



Spatial and temporal variation in the distribution of burrowing mayfly nymphs (Ephemeroptera: *Hexagenia limbata* and *H. rigida*) in western Lake Erie

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ABSTRACT

In the early 1990s, burrowing mayfly species reappeared in sediments of the western basin of Lake Erie after an absence of over 30 years due to episodic hypoxia at the sediment–water interface. Long-term monitoring of adult mayflies at shoreline areas had revealed that *Hexagenia rigida* was more abundant than *Hexagenia limbata* during the initial recolonization period, but was gradually replaced by *H. limbata*. We hypothesized that this shift in dominance would be confirmed by the distribution and abundance of nymphs. We identified nymphs collected each spring throughout western Lake Erie from 1997 to 2004. The relative abundances of *H. rigida* and *H. limbata* nymphs exhibited the same temporal sequence as adults. Furthermore, the number of sites in the western basin in which *H. rigida* occurred decreased as the occurrence frequency of *H. limbata* increased. *H. limbata* were dominant in the basin by 2004. *Hexagenia limbata* nymphs persisted in the center-most part of the basin, whereas *H. rigida* did not, possibly due to differences in tolerance to hypoxia. There were no significant differences in body size between the two populations. Differences in dispersal distance from source populations and the timing and success of egg hatching likely accounted for the initial colonizing success of *H. rigida*, but the differential ability of *H. limbata* eggs to overwinter in sediments and possible tolerance of nymphs to hypoxia has possibly led to its current dominance in the western basin.

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Introduction

Species replacement occurs when a dominant species is overtaken by another in terms of population density and/or distribution. This may result from interspecific competition or differing predation pressures, among other factors or from changing environmental conditions that alter the species' relative abilities to persist (Juliano, 1998). Replacement of native species by invasive species has been widely studied (Bøhn et al., 2008; Juliano, 1998; Kiesecker et al., 2001) as have replacements among invaders (Lohrer and Whitlatch, 2002; Ricciardi and Whoriskey, 2004). Invaders can influence the population dynamics of other species by acting as predators (Woodward and Hildrew, 2001), by increasing competition (Human and Gordon, 1996) and by altering habitats making them unsuitable for existing species (Wallentinus and Nyberg, 2007).

Species replacement can also occur among native species. Most of these studies, however, focus on the effects of changes in one species' dominance on other taxa (often through succession), but mechanisms responsible for the replacement are seldom explored or are difficult to discern because multiple factors (e.g., predation, disease, and adverse

weather) may occur simultaneously or successively (Halpern et al., 1997; Hargeby et al., 1994).

In the absence of apparent causal external factors, it becomes difficult for researchers to explain turnover among native species, especially when population trends are not observed from the onset of colonization (as they often are in studies with invasive species). In this study, we documented the replacement of populations of one native species by another following their reestablishment after an extended absence, caused by environmental disturbance.

During the early 1990s, populations of two species of burrowing mayflies, *Hexagenia limbata* (Serville) and *Hexagenia rigida* McDunnough (Ephemeroptera: Ephemeridae), reappeared and rapidly became established in extensive areas of the western basin of Lake Erie after their near-absence of over 30 years (Krieger et al., 1996). *Hexagenia* were the dominant benthic invertebrates in western Lake Erie before the 1950s (Wright and Tidd, 1933). However, comparison of nymphal densities from surveys conducted in 1929–1930 (Wright and Tidd, 1933) with 1951–1952 (Wood, 1973) showed a 90% decline in the *Hexagenia* population in the open waters of western Lake Erie (Wood, 1973). The disappearance of *Hexagenia* from most of the western basin was attributed to increased loadings of nutrients to the lake that resulted in eutrophication and frequent episodes of hypoxia at the sediment–water interface (Beeton, 1965; Reynoldson et al., 1989). From the early 1960s onward, *Hexagenia* were limited to a small area southeast of the mouth of the Detroit River (Krieger et al.,

