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

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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*$\cdot m^{-2}$ *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-

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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.*

TABLE 1. Summary of amphipod collections examined for the presence of **Gammarus tigrinus***. Values in parentheses indicate mean density (***G. tigrinus** *no. m^{-2}) in quantitative samples. Other Gammaridae identified: †,* **Crangonyx pseudogracilis***; ‡,* **Echinogammarus ischnus***; ∫, immature instar stages of the Gammaridae.*

Location	Date	Habitat	Sampling method	No. of Amphipods Collected	% G. tigrinus	% G. fasciatus	% G. pseudo-limnaeus	% other Gammaridae	% Hyalella	% Diporeia
Superior Bay Lake Superior	24/06/01– 21/08/01	silty sand, mud	Ponar sampling sled dredging	14	(88) 14	14	—	0	0	71
Muskegon Lake Lake Michigan	16/08/03– 17/08/03	mud, sand *Sagittaria, Typha* *Lemna, Nymphaea*	Ponar and core sampling D-frame net sweeping	2,852	13	15	46	8 ∫	18	—
Saginaw Bay Lake Huron	26/07/02– 01/06/04	sand emergent vegetation	Ponar and core sampling sledge dredging D-frame net sweeping	216	(283) 31	15	0	32 ‡∫	22	0
St. Clair—Shoreline Lake St. Clair	15/07/04	*Typha*	D-frame net sweeping	120	29	3	39	23 ∫	5	0
St. Clair Marches Lake St. Clair	12/07/04– 13/07/04	*Typha*	D-frame net sweeping	168	0	0	0	1 †	99	0
Mitchell's Bay Marsh Lake St. Clair	15/07/04	*Typha*	D-frame net sweeping	94	3	3	7	1 ∫	85	0
Long Point Lake Erie	26/07/04 27/07/04	*Typha*, *Phragmites*	D-frame net sweeping	354	1	1	5	1† ∫	92	0
Middle Sister Island Lake Erie	17/08/01	cobble, *Cladophora* zebra mussels	Ponar sampling sled dredging	533	3	10	0	86 ‡∫	1	0
Rouge River Marshes Lake Ontario	06/07/04	*Typha*	D-frame net sweeping	69	14	19	54	12	1	0
Frenchman's Bay Lake Ontario	06/07/04	*Typha*	D-frame net sweeping	77	14	6	42	38 †∫	0	0
Hydro Marsh Lake Ontario	06/07/04	*Typha*	D-frame net sweeping	130	32	8	42	14 ∫	4	0
Duffins Creek Lake Ontario	06/07/04	*Typha*	D-frame net sweeping	199	18	8	26	47 †∫	2	0

(Continued)

TABLE 1. (Continued).

Location	Date	Habitat	Sampling method	No. of Amphipods Collected	% G. tigrinus	% G. fasciatus	% G. pseudo-limnaeus	% other Gammaridae	% Hyalella	% Diporeia
Carruther's Creek Lake Ontario	05/07/04	*Typha*	D-frame net sweeping	289	27	7	37	16 †∫	14	0
Cranberry Marsh Lake Ontario	05/07/04	*Typha*	D-frame net sweeping	99	0	0	0	0	99	0
Lynde Creek Lake Ontario	05/07/04	*Typha*	D-frame net sweeping	307	18	8	63	11 ∫	0	0
Corbett Creek Marsh Lake Ontario	07/07/04	*Typha*, *Lemna*	D-frame net sweeping	183	23	9	33	11 †∫	23	0
McLaughlin Bay Lake Ontario	08/07/04	*Typha*	D-frame net sweeping	290	20	8	53	18 †∫	1	0
West Side Beach Marsh; Lake Ontario	06/07/04	*Typha*	D-frame net sweeping	351	23	11	40	20 †∫	7	0
Port Darnlington Lake Ontario	07/07/04	*Typha*	D-frame net sweeping	317	14	8	63	14 †∫	1	0
Wilmot Creek Lake Ontario	07/07/04	*Typha*	D-frame net sweeping	46	24	0	15	15 †∫	46	0
Port of Newcastle Lake Ontario	05/07/04	*Phalaris*, *Typha*	D-frame net sweeping	33	39	0	48	9	3	0
Huyck's Bay Lake Ontario	08/07/04	*Typha*	D-frame net sweeping	128	10	3	13	0	73	0
Big Sand Bay Lake Ontario	08/07/04	*Scirpus*, *Typha*	D-frame net sweeping	131	0	0	0	0	100	0
Hay Bay North Lake Ontario	09/07/04	*Typha*	D-frame net sweeping	374	6	0	11	6 ∫	77	0
Amherst Island Lake Ontario	20/07/04–21/07/04	*Typha*	D-frame net sweeping	27	15	0	33	4 ∫	48	0
Parrot's Bay Lake Ontario	09/07/04	*Typha*	D-frame net sweeping	454	6	0	17	2	76	0

