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Colonization of the Laurentian Great Lakes by the Amphipod *Gammarus tigrinus,* a Native of the North American Atlantic Coast

Igor A. Grigorovich[1,*], Misun Kang[2], and Jan J.H. Ciborowski[2]

[1]*Department of Fisheries and Wildlife Sciences*
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061

[2]*Department of Biological Sciences and Great Lakes Institute for Environmental Research*
University of Windsor
Windsor, Ontario N9B 3P4

ABSTRACT. Gammarus tigrinus, *whose natural distribution is restricted to the North American Atlantic coast, has been found at numerous localities across the Laurentian Great Lakes. This amphipod was first discovered in Saginaw Bay of Lake Huron in 2002. However, analysis of archived samples and new material collected during 2001–2004 revealed that* G. tigrinus *is present in all of the Great Lakes. During August 2002, it occurred at an average density of 283 individuals·m^{-2} in Saginaw Bay, where it was outnumbered by the resident amphipods* G. fasciatus *and* Hyalella azteca. *In terms of frequency of occurrence,* G. tigrinus *was the second most numerous amphipod in beds of* Typha *in lower Great Lakes coastal wetlands during July 2004, being outnumbered only by native* G. pseudolimnaeus. Gammarus tigrinus *has a history of ballast water transfer in Europe and it likely exploited this transport vector during its recent colonization of the Great Lakes.*

INDEX WORDS: *Amphipod, nonindigenous species,* Typha *beds, invasion, nekton, Great Lakes.*

INTRODUCTION

The Laurentian Great Lakes have experienced a dramatic sequence of invasions by nonindigenous species (NIS) since the early 1800s (Mills *et al.* 1993). Most of these NIS were native to geographical areas of Europe and Asia, with another sizable contribution from the Atlantic coast of North America (Mills *et al.* 1993). Since completion of the St. Lawrence Seaway in 1959, species native to Eurasia have accounted for approximately 70% of NIS introduced into the Great Lakes, and American Atlantic coast natives for 7% of NIS (Grigorovich *et al.* 2003). These introductions could originate directly from native regions of NIS or indirectly via recently colonized areas linked with the Great Lakes by strong shipping vectors. Several NIS native to the Ponto-Caspian region of Eurasia (i.e., Black, Azov, and Caspian sea basins) have expanded their range into the Great Lakes after becoming established in the Baltic Sea or lower Rhine River basins (MacIsaac *et al.* 2001). Studies exploring dispersal patterns for two of these NIS—the cladoceran *Cercopagis pengoi* and the amphipod *Echinogammarus ischnus*—yield strong evidence for a stepwise colonization from the native northern Black Sea region to the Baltic or lower Rhine River regions to the Great Lakes (Cristescu *et al.* 2001, 2004).

In this study, we describe the first Great Lakes record of *Gammarus tigrinus* Sexton, 1939, an euryhaline amphipod native to the North American Atlantic coast. We demonstrate that *G. tigrinus* is now colonizing shallow coastal margins of the Great Lakes. Native to the mixohaline waters of the North American Atlantic coast, it was first described in 1939 from western England (Sexton 1939). Its European distribution has since expanded to the European mainland, now encompassing the Rhine River, Baltic Sea, and adjacent canals and river drainages (Nijssen and Stock 1966, Jazdzewski and Konopacka 1999, Van der Velde *et al.* 1999). This amphipod currently continues to ex-

*Corresponding author. Present address: 320 Dixon Road, Suite 1016, Toronto, Ontario M9R 1S8. E-mail: IgorGrigorovich@yahoo.ca

tend its range in the Baltic Sea, where it recently colonized the Vistula Lagoon, Puck Bay, and Gulf of Finland (Jazdzewski and Konopacka 1999, Szaniawska *et al.* 2003). *Gammarus tigrinus* has been identified as a potential invader to the Great Lakes based on its invasion history in Europe, physicochemical requirements that enhance survival in ballast tanks, and inbound shipping traffic to the Great Lakes (Grigorovich *et al.* 2003). As with other recent invaders of the Great Lakes (Cristescu *et al.* 2001, 2004), *G. tigrinus* may have followed a stepwise route of invasion from the Rhine River or Baltic Sea to the Great Lakes.