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2007), presumably sustained by recruitment from populations in the Detroit River (Thornley, 1985). The reduction of phosphorus loadings into Lake Erie during the 1970s and 1980s (Makarewicz and Bertram, 1991) and the establishment of filter-feeding dreissenids (Holland, 1993), preceded the reappearance of *Hexagenia* beginning as early as 1991 (Krieger et al., 1996). The re-establishment of *Hexagenia* in the western basin occurred rapidly, especially along the shorelines (Krieger et al., 1996). Cooperative efforts to annually assess the distribution of zoobenthos in western Lake Erie, subsequent to the first observations of *Hexagenia*'s reappearance (e.g., Krieger et al., 1996; Schloesser et al., 2000), provided samples from which to document changes in *Hexagenia* distribution patterns from the onset of colonization.

Corkum (2010) determined that *H. rigida* male adults predominated over *H. limbata* in light traps along Ontario shorelines of the western basin of Lake Erie during the initial colonizing period. However, over the ensuing 8 years, *H. limbata* became more prevalent. Collection of adult males alone, however, provides only limited information on the distribution of the two species within the basin. *Hexagenia* females and nymphs could not reliably be identified to the species level until recently. Newly described characters (pigmented structural markings on the head and abdomen) now permit one to distinguish males, females and nymphs of the two species (Elderkin et al., 2012).

The purpose of this study was to determine the species identity of *Hexagenia* nymphs in archived samples from the western basin of Lake Erie and to document patterns of species replacement between *Hexagenia* populations over 8 years, following their reappearance. Furthermore, we postulate explanations for the observed dominance shift by contrasting the populations' life history patterns as well as differences in morphological characteristics that could lead to differences in potential competitive ability. We hypothesized that changes in the relative abundance of nymphs through time would reflect those of adults. We also expected the spatial distributions of each population to expand in parallel with these shifts. For example, as *H. limbata* increases in dominance, its distribution (the number of sites at which the species is found) in the western basin should also increase.

Material and methods

Data collection

Hexagenia nymphs were examined from archived samples originally collected as part of an annual reconnaissance that began in 1995 at a series of stations throughout the western basin of Lake Erie (J.J.H. Ciborowski, University of Windsor, pers. comm.). Although populations had become re-established in the western-most portions of the basin as early as 1993, nymphs were only sporadically encountered at more easterly stations prior to 1996 (Krieger et al., 2007).

Specimens examined in this study were collected from 1997 to 2004. From 1997 to 2003, they were collected within a grid of up to 41 sites (5 replicate petite ponar grabs per site, with sites located 6 km apart). Not all sites were sampled each year due to logistic difficulties. In 2004, triplicate Ponar grabs were collected from over 200 sites stratified-randomly with respect to basin, depth and substrate type throughout all of Lake Erie, as part of the Lake Erie Collaborative Comprehensive Survey (Environment Canada and US Environmental Protection Agency, 2008; Krieger et al., 2007). Samples from the 2004 whole lake survey revealed that *Hexagenia* nymphs were present only in the western basin. Selected data from these surveys were also previously used by Krieger et al. (2007). In particular, *Hexagenia* densities (both species combined) from all western basin stations in the 2004 survey, and from the easternmost stations (east of Pelee Island) in earlier years were incorporated with other collections to estimate year-to-year variation in the Island area of western Lake Erie and along the south shore of the central basin.

Samples were collected between April and June each year (except in 2000 when samples were obtained in June and July). In the field, samples were emptied into a 250- μ m mesh sieve bucket and rinsed in lake water to remove fine material. The retained contents were preserved in a formal-ethanol solution (5:2 95% ethanol:phosphate-buffered 100% formalin, diluted 1:1 with water) (Zhang, 2008). In the laboratory, samples were sieved again into four size classes using brass U.S.A Standard Soil Testing Sieves (4.00, 1.00, 0.50 and 0.25 mm size fractions). All zoobenthos were sorted from each size fraction beneath a dissection microscope, and preserved and stored in 70% ethanol. Only *Hexagenia* nymphs retained in the 4-mm and 1-mm sieve fractions were used in this study. Smaller nymphs could not be reliably identified to species level. In instances where individuals in storage had become desiccated, the samples were reconstituted in a solution of 3.5 g/L trisodium phosphate for 24 h, rinsed in dechlorinated water and returned to storage in fresh 70% ethanol (J.J.H. Ciborowski, University of Windsor, pers. comm.).