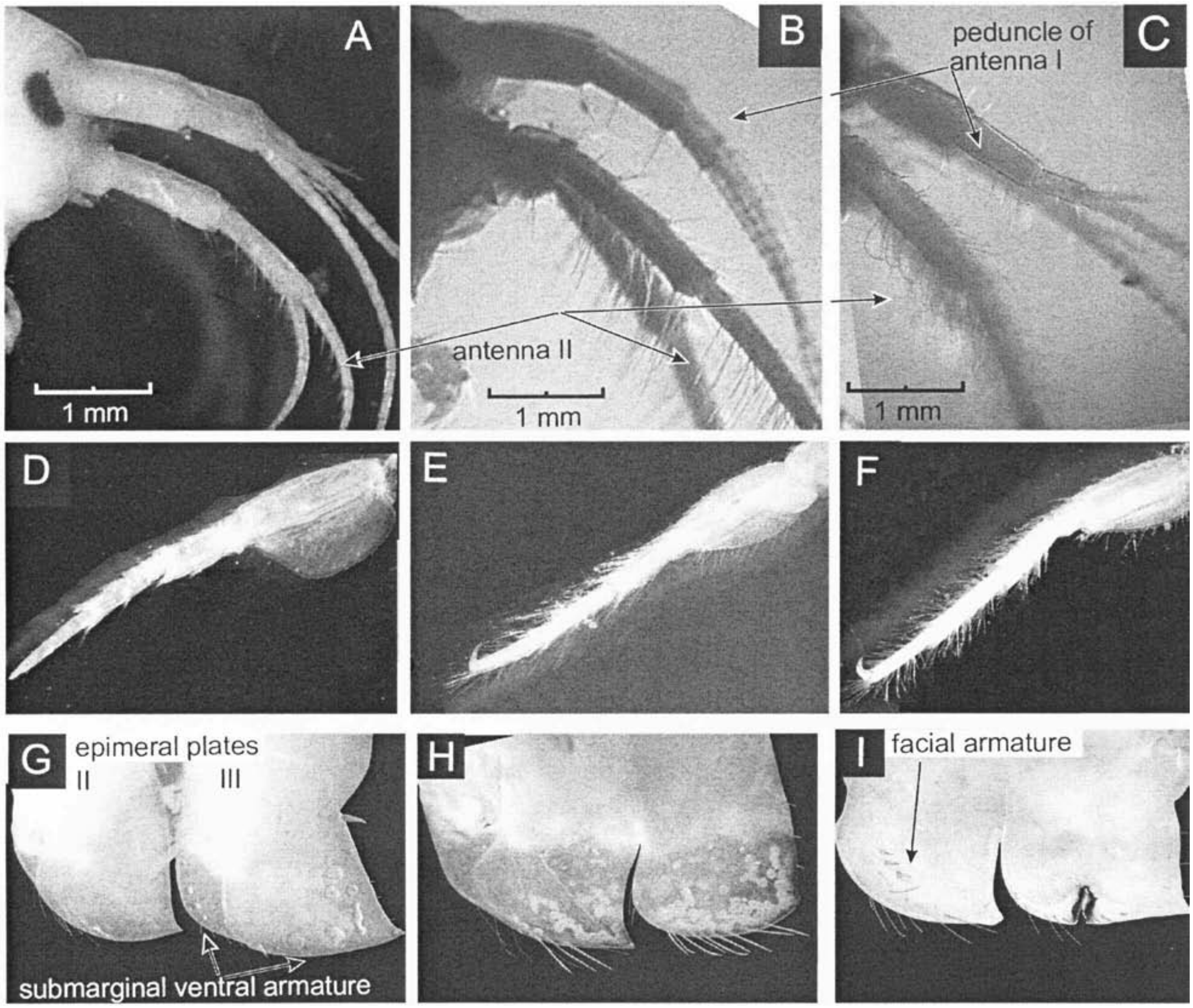

FIG. 1. Morphological features of **Gammarus pseudolimnaeus** ***Bousfield, 1958,*** **G. fasciatus** ***Say, 1818, and*** **G. tigrinus** ***Sexton, 1939. Male*** **Gammarus pseudolimnaeus** ***from Lake Ontario: antennae I and II (A), pereopod V (D), and epimeral plates I and II (G). Male*** **Gammarus fasciatus** ***from Saginaw Bay of Lake Huron: antennae I and II (B), pereopod V (E), and epimeral plates I and II (H). Male*** **Gammarus tigrinus** ***from Saginaw Bay of Lake Huron: antennae I and II (C), pereopod V (F), and epimeral plates I and II (I).***

pseudolimnaeus is distinguishable from other species of *Gammarus* by the armature of epimeral plates II and III. The facial setae on the epimeral plates II are often arranged in groups of two or four (although sometimes the facial setae may occur only singly) in *G. pseudolimnaeus*, whereas those in *G. fasciatus* and *G. tigrinus* are typically single (Cole 1970; Fig. 1G-I). *Gammarus pseudolimnaeus* possesses epimeral plates III that bear the ventral spines, each of which is accompanied by a short seta, whereas ventral insertions on the epimeral plates III are typically single in *G. fasciatus* and *G. tigrinus* (Cole 1970; Fig. 1G-I).

Male *G. tigrinus* and male *G. fasciatus* differ in the setation of the antennae II and pereopods I and II. Setae are long and curly in male *G. tigrinus*, whereas those in male *G. fasciatus* are usually short and lack curled tips (Fig. 1B, C). Ventral margins of the second peduncular segment of antennae I have 2-4 equally strong clusters of setae in *G. tigrinus* and one prominent cluster of setae in *G. fasciatus* (Fig. 1B, C). In both species, female antennae and

