does not occur for *G. fasciatus* and *E. ischnus* in the Great Lakes sites examined. Support for Baltz and Moyle's hypothesis would be achieved if *E. ischnus* was detected wherever *G. fasciatus* was encountered. Baltz and Moyle's hypothesis would be falsified when *E. ischnus* is detected at sites that do not provide "suitable" abiotic conditions (i.e., at sites that do not support *G. fasciatus*).

All analyses were performed using in the Statistica © software package (StatSoft, Inc., 2001), except for runs tests.

A hierarchical approach was taken with statistical analyses to determine if the distribution of *E. ischnus* is associated with specific types of stress. Data were first examined at a Great Lakes basin scale and then on a lake-by-lake and ecosystem type basis. This method was employed to take into account varying

population densities of *E. ischnus* and dispersal trends of invaders in the Great Lakes, since some lakes have a higher propensity for invader establishment (e.g., Lake Erie) than others (e.g., Lake Superior). For this reason, analyses were also performed with Lake Superior data excluded, because the establishment of *E. ischnus* is yet to be documented for this lake and no Lake Superior *E. ischnus* specimens were collected during this study. Lake Superior is argued to support few nonindigenous species for a variety of reasons (reviewed by Grigorovich *et al.*, in review). Some types of ecosystems are also more likely to support *E. ischnus* than others because of inherent accessibility. For example, coastal wetland site types are likely more easily accessible than protected wetlands.

Past studies of *E. ischnus* invasion of the Great Lakes have illustrated the close association between the amphipod and the nonindigenous bivalve, *Dreissena polymorpha* (Dermott *et al.*, 1998; van Overdijk *et al.*, 2003). Both species occupy the same native habitat of the Ponto-Caspian region and it is speculated that the co-evolution of the two species has assisted the establishment of *E. ischnus* (refer to Study Species section of Chapter 1). *Echinogammarus ischnus* is also associated with *Dreissena bugensis* (Kohn and Waterstraat, 1990) so the distribution of the amphipod may correspond with the distribution of dreissenids. Given this factor in establishment of *E. ischnus*, the presence of dreissenids at sites that supported gammarids was taken into account. The presence of *E. ischnus* was compared with that of dreissenids, using frequency analyses (Yates corrected chi-square on presence/absence data). In turn, the same analysis was performed for *G. fasciatus*

RESULTS

Spatial Distribution

A total of 74 sites distributed across the Great Lakes was sampled during the 2002 sampling season (22 in Lake Superior, 23 in Lake Michigan, 16 in Lake Huron, 11 in Lake Erie, and 2 in Lake Ontario; Figures 2-6; Table 2). *Gammarus fasciatus* was the predominant species of *Gammarus* in samples, although *G. tigrinus, and G. pseudolimnaeus* specimens were also found. The *G. tigrinis* record is a first for the Great Lakes (I. Grigorovich, University of Windsor, Windsor, Ontario, pers. comm.).

Gammarus fasciatus was found at 39 of the 74 sampled sites (52.7%) (Fig. 2-6; Table 1, 2). *Echinogammarus ischnus* was found at 8 of the 74 sampled sites (10.8%) (Fig. 3-6; Table 1, 2), which comprises 20.5% of the *G. fasciatus* sites. *Echinogammarus ischnus* is over-represented in Lake Huron, Lake Erie, and Lake Ontario, whereas it is under-represented in Lake Superior and Lake Michigan (Table 2). *Gammarus fasciatus* is over-represented in Lake Huron (Table 2). A highly significant association was detected between the presence or absence of *E. ischnus* and that of *G. fasciatus* (Yates corrected $\chi^2 = 7.94$, d. f. = 1, $p < 0.02$, n = 74) (Table 3).

These results do not take into account the fact that *E.* ischnus may not yet have dispersed to some areas, such as Lake Superior. *Echinogammarus ischnus* has been reported from the Thunder Bay, Ontario, Canada area of Lake Superior (Grigorovich *et al.*, in review) but it is unknown whether it has become established in this lake (i.e., maintaining a reproducing population). Given that Lake Superior does not provide optimum habitat for *G. fasciatus* or *E. ischnus*, it is possible that *E. ischnus* may not establish in this lake (see Discussion section). Consequently, the analyses were repeated excluding the Lake Superior sites. *Echinogammarus ischnus* was found at 8 of 52 sampled sites (15%) when Lake Superior sites were excluded from analyses (Fig. 3-6; Table 2). *Gammarus fasciatus* was found at 30 sites (58%) (Fig. 3-6; Table 2), and *E. ischnus* was found at 27% of these sites. A significant association was detected between the

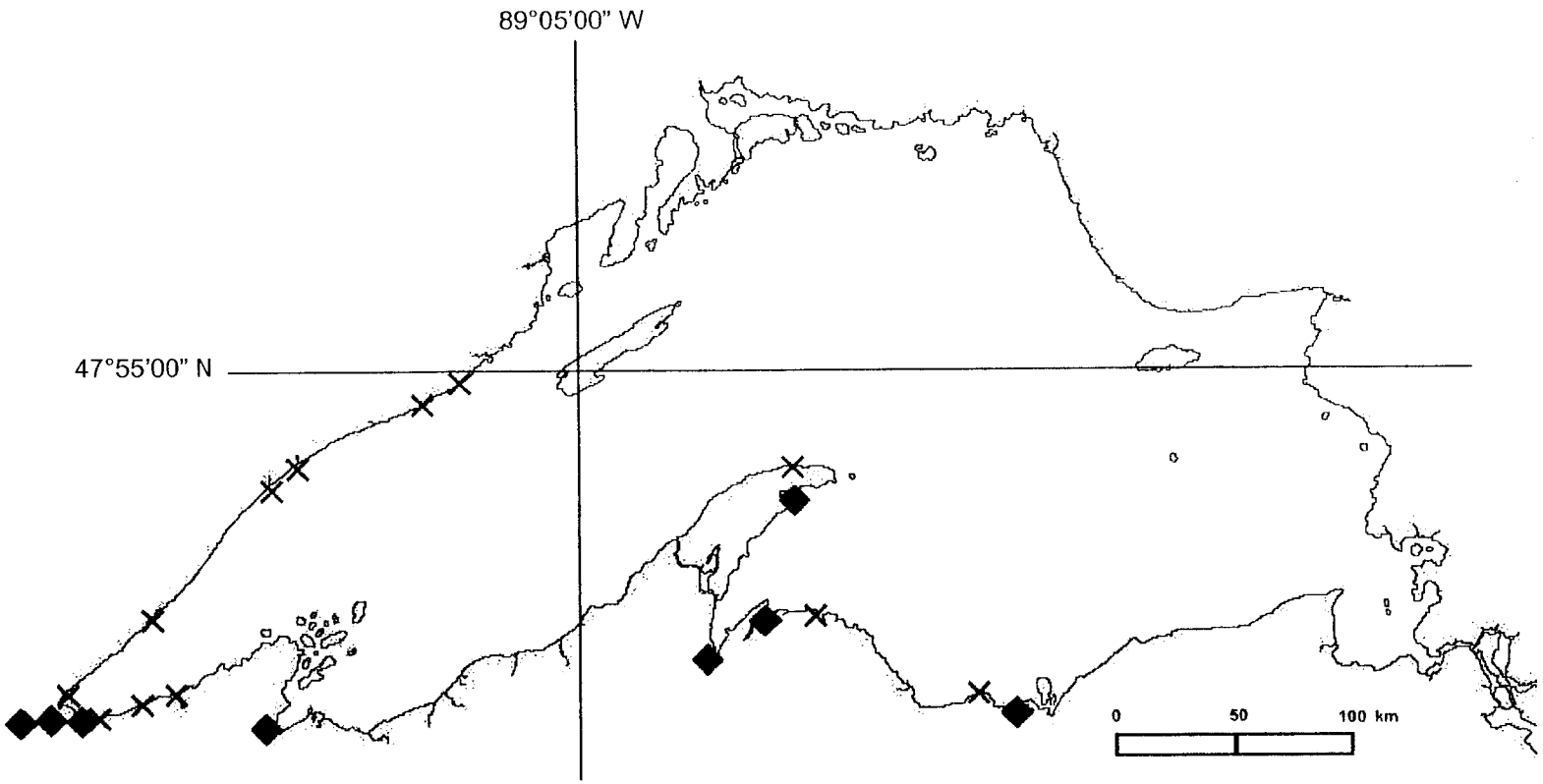

Figure 2: Distribution of sites sampled from Lake Superior. ◆ = *Gammarus fasciatus* present; × = *Gammarus fasciatus* and *Echinogammarus ischnus* absent.

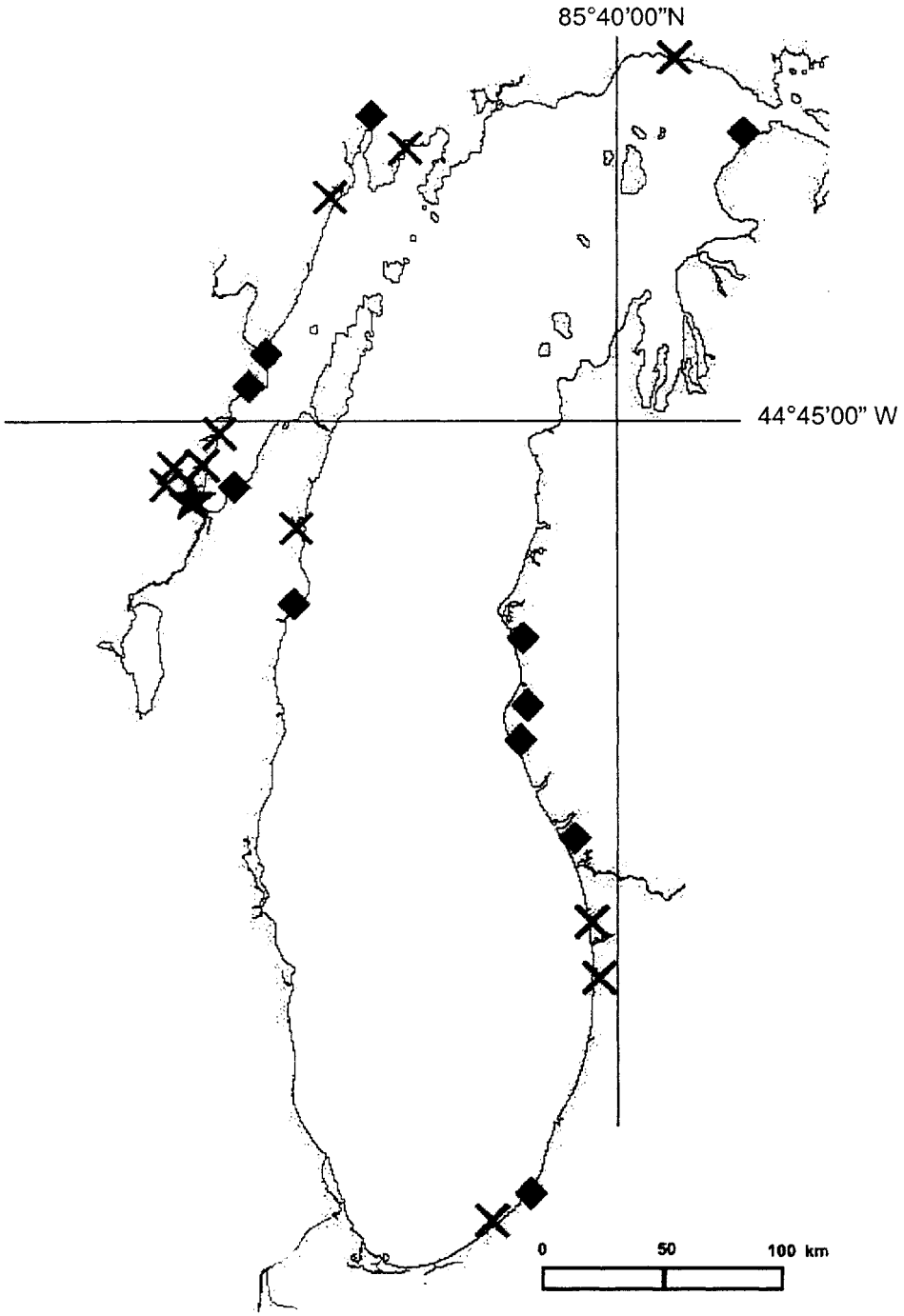

Figure 3: Distribution of sites sampled from Lake Michigan.
★ = *Echinogammarus ischnus* and *Gammarus fasciatus* present;
◆ = *Gammarus fasciatus* present; × = *Gammarus fasciatus* and *Echinogammarus ischnus* absent.

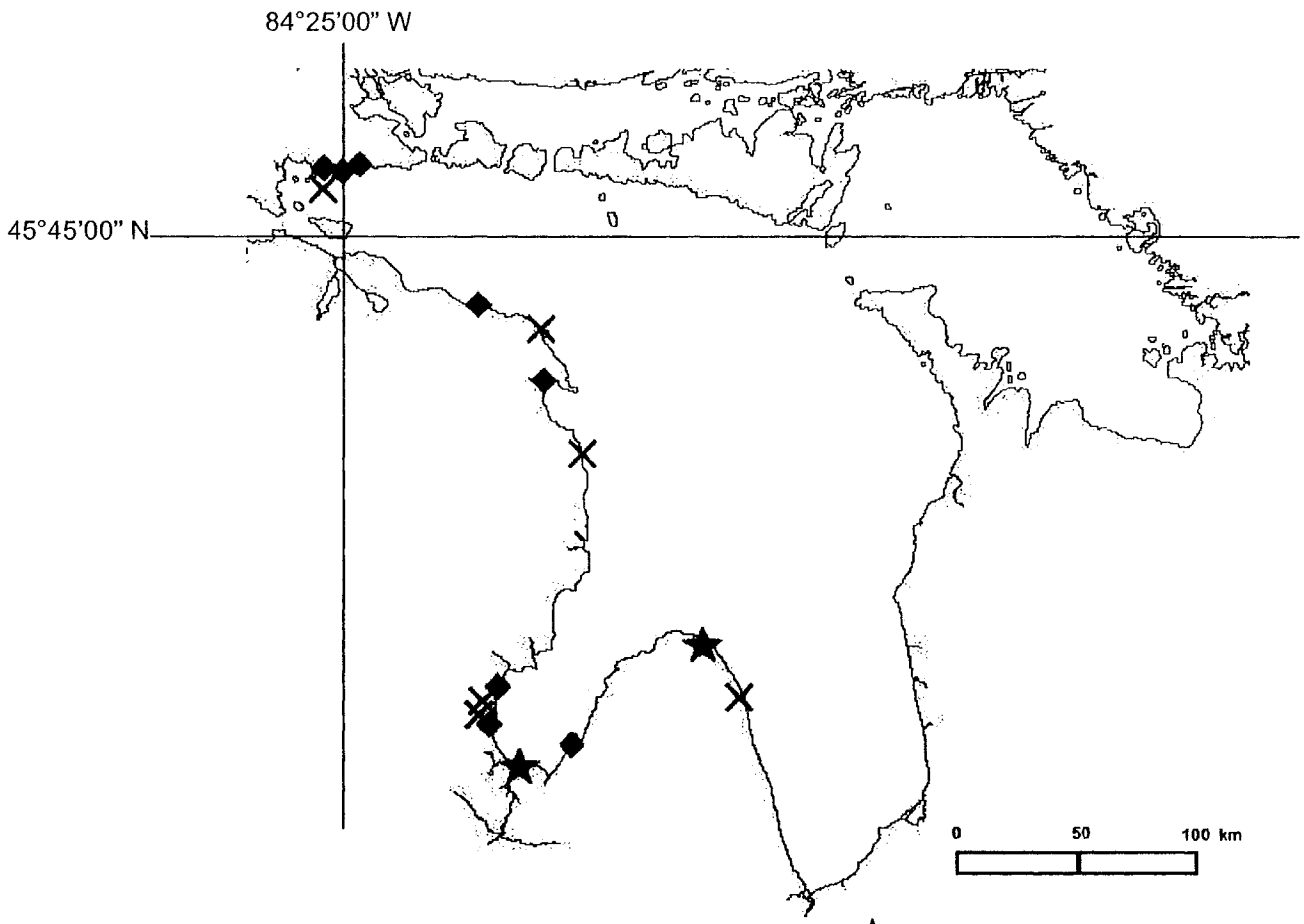

Figure 4: Distribution of sites sampled in Lake Huron. ★ = *Echinogammarus ischnus* and *Gammarus fasciatus* present; ◆ = *Gammarus fasciatus* present; × = *Gammarus fasciatus* and *Echinogammarus ischnus* absent.

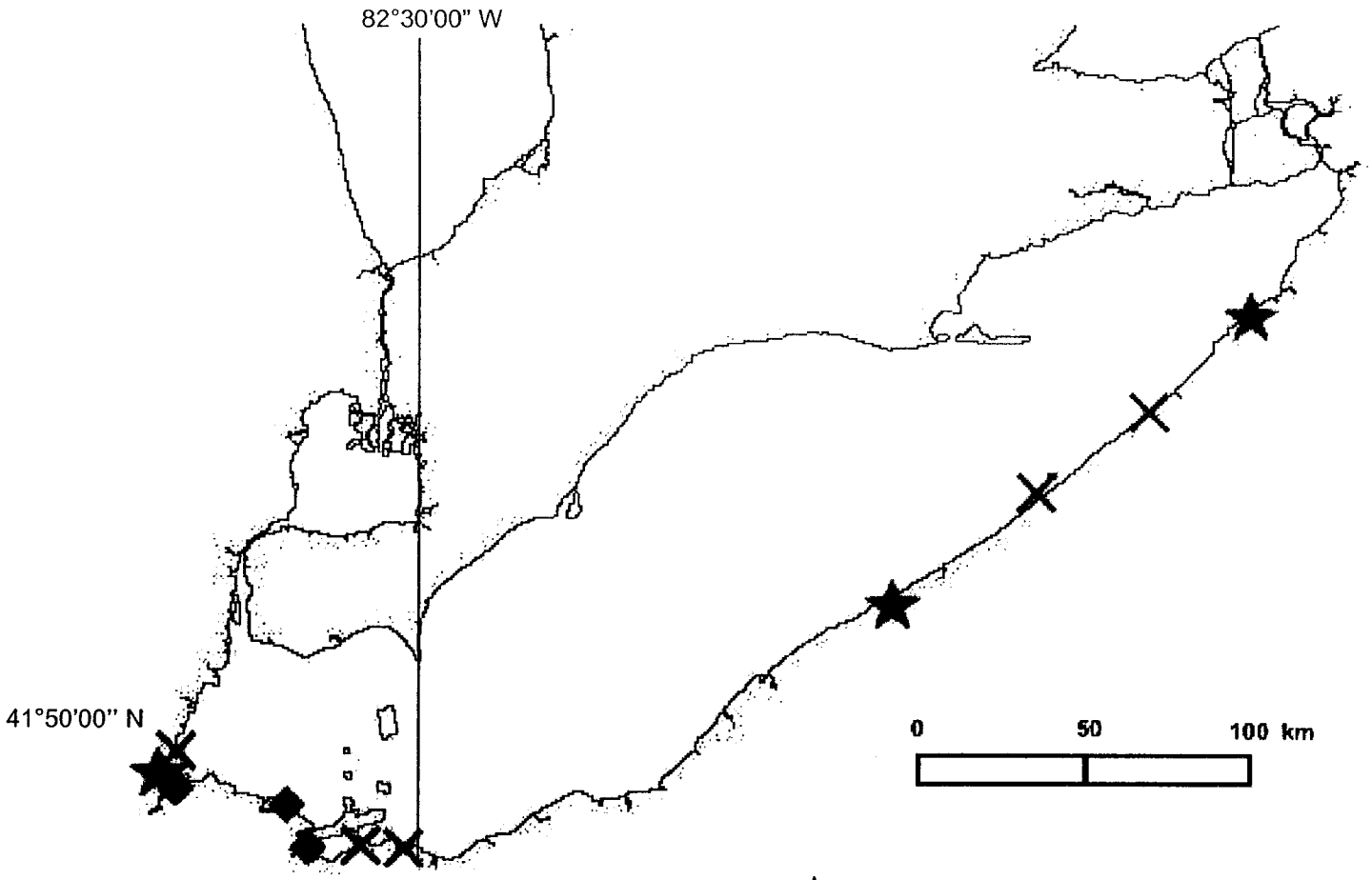

Figure 5: Distribution of sites sampled in Lake Erie. ★ = *Echinogammarus ischnus* and *Gammarus fasciatus* present; ◆ = *Gammarus fasciatus* present; × = *Gammarus fasciatus* and *Echinogammarus ischnus* absent.