Nymphs were identified to species by examining patterns of pigmented markings on the abdomen and the head (Corkum, 2010; Elderkin et al., 2012). A very small number of damaged or faded individuals could not be identified. They were assigned a species identity (*H. limbata* or *H. rigida*) based on the relative abundance of each species present at a particular site. If none of the nymphs at a site could be identified, they were assigned a species identity based on relative abundances at neighboring sites.

After each individual had been identified, body length (from the tip of the head to the end of the abdomen) and head width were measured using a Mitutoyo digimatic caliper (Model No. CD-6" CS) and an ocular micrometer on a Wild Leitz dissecting microscope (Model No. 228720), respectively.

Data analysis

To assess changes in interannual abundance, the mean density of individuals for each species collected at each of the n sites sampled each year ($\text{no./m}^2 = \text{average of 5 replicates}$) was calculated. Site-specific means were \log_{10} -transformed, and the grand mean difference between the mean densities of individuals of each species for each year, were determined using a paired-comparison t -test (with $n-1$ degrees of freedom). Relative proportions of each species were also determined for each year using pooled data from the total numbers sampled at each site (rather than the average of the mean densities) of individuals. Proportions were compared to historical observations made in the western basin prior to 1947 (cited in Manny, 1991) as well as to collections of adult males made on the shorelines of Lake Erie from 1997 to 2004 (Corkum, 2010).

To illustrate spatial distributions, maps showing the mean density of nymphs of each species at each site were plotted using ArcGIS version 9.3 software (ESRI, 2008).

Comparisons of nymphal size between species were calculated by pooling the size measurements of individuals at each site and then calculating the mean size (body length and head width) for each species at each site. This analysis used data from only those sites at which both species were present. The raw values were \log_{10} -transformed from which the mean size of nymphs of each species at a site was calculated for each year. Differences in mean size between species overall and for each year were analyzed using paired-comparison t -tests.

Results

Interannual variation in density

H. rigida was initially the more abundant of the two species, but after 1999, *Hexagenia limbata* became increasingly dominant, representing over 90% of the nymphs collected by 2004 (Table 1). In 1997 and 1998, there was a significant difference between the

densities of each species occurring ($t_{(29)} = 4.543$, $p < 0.001$ and $t_{(30)} = 2.679$, $p = 0.012$, respectively), with *H. rigida* being the more abundant of the two. In 1999, there was no significant difference between the densities of each species ($t_{(36)} = 0.817$, $p = 0.420$). However, in the years following 1999 (2000–2004), *H. limbata* was significantly and progressively more abundant than *H. rigida* ($t_{2000(30)} = 4.698$, $p < 0.001$; $t_{2001(33)} = 6.471$, $p < 0.001$; $t_{2002(24)} = 3.609$, $p = 0.001$; $t_{2003(28)} = 9.425$, $p < 0.001$; and $t_{2004(82)} = 9.657$, $p < 0.001$). Densities of *H. rigida* gradually declined across years from 1999 onward (Table 1). In contrast, overall mean density of *H. limbata* fluctuated in a relatively narrow range of 100–150 nymphs/m² over the 5 years between 1999 and 2003. Density of *H. limbata* was fourfold higher in 2004. When all numbers were combined on a year-by-year basis, the proportion of *H. limbata* nymphs gradually rose from around 20% of the total in 1997 to approximately 90% in 2003 and 2004 (Table 1). A similar trend was observed in the relative proportion of the sites at which *H. limbata* density exceeded that of *H. rigida* (see below).

Spatial distribution

The breadth of distribution of *H. rigida* narrowed across the western basin of Lake Erie from 1997 to 2004, while the distribution of *H. limbata* expanded throughout the basin (Figs. 1 and 2). In 1997, more sites were occupied by *H. rigida* than by *H. limbata*, specifically in the western part of the basin. Of the 30 sites sampled, *H. rigida* occurred in higher densities at 27 (Table 1). However, by 1999, almost all sites across the basin were occupied by both species (Fig. 1). In 2000, both species occurred in lower densities, but *H. limbata* began to become more widespread than *H. rigida* (Fig. 1). Subsequent to 1999, *H. limbata* densities exceeded those of *H. rigida* at between 80 and 100% of the sites (Table 1).