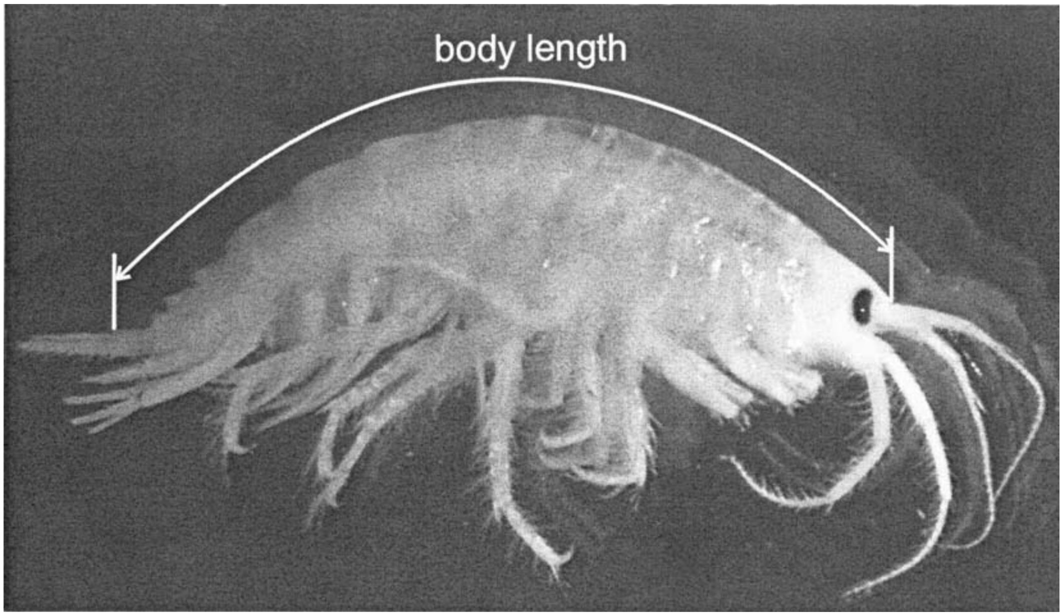

FIG. 2. Lateral view of male* Gammarus tigrinus *from Saginaw Bay of Lake Huron showing body length measurement (body length = 11.0 mm).

pereopods are less richly setose than those of the male. Newly mature males of *G. tigrinus* may not exhibit the curly setae "characteristic" of this species (Nijssen and Stock 1966). Males of *G. tigrinus* from British waters acquire curly setae during the winter months (Hynes 1994). The facial and submarginal ventral setation of epimeral plates II is typically dense in *G. fasciatus*, but sparse in *G. tigrinus* (Fig. 1H, I). *Gammarus tigrinus* possesses ventral spines on the epimeral plates III, while the spines are extremely rare on the epimeral plates III in *G. fasciatus* (Fig. 1H, I). Some variability in the armature of the epimeral plates of *G. tigrinus* is documented in Sexton (1939) and Nijssen and Stock (1966) and was observed in this study.

Specimens of *G. tigrinus* were sorted into males, females, and juveniles, and measured from rostrum to telson using an image analysis system (Fig. 2). We counted ovigerous females and measured clutch size.

RESULTS AND DISCUSSION

Gammarus tigrinus was initially discovered in samples collected in August 2002 in Saginaw Bay of Lake Huron (Fig. 3). Of the 23 individuals of *G. tigrinus* collected, most were found in shallow water (20–40 cm deep) on silty sand overgrown by *Cladophora*. *Gammarus tigrinus* occurred at an average density of 283 individuals$\cdot$m^{-2} (SD = 234, n = 4). The presence of *G. tigrinus* in Saginaw Bay and its tributary, Saginaw River, was confirmed in June 2004 (Fig. 3) when *G. tigrinus* was collected by sweeping a dip net through vegetation and debris in Saginaw Bay and Saginaw River, though none was found in 12 Ponar samples taken at depths of 1.4–2.3 m. Thus, in Saginaw Bay the species inhabited shallow-water sandy habitats and beds of aquatic macrophytes including *Phragmites communis*, *Typha* sp., *Scirpus* sp., and *Cladophora* sp. at depths < 2.1 m.

Analysis of archived samples revealed that *G. tigrinus* was present in the Great Lakes at least a year prior to its discovery in Lake Huron in 2002. The species was found in samples collected in 2001 in Superior Bay of Lake Superior and Middle Sister Island in Lake Erie (Fig. 3). However, the qualitative nature of the samples collected from lakes Superior and Erie (Table 1) prevented us from providing a more quantitative indication of its abundance. *Gammarus tigrinus* was also found at a soft-bottomed site on the eastern shoreline of Lake Michigan adjacent to Muskegon Lake in August 2002 (Fig. 3). During July 2004, *G. tigrinus* was detected at numerous localities in the lower Great Lakes coastal wetlands, from which a total of 586 individuals was collected (Table 1). Based on relative estimates of catch per sampling location (Table 1), *G. tigrinus* was the second most numerous amphipod, being outnumbered only by *G. pseudolim-*