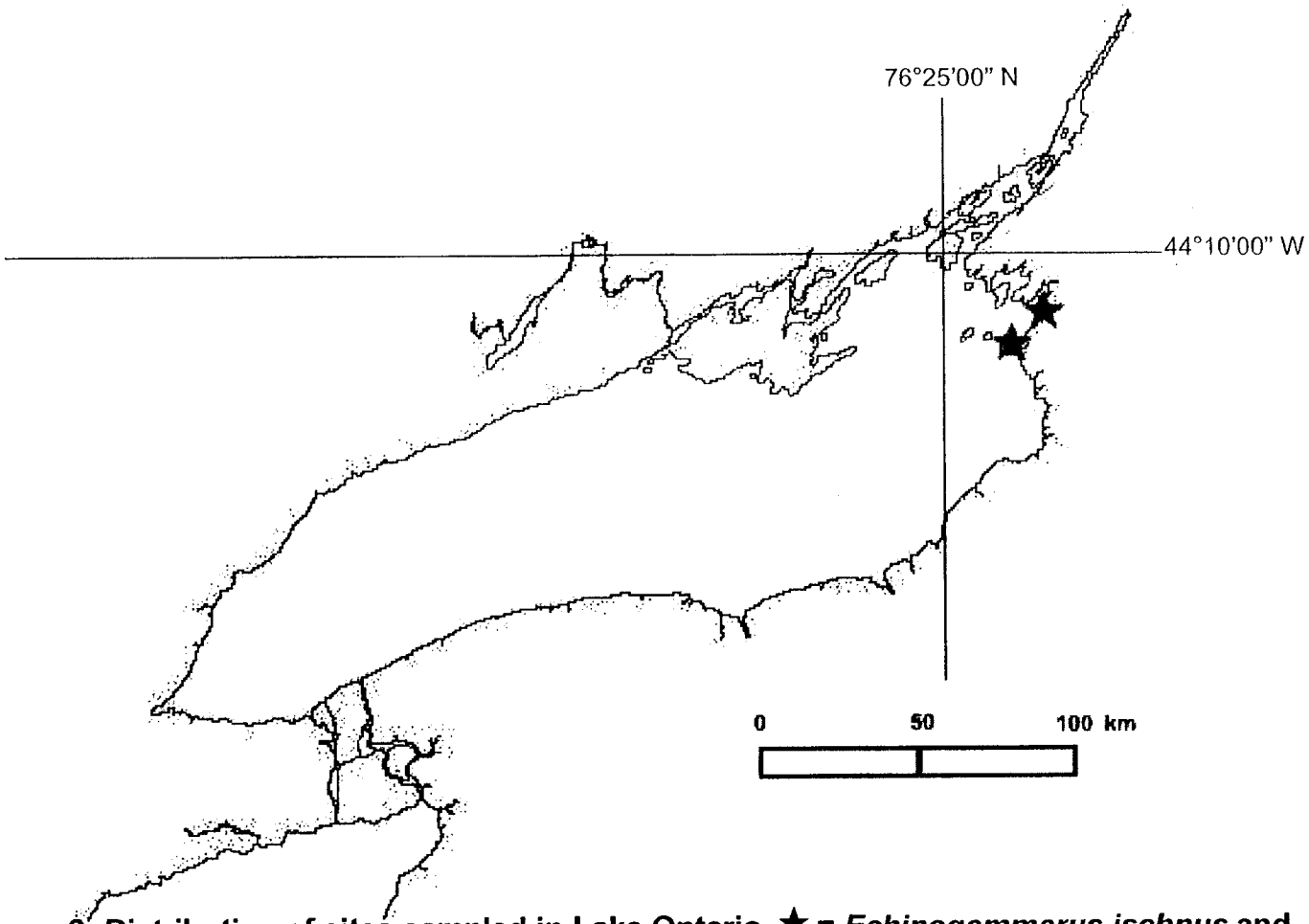

Figure 6: Distribution of sites sampled in Lake Ontario. ★ = *Echinogammarus ischnus* and *Gammarus fasciatus* present.

Table 2: Distribution of *Echinogammarus ischnus*, *Gammarus fasciatus*, and total sites sampled in the Great Lakes. Dates of the first record of *Echinogammarus ischnus* in each Great Lake are listed.

Number of Sites Sampled	**Superior** (2002)	**Michigan** (1998)	**Huron** (1996)	**Erie** (1993)	**Ontario** (1996)	**Taxa Total**
Echinogammarus ischnus	0	1	2	3	2	**8**
Gammarus fasciatus	9	12	10	6	2	**39**
Lake Total	22	23	16	11	2	**74**

Table 3: A 2 x 2 contingency table testing the independence of occurrence of *Echinogammarus ischnus* and *Gammarus fasciatus* at all sampled sites. χ^2 (Yates corrected) = 6.06 ($p < 0.02$).

	***G. fasciatus* present**	***G. fasciatus* absent**	**Row Totals**
***E. ischnus* present**	8 (11%)	0 (0%)	8 (11%)
***E. ischnus* absent**	31 (42%)	35 (47%)	66 (89%)
Column Totals	39 (53%)	35 (47%)	74
χ^2 (d.f. = 1)	8.05	$p < 0.005$	
Yates corrected χ^2 (d.f. = 1)	6.06	$p < 0.020$	

presence of *E. ischnus* and that of *G. fasciatus* (Yates corrected $\chi^2 = 5.04$, d. f. = 1, $p < 0.05$, n = 52) (Table 4).

Spatial Distribution by Lake

A single site was occupied by *Echinogammarus ischnus* of 23 sites sampled (4%) from Lake Michigan (Figure 3; Table 2). *Gammarus fasciatus* was found at 12 sites (52%) and *E. ischnus* was found at 8% of these sites (Table 2).

Echinogammarus ischnus was found at 2 of 16 (12.5%) sites sampled in Lake Huron (Figure 4). *Gammarus fasciatus* was found at 10 sites (62.5%) and *E. ischnus* was found at 20% of these sites (Table 2).

Lake Erie sampling consisted of 11 sites (Figure 5). *Gammarus fasciatus* was found at 6 sites (54.55%) and *E. ischnus* was found at 50% of these sites (27% of Lake Erie sites) (Table 2).

Only 2 sites were sampled in Lake Ontario and both were found to support *E. ischnus*, as well as *G. fasciatus* (Figure 6; Table 2).

Spatial Distribution by Geomorphic Type

The largest proportion of sites was classified as high-energy (25/74). *Echinogammarus ischnus* was found at 4 of 25 sampled high-energy sites (16%). *Gammarus fasciatus* was found at 9 sites (36%) and *E. ischnus* was found at 44% of these sites.

When Lake Superior sites were excluded from the analyses, *E. ischnus* was found at 4 of 14 (29%) high-energy sites that were sampled. *Gammarus fasciatus* was found at 8 sites (57%) and *E. ischnus* was found at 50% of these sites.

Sites characterized as coastal wetland encompassed 16 sampled sites. *Gammarus fasciatus* was found at 8 of these sites (50%), while *E. ischnus* was found at 3 sites (19% of all coastal wetland sites and 38% of coastal wetland sites that supported *G. fasciatus*). No coastal wetland sites were sampled from Lake Superior.

Table 4: A 2 x 2 contingency table testing the independence of occurrence of *Echinogammarus ischnus* and *Gammarus fasciatus* at sampled sites, excluding Lake Superior. χ^2 (Yates corrected) = 5.04 ($p < 0.05$).

	***G. fasciatus* present**	***G. fasciatus* absent**	**Row Totals**
***E. ischnus* present**	8 (15%)	0 (0%)	8 (15%)
***E. ischnus* absent**	22 (42%)	22 (42%)	44 (85%)
Column Totals	30 (58%)	22 (42%)	52
χ^2 (d.f. = 1)	6.93	$p < 0.010$	
Yates corrected χ^2 (d.f. = 1)	5.04	$p < 0.050$	

E. ischnus was found at 1 of 6 embayment sites (17%). *Gammarus fasciatus* was found at 5 sites (83%) and *E. ischnus* was found at 20% of these sites.

When Lake Superior sites were excluded from the analyses, *E. ischnus* was found at 1 of 5 sampled embayment sites (20%). *Gammarus fasciatus* was found at 4 sites (80%) and *E. ischnus* was found at 20% of these sites.

No *E. ischnus* specimens were found at the 21 river-influenced wetland or the 6 protected wetland sites that were sampled. *Gammarus fasciatus* was found at 14 of the river-influenced sites (67%) and at 3 of the protected wetland sites (50%).

Further analyses were not performed on Lake Ontario (0's = 2, 1's = 2), river-influenced wetland (0's = 14, 1's = 0), and protected wetland (0's = 3, 1's = 0) sites because these geomorphic types had either too few data to conduct meaningful tests or *E. ischnus* was completely absent.

Spatial Distribution with respect to *Dreissena* spp.

A highly significant association was detected between the occurrence of *E. ischnus* and that of *Dreissena* spp. (Yates corrected $\chi^2 = 16.45$, d. f. = 1, $p < 0.0005$, n = 74) (Table 5). *Echinogammarus ischnus* was found at 8 of the 74 sampled sites (11%) (Fig. 3-6; Table 1-2). *Dreissena* spp. were found at 23 sites (31%).

A highly significant association was also detected between the presence or absence of *G. fasciatus* and that of *Dreissena* spp. (Yates corrected $\chi^2 = 7.32$, d. f. = 1, $p < 0.01$, n = 74) (Table 6). *Gammarus fasciatus* was found at 39 of the 74 sampled sites (53%) (Fig. 2-6).

Distribution of *Echinogammarus ischnus* along Stressor Gradients

Great Lakes Basin

Echinogammarus ischnus distribution at all sites that supported *G. fasciatus* was independent of the degree of stress for 5 of the 6 variables evaluated. The critical number of runs for the one-tailed test is ≤ 8 ($p < 0.05$,

Table 5: A 2 x 2 contingency table testing the independence of occurrence of *Echinogammarus ischnus* and *Dreissena* spp. at all sampled sites. χ^2 (Yates corrected) = 16.45 ($p < 0.0005$).

	***Dreissena* spp. present**	***Dreissena* spp. absent**	**Row Totals**
***E. ischnus* present**	8 (11%)	0 (0%)	8 (11%)
***E. ischnus* absent**	15 (20%)	51 (69%)	66 (89%)
Column Totals	23 (31%)	51 (69%)	74
χ^2 (d.f. = 1)	19.89	$p < 0.0001$	
Yates corrected χ^2 (d.f. = 1)	16.45	$p < 0.0005$	

Table 6: A 2 x 2 contingency table testing the independence of occurrence of *Gammarus fasciatus* and *Dreissena* spp. at all sampled sites. χ^2 (Yates corrected) = 7.32 ($p < 0.01$).

	***Dreissena* spp. present**	***Dreissena* spp. absent**	**Row Totals**
***G. fasciatus* present**	18 (24%)	21 (28%)	39 (53%)
***G. fasciatus* absent**	5 (7%)	30 (41%)	35 (47%)
Column Totals	23 (31%)	51 (69%)	74
χ^2 (d.f. = 1)	8.75	$p < 0.005$	
Yates corrected χ^2 (d.f. = 1)	7.32	$p < 0.010$	

n = 39) for rejection of the hypothesis of random arrangement of the dichotomous data. The runs test for the Overall Pollution Loading stressor variable identified nonrandom distribution of *E. ischnus* at Great Lakes sites, with 8 runs. The number of runs was > 10 for all other stressor variables. Therefore, the null hypothesis of random arrangement of these data could not be rejected for the 5 other stressor variables. Similar results were obtained when Lake Superior sites were excluded from analyses. The association of *E. ischnus* with Overall Pollution Loading was not affected by the exclusion of Lake Superior sites, as the scatterplot revealed 8 runs. Scatterplots for all other stressor variables without Lake Superior sites gave > 10 runs.

None of the logistic regression plots showed a significant relationship between *E. ischnus* presence/absence with the principal component scores of the stressor variables (Table 7). The negative coefficient values for all stressor variables indicate that for every unit increase in PC score, the log odds of *E. ischnus* presence at a site decreases. Thus, the probability of finding *E. ischnus* apparently decreased along gradients of increasing stress. None of the p-levels associated with the Chi-square were significant. Thus, the estimated models did not yield a better fit to the data than the null models (where slope parameters are zero).

Excluding Lake Superior sites from analyses did not improve the fit of *E. ischnus* occurrence to a logistic curve. Chi-square p-values were not significant so the estimated models did describe the data better than the null models, and the regression parameters were not statistically significant (Table 8). However, unlike the former 'whole basin' logistic regression analyses, the coefficient values for the principal component scores of the stressor variables were positive. This indicates that for every unit increase in PC score, the log odds of *E. ischnus* presence at a site increases. Thus, the probability of finding *E. ischnus* increases as well.

Table 7: Critical values from runs tests and logistic regression analyses for sites at all sampled lakes (n = 39). Bolded item(s) exhibit significant association(s) with *Echinogammarus ischnus* distribution.

	Coefficient	**Intercept**	χ^2 **(1)**	**p**	**Odds ratio (unit change)**	**Number of Runs**
Nutrient Input	-0.427931	-1.30376	0.63441	0.42575	0.651856	12
Total N + P Load	-1.23645	-1.33631	0.69906	0.40311	0.29041	17
Agricultural Stress	-0.605731	-1.30391	0.35445	0.55161	0.545675	14
Population Density	-0.798866	-1.34421	0.65421	0.41862	0.449839	11
Pollution Loading	-0.847876	-1.31315	1.1635	0.28075	0.428324	**8**
Relative Maximum	-0.082123	-1.30038	0.01177	0.91359	0.921158	13

Table 8: Critical values from runs tests and logistic regression analyses for sites at sampled lakes, excluding Lake Superior sites (n = 30). Bolded item(s) exhibit significant association(s) with *Echinogammarus ischnus* distribution.

	Coefficient	**Intercept**	**χ^2 (1)**	**p**	**Odds ratio (unit change)**	**Number of Runs**
Nutrient Input	0.92674	0.775467	2.6835	0.10140	2.52626	12
Total N + P Load	1.263268	0.979076	0.82428	0.36394	3.536962	15
Agricultural Stress	1.223119	0.857304	1.2699	0.25979	3.397771	14
Population Density	0.926589	0.986949	0.84380	0.35832	2.525879	11
Pollution Loading	0.934908	0.946526	1.4194	0.23350	2.546980	**8**
Relative Maximum	0.638190	0.547009	0.59577	0.44020	1.893051	13

Lake Michigan

The number of runs formed by most of the stressor variables (Overall Nutrient Input, N + P Load, Agricultural Stress, and Relative Maximum PC Score) for Lake Michigan sites did not support Elton's hypothesis (critical number of runs > 2, $p < 0.05$, $n_1 = 1$, $n_2 = 11$). The two remaining stressor variables, Overall Population Density and Overall Pollution Loading, suggested the occurrence of nonrandom distributions, with 2 runs displayed in their respective scatterplots. The range of the Overall Population Density PC scores that span the point of inflection of the logistic regression line is 0.742 to 1.161, validating Elton's hypothesis. Conversely, the Overall Pollution Loading stressor variable shows the presence of *E. ischnus* at lower PC scores and its absence at higher PC scores, contradicting Elton's hypothesis. The range of the point of inflection spans from -0.336 to -0.312. These analyses are based on the presence of *E. ischnus* at a single site bringing uncertainty to the validity to these results.

At Lake Michigan sites, Overall Population Density and Overall Pollution Loading showed significant relationships between respective principal component scores and *E. ischnus* presence/absence (Overall Population Density $\chi^2 = 6.8841$, d. f. = 1, $p = 0.00870$, $n = 12$; Overall Pollution Loading $\chi^2 = 6.8330$, d. f. = 1, $p = 0.00895$, $n = 12$; Table 9), although they are not significant at the 0.0083 level (Fig. 7). The p-values associated with the Chi-square tests suggest that there is a significant difference between the estimated models and the null model for the Overall Population Density and Overall Pollution Loading variables. However, the logistic regression curves are very different from each other, with Overall Population Density purportedly supporting Elton's hypothesis, while Overall Pollution Loading contradicts Elton's hypothesis. The logistic regression for Overall Population Density gave a coefficient of 142, implying that for every unit increase in PC score, the log odds of finding *E. ischnus* at that site increases by 142, on average. Alternatively, the logistic regression for Overall Pollution Loading gives a coefficient of -404, meaning that for each unit increase in PC score, the log odds of finding *E. ischnus* at that site decreases by 404, on average. Results were nonsignificant for the other three stressor variables.

Table 9: Critical values from runs tests and logistic regression analyses for Lake Michigan sampled sites (n = 12). Bolded item(s) exhibit significant association(s) with *Echinogammarus ischnus* distribution.