In the years after 2000, the *H. limbata* population gradually expanded back into the centermost part of the basin, whereas *H. rigida* nymphs did not reappear in that area. By 2004, *H. limbata* dominated the western basin in terms of both spatial distribution and population density (Fig. 2). Densities of *H. limbata* were greater at 80 of the 83 sites sampled in that year.

Highest densities of both species occurred in the western part of the basin, specifically in the offshore regions near the mouth of the Maumee River (Figs. 1 and 2). High densities also occurred along the northern part of the basin near Colchester and, in some years, at the mouth of the Detroit River. Lowest densities occurred in the central area of the basin as well as in the eastern part of the basin near Pelee Island and central Lake Erie. In 2001, both species occurred in highest densities at the northern part of the basin between Colchester and Point Pelee (Fig. 2).

Table 1

Densities of *Hexagenia limbata* and *H. rigida* nymphs and the mean relative abundance (%) of *H. limbata* nymphs in western Lake Erie proportion of sites (%) with *H. limbata* > *H. rigida* in benthic collections, 1997–2004. Standard error (SE) on density estimates are given in parentheses.

Year	Total # of sites (n)	Mean (\pm SE) density of nymphs (no./m ²)		Proportions (%)	
		<i>H. limbata</i>	<i>H. rigida</i>	% <i>H. limbata</i>	% of sites <i>H. limbata</i> > <i>H. rigida</i>
1997	30	85.5 (18)	317.1 (70)	21.2	10
1998	31	43.9 (8.4)	72.0 (13)	37.9	39
1999	37	159.2 (28)	136.4 (20)	51.4	51
2000	31	130.2 (31)	48.8 (17)	73.4	84
2001	34	163.7 (36)	57.7 (17)	73.9	94
2002	25	110.3 (22)	64.7 (15)	63.0	83
2003	29	105.6 (30)	26.4 (8.6)	80.0	100
2004	83	422.8 (42)	37.5 (7.7)	91.9	98

Morphological characteristics

Overall, there was no significant difference in either mean body length or head width between *H. rigida* and *H. limbata* (Table 2). On a year-by-year basis, however, *H. rigida* was consistently larger than *H. limbata* except for 2002 (body length only) and 2003 (both head width and body length) in which the reverse occurred. None of these differences were statistically significant, except for 2001, during which *H. rigida* was significantly larger than *H. limbata*.

Discussion

During periods of recolonization following a disturbance, species composition can change through successional processes. These processes are affected by several factors that can contribute either to the increase or decrease of species populations. Life history traits – fecundity, developmental rates, longevity and dispersal – can facilitate species establishment, whereas competitive interactions can inhibit population growth (Halpern et al., 1997). However, it becomes difficult to understand species replacement when species' niches overlap and when species exhibit similar life history patterns, as do *H. limbata* and *H. rigida* (Bustos and Corkum, 2013; Giberson and Rosenberg, 1992, 1994).

Following their reestablishment in the western basin of Lake Erie, the burrowing mayfly community exhibited a shift from *H. rigida* to *H. limbata* dominance. These findings are consistent with previous observations of the adults of these two species collected along the northern shoreline of Lake Erie's western basin (Corkum, 2010). Analyses of adult abundances showed that *H. rigida* were much more numerous in the western basin in 1997 but by 2004, *H. limbata* represented over 90% of the adults captured. The shift of dominance in favor of *H. limbata* is also reflected by data that showed that *H. limbata* was the historically dominant species in the western basin in the 1940s. Data collected by Dr. David D. Chandler from 1942 to 1944 revealed that the burrowing mayfly population in Lake Erie consisted of 75% *H. limbata* and 25% *H. rigida* (cited in Manny, 1991). Similar results have also been found in other areas of North America. In Lake Winnipeg, for example, *H. limbata* has historically dominated *H. rigida*, representing almost 88% of the population in 1932 (Neave, 1932) and 80% in 1969 (Flannagan, 1979). Although relative proportions showed that *H. limbata* gradually became the more dominant of the two species in western Lake Erie, there were no clear increases in the numbers of *H. limbata* nymphs in the years before 2004 (Table 1). Rather, the changing relative proportions reflected declining densities of *H. rigida*.