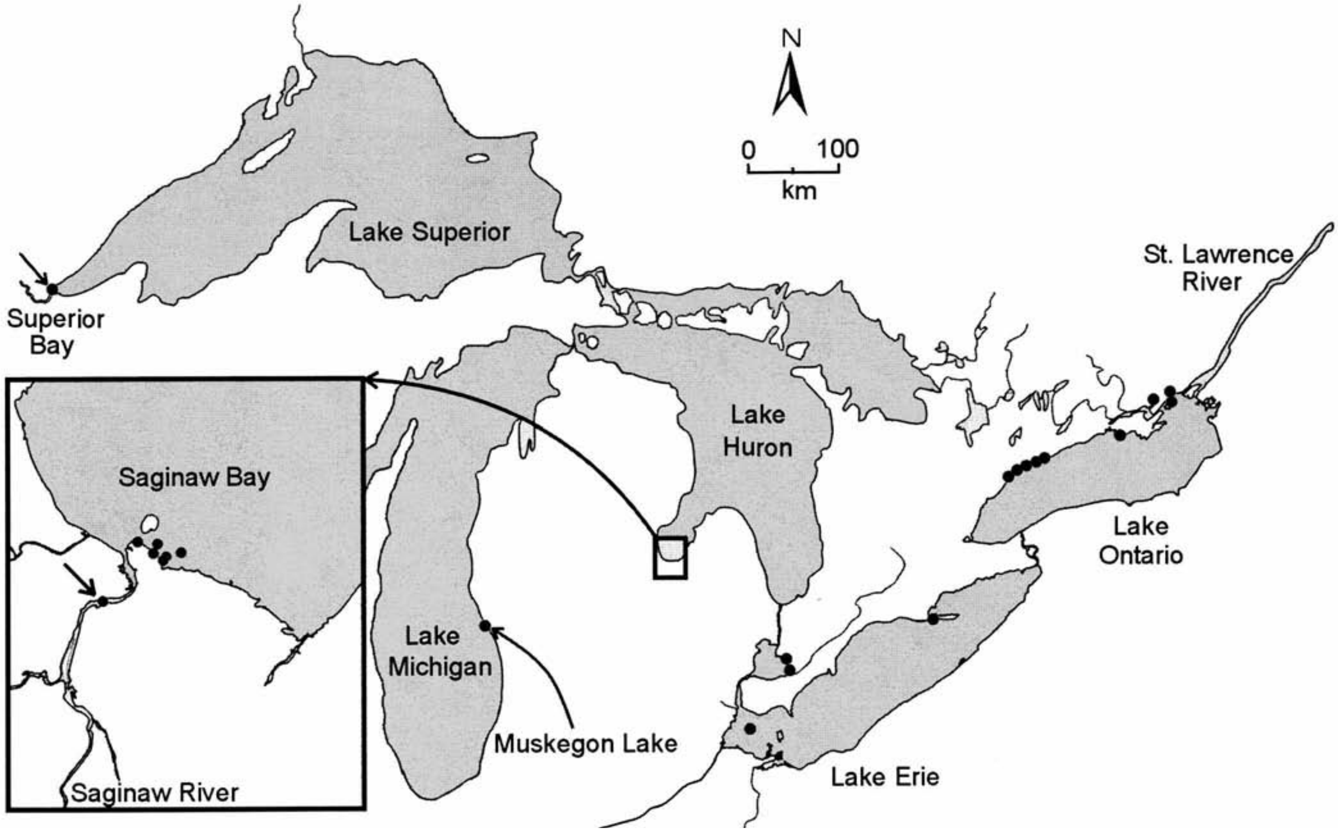

FIG. 3. Occurrence of* Gammarus tigrinus *in the Laurentian Great Lakes during 2001–2004.

naeus (Table 1). These records indicate that *G. tigrinus* has broadly colonized shallow-water habitats around the perimeter of the Great Lakes. Prior studies have documented the rapid spread of this species in the Rhine River and the Baltic Sea, covering nearly 40 km per year (Pinkster *et al.* 1977, Jazdzewski and Konopacka 1999). Between 1975 and 1998, it dispersed along the Baltic coast by some 1,000 km (Jazdzewski and Konopacka 1999).