	Coefficient	**Intercept**	**χ^2 (1)**	**p**	**Odds ratio (unit change)**	**Number of Runs**
Nutrient Input	2.525	-5.24701	2.0718	0.15005	12.495	3
N + P Load	-2.87575	-2.33843	0.48439	0.48645	0.05637	3
Agricultural Stress	1.488520	-3.10440	0.37840	0.53847	4.430534	3
Population Density	**142.0440**	**-127.677**	**6.8841**	**0.00870**		**2**
Pollution Loading	-403.694	-130.537	6.8330	0.00895	0.000	**2**
Relative Maximum	2.9934	-6.17160	1.7427	0.18681	19.9531	3

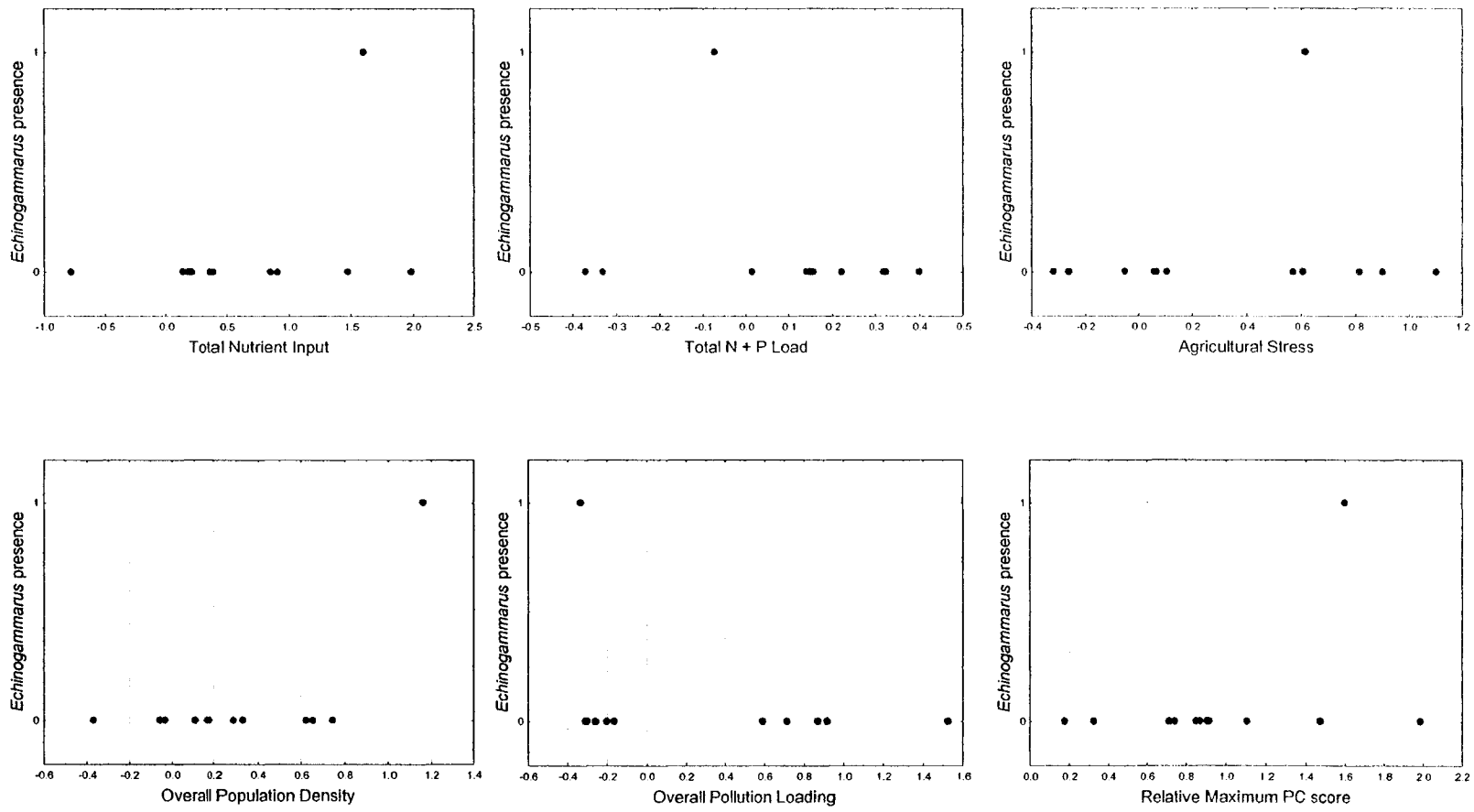

Figure 7: Scatterplots of *Echinogammarus ischnus* presence/absence at sites sampled from Lake Michigan, influenced by varying degrees of stressor variables.

The data for Overall Population Density and Overall Pollution Loading appear to indicate significant associations with *E. ischnus* presence/absence but there are so few data points (only a single site documents *E. ischnus* presence in Lake Michigan) that the patterns could have easily arisen by chance (probability = 1/12 = 0.08). In addition, the validity of the significance of nonrandomness and associations of *E. ischnus* distribution with stressor variables is questionable given that none of the analyses were significant at the Bonferroni corrected 0.0083 level to verify Elton's hypothesis.

Lake Huron

Scatterplots of *E. ischnus* presence/absence at Lake Huron sites revealed > 2 runs, thus contradicting the expectations of Elton's hypothesis. The critical number of runs for rejection of random distribution is 2 runs ($p < 0.05$, $n_1 = 2$, $n_2 = 8$).

The logistic regression curves did not fit well with the observed data. The probability of finding *E. ischnus* at sites sampled from Lake Huron was independent of principal component scores for all of the stressor variables (Table 10). *E. ischnus* was no more likely to occur at stressed than at unstressed sites. There may be too few data points for Lake Huron sites to permit a proper comparison of *E. ischnus* presence/absence with stressor variables. Intuitively, this seems to be a small sample of *E. ischnus* sites, however, the probability of finding *E. ischnus* at the 2 most extreme sites (sites with the highest PC score for a stressor variable) would be 0.01 (=1/10x1/9).

Lake Erie

None of the plots of *Echinogammarus* distribution in Lake Erie resembled the pattern predicted by Elton's hypothesis (Fig. 8). The scatterplot of *E. ischnus* presence/absence at sites influenced by varying degrees of Overall Pollution Loading displayed 2 runs, implying a nonrandom distribution. However, the distribution of PC scores indicates that the presence of *E. ischnus* occurred at lower PC scores, while *E. ischnus* were consistently absent at higher PC scores,

Table 10: Critical values from runs tests and logistic regression analyses for Lake Huron sampled sites (n = 10).

	Coefficient	**Intercept**	χ^2 **(1)**	**p**	**Odds ratio (unit change)**	**Number of Runs**
Nutrient Input	-0.098808	-1.35106	0.00744	0.93125	0.905917	5
Total N + P Load	-1.48807	-1.56824	0.34281	0.55821	0.22581	5
Agricultural Stress	-2.44114	-1.52833	1.0549	0.30438	0.08706	4
Population Density	-3.27770	-2.05810	1.8098	0.17854	0.03772	4
Pollution Loading	1.645460	-1.39889	0.74551	0.38791	5.183392	3
Relative Maximum	0.263744	-1.56166	0.3472	0.85218	1.301794	5

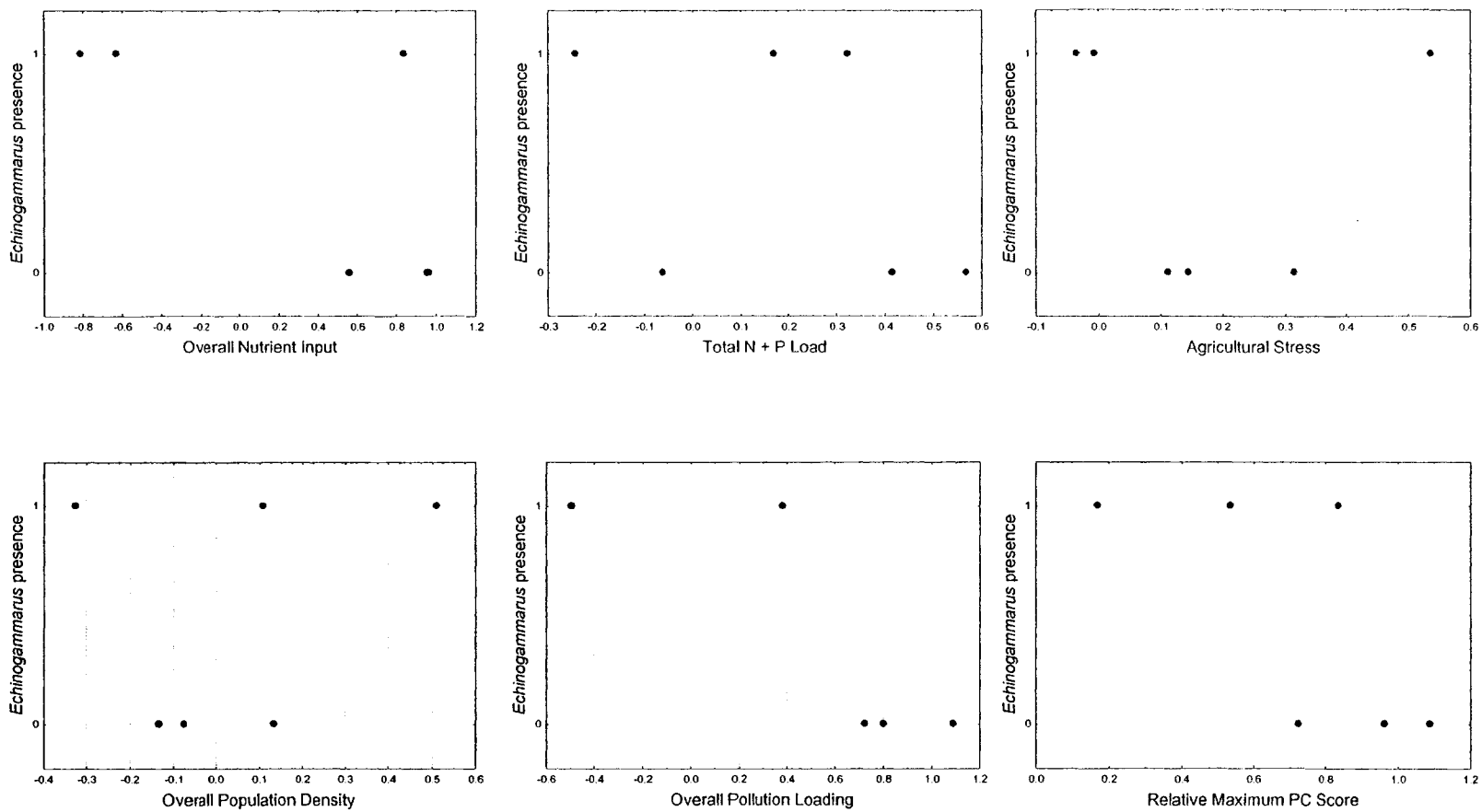

Figure 8: Scatterplots of *Echinogammarus ischnus* presence/absence at sites sampled from Lake Erie, influenced by varying degrees of stressor variables.

contradicting Elton's hypothesis. The range of the point of inflection spans from 0.382 to 0.722. All other scatterplots used in analyses displayed > 2 runs, and thus, did not resemble that expected by Elton's hypothesis.

There was a significant relationship between *E. ischnus* presence/absence and Overall Pollution Loading at the Bonferroni corrected level ($\chi^2 = 8.318$, d. f. = 1, $p < 0.0040$, n = 6; Table 11). The coefficient for Overall Pollution Loading indicates that the log odds of finding *E. ischnus* at a site increases by 70 with every unit increase in PC score. The data for Overall Pollution Loading appear to correspond with the expectations of Elton's hypothesis but there are so few data points (only 3 sites document *E. ischnus* presence) that the patterns could have arisen by chance (probability = 1/6 x 1/5 x 1/4 = 0.008).

High Energy

Data incorporating high-energy sites from all of the Great Lakes produced scatterplots that were not consistent with Elton's hypothesis. There were > 2 runs for all stressor variables (critical number of runs = 2, $p < 0.05$, $n_1 = 4$, $n_2 = 5$). However, the exclusion of Lake Superior high-energy sites produced a scatterplot with 2 runs for the Relative Maximum PC Score variable (critical number of runs for embayment sites without Lake Superior sites is 2, $p < 0.05$, $n_1 = 4$, $n_2 = 4$).

Logistic regression curves did not fit well with data. None of the 6 stressors were good predictors of *E. ischnus* distribution at high-energy sites from all of the Great Lakes considered together (all p-values > 0.15; Table 12).

When Lake Superior sites were excluded from analyses (Fig. 9), the Overall Nutrient Input stressor variable was significantly related to *E. ischnus* presence ($\chi^2 = 3.9423$, d. f. = 1, $p < 0.05$, n = 8), but it was not significant at the 0.0083 level (Table 13). A relatively high principal component score of Overall Nutrient Input was significantly related to *E. ischnus* presence at sites. The coefficient of Overall Nutrient Input implied that the log odds of finding *E. ischnus* at a site increases by 2.2 with every unit increase in PC score. The estimated

Table 11: Critical values from runs tests and logistic regression analyses for Lake Erie sampled sites (n = 6). Bolded item(s) exhibit significant association(s) with *Echinogammarus ischnus* distribution.

	Coefficient	**Intercept**	**χ^2 (1)**	**p**	**Odds ratio (unit change)**	**Number of Runs**
Nutrient Input	3.0928	-1.46799	3.4632	0.06276	22.0385	4
Total N + P Load	3.24656	-0.645610	1.0310	0.30992	25.70167	4
Agricultural Stress	0.642291	-0.113555	0.02372	0.87760	1.900830	3
Population Density	-1.87799	0.061906	0.33863	0.56063	0.15290	5
Pollution Loading	**70.04194**	**-39.1170**	**8.3177**	**0.00393**		**2**
Relative Maximum	9.118	-6.94754	3.7263	0.05357	9114.592	4

Table 12: Critical values from runs tests and logistic regression analyses for all high-energy sampled sites (n = 9).

	Coefficient	Intercept	χ^2 (1)	p	Odds ratio (unit change)	Number of Runs
Nutrient Input	-0.995112	0.145149	1.6260	0.20226	0.369682	6
Total N + P Load	0.734582	-0.179657	0.07937	0.77815	2.084611	5
Agricultural Stress	-1.39437	-0.029548	1.0948	0.29541	0.24799	4
Population Density	-1.57576	-0.135913	1.1029	0.29364	0.20685	8
Pollution Loading	-1.69737	-0.315753	1.9164	0.16626	0.18316	4
Relative Maximum	-2.00409	1.303678	2.0578	0.15144	0.13478	3

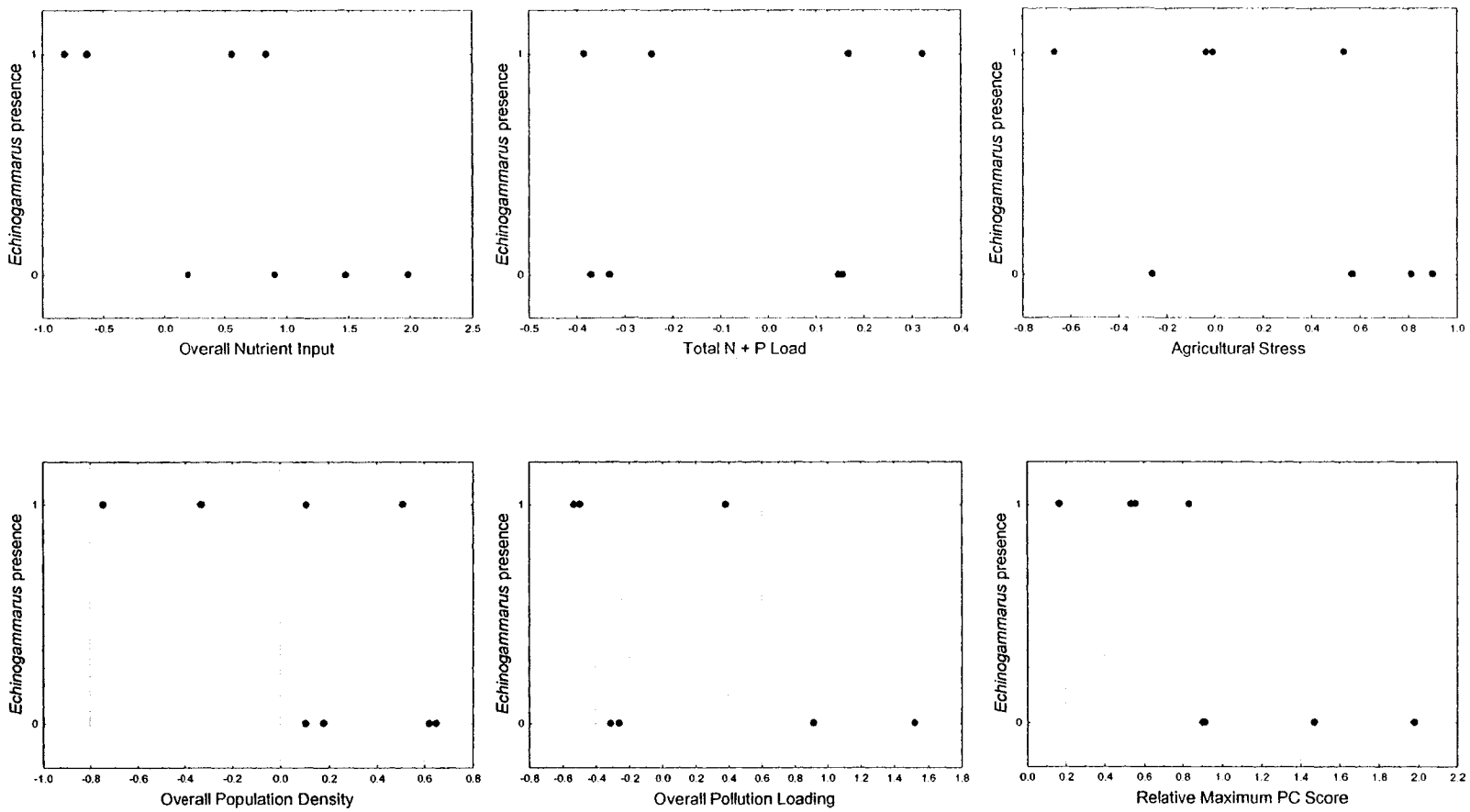

Figure 9: Scatterplots of *Echinogammarus ischnus* presence/absence at high-energy sites, excluding Lake Superior sites, influenced by varying degrees of the stressor variables.

Table 13: Critical values from runs tests and logistic regression analyses for high-energy sampled sites, excluding Lake Superior sites (n = 8). Bolded items exhibit significant associations with *Echinogammarus ischnus* distribution.

	Coefficient	Intercept	χ^2 (1)	p	Odds ratio (unit change)	Number of Runs
Nutrient Input	**2.1956**	**-1.30626**	**3.9423**	**0.04710**	**8.9850**	**4**
Total N + P Load	-0.878214	-0.059296	0.11416	0.73546	0.415524	5
Agricultural Stress	2.46983	-0.604904	2.4387	0.11839	11.82039	4
Population Density	3.4993	-0.613846	2.9044	0.08835	33.0930	6
Pollution Loading	1.93264	-0.020299	2.4781	0.11546	6.90771	4
Relative Maximum	**32.29865**	**-27.0026**	**9.3829**	**0.00219**		**2**

relative odds of finding *E. ischnus* in a non-Lake Superior high-energy site was 9.0 with a one-unit increase in PC score of Overall Nutrient Input. The Relative Maximum PC Score of stressor variables also showed a significant relationship with *E. ischnus* presence at the 0.0083 level ($\chi^2 = 9.38$, d. f. = 1, $p < 0.0022$, n = 8). The Relative Maximum PC Score coefficient implies that the log odds of finding *E. ischnus* at a site increases by 32 with every unit increase in PC score.

Coastal Wetlands

Runs tests for coastal wetland sites did not demonstrate that *E. ischnus* was absent at sites with lower PC scores of stressors and present at sites with higher PC scores. All scatterplots for stressor variables produced > 3 runs (critical number of runs = 2, $p < 0.05$, $n_1 = 3$, $n_2 = 5$).

The logistic regression curves did not fit well to observed data. Chi-square p-values were all > 0.4 (Table 14). Thus, principal component scores of stressor variables were not able to predict the probability of finding *E. ischnus* at coastal wetland sites.

Embayments

The runs test for Overall Nutrient Input gave a nonrandom distribution (2 runs). This result does not verify Elton's hypothesis, as *E. ischnus* occurred at sites with lower PC scores but was absent at sites with higher PC scores.

