Journal of Great Lakes Research 39 (2013) 280–286

Contents lists available at SciVerse ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

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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ARTICLE INFO

Article history:
Received 29 August 2012
Accepted 28 March 2013
Available online 23 April 2013

Communicated by David Barton

Keywords:
Hexagenia
Lake Erie
Recolonization
Species replacement
Succession

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.

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 Whitlach, 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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http://dx.doi.org/10.1016/j.jglr.2013.03.013

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-μm 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 (no./m^2 = 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