MATERIALS AND METHODS

Collection and Processing of Samples

Samples examined for the presence of *G. tigrinus* were collected from each of the Great Lakes during the summer months of 2001–2004 using a variety of sampling techniques (Table 1). In Superior Bay of Lake Superior and in the vicinity of Middle Sister Island in western Lake Erie, amphipods were gathered using a Petite Ponar grab (area 225 cm^2; 2–5 grabs per location) and/or bottom sled dredge (width 0.38 m, mesh 500 μm; duration 7–12 min, depending on volume of material retrieved). Saginaw Bay of Lake Huron and the eastern shoreline of Lake Michigan were surveyed using a combination of D-frame dip net (mesh 500 μm; 8–16 sweeps per location), core grab (area 33 cm^{-2}; 8–16 grabs per location), and Petite Ponar (8–16 samples per location). These two localities were sampled at discrete depths, corresponding to the location of the emergent macrophyte zone (20–50 cm deep), submergent macrophyte zone (40–75 cm deep), and the deepest point (1.4 to 2.3 m) of visible vegetation, no farther than 500 m offshore. The samples were preserved in bulk with ethanol-formalin solution (containing 2.5:1 v/v 95% ethanol:100% formalin, diluted 1:1 with water), and all zoobenthos were sorted from debris in the laboratory.

In the lower Great Lakes wetlands and Saginaw River, amphipods were gathered by sweeping a D-frame dip net (mesh 500 μm; typically three sweeps per site) through the entire water column from immediately above the sediment layer to the surface, thereby covering all microhabitat types. Material was immediately emptied into a white pan, and the first 150 invertebrates observed were hand-picked into 70% ethanol. Coastal wetland emergent vegetation in the lower Great Lakes was generally dominated by cattail (*Typha* sp.) (G. Grabas, Environment Canada, pers. comm.).

Sampling sites represented a combination of littoral coastal (< 0.5 km from shore) and wetland habitats at depths < 2.0 m.

In the laboratory, amphipods were separated from other material beneath a dissection microscope, identified to species, and enumerated.

Representative voucher specimens of *G. tigrinus* from Saginaw Bay of Lake Huron have been deposited in the Canadian Museum of Nature, Ottawa, Ontario (entire specimens preserved in ethanol; catalogue numbers CMNC 2004-2582 to 2584).

Identification of Amphipods

Amphipod species were identified using the taxonomic keys by Bousfield (1958, 1989), Holsinger (1976), and Grigorovich (1989). Based upon traditional taxonomic characteristics, at least four amphipod species residing in the Great Lakes could be readily recognized by their distinctive exoskeletal features (e.g., Bousfield 1958, 1989). These species, belonging to the families Talitridae, Gammaridae, and Pontoporeiidae, are *Hyalella azteca* (Saussure, 1858), *Crangonyx pseudogracilis* Bousfield, 1958, *Echinogammarus ischnus* (Stebbing, 1899), and *Diporeia* sp. Representatives of the gammarid genus *Gammarus*, which includes several species native to the Great Lakes (Holsinger 1976), are much more difficult to identify because their taxonomic classification depends on a series of instar- and gender-specific characters, including: 1) the shape of the interantennal lobe of the head; 2) the setosity of the peduncular and flagellar segments of antennae I and II; 3) the shape and armature of pereopods V; and 4) the armature of the epimeral plates (Sexton 1939, Bousfield 1958, Cole 1970, Holsinger 1976). Within the genus *Gammarus* however, species boundaries are confounded by extreme sexual dimorphism and instar-related variability, posing a problem in identification of females and younger instars. Based upon the examination of the aforementioned characters, we identified the three species of *Gammarus*: *G. fasciatus* Say, 1818; *G. tigrinus* Sexton, 1939; and *G. pseudolimnaeus* Bousfield, 1958. *Gammarus pseudolimnaeus* was discriminated from other species of *Gammarus* by its possession of an interantennal cephalic lobe with a rounded upper angle and basal segments of pereopods V bearing a characteristic, free, posterior lobe, which is markedly concave distally (Fig. 1A–F). In addition, *G.*