Densities of *G. tigrinus* observed in the Great Lakes appear to be low compared to those recorded from invaded habitats in Britain and continental Europe. Densities on Rhine River stones rose in excess of several thousand individuals$\cdot$m^{-2} (Van der Velde *et al.* 1999). Densities in Lake Tjeukemeer reed beds peaked at 24,000 individuals$\cdot$m^{-2} during the growth season (Chambers 1977). The Saginaw Bay population consisted of reproducing adults and juveniles during August 2002 and June 2004 (Fig. 4), with females carrying broods as large as 79 individuals (mean brood size = 32, SD = 25, n = 14). Immature instars and females outnumbered sexually mature males by a ratio of 7:1. This observation is consistent with Hynes' (1994) inference that the males of old generations of *G. tigrinus* may die before the females. Mean body length of females from Saginaw Bay (7.6 mm, SD = 3.1 mm, n = 35) was significantly (t = 2.8, P = 0.007) smaller than that of males (10.5 mm, SD = 1.3 mm, n = 10). In the Rhine River, the Netherlands, *G. tigrinus* females begin reproducing at body length ≥4 mm (Pinkster *et al.* 1977). Comparisons of our measurements with published data (Szaniawska *et al.* 2003) showed that both males and females from Saginaw Bay were significantly larger than their counterparts from Puck Bay, Baltic Sea (Kolmogorov-Smirnov two-sample test, P < 0.05). Body length varies greatly among the introduced populations of *G. tigrinus* in Europe, possibly in response to factors such as water temperature, salinity, food supply, etc. (e.g., Hynes 1994, Szaniawska *et al.* 2003).

The date of initial colonization of *G. tigrinus* into the Great Lakes basin is unknown. The species may have been present but remained undetected for an extended period of time due to its superficial resemblance to *G. fasciatus* or other congeners (e.g.,

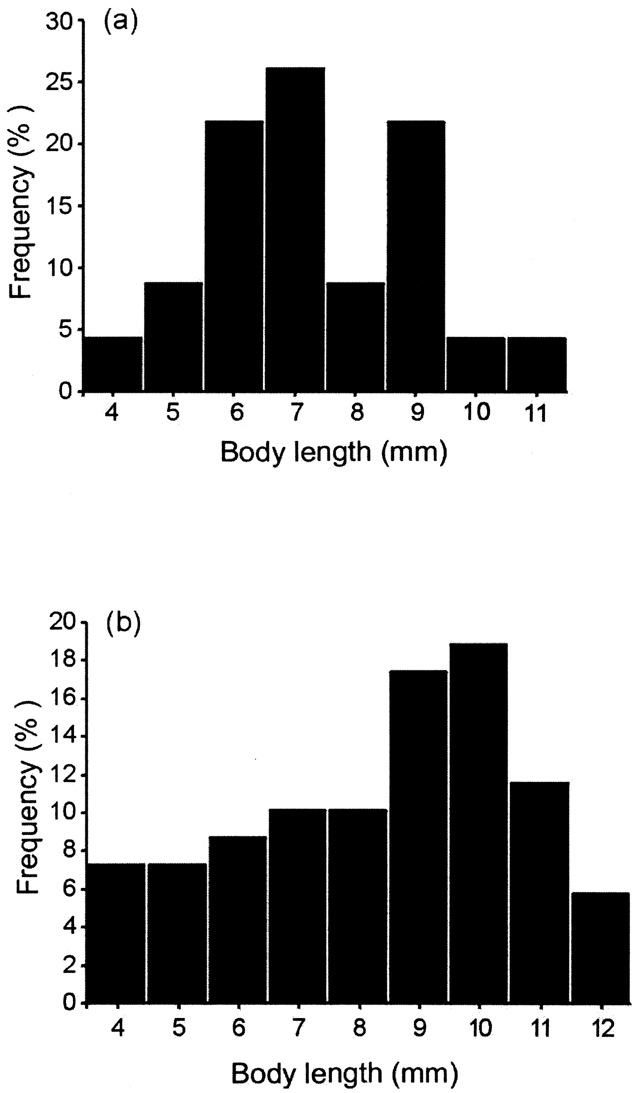

FIG. 4. Body length distribution of* Gammarus tigrinus *in Saginaw Bay of Lake Huron: A—August 2002. n = 23; B—June 2004. n = 69.