Nymphal densities also varied greatly among years, with declines in both species occurring in 1998, 2000, 2002 and 2003. Interannual variation has been documented in other studies of Lake Erie *Hexagenia* populations (e.g., Krieger et al., 2007; Schloesser et al., 2000) and could be attributed to a number of factors. The low densities recorded in 2000 could be an artifact of the lateness of sampling in that year (June and July vs. May to mid June in all other years). *Hexagenia* emergence usually occurs in June and July across its geographic range (Heise et al., 1987). Emergence typically begins in western Lake Erie when water temperature reaches 20 °C and peak emergence occurs in late June (Corkum, 2010; Corkum et al., 2006). *Hexagenia* nymphs are also oxygen sensitive and can suffer high mortality when oxygen levels are low (Winter et al., 1996). Hypoxic conditions still commonly occur in the western basin as a result of thermal stratification. Bridgeman et al. (2006) attempted to backcast years of high and low densities of western basin *Hexagenia* based on spring meteorological records from which periods of high sediment oxygen demand might be inferred (extended episodes of warm, calm weather). They found that 1997 and 2002 had the highest levels of summer stratification (and subsequently the highest occurrence of hypoxia), resulting in the lowest fall recruitment of nymphs. This could account for the lower recruitment of nymphs observed in the

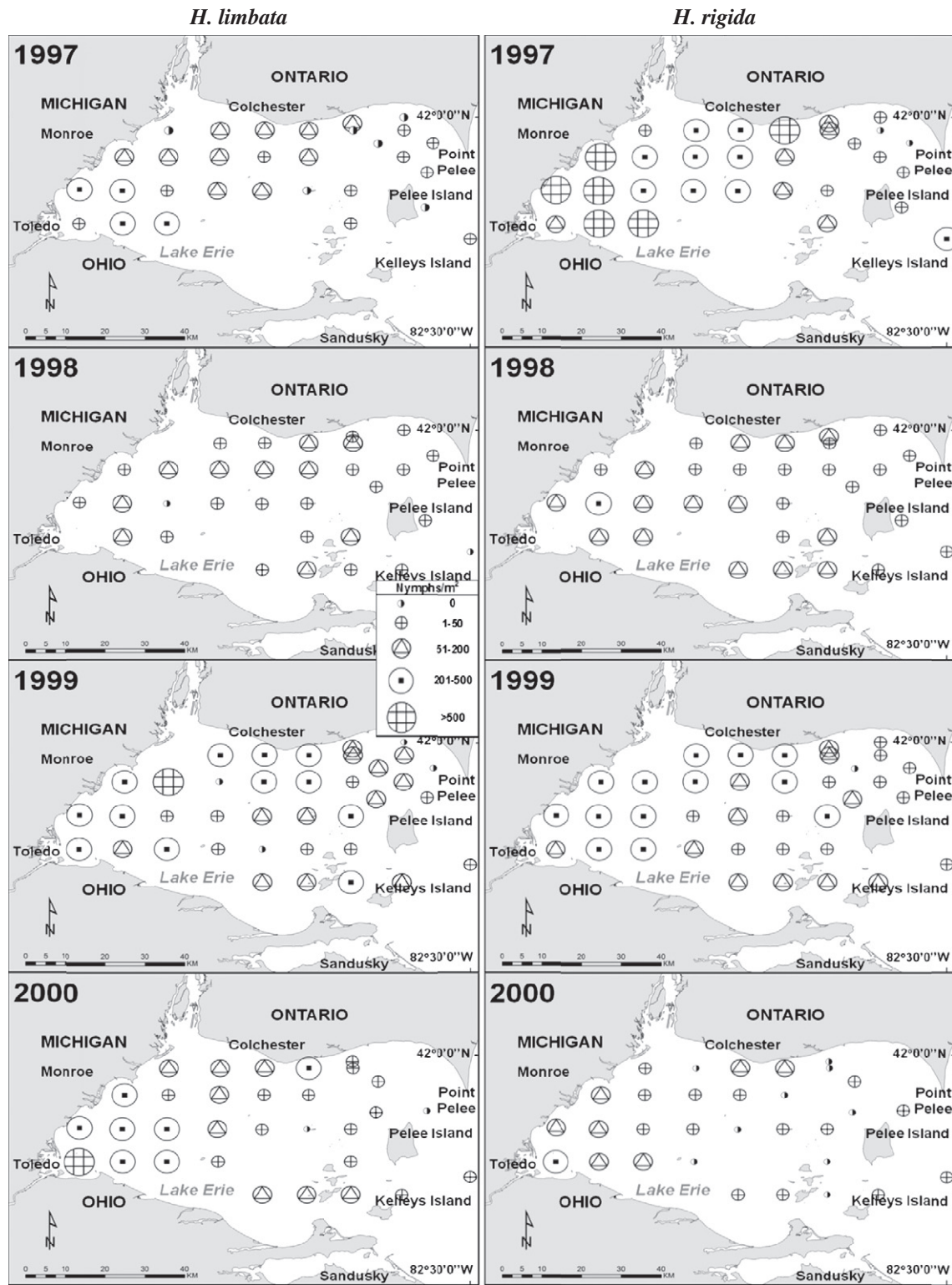


Fig. 1. Spatial distribution of *Hexagenia limbata* and *H. rigida* in the western basin of Lake Erie from 1997 to 2000. Symbols represent different densities of nymphs collected at each sampled site. Areas without symbols indicate sites that were not sampled.

spring of subsequent years (1998 and 2003). The year 2000 had the lowest occurrence of stratification, possibly accounting for the higher recruitment of nymphs observed in the following year (2001).

The relative proximity of source populations of *H. rigida* to the western basin likely contributed to its role as the initial colonizer. *H. rigida* are more commonly found than *Hexagenia limbata* in the Detroit River (Corkum, 2010), which contributes approximately 90% of the water

flowing into Lake Erie (Carter and Hites, 1992). In comparison, *Hexagenia limbata* are more commonly found in Lake St. Clair (Corkum, 2010), which drains into the Detroit River approximately 50 km upstream of Lake Erie. *H. rigida*, therefore, has a shorter dispersal distance to the western basin through the Detroit River. Adult mayflies are relatively weak fliers and their flight is primarily wind-dependent. Observations of inland dispersal of *Hexagenia* adults revealed travel

