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Research Article

The Baltic prawn *Palaemon adspersus* Rathke, 1837 (Decapoda, Caridea, Palaemonidae): first record, possible establishment, and illustrated key of the subfamily Palaemoninae in northwest Atlantic waters

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Abstract

This study documents the introduction of the European Baltic prawn, *Palaemon adspersus* Rathke, 1837 to the coastal waters of northeastern North America, specifically the west coast of Newfoundland and the Magdalen Islands in the Gulf of St. Lawrence, Canada. Species identification was verified using morphological and genetic criteria. In September 2011, the first specimens of *P. adspersus* were collected in Gulf of St. Lawrence waters near Stephenville Crossing, Newfoundland, Canada. In 2012, additional *P. adspersus* specimens were collected in this area and at St. Andrew