Principal component score of Overall Nutrient Input exhibited a significant relationship with *E. ischnus* presence ($\chi^2 = 5.00$, d. f. = 1, $p = 0.02530$, n = 5), although the relationship is not significant at the 0.0083 level (Table 15). The coefficient implies that the log odds of finding *E. ischnus* at a site decreases by 173 with every unit increase in PC score.

When Lake Superior sites were excluded, Overall Nutrient Input showed a significant relationship with *E. ischnus* presence ($\chi^2 = 4.4987$, d. f. = 1, $p = 0.03393$, n = 4; Table 16), but again was not significant at the 0.0083 level. The coefficient of Overall Nutrient Input indicates that the log odds of finding *E. ischnus* at a site decreases by 151 with every unit increase in PC score.

Table 14: Critical values from runs tests and logistic regression analyses for all coastal wetland sampled sites (n = 8).

	Coefficient	Intercept	χ^2 (1)	p	Odds ratio (unit change)	Number of Runs
Nutrient Input	-0.521349	-0.254985	0.37553	0.54001	0.593719	6
Total N + P Load	2.63033	-0.250005	0.57553	0.44808	13.87834	3
Agricultural Stress	-0.009970	-0.508725	0.00002	0.99628	0.990079	6
Population Density	-0.217774	-0.475308	0.03171	0.85867	0.804307	5
Pollution Loading	1.179590	-0.384414	0.42685	0.51354	3.253041	3
Relative Maximum	-0.243579	-0.304473	0.03990	0.84168	0.783818	6

Table 15: Critical values from runs tests and logistic regression analyses for all embayment sampled sites (n = 5). Bolded item(s) exhibit significant association(s) with *Echinogammarus ischnus* distribution.

	Coefficient	Intercept	χ^2 (1)	p	Odds ratio (unit change)	Number of Runs
Nutrient Input	**-172.809**	**-103.060**	**5.0040**	**0.02530**	**0.000**	**2**
Total N + P Load	-3.27168	-0.857217	0.77544	0.37855	0.03794	3
Agricultural Stress	-7.70252	-1.73726	1.3342	0.24807	0.00045	3
Population Density	-13.4478	-4.59391	1.9609	0.16143	0.0000	3
Pollution Loading	1.86906	-2.09674	0.86152	0.35332	6.48221	3
Relative Maximum	0.355579	-1.61565	0.01965	0.88853	1.427007	3

Table 16: Critical values from runs tests and logistic regression analyses for all embayment sampled sites, excluding Lake Superior sites (n = 4). Bolded item(s) exhibit significant association(s) with *Echinogammarus ischnus* distribution.

	Coefficient	Intercept	χ^2 (1)	p	Odds ratio (unit change)	Number of Runs
Nutrient Input	**-151.291**	**-94.5832**	**4.4987**	**0.03393**	**0.000**	**2**
Total N + P Load	-2.94979	-0.479536	0.86639	0.35196	0.05235	3
Agricultural Stress	-7.41251	-1.69062	0.84035	0.35930	0.00060	3
Population Density	-13.4411	-4.59172	1.4556	0.22764	0.0000	3
Pollution Loading	1.526845	-1.78615	0.51711	0.47208	4.603627	3
Relative Maximum	0.098524	-1.16436	0.00178	0.96634	1.103541	3

The data for Overall Nutrient Input appear to have a significant association with *E. ischnus* distribution, but there are so few data points (*E. ischnus* was present at only a single site) that the patterns could have easily arisen by chance. The probability of finding *E. ischnus* at the single most stressed embayment site is 1/5 = 0.2 (1/4 = 0.25 for embayment sites without Lake Superior sites). Despite this high probability of finding *E. ischnus* at stressed sites by chance, the critical level for rejection at the 0.05 level for all 6 stressor variables is 0.0083 when the Bonferroni correction is applied. Thus, results are nonsignificant at the 0.0083 level and are not consistent with Elton's hypothesis.

DISCUSSION

All 8 of the 2002-sampled sites that supported *Echinogammarus ischnus* also supported *Gammarus fasciatus*. *Gammarus fasciatus* alone was found at 39 sites, and 35 locations contained neither *G. fasciatus* nor *E. ischnus*. A total of 74 sites were included in the survey. This gives a strong indication that the habitat preferences of both amphipod species are similar. The association remained statistically significant even when data from Lake Superior, throughout which *E. ischnus* has likely not yet dispersed (I. Grigorovich, University of Windsor, Windsor, Ontario, Canada, pers. comm.) were excluded from the analysis.

In cases where the sample sizes were very small (i.e., Lake Erie, Lake Michigan, and embayment sites), the runs test was not appropriate for evaluating randomness of presence/absence events. A few results from the 60 runs tests implied that there was a statistically significant pattern. However, there were so few data points for some lakes that the likelihood of getting the observed results by chance was high. Ultimately, the runs test was only suitable for analyses of the whole Great Lakes basin, the Great Lakes basin excluding Lake Superior, Lake Huron sites, high-energy sites, and coastal wetland sites. More sites must be incorporated into analyses for those domains with small sample sizes.

Logistic regression analyses at the Great Lakes basin scale did not show any significant relationships between *E. ischnus* presence/absence and principal component scores of stressor variables. The significant association of *E. ischnus* distribution and Overall Pollution Loading score of sites revealed by the runs test was not corroborated by the corresponding logistic regression analysis. The analysis was not able to produce a reliable description of the relationship by estimating a threshold stressor PC score at which the status of *E. ischnus* presence/absence at sites changes. There may be too much variability among lakes for an overall pattern to show. For example, perhaps too few sites from Lake Huron possessing high principal component scores for stressor variables were sampled, as compared to Lake Erie. The overall sampling design was derived to provide a complete stressor gradient that covered all of the Great

Lakes, and more high-disturbance segments may have been inadvertently chosen for certain lakes by the stratified random site selection design. This would not, however, necessarily accurately depict the specific type and range of stress influencing each lake. Lake Erie might inherently be more developed than Lake Huron, but the gradient of stressor scores of selected sites do not necessarily characterize the extent of stress influencing each lake and does not rule out the possibility that Lake Huron is subject to the same types and degree of disturbance as Lake Erie. Lake Huron may have sites that are just as stressed as Lake Erie sites but were not chosen in the site selection.

When analyses were performed at the individual lake and site type scales, several significant relationships were observed, although sample sizes tended to be small, and most analyses were not significant at the Bonferroni-corrected probability level (nominally $p < 0.0083$). Those analyses that revealed unadjusted probability levels that were < 0.05 are discussed in the following paragraphs with the expectation that incorporation of 2003 samples will make the analyses more powerful.

The logistic regression analysis of *E. ischnus* presence/absence was found to be significantly associated with the Overall Population Density stressor variable at Lake Michigan sites ($p < 0.009$, $n = 12$) and supports Elton's hypothesis. The Overall Population Density stressor variable may be spuriously associated with *E. ischnus* distribution, as ports of call are often located in areas that are influenced by high density and pollution loading. Most sites found to contain *E. ischnus* were located near ports of call (Fig. 10). A port of call is the port where a transoceanic ship first discharges ballast water once entering the Great Lakes. Ballast tanks of these ships are considered a predominent vector for Ponto-Caspian organisms that invade the Great Lakes (Ricciardi and MacIsaac, 2000). Many organisms are able to survive the voyage, often as dormant stages, and are emptied from ballasts tanks into the Great Lakes (Ricciardi and MacIsaac, 2000). These organisms flourish in their new habitat especially if it matches conditions of their native habitat (Moyle and Light, 1996; Williamson and Fitter, 1996). These positive associations may be explained by

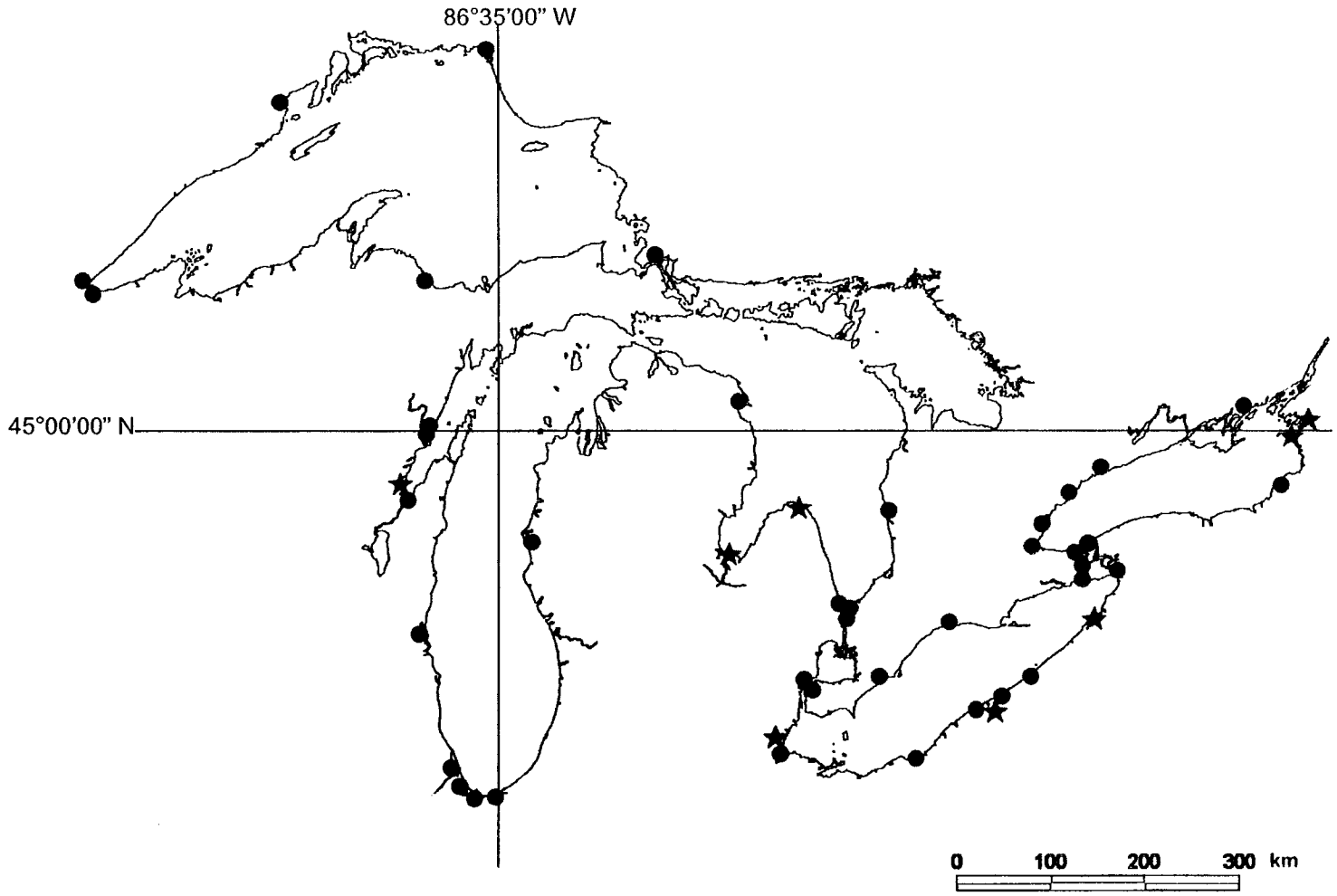

Figure 10: Distribution of major Great Lakes ports of call (●) and *Echinogammarus ischnus* sites (★).

the fact that *E. ischnus* has not had time to disperse from these areas of inoculation, especially for regions where it has recently arrived. With time, associations with other types of stressors may become detectable as *E. ischnus* expands its range over larger geographic areas. As well, the positive association may no longer exist at port locations after enough time has passed for *E. ischnus* to disperse.

Logistic regression analyses suggested that *E. ischnus* presence/absence was significantly related to principal component scores for Overall Nutrient Input at embayment ($p < 0.04$, $n = 4$) and high-energy ($p < 0.05$, $n = 8$) sites when Lake Superior sites were excluded, as well as for all embayment sites ($p < 0.03$, $n = 5$). However, no significant association was found when high-energy and embayment sites (which also make up the main shoreline of the lakes) were pooled ($p > 0.05$). None of these analyses were significant at the Bonferroni-corrected probability level.

Echinogammarus ischnus presence/absence at high-energy sites was also significantly associated with the Relative Maximum PC Score of stressor variables when Lake Superior sites were excluded ($p < 0.003$, $n = 8$). This association was stronger than those of the other analyses. This implies that there may be an association between *E. ischnus* distribution and generalized stress, rather than specific types of stress. Elton's hypothesis would be corroborated in this case, since any disturbance that modifies species interactions or the nature of the environment should facilitate nonindigenous species establishment, regardless of the type of stress. If Overall Pollution Loading or another type of stressor is ultimately demonstrated to be the primary attribute of sites supporting *E. ischnus*, this finding would detract from Elton's hypothesis since the disturbance that determines nonindigenous species establishment is attributed to a certain type of stress. Accordingly, this would imply that the degree to which interactions or resources are altered to favour nonindigenous species depends on the type of stress, which could explain the varying strengths of associations in analyses of this study. Certain types of stress may disrupt specific key interactions or resources, or the magnitude of disruption may vary among

stressors, indicating that stressors do not have equal influence on nonindigenous species establishment.

The small sample sizes used in these analyses means that the events could have occurred by chance. The Bonferroni correction, which was used to adjust the detection level for significance of the numerous tests to correct for inflated Type I Error rendered many of the nominally significant relationships nonsignificant. Incorporation of data from samples collected from the 2003 sampling season will make my analyses more powerful.

Adequacy of Site Selection for Stressor Representation

As a result of site sampling protocols and logistics, the sites used in this study are not uniformly spread across the Great Lakes Basin. Large sections of some lakes were not sampled in 2002 (e.g., Lake Ontario) and consequently were not incorporated into this study to provide a complete assessment of the scope of *E. ischnus* distribution in the Great Lakes. Integration of 2003 samples into this study will more effectively depict the distribution of *E. ischnus* along the U. S. coastal margins of the Great Lakes. However, the present data does provide an adequate gradient of stressed sites to investigate the association between nonindigenous species distribution and stressor variables in an attempt to test Elton's and Baltz and Moyle's hypotheses (Fig. 11-16). The range of stress covered by the 74 sites examined in this study (PC score range = -1.008 – 2.398) is representative of the range of stress encountered in the Great Lakes (PC score range = -1.399 – 3.203) and is suitable for tests.

Results from this study show inconsistency in the proportion of *E. ischnus* occurrences at Lake Erie and Lake Ontario sites with those from the other lakes (Table 2). Lakes Erie and Ontario have a history of invasion, while other lakes, such as Lake Superior, have few invasion records in the literature. This may be a result of several factors, including inadequate sampling effort. This may reflect bias in research efforts to survey flora and fauna in these areas, resulting in under-reporting of nonindigenous species in less explored areas. Alternatively, Lake Erie and Lake Ontario may provide better habitat match with native regions

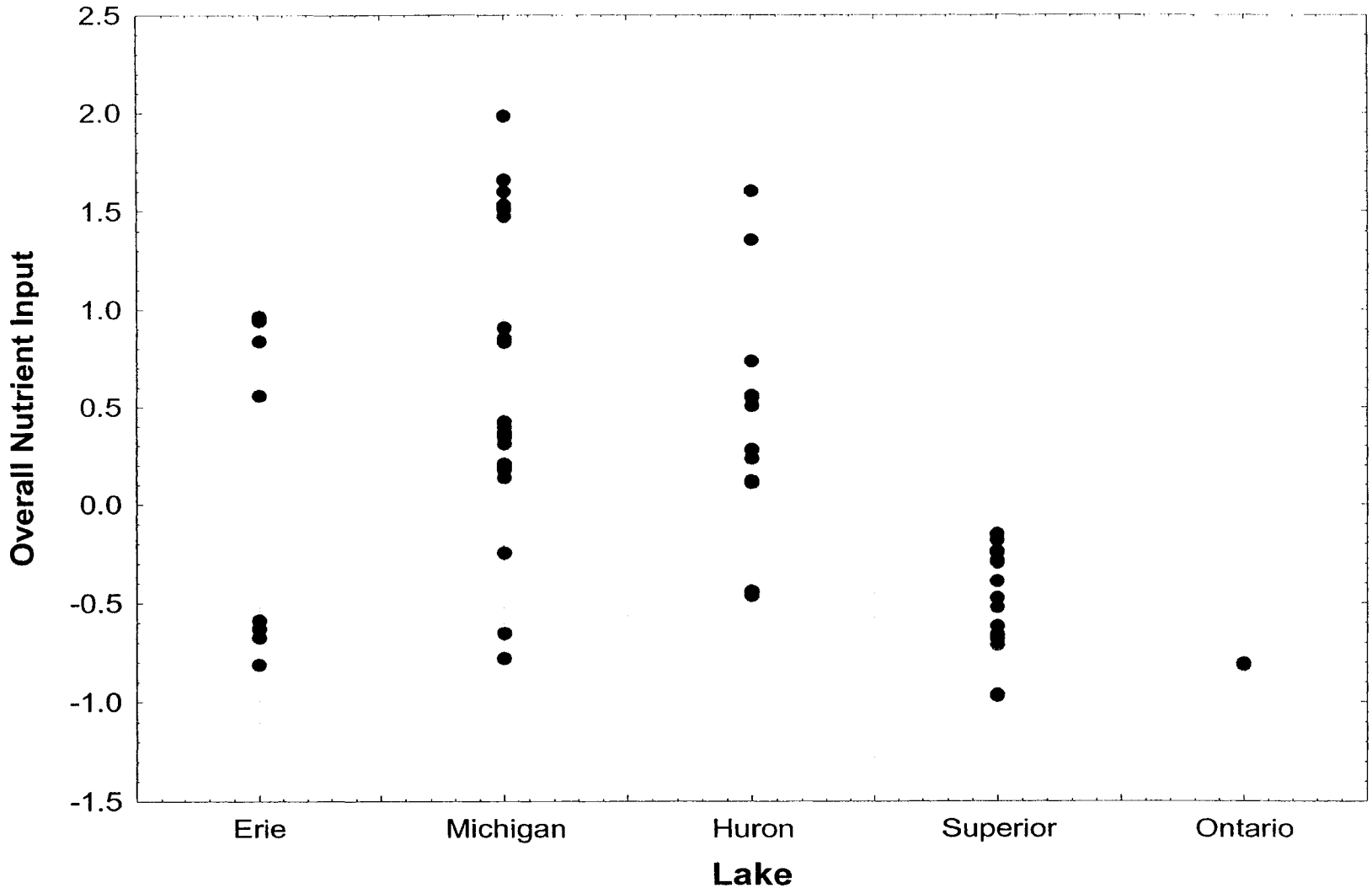

Figure 11: Range of Overall Nutrient Input principal component scores of sites sampled in each lake.

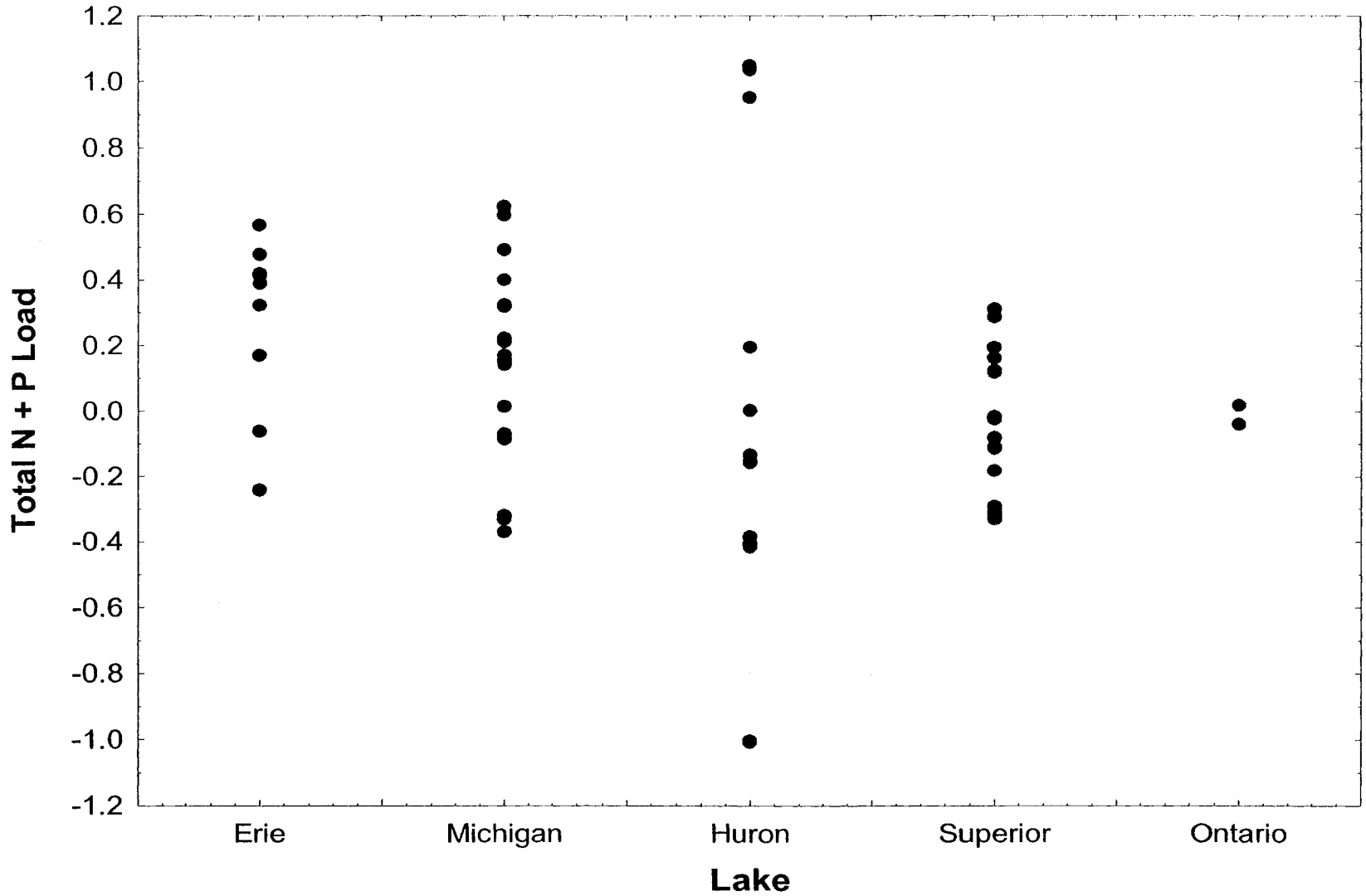

Figure 12: Range of Total N + P Load principal component scores of sites sampled in each lake.

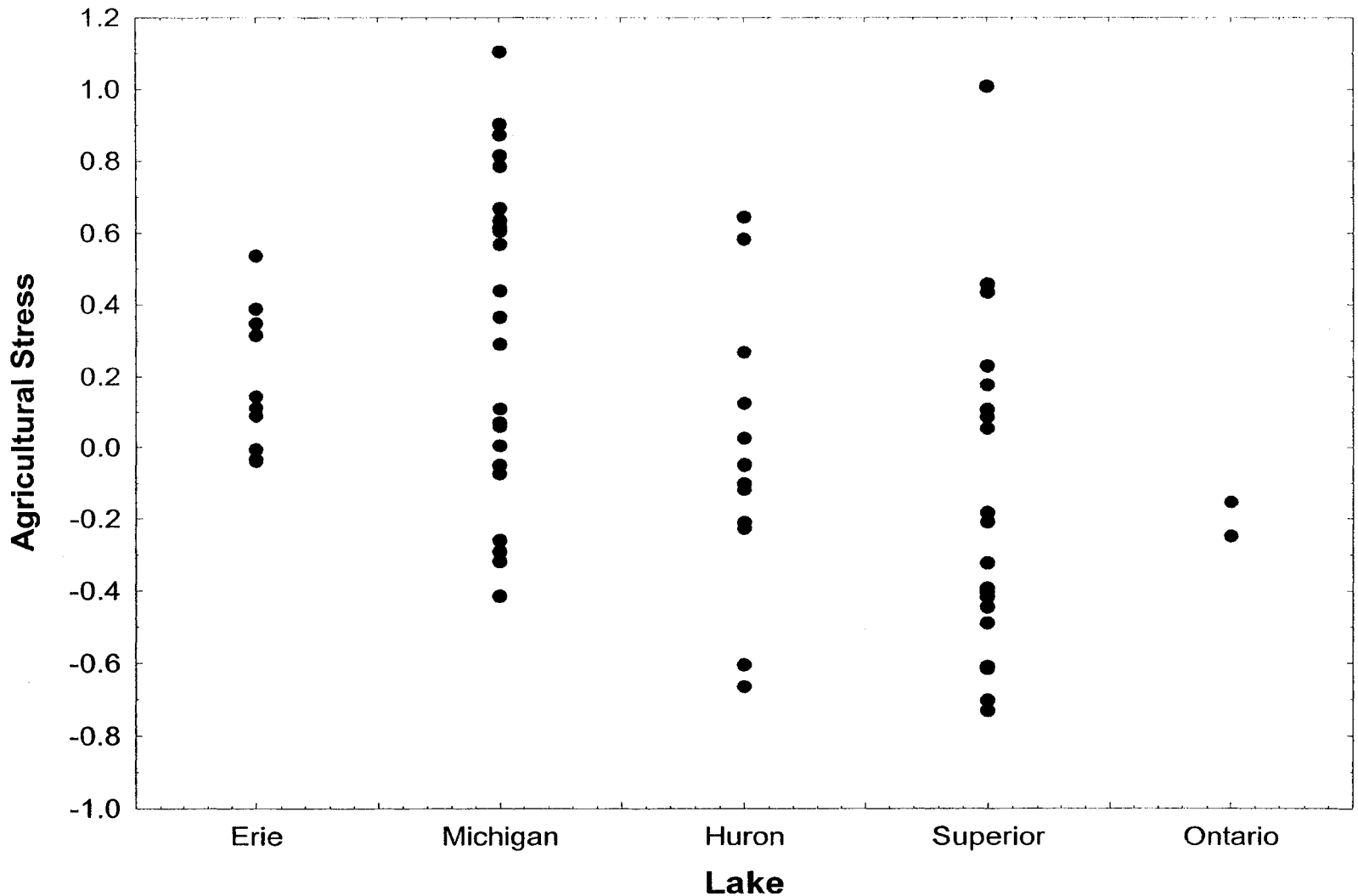

Figure 13: Range of Agricultural Stress principal component scores of sites sampled in each lake.

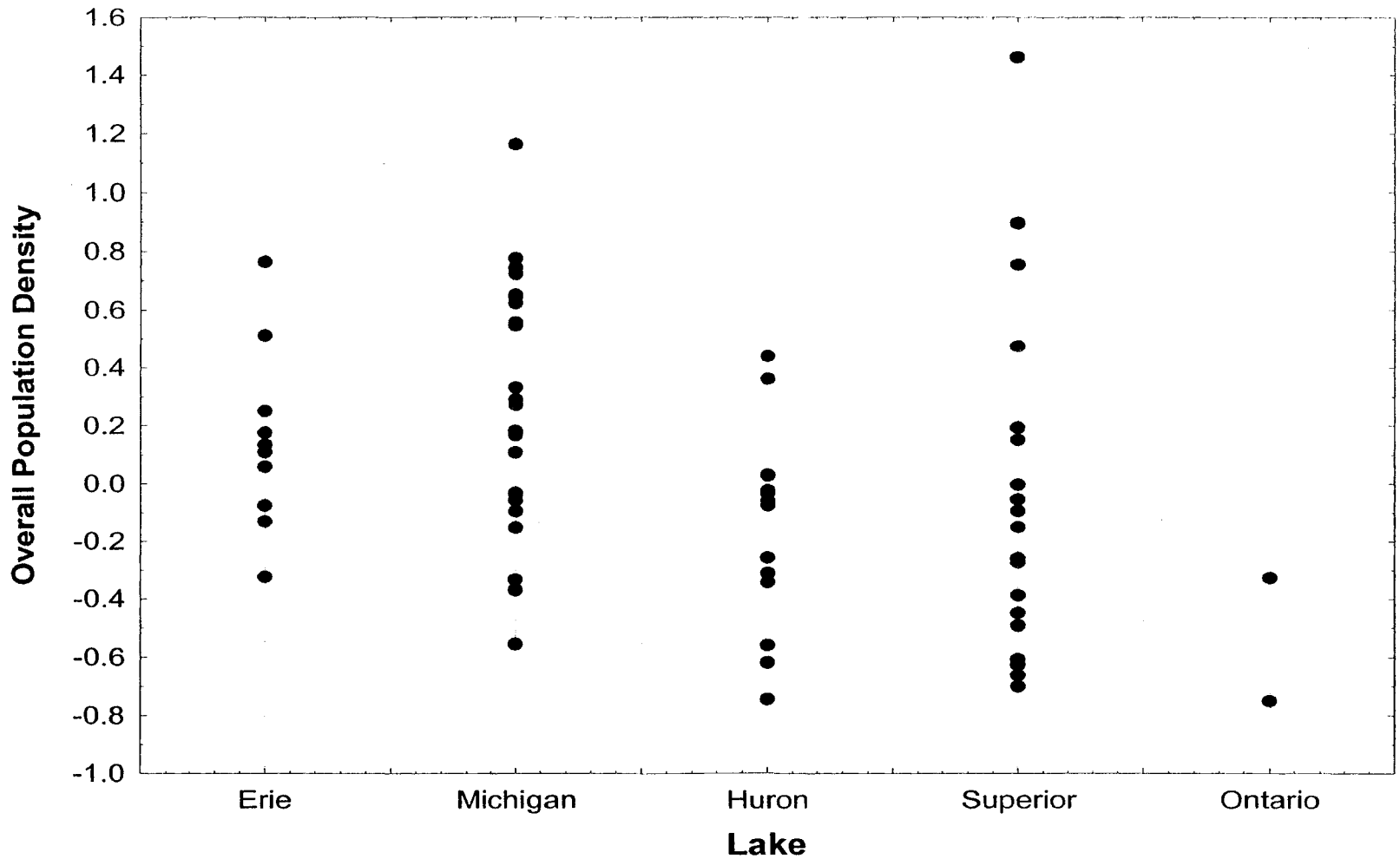

Figure 14: Range of Overall Population Density principal component scores of sites sampled in each lake.

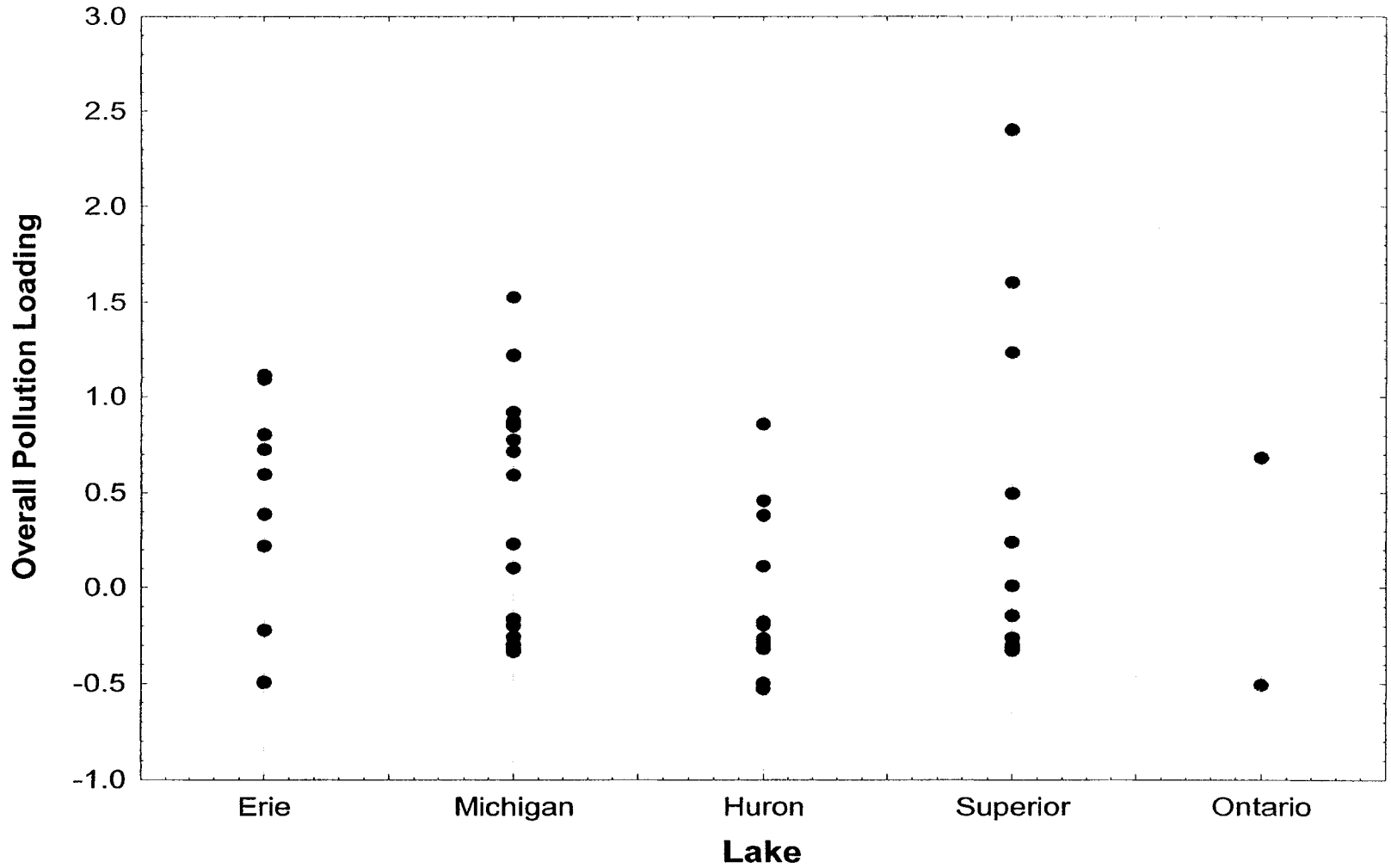

Figure 15: Range of Overall Pollution Loading principal component scores of sites sampled in each lake.

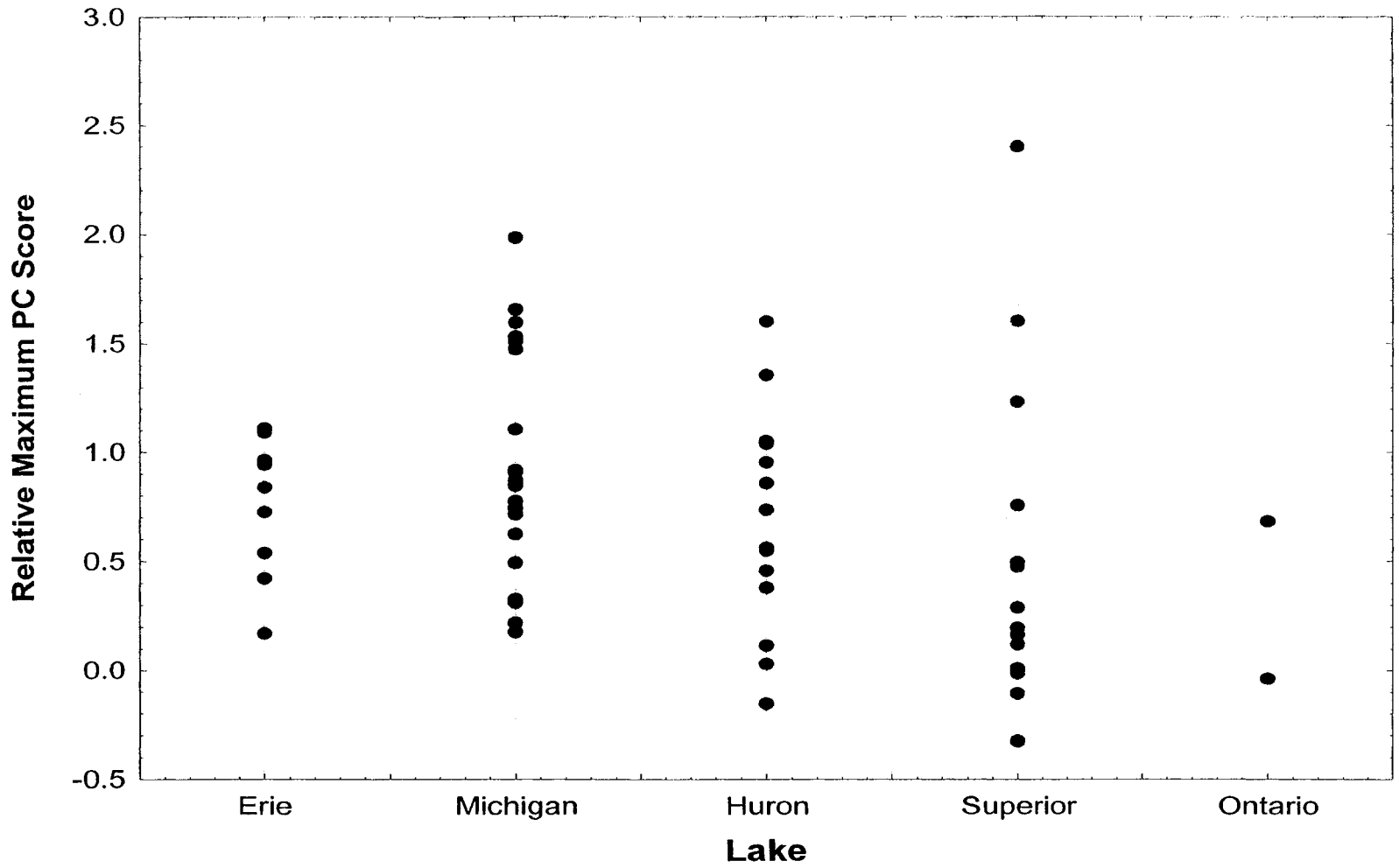

Figure 16: Range of Relative Maximum Principal Component Score of stressor variables for sites sampled in each lake.

for nonindigenous species entering the basin than the other Great Lakes. The lower Great Lakes' physicochemical properties and resources may best match the nonindigenous species physiological processes and life history strategies. The lower Great Lakes are more eutrophic and warmer than the upper Great Lakes, so may be more similar to the native habitat of newly arriving species. This habitat matching becomes even more apparent when considering that shipping intensity and ballast discharges (which are important entry and dispersal vectors) are greater in Lake Superior than in the other Great Lakes (Colautti, 2001). Yet, Lake Superior seemingly supports few nonindigenous species (Grigorovich *et al.*, in review). The absence of nonindigenous species in Lake Superior is exemplified by this study of *E. ischnus* distribution.

Potential versus Present Distribution of *Echinogammarus*

Although, *E. ischnus* has been reported from all of the Great Lakes, the discrepancy in occurrences among lakes may be due to its dispersal capabilities (Table 2). *Echinogammarus ischnus* has perhaps not had time to disperse throughout the lakes. Dates of the first record of *E. ischnus* in each Great Lake show that the distribution of *E. ischnus* radiates from Lake Erie. The first report of *E. ischnus* in Lake Superior is recent (Grigorovich *et al.*, in review), and the detection site was located close to a busy port of call, which is most likely a point of inoculation. Dispersal rates in the lower Great Lakes are likely more rapid than rates of the upper Great Lakes, since the upper lakes are both less densely populated (providing less chance for anthropogenic transport) and colder (resulting in slower population growth). *Echinogammarus ischnus* may have not yet dispersed to all potential habitats of the Great Lakes.

The sites used in this study covered a range of principal component scores for the six variables examined (Fig. 11-16). *Echinogammarus ischnus* sites spanned the complete range of most stressor variable PC scores, and did not seem to be concentrated at specific levels of stress for any of the stressor variables (Fig. 17-22). *Echinogammarus ischnus* was found at relatively pristine sites (e.g., Muskalonge Bay, Lake Ontario), which scored low for all of the

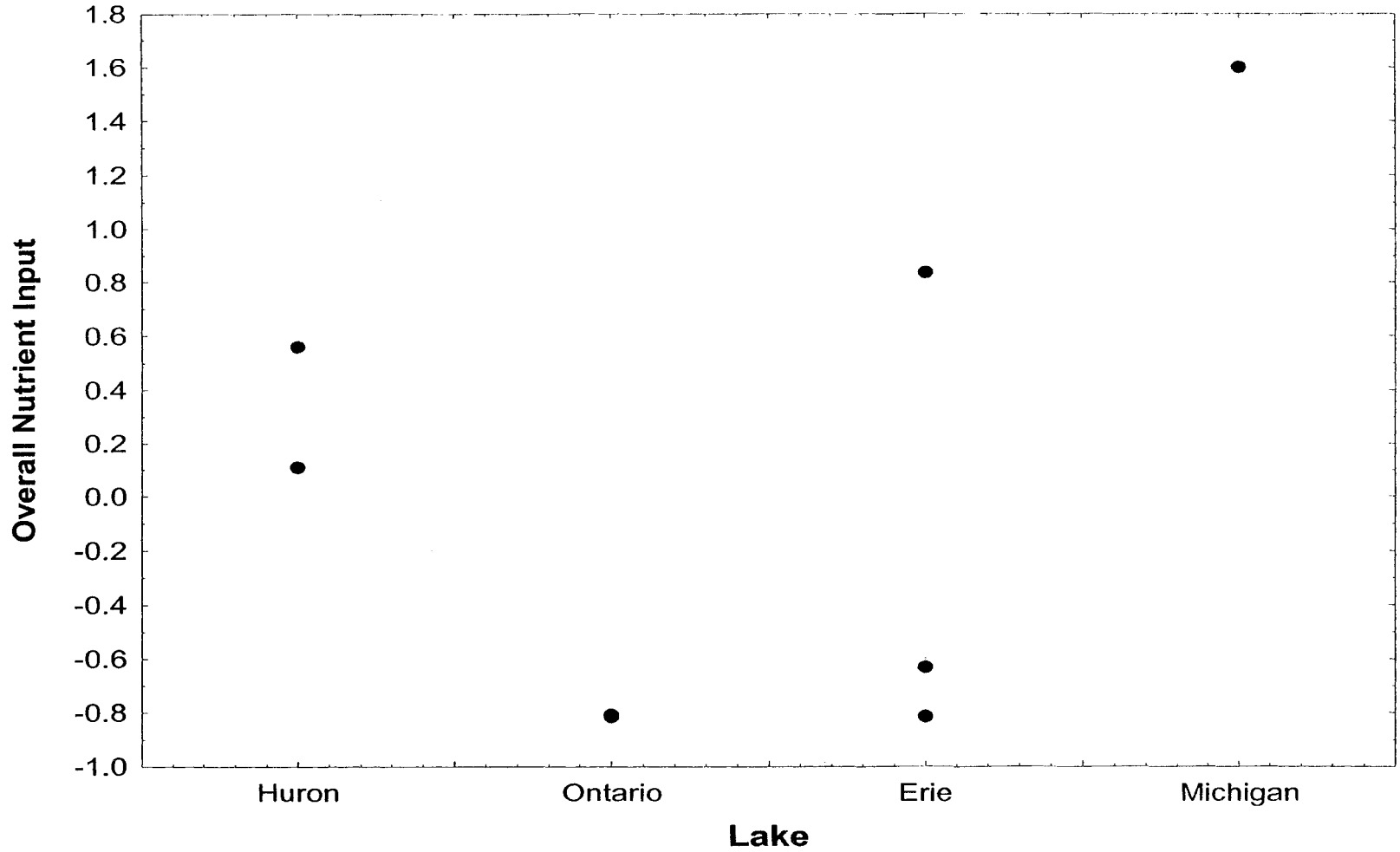

Figure 17: Range of Overall Nutrient Input principal component scores for *Echinogammarus ischnus* sites sampled in each lake.

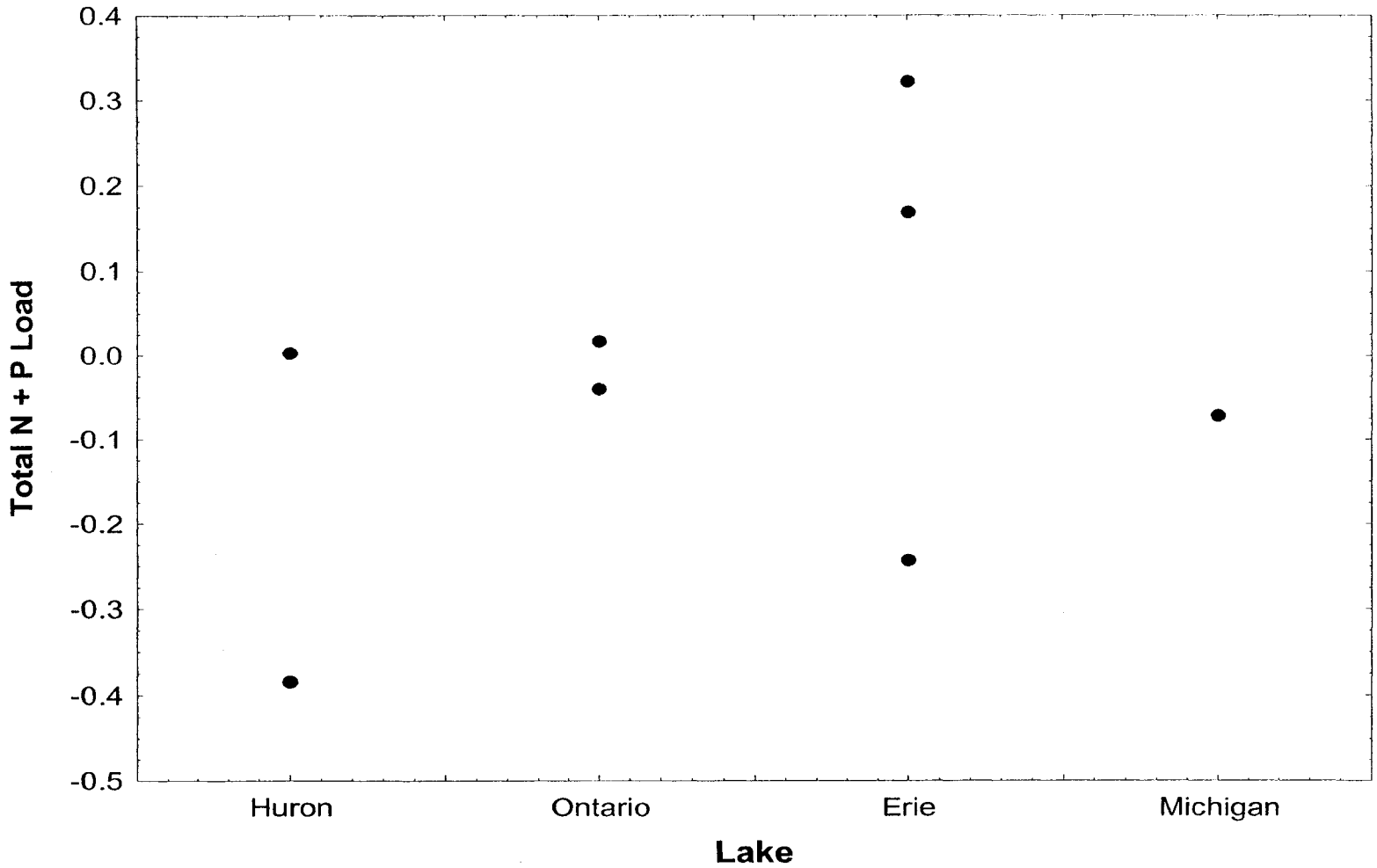

Figure 18: Range of Total N + P Load principal component scores for *Echinogammarus ischnus* sites sampled in each lake.

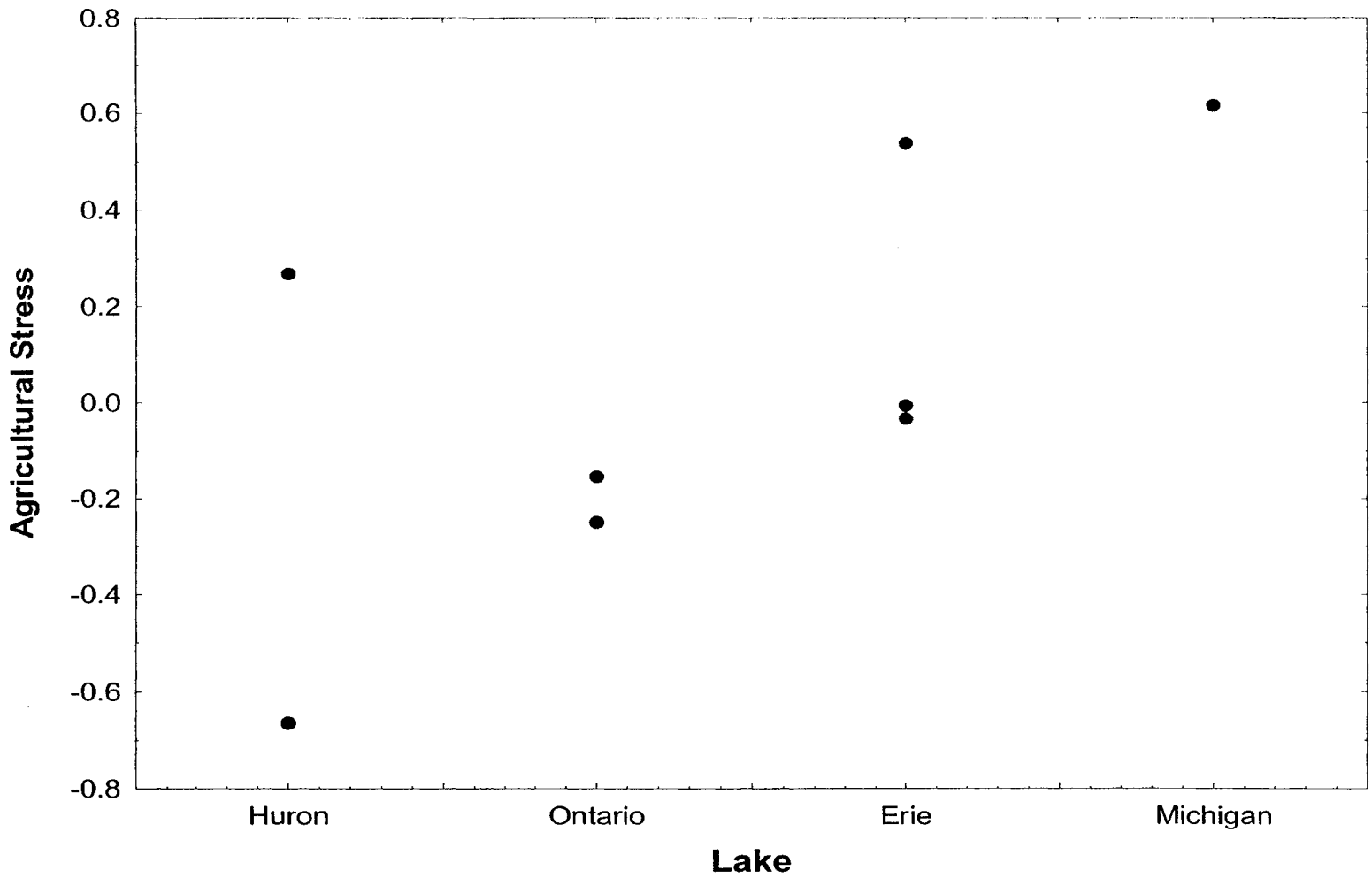

Figure 19: Range of Agricultural Stress principal component scores for *Echinogammarus ischnus* sites sampled in each lake.

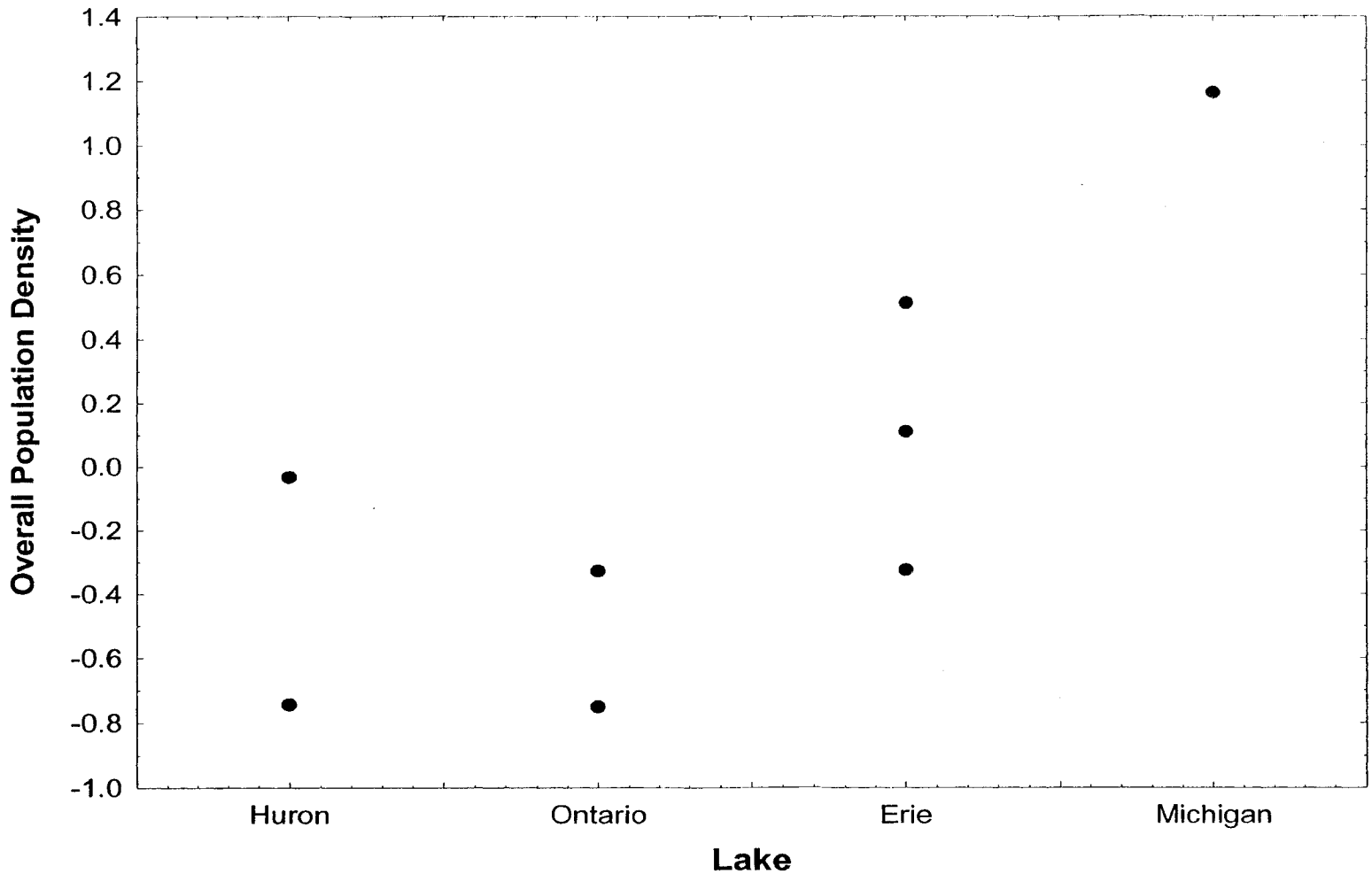

Figure 20: Range of Overall Population Density principal component scores for *Echinogammarus ischnus* sites sampled in each lake.

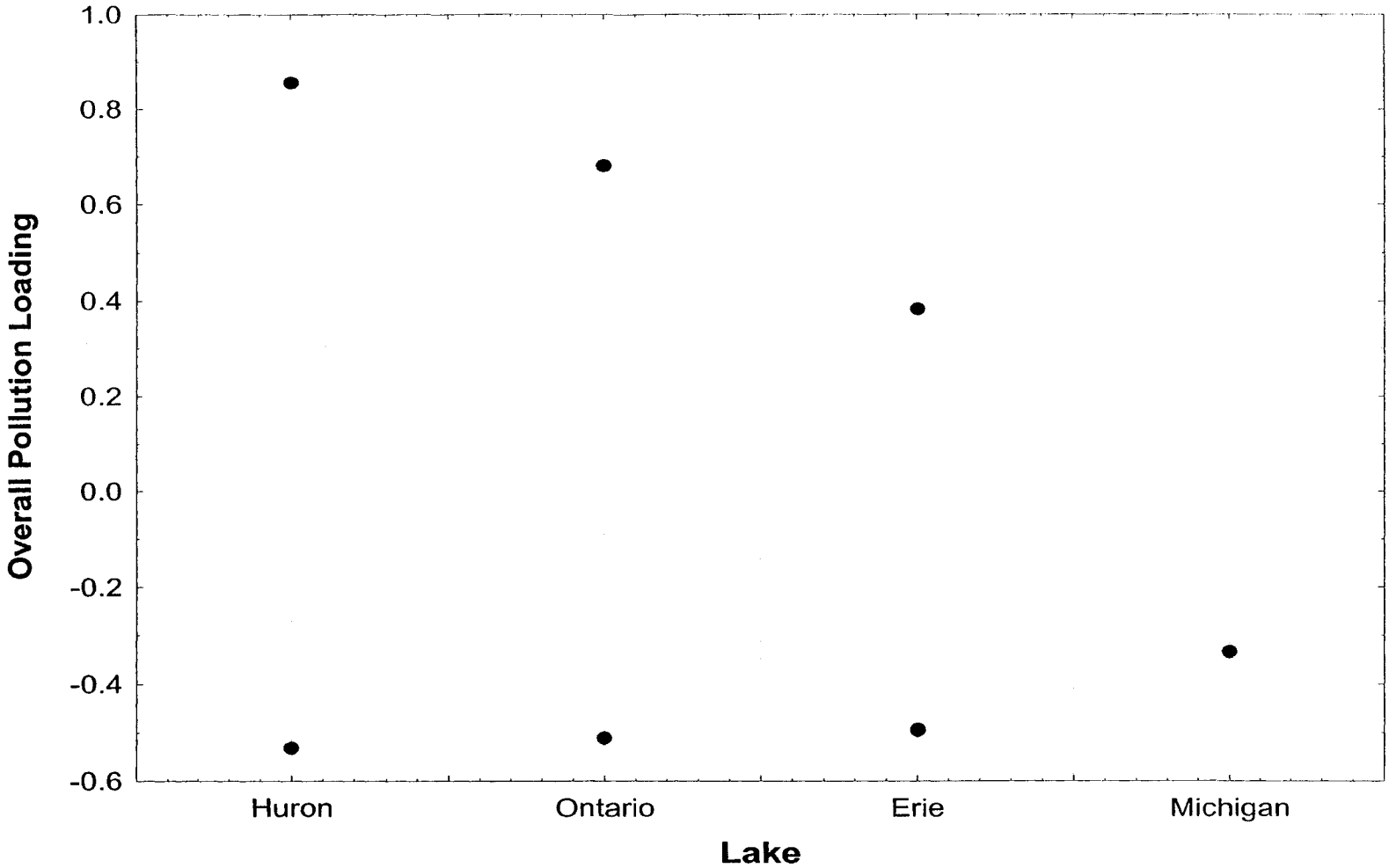

Figure 21: Range of Overall Pollution Loading principal component scores for *Echinogammarus ischnus* sites sampled in each lake.

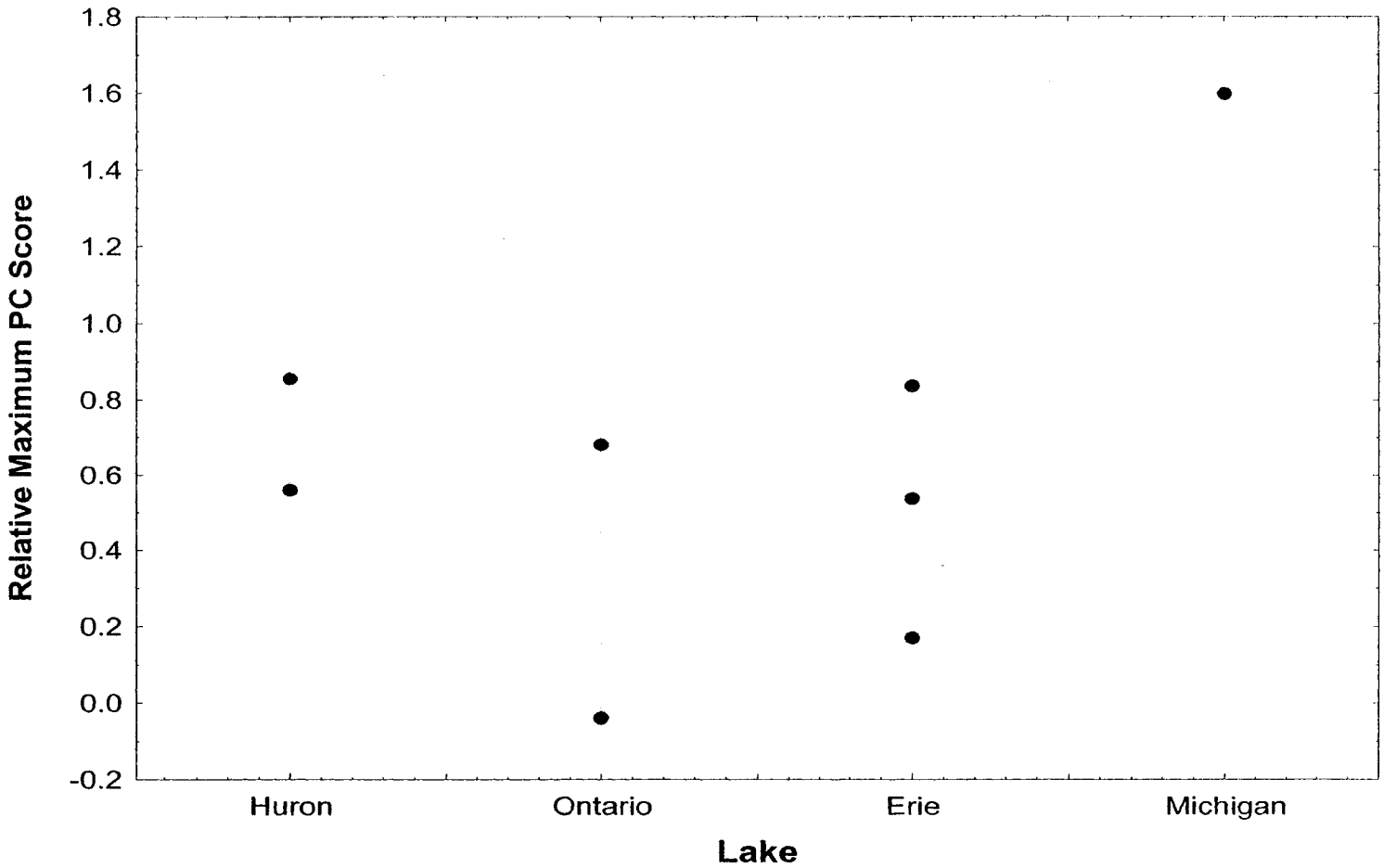

Figure 22: Range of Relative Maximum Principal Component Score of stressor variables for *Echinogammarus ischnus* sites sampled from each lake.

stressor variables, as well as at more polluted sites (e.g., Green Bay Shores, Lake Michigan and Saginaw Bay, Lake Huron) that scored relatively high for all stressor variables. Significantly, Lake Ontario and Lake Erie sites, which make up the most occurrences of *E. ischnus* compared to the other Great Lakes sites, appear to have relatively low PC scores for all stressor variables, although scores of the Overall Pollution Loading variable are comparatively high (Fig. 17-22). The range of stressor scores across which *E. ischnus* occurs indicates the broad environmental tolerances of the amphipod, an attribute often ascribed to successful nonindigenous species (Mills *et al.*, 1994). Areas that it occurs do not appear to consistently be disrupted by a stressor. This corresponds with Baltz and Moyle's hypothesis that nonindigenous species become established wherever conditions are suitable.

Results from this study ultimately do not support Elton's hypothesis. The significant associations I found may be the result of *E. ischnus* presence at sites spuriously correlating with stressors. The stressors found to have significant associations with *E. ischnus* distribution have their highest values at city centers influenced by various stressors, along with shipping activities. Invasion by Ponto-Caspian species, such as *E. ischnus*, is believed to be mediated by ships' ballast water (Ricciardi and MacIsaac, 2000). The distribution of nonindigenous species expelled from ballast tanks at Great Lakes ports of call may appear to be associated with stressors that affect sites coincidentally. However, the stressors at these sites may not necessarily influence nonindigenous species establishment. *Echinogammarus ischnus* might have the potential to be successful in relatively pristine areas but may not yet be distributed in these areas due to their limited dispersal abilities. Pristine areas may be protected from the influence of possible dispersal vectors (lake currents and activities related to shipping/boating). If given the opportunity to disperse to these remote areas, *E. ischnus* will likely prosper, particularly if they already support *G. fasciatus* and/or *Dreissena* spp. Sites that are relatively stressed and do not support *E. ischnus* may lack suitable conditions for establishment. Environmental conditions at the

most stressed sites may be so poor that, possibly no organisms, including *E. ischnus* can tolerate them.

Dreissena spp. co-occurred with *E. ischnus* and *G. fasciatus* at many locations. Dreissenids were found at 23 sites, which includes all sites that supported *E. ischnus.* There was a highly significant association between *Dreissena* spp. and *E. ischnus* distribution, a novel finding at the landscape scale. In fact, unlike *G. fasciatus, E. ischnus* was only found in samples that contained *Dreissena* spp. Although *G. fasciatus* and dreissenid distributions were significantly associated, *Dreissena* spp. were not present at all sites that contained *G. fasciatus* and vice versa. *Dreissena* spp. and *G. fasciatus* co-occurred at 18 sites (78% and 46% of sites, respectively) and this common distribution was observed to be a significant association.

These results are consistent with past findings that suggest that *Dreissena* spp distribution and dispersal are good predictors of *E. ischnus* distribution at the microhabitat scale (Witt *et al.*, 1997; Dermott *et al.*, 1998; Stewart *et al.*, 1998; Bially and MacIsaac, 2000; Vanderploeg *et al.*, 2002; van Overdijk *et al.*, 2003). Both *E. ischnus* and *G. fasciatus* have been associated with *D. polymorpha.* Field and laboratory studies have shown that *G. fasciatus* and *E. ischnus* prefer *Dreissena*-encrusted substrata to bare rocks (Dahl *et al.*, 1995; Witt *et al.*, 1997; Dermott *et al.*, 1998; Stewart *et al.*, 1998; Bially and MacIsaac, 2000; Vanderploeg *et al.*, 2002; van Overdijk *et al.*, 2003). My data further verify that *E. ischnus* occurs wherever habitat is suitable, as *Dreissena* spp. provides suitable, and perhaps obligate habitat for the amphipod. Given that *E. ischnus* only occurred at sites that supported dreissenids and both were often found together in the same sample, *Dreissena* spp. distribution could perhaps be used as an estimate of *E. ischnus* distributional limits. The strong association between *E. ischnus* and *Dreissena* spp. distribution may be due to habitat alterations caused by the dreissenids themselves. Colonization of fine sediments in western Lake Erie by *Dreissena* spp. is suspected to have facilitated the expansion of *E. ischnus* into habitats that were previously unsuitable (Bially and MacIsaac, 2000). Areas that support *Dreissena* spp. without *E. ischnus* likely represent areas that

the amphipod has not yet reached. This would indicate that *E. ischnus* has not yet reached the extent of its dispersal limits in the Great Lakes. Continued expansion of *E. ischnus* distribution to these locations would provide further evidence in support of Baltz and Moyle's hypothesis.

Similarities in *E. ischnus* distributional patterns found in this study with those described from the Ukraine support the generalization that nonindigenous species are likely to become successfully established in a new environment if it resembles the environment from whence they came (Moyle and Light, 1996; Williamson and Fitter, 1996). Characteristics of the Great Lakes areas supporting *E. ischnus* that parallel those of its native habitat are shallow, littoral, cobble or rocky substrates that often have slow-moving water currents (Witt *et al.*, 1997; Dermott *et al.*, 1998; Stewart *et al.*, 1998).

Conjecture generated from observations of co-evolved nonindigenous species is exemplified by the Ponto-Caspian trio formed by *Dreissena polymorpha*, *Echinogammarus ischnus*, and the round goby, *Neogobius melanostomus* Pallas 1811. All three species are closely linked in the Great Lakes, mirroring their close association in their native habitat. The introduced mussels provide a food resource for juvenile round gobies, which feed predominantly on gammarid amphipods in their native range, whereas adult gobies feed preferentially on the mussels (Shorygin, 1952; Ray and Corkum, 1997). This relationship helped to form the basis of the invasional meltdown hypothesis (Simberloff and Von Holle, 1999; Ricciardi, 2001), which proposed that direct interactions between nonindigenous species are important in facilitating invasions. This facilitation may become synergistic, resulting in an "invasional meltdown", i.e., an accelerated accumulation of introduced species and effects. This process is thought to be especially potent in coevolved species complexes, such as the trio outlined above, and may explain the success of all three nonindigenous species in the Great Lakes. Grigorovich *et al.* (in review) postulated that established populations of *D. polymorpha* may facilitate the subsequent establishment of *E. ischnus*, and *Neogobius melanostomus* in areas of Lake Superior. Interactions among the Ponto-Caspian trio indicate that a

specific sequence of invasion is required for successful facilitation. It is unlikely that either *E. ischnus* or *N. melanostomus* would have been successful in the Great Lakes without the prior arrival of *D. polymorpha*, which provides both nonindigenous species with resources. This sequence of arrival would be important for *N. melanostomus* establishment, as adult stages would strongly rely on the preferred *D. polymorpha* food supply (Ray and Corkum, 1997) for their own establishment. *Echinogammarus ischnus* would also depend on the prior establishment of *D. polymorpha* that provides suitable substrate for shelter and food for establishment of stable populations in the Great Lakes. Thus, *D. polymorpha* can be regarded as the primary facilitator species for establishment by the other 2 nonindigenous species. Establishment of *E. ischnus* is unlikely to have been influenced by prior establishment of *N. melanostomus* given that the goby feeds on the amphipod. The commensal relationship between *E. ischnus and D. polymorpha* (the interaction is positive for the amphipod while the bivalve is unaffected) implies that prior establishment of *E. ischnus* would not have influenced establishment of the bivalve.

Displacement of *Gammarus fasciatus* Say

Past studies predicted that the strong association between *Dreissena* and *E. ischnus* would result in displacement of native *G. fasciatus* in the Great Lakes (Witt *et al.*, 1997; Dermott *et al.*, 1998; Nalepa *et al.*, 2001; van Overdijk *et al.*, 2003). Sampling conducted in 1995 to 1999 (Witt *et al.*, 1997; Nalepa *et al.*, 2001) and 2001 to 2002 (Barton *et al.*, 2003), demonstrated declines in *G. fasciatus* abundance at sites where it had previously been found. *Echinogammarus ischnus* was often the only amphipod found at sites, such as along the eastern shoreline of Lake Michigan (Nalepa *et al.*, 2001) and the eastern and central basin shores of the Canadian side of Lake Erie (Barton *et al.*, 2003). Competitive displacement predicted to occur at sites that support *G. fasciatus* by *E. ischnus* is not supported by the preliminary findings of this study. All sites that supported *E. ischnus* in 2002 also supported *G. fasciatus*, indicating that both species are able to co-occur and utilize resources at the same site.

Paralleling these findings are observations of the decline in *Dreissena* spp. abundance (Vanderploeg *et al.*, 2002; Barton *et al.*, 2003). *Dreissena* populations are decreasing in abundance in many areas where they were once densely distributed, especially in Lake Erie (Barton *et al.*, 2003). Given that *E. ischnus* distributions are strongly governed by *Dreissena* spp. distributions, declines in *E. ischnus* abundance may be a direct consequence of declining *Dreissena* spp abundances (pers. observ). This trend might be mirrored by *Gammarus fasciatus*, since its abundance has also been found to be positively influenced by distributions of *Dreissena* spp. (Stewart and Haynes, 1994; Dahl *et al.*, 1995; Hime and Ciborowski, 1995; Stewart *et al.*, 1998). Conversely, the competitive release achieved by decreases in *E. ischnus* abundance may possibly exert a stronger influence than decreases in *Dreissena* spp. abundance, since the native amphipod does well in substrates lacking *Dreissena* spp. *Echinogammarus ischnus* has a stronger preference for *Dreissena* druses than for any other type of substrate (van Overdijk *et al.*, 2003), so fluctuations in *Dreissena* spp. populations will have a stronger impact on the *E. ischnus* than on native amphipods. If these dynamics are real, it is unlikely that *E. ischnus* will displace *G. fasciatus* in the Great Lakes. Areas that have experienced the introduction and subsequent rapid spread of *Dreissena* spp. may have reached a steady state of some form, causing populations to plateau. Records show that *D. polymorpha* abundances have decreased in eastern Lake Erie (Barton *et al.*, 2003) and distributions have contracted (pers. obs.). This is possibly a consequence of *Neogobius melanostomus* predation, as populations have become noticeably more abundant in the Eastern Basin (Barton *et al.*, 2003). Consequently, I expect that *E. ischnus* populations will continue to radiate until it reaches the furthest extents of dreissenid distributions resulting from recessions.

Ports of Call

Since ballast discharge of transoceanic ships is considered to be the key entry vector of nonindigenous species in the Great Lakes, large numbers of propagules of various species would be expected to be located at ports of call.

One would then predict that nonindigenous species will occur close to those areas of inoculation (i.e., close to ports of call and marinas) and expect nonindigenous species success wherever biotic and abiotic requirements are fulfilled. Duluth and Thunder Bay harbours (Lake Superior) receive a disproportionate number of visits by transoceanic ballasted and NOBOB vessels (ships with no-ballast-on-board status) compared to other ports of the Great Lakes (Colautti, 2001), but do not support many nonindigenous species in their vicinity (Grigorovich *et al.*, in review). Lack of suitable habitat is argued to be the major barrier for potential nonindigenous species of Lake Superior (barriers reviewed by Grigorovich *et al.*, in review).

One would predict that sites that are located near ports of call would be more likely to contain *E. ischnus* than sites that are located farther away. Figure 10 shows the distribution of sites supporting *E.* ischnus and the location of ports of call. Lake Huron *E. ischnus* sites do not appear to be near ports of call. Two Lake Huron ports of call nearest the sites supporting *E. ischnus* are located at Alpena, Michigan and Goderich, Ontario, over 100 km away. Boat traffic between ports of call and *E. ischnus* sites may somehow link the sites. Other watercraft such as recreational boats that contain holding tanks are often emptied of water that may contain nonindigenous species, consequently aiding their dispersal (Mills *et al.*, 1993). Lake currents may also act as a dispersal vector carrying introduced species to distant areas.

Areas around ports of call would presumably be disturbed relative to other areas. The type of stress influencing these areas would most likely be linked to those related to industrial/urban development such as the stressor variables characterized by Overall Pollution Loading or Overall Population Density in this study. Coincidentally, these stressor variables were found to have significant associations with *E. ischnus* distribution and the association involving Overall Population Density was found to be particularly strong. Ports of call and surrounding areas will have low diversity and abundances of native fauna that are sensitive to these stressors. The combination of substantial propagule pressure and presence of the stressor variables may aid establishment of *E.*

ischnus. Areas remote to ports of call would be less subject to propagule pressure. The 2 Lake Huron sites at which *E. ischnus* occurred had intermediate values of the stressors variables, except for the Overall Pollution Loading stressor variable. They appear on the two extreme ends of the range of Overall Pollution Loading principal component scores for sampled sites. This may be a reflection of the dispersal pattern of *E. ischnus* in Lake Huron. Elucidation of the dispersal of *E. ischnus* in Lake Huron and the other lakes is needed to understand trends in its dispersal. Incorporation of data from the 2003 GLEI sampling season will make analyses more powerful.

The regions surrounding the ports of call are simultaneously influenced by various anthropogenic activities, given that ports are often subject to intense human/commercial development. The propagule pressure supplied by ballasting activities at ports may confound our ability to interpret the impact of anthropogenic stressors on native biota and facilitation of nonindigenous species establishment in these areas. Areas near ports of call are key invasion sites due to the ballasting activities of ships (Grigorovich *et al.*, 2003). The condition of habitats at these sites is often not taken into consideration when investigating factors involved in invasion events. Sites close to ports likely experience higher propagule pressure of *E. ischnus* than sites remote from ports of call, and its establishment would be expected, especially if *G. fasciatus* and/or *Dreissena* spp. are located there, as these indicate (or provide in the case of *Dreissena* spp.) suitable habitat for the nonindigenous amphipod.

Two pairs of sites within 25 km of ports of call were compared to assess stressor level differences and *E. ischnus* presence/absence. For each pair, one site supported both *E. ischnus* and *G. fasciatus*, while the other only harboured *G. fasciatus.* One pair was made up of sites adjacent to Green Bay Harbour: Green Bay Shores (supporting both amphipod species) and Sugar Creek (supporting *G. fasciatus* only). The second pair of sites was adjacent to Toledo Harbor: Toledo Beach (supporting both species) and Maumee River (supporting *G. fasciatus* only). All sites supported *Dreissena* spp. Pairs of sites had similar values for most stressor variables when all 74 sampled sites were ranked (from

lowest to highest PC score), except for Overall Pollution Loading and Total N + P Loading. Green Bay Shores (*Echinogammarus* present) ranked 8th in degree of Overall Pollution Loading whereas Sugar Creek (*Echinogammarus* absent) ranked 27th. However, the reverse order was true for degree of Total N + P Loading. Green Bay Shores ranked 30th while Sugar Creek ranked 8th. Toledo Beach (*Echinogammarus* present) ranked 6th in degree of Overall Pollution Loading, while Maumee River (*Echinogammarus* absent) ranked 67th. Toledo Beach ranked 16th in Total N + P Loading while Maumee River ranked 69th. It is noteworthy that there was a large discrepancy in Overall Pollution Loading scores for both pairs, especially since this is the stressor variable identified to be highly associated with *E. ischnus* distribution overall. For both pairs, the site that supported *E. ischnus* scored low for Overall Pollution Loading. This contradicts the earlier finding for the Great Lakes basin that supported Elton's hypothesis. Given that these sites near ports of call do not score highly for Overall Pollution Loading, a determinant of propagule success might be that newly arriving *E. ischnus* from ballast discharge must meet habitat that is not highly affected by pollution loading. Sites that are distant from ports of call seem to be characterized by high principal component scores of Overall Pollution Loading. This might be a general factor that influences dispersal of *E. ischnus* and suggests that dispersal depends on currents and water plumes that carry the products of pollution loading. The current and water plumes may act as a transport vehicle for *E. ischnus* and pollution loading dispersal. The movement of these water masses may coincidentally decrease native species richness and facilitate dispersal for *E. ischnus*. Overall Pollution Loading might also be affecting establishment of other nonindigenous species in a similar manner. Further studies need to be executed to reveal what factors may covary with propagule pressure to facilitate nonindigenous species establishment at ports.

Lozon and MacIsaac (1997) concluded from a literature survey of the relationship between disturbance and invasion success that although plants are significantly more dependent on disturbance for establishment than animals, both are reported to rely equally on disturbance for range expansion. Mechanisms

associated with successful animal invasions consisted of introduction via ballasting by ships, environmental disturbance (unspecified), and forestry and associated soil disturbance (involved earthworm species). Close examination of the papers cited in their review showed that none dealt directly with the influence of anthropogenic disturbance on success of aquatic invasions. Most animal studies documented invasions of terrestrial animals or dealt with activities of aquatic organisms associated with shipping activities (boring, fouling, dwelling in ballast tanks) that provided an entry mechanism to invasion sites. Most animal introductions (39%) were reported in aquatic habitats adjacent to urbanized areas, consistent with established patterns of ballast water discharge, species additions from fish release, and habitat destruction or degradation near cities. However, direct influence of urban-related stress was not assessed in these studies. This is most likely due to the difficulty in directly linking and assessing the contribution of disturbance to invasion success, especially for aquatic fauna.

Alternatively, Ricciardi (2001) reviewed articles that explicitly tested biotic resistance to establishment in aquatic communities. Two of the four studies support the biotic resistance model. These were composed of small communities (0 – 4 epifaunal species) and may have little predictive power if the relationship between invasibility and species richness is asymptotic over the range of community sizes commonly found in nature (Ricciardi, 2001).

Relatively sessile benthic macroinvertebrates are the closest animal equivalent to terrestrial plant communities. However, my research suggests that disturbance does not seem to factor into aquatic invertebrate invasion processes as it does with terrestrial plants. Aquatic habitats are thought to be highly vulnerable to invasions (Mills *et al.*, 1993) due to their generally low level of native species diversity and high level of invasion opportunities. Entry into potential habitats and dispersal limitations may be the primary obstacles for aquatic invasions but this does not explain why all aquatic nonindigenous species that arrive in a new habitat do not succeed. Factors such as habitat match, physiology and life history requirements of nonindigenous species that inhibit establishment successare almost certainly involved. Further studies

attempting to elucidate the disparity between the dependence of plant and animal nonindigenous species on disturbance for establishment would be helpful in understanding the dynamics of invasion biology, particularly for aquatic environments.

FUTURE RESEARCH

Results from this study indicate that establishment of *Echinogammarus ischnus* in the Great Lakes is not associated with anthropogenic activities such as those related to the Overall Nutrient Input, Total N + P Load, Agricultural Stress, Overall Population Density, and Overall Pollution Loading stressor variables. This finding is inconsistent Elton's (1958) hypothesis that biotic resistance against exotic species establishment is greater in intact communities than in those disturbed by human activities. It is more consistent with Baltz and Moyle's (1993) hypothesis that establishment of nonindigenous species is likely to occur wherever abiotic conditions are appropriate.

A few of the analyses suggested that *E. ischnus* distribution was consistent with the expectations of Elton's hypothesis, although none had enough power to provide strong support for the hypothesis. If biotic resistance to invasion is indeed weakened by anthropogenic disturbance, a factor that may have prevented my results from revealing this trend is the ongoing expansion of *E. ischnus* distributions. *Echinogammarus ischnus* populations may have not yet dispersed to reach boundaries of suitable habitat to occupy all possible locations at which they are able to persist. Distribution of *E. ischnus* was found to be significantly associated with that of *Gammarus fasciatus* and *Dreissena* spp. The association between *E. ischnus* and *Dreissena* spp. distributions was particularly strong. Past studies have revealed the preference of *E. ischnus* for *Dreissena* druses as substrate in the Great Lakes (Witt *et al.*, 1997; Dermott *et al.*, 1998; Stewart *et al.*, 1998; Bially and MacIsaac, 2000; Vanderploeg *et al.*, 2002; van Overdijk *et al.*, 2003). *Dreissena* spp. distribution could perhaps be used as an estimate of *E. ischnus* distributional limits. Samples failed to reveal *E. ischnus* at all sites that supported *G. fasciatus* and *Dreissena* spp., indicating that it has not yet reached the potential boundaries of its distribution.

A better test of Elton's hypothesis would be to evaluate the distribution of *Dreissena* spp. along stressor gradients because *Dreissena* spp. have both greater dispersal rates and have had more time to reach all of the boundaries of

the Great Lakes basin. Analyses could be conducted again using *Dreissena* spp. as a case study. *Dreissena* spp. distribution in Great Lakes coastal margins can be evaluated for areas that supply preferred hard substrate for the invader. The dispersal abilities of *Dreissena* spp. are likely higher than that of *E. ischnus* given that the larval stage of the bivalve consists of pelagic veligers that are broadly transported by currents. *Dreissena polymorpha* populations appear to be declining (Vanderploeg *et al.*, 2002; Barton *et al.*, 2003), suggesting that their rapid expansion in the Great Lakes is being followed by a period of recession as populations begin to stabilize and that *D. polymorpha* may have reached its dispersal limits in the Great Lakes.

Nonindigenous Species As Environmental Indicators

The indicators that will be proposed from the GLEI project may permit us to identify stressors and/or indicators that characterize areas where nonindigenous species establishment will likely occur. These areas may contain shipping port(s) and the presence of high PC scores of Overall Population Density. If nonindigenous species distribution can be predicted by the influence of environmental variables (including but not limited to locations of maximum propagule pressure), the occurrence of nonindigenous species could potentially be used as an environmental indicator. Results from this study indicate that *E. ischnus* could be used as an indicator of population density. Confirmation of this association would require observations of *E. ischnus* at all sites that are influenced by heavy population density. However, there may be upper threshold levels of population density at which conditions become unsuitable even for invaders. Stressor levels that are too low may be unsuitable for invasion of sites due to strong biotic resistance.

Addendum to the Invasional Meltdown Hypothesis

Communities can be considered to be the outcome of nonrandom sorting and adjustment processes. Simberloff and Von Holle (1999) proposed ways that species introductions may generate an increasing threat to community integrity.

As the cumulative number of attempted (including unsuccessful) introductions increases, populations of resident species are disrupted and the community thus becomes more easily invaded. Invasion can consequently be regarded as a form of disturbance. Certain established nonindigenous species alter habitat conditions in ways that favour other nonindigenous species, thereby creating a positive feedback system that accelerates the accumulation of nonindigenous species and their synergistic impacts. This "invasional meltdown" model is an alternative to the biotic resistance model that emphasizes facilitative rather than antagonistic interactions among introduced species. Some of the most successful nonindigenous species of the Great Lakes come from the Ponto-Caspian region, and the invasional meltdown hypothesis implies that these nonindigenous species alter conditions to resemble those of native regions through mutualism, commensalism, and/or habitat modification. However, positive interactions do occur between species that share no evolutionary history, such as *G. fasciatus* and *Dreissena* spp. (Ricciardi *et al.*, 1997). Biotic resistance to establishment is perhaps sensitive to the frequency of introductions. Accordingly, Ricciardi (2001) proposed that invasional meltdown is a threshold effect of inoculation pressure. Theoretically, establishment of nonindigenous species might be hindered by biotic resistance that is able to exist when the frequency of introductions is low.

Interpretations of mechanisms of invasion can be scale-dependent. Native and exotic species diversity are proposed to be negatively correlated at the small scale, suggesting that biotic resistance operates at this level (Levine and D'Antonio, 1999). Alternatively, invasional meltdown is hypothesized by others to operate at multiple scales – from communities to ecosystems (Simberloff and Von Holle, 1999).

Establishment of nonindigenous species in the Great Lakes has apparently increased with time over the last two centuries, and none have subsequently become extirpated (Ricciardi, 2001), providing evidence for invasional meltdown. Undeniably, many invasions have also gone undetected, and some species are cryptogenic (i.e., species of unknown origin) that may

have been introduced to the Great Lakes in the past (Mills *et al.*, 1993). Alternatively, this apparent increasing accumulation of nonindigenous species may simply reflect increased awareness and monitoring efforts. The increased invasion rate might also be attributed to the increased shipping activity in the Great Lakes. Most invasions since 1970 likely had their sources in transoceanic shipping (Mills *et al.*, 1993; Ricciardi, 2001). Ricciardi (2001) posits that invasions may be succeeding more easily now because of facilitation among nonindigenous species. A positive feedback cycle of invasion should yield a stronger correlation involving all nonindigenous species rather than only a subset of species associated with a particular vector. This is admittedly difficult to assess since separation of effects of facilitation and inoculation pressure on the rate of invasion is not possible.

Ricciardi (2001) found that in about one-third of the cases of exploitative interactions among Great Lakes nonindigenous species reported in the literature, the newcomer benefited from the presence of a previously established nonindigenous species. If facilitation of invasion by other nonindigenous species is occurring in the Great Lakes, fundamental (i.e., 'pioneer') nonindigenous species must alter conditions, resources, or interactions at sites in some way to make them more hospitable for subsequent nonindigenous species. This is the case with the Ponto-Caspian trio made up of *Dreissena polymorpha*, *Echinogammarus ischnus*, and *Neogobius melanostomus*. *Dreissena polymorpha* is the fundamental nonindigenous species that facilitated the establishment of the two subsequent nonindigenous species, since it provides food for *N. melanostomus*, and shelter from predators and food through its pseudofeces for *E. ischnus*. This form of facilitation is similar to successional processes of forests after a disturbance such as fire. Fundamental nonindigenous species behave similarly to the first plants that establish a disturbed area by changing the conditions of the environment and effectively aiding the establishment of subsequent species. As discussed, establishment success of the Ponto-Caspian trio likely depended on the sequence of entry into the Great Lakes, initiated by *D. polymorpha*. Facilitation is a critical aspect of this

process in that the success of newly arriving species depends on the benefit derived from interactions with established nonindigenous species. Dynamics involving nonindigenous species may also break down interspecific interactions, suppressing resistance of established species (both native and nonindigenous). This interpretation differs from the current invasional meltdown model, which proposes that establishment of nonindigenous species is mutually facilitated (protocooperation), creating a positive feedback system. It is unlikely that all nonindigenous species facilitate one another. Moreover, accumulation of additional nonindigenous species through facilitated establishment will diminish when competitive interactions become predominant over beneficial interactions.

A specific observation in the Great Lakes that would corroborate the idea that this process is important would be the strict limitation of *E. ischnus* to locations where *D. polymorpha* and *D. bugensis* occur, or have become newly established (e.g., Lake Superior). Field experiments have shown that *E. ischnus* is able to colonize single stones that are not encrusted with *Dreissena* spp. (van Overdijk *et al.*, 2003). As well, other field observations revealed *E. ischnus* unassociated with *Dreissena* spp. (Nalepa *et al.*, 2001). However, this occurrence is unusual (Nalepa *et al.*, 2001) and may reflect forced dispersal of the amphipod from microhabitats where it is well established and very abundant. This does not negate the fact that *E. ischnus* dispersal is highly governed by the distribution of *Dreissena* spp.

Examination of historic data will further elucidate possible succession of establishment. Locations for which there are long-term data sets may permit one to reconstruct the sequence of establishment and corroborate that *Dreissena* spp. establishment occurred prior to that of *E. ischnus* and *N. melanostomus* during the range expansion of these three species.

Intermediate Disturbance Hypothesis

The results from this study indicate that *E. ischnus* is not distributed in the Great Lakes according to the expectations of Elton's hypothesis. It may be that all sites in the Great Lakes are so greatly influenced by stressors that *E. ischnus*

cannot disperse to many areas that are highly stressed. Individual nonindigenous species' relative tolerances to conditions will ultimately dictate whether they are able to establish in the Great Lakes.

The intermediate disturbance hypothesis predicts that biotic diversity is greatest in communities subjected to moderate levels of disturbance. If biotic resistance to invasion is not occurring in the Great Lakes and the intermediate disturbance hypothesis holds, observations of more nonindigenous species may occur where there are intermediate levels of disturbance. This can be evaluated by comparing the distribution of *Dreissena* spp. at rocky substrate sites along stressor gradients using runs tests. The intermediate disturbance hypothesis would be supported if runs tests revealed 3 runs, with *Dreissena* spp. occurring predominantly in the middle range of stressor gradients. A binomial distribution would theoretically result from this analysis if the intermediate disturbance hypothesis holds and the fit of this curve can be tested. The alternative hypothesis would be that that *Dreissena* spp. distribution is not binomial.

Scale Dependent Biotic Resistance

Levine and D'Antonio (1999) note that mathematical models are based on communities that are at equilibrium prior to invasion, whereas many natural communities appear to be unsaturated or in early successional states (Cornell, 1999). Depending on the study, the relationship between invasion success and community diversity has been found to be negative, positive, or nonsignificant (reviewed by Levine and D'Antonio, 1999). Negative relationships, when observed, occur at small spatial scales (e.g., ~1 m^2 or less). Positive relationships tend to occur at regional scales (thousands of square meters) and suggest that the same environmental properties that support a rich diversity of native species may also support a rich diversity of introduced species (Levine and D'Antonio, 1999).

Byers and Noonburg (2003) developed a model that proposed that native and exotic species diversity should often be positively correlated in large-scale observational studies, but negatively correlated in small-scale experimental

studies. This discrepancy suggests that the scale of invasion studies may be an important influence on the perceived outcome. They also showed that changes in the number of available resources across communities may cause invasion success to appear to be positively correlated with native species diversity at larger scales. The strength of the positive correlation, however, was found to depend on the relationship between niche breadth and species diversity in natural communities. Adding species to a community or removing resources has a similar effect – increasing the sum of interspecific interaction strengths, which decreases invasion success.

The ability to examine data at various scales in my study allows testing of Byers and Noonburg's model. Results from my study suggest that examination of the Great Lakes at a range of scales produces different associations of *E. ischnus* with stressor variables, and they may be evidence in support of Byers and Noonburg's model. This can be further investigated to see if resources, niche breadth, and species diversity influence the strength of correlations.

Using 2002 and 2003 data, scale dependent biotic resistance can be evaluated for the Great Lakes. Examination of nonindigenous species diversity and native species diversity on a lake-by-lake, site-type-by-site-type, and site-by-site basis could confirm the scale dependent correlations proposed by Byers and Noonburg (2003).

Biotic resistance at various scales could be assessed by incorporating 2003 data to runs tests and logistic regressions performed in this study for either *E. ischnus* or *Dreissena* spp. Significant associations were suggested by the 2002 data, although they were not significant at the Bonferroni-corrected 0.0083 level. Power of these tests will also be improved with the incorporation of the later samples. A finding of nonsignificance of analyses at large scales (all the lakes) and significance of analyses at small scales (e.g., individual Great Lakes, site-type, and/or site) would support Byers and Noonburg's model that biotic resistance occurs at small scales. This may also imply that invasional meltdown is occurring at the larger scales, rather than biotic resistance. Biotic resistance

that purportedly occurs at small scales can be evaluated by performing analyses on smaller sections of lakes.

CONCLUSIONS

This study did not reveal an association between *E. ischnus* distribution in the Great Lakes and stress exerted on watershed-scale habitats (Overall Nutrient Input, Total N + P Loading, Agricultural Stress, Overall Population Density, Overall Pollution Loading, and Relative Maximum PC Score). Analyses that revealed unadjusted probability levels that were < 0.05 (i.e., Overall Population Density for Lake Michigan sites, Overall Pollution Loading for Lake Erie sites, and Relative Maximum PC Score for high-energy sites) may become more powerful with the incorporation of 2003 samples. None of the analyses provided support for Elton's hypothesis that invasion is more likely to occur in disrupted communities than in those that are intact. *Echinogammarus ischnus'* presence at sites that are influenced by varying degrees of these stressors and concurrently occupied by *Gammarus fasciatus* and *Dreissena* spp. suggests that the nonindigenous species occurs wherever conditions are suitable, giving precedence to Baltz and Moyle's hypothesis over Elton's hypothesis. The validity of these conclusions is uncertain given that *E. ischnus* may have not yet dispersed to all possible locations at which they are able to persist, and the low power of the tests. A better method of testing the hypotheses may be to evaluate the distribution of *Dreissena* spp. along stressor gradients because *Dreissena* have both greater dispersal rates and have had more time to reach all of the boundaries of the Great Lakes basin.

A factor that seems to determine the distribution of *E. ischnus* more strongly than disturbance alone is the distribution of *Dreissena* spp., which provides necessary microhabitat for the amphipod. This novel finding at a large geographic scale suggests that dreissenids may regulate the distribution of *E. ischnus* at the landscape scale as well as at the microhabitat scale. This also suggests that the successful invasion of the Great Lakes by *E. ischnus* was a consequence of the prior establishment of *Dreissena polymorpha* and implicates invasional meltdown as a real and important invasion process. Dependence of *E. ischnus* establishment on the prior establishment of *D. polymorpha* suggests that the sequence of establishment is critical for facilitative interactions to occur.

The entry mechanism (provided by shipping and ballasting activities), and the condition of the receiving habitat appear to be important for establishment, whereas disturbance regimes imparted by population density may be important for the dispersal of *E. ischnus*. Several factors seem to interact to determine establishment success when using *E. ischnus* as a case study. Successful establishment seems be determined by the nonindigenous species being at the right place at the right time. As shipping and impacts of population density will continue in the Great Lakes with ongoing urban/industrial development and human population growth, species such as *E. ischnus*, can be expected to continue to invade and thrive.

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