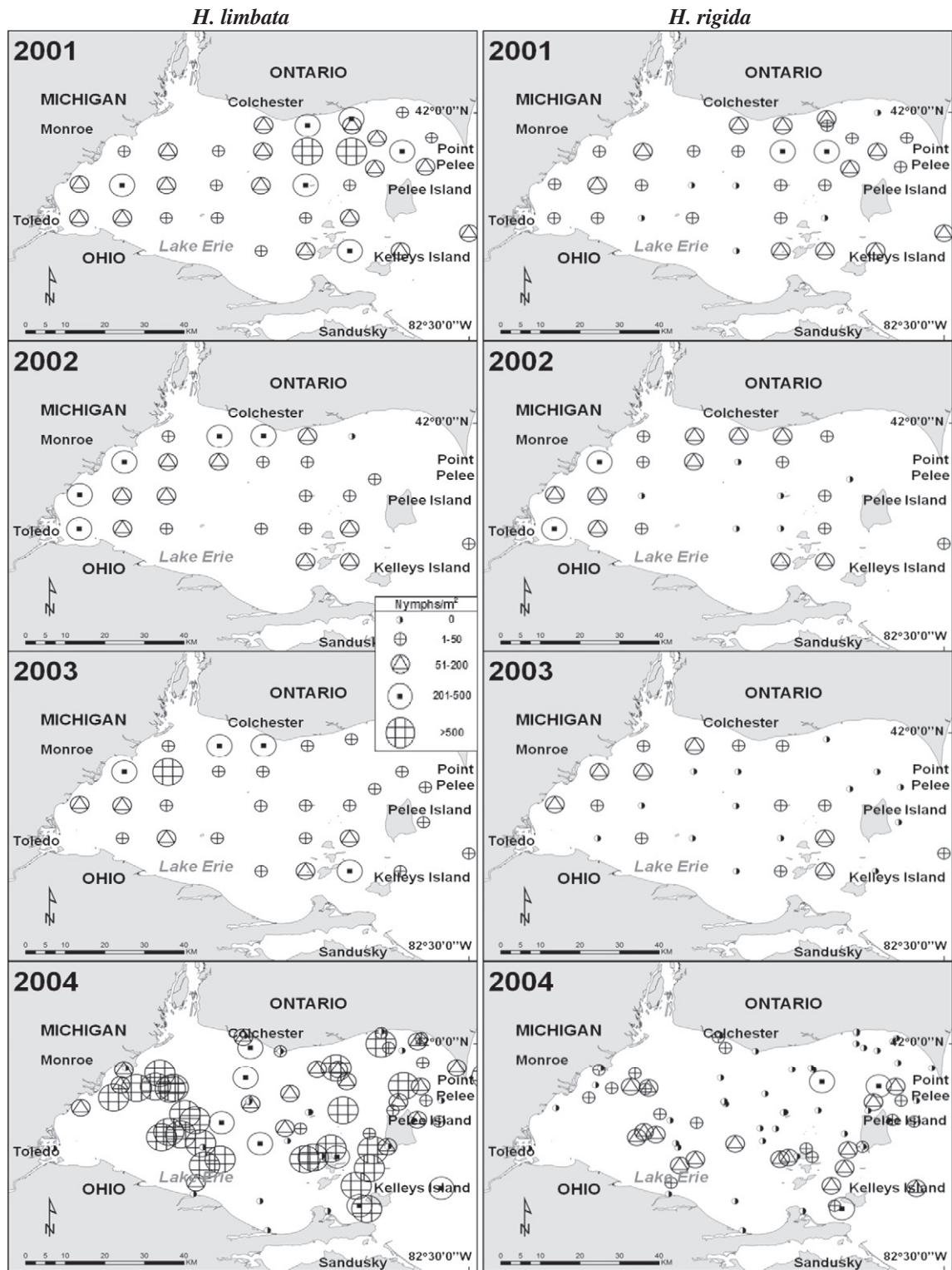


Fig. 2. Spatial distribution of *Hexagenia limbata* and *H. rigida* in the western basin of Lake Erie from 2000 to 2004. Symbols represent different densities of nymphs collected at each sampled site. Areas without symbols indicate sites that were not sampled.

distances of only 1.2 km on average (Kovats et al., 1996). However, *Hexagenia* emerging from offshore locations may have to travel longer distances (10 km or more) before reaching land. Therefore, Lake Erie was originally more accessible to *H. rigida* than to *H. limbata*.

Observed shifts in dominance from *H. rigida* to *Hexagenia limbata* could be attributed to a number of factors. *H. rigida* were found to be consistently larger than *H. limbata* (except for in 2002, in which the

reverse occurred), but these differences were not significant and therefore do not likely account for observed shifts in dominance. However, differential persistence of aquatic stages through unfavorable periods could contribute to changes in relative abundances following an initial colonization period. Laboratory studies have demonstrated that *H. rigida* eggs have a higher survival and hatching rate in a non-overwintering period (Bustos and Corkum, 2013). Eggs that successfully hatch soon

Table 2

Mean body length and mean head width of *H. limbata* and *H. rigida* nymphs for each year and for all years (1997–2004) combined. “n” represents the number of sites (or years at the bottom of the table) included in the analysis for each year. Annual and overall means were evaluated by within year paired-comparison *t*-tests of Log-transformed values. “NS” means that the differences in size between the two species were not significant ($p > 0.05$).