G. pseudolimnaeus) indigenous to the Great Lakes (see Grigorovich *et al.* 2003 for discussion on time lags between the initial invasions and detections of NIS). In the mid 1980s, unidentified, large-bodied amphipods belonging to the genus *Gammarus* were observed to occur in the Detroit River (R. Dermott, Fisheries and Oceans Canada, pers. comm.). Although these individuals were not identified to species, they did not fit the range of morphological variability of *G. fasciatus* and, thus, may be the first sighting of *G. tigrinus* in the Great Lakes (R. Dermott, pers. comm.).

Entry vectors invoked for the European invasions of *G. tigrinus* include deliberate stocking, canal development, and ballast-mediated transfer by ships (Van der Velde *et al.* 1999). The likelihood of its introduction into the Great Lakes via discharge of ballast water was predicted using a risk-assessment framework (Grigorovich *et al.* 2003). A survey of residual ballast water and sediment from transoceanic vessels that entered the Great Lakes during 2001 revealed a live *G. tigrinus* individual (I. Grigorovich, unpubl. data), which must have survived conditions in the ballast tank during the trans-Atlantic trip.

The occurrence of *G. tigrinus* in the shallow-water zone of the Great Lakes is in agreement with Bousfield's (1958) reports on the species' associations with shores and shallow habitats in both lotic and lentic waters. Its native habitats include shorelines and shallows of turbid estuaries and river mouths of the North American Atlantic coast (Bousfield 1958), where it occurs at salinity levels of 0–25‰ (Van der Velde *et al.* 1999; D. Kelly, University of Windsor, pers. comm.). As with many coastal species, *G. tigrinus* is capable of rapid ion exchange regulation when moving between salt- and fresh-water zones (Koop and Grieshaber 2000). Euryhaline adaptations of this amphipod could facilitate its survival in ships' ballast tanks, suggesting the current ballast management strategy may not fully protect the Great Lakes from additional invasions (Grigorovich *et al.* 2003). Pinkster *et al.* (1977) believed that *G. tigrinus* require mixohaline waters for reproduction. However, we observed reproducing males, females carrying broods, and offspring indicating that this amphipod is physiologically capable of reproduction in the Great Lakes milieu.

High reproductive capacity, rapid growth and maturation, and efficient feeding strategies have been invoked to explain the development of abundant populations of *G. tigrinus* in the Rhine River (Pinkster *et al.* 1977, Van der Velde *et al.* 1999). For example, *G. tigrinus* was reported to produce up to 16 generations during one reproductive season in the Rhine River, whereas aboriginal species of *Gammarus* produce four or fewer generations a season (Pinkster *et al.* 1977). *Gammarus tigrinus* had a short maturation time in the Rhine River, with females born in the beginning of the season starting to breed in the early summer; females of aboriginal *Gammarus* species need 1 year to reach sexual maturity (Pinkster *et al.* 1977). Likewise, the British populations of *G. tigrinus* mature rapidly, with specimens born in early summer beginning to breed in the autumn (Hynes 1994).

Gammarus tigrinus is omnivorous, feeding on animals, plants, algae, and detritus (Van der Velde *et al.* 1999). As with other amphipods, this species can likely graze on suspended organic matter and algae by filter feeding. This may facilitate development of abundant populations of this species in polluted and nutrient-rich habitats like the Rhine River (e.g., Van der Velde *et al.* 1999).

The adverse impact of *G. tigrinus* on indigenous faunas has been documented in the Rhine River and Baltic Sea where it has been eliminating native species of *Gammarus* (Pinkster *et al.* 1977, Van der Velde *et al.* 1999, Szaniawska *et al.* 2003). Pinkster *et al.* (1977) demonstrated that *G. tigrinus* is significantly more predacious than amphipods native to the Rhine River—*G. duebenii*, *G. zaddachii*, and *G. pulex*. One considerable smaller amphipod *Crangonyx pseudogracilis*, co-occurring with *G. tigrinus* at many localities in lower Great Lakes wetlands, was reported to be heavily preyed upon by the latter species in Lough Neagh, Northern Ireland (Dick 1996). We anticipate that the establishment of an abundant population of *G. tigrinus* will affect the Great Lakes populations of *C. pseudogracilis* via predation and competition for food and habitat. Close monitoring is necessary to establish how other Great Lakes amphipods will interact with *G. tigrinus*.

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