Year	Mean body length (mm)					Mean head width (mm)				
	<i>H. limbata</i>	<i>H. rigida</i>	n	t	p	<i>H. limbata</i>	<i>H. rigida</i>	n	t	p
1997	8.7	11	20	−1.3	NS	1.2	1.4	20	−1.2	NS
1998	16	17	22	−1.6	NS	2.0	2.3	23	−1.9	NS
1999	11	12	31	−1.4	NS	1.5	1.5	32	−1.7	NS
2000	14	14	13	−0.77	NS	1.7	1.6	13	−0.76	NS
2001	11	13	24	−3.2	0.004	1.4	1.7	24	−4.1	<0.001
2002	19	17	13	1.0	NS	2.3	2.2	15	−0.32	NS
2003	15	12	15	1.8	NS	1.8	1.5	15	1.0	NS
2004	14	15	19	−0.7	NS	1.7	1.9	20	−0.5	NS
1997–2004	13	14	8	−0.77	NS	1.7	1.8	8	−1.2	NS

after being oviposited and sink to the lake substrate are more likely to be *H. rigida* than *H. limbata*, thus possibly contributing to the initial dominance of *H. rigida* in the western basin. Differences in egg hatching in these species also may influence long term establishment. Despite *H. rigida*'s greater egg hatching success in warm water, *H. limbata* eggs are more likely to survive extended periods of cold storage, such as occurs over winter. Bustos and Corkum (2013) showed that the longer eggs remain in cold sediment (which is anoxic), the less likely *H. rigida* eggs are to hatch. After a year of cold storage, *H. rigida* had a 0% survival and egg hatching rate, whereas approximately 45% of *H. limbata* eggs remained viable into the following spring (Bustos and Corkum, 2013).

The changes in relative distributions of both species may reflect a difference in relative tolerance of the two species to periods of reduced oxygen. As *H. limbata* came to represent a larger proportion of the population, we also observed that *H. limbata* became more broadly distributed, whereas *H. rigida* became more restricted in distribution. This was especially evident in the most central offshore portions of Lake Erie's western basin in which *H. limbata* was more likely to occur than *H. rigida*. Hypoxia is more prevalent in deeper, more remote areas of the basin than along the shorelines (Bridgeman et al., 2006). *Hexagenia limbata* may owe its increasing dominance over *H. rigida* either to an ability of nymphs to better tolerate or recover from hypoxic epibenthic conditions, or alternatively from differential viability of eggs buried in sediments (a seed bank) that are subsequently returned to oxic conditions at the sediment surface by storms (Gerlofsma, 1999). Further study is warranted to investigate the physiological characteristics of both species in relation to oxygen depletion.

From 1997 to 2004 (Figs. 1 and 2), highest densities of both species occurred in the westernmost part of the basin in all years except for 2001, at which time densities were highest in the northern part of the basin between Colchester and Point Pelee. In all years, lowest densities occurred on the eastern side of the basin. Existing populations in the Detroit and Maumee rivers as well as in Lake St. Clair likely facilitated initial recolonization, leading to higher densities in the western area (Corkum et al., 1997; Krieger et al., 1996; Thornley, 1985). Water flowing into the basin from the Detroit and Maumee rivers could transport eggs deposited by adults into these tributaries. The higher densities of nymphs around the Maumee River as opposed to the Detroit River could be attributed to the intensity of flow (Carter and Hites, 1992; Moorhead et al., 2008). Eggs oviposited into the Detroit River may be carried farther into the basin than those released into Maumee River waters (DeVanna, 2011). Differences in sediment quality may also have an effect on egg and nymphal survival (J.J.H. Ciborowski, University of Windsor, unpubl. data). Lower nymphal densities in the east could be attributed to mortality due to the episodic intrusion of hypoxic hypolimnetic water from the central basin into the eastern portion of the western basin (Bartish, 1987; Krieger et al., 2007; Rosa and Burns, 1987; Schertzer et al., 1987), thus reducing epibenthic oxygen concentrations (Bridgeman et al.,

2006). This same principle was proposed by Krieger et al. (2007) to explain low *Hexagenia* density in shallow areas of the central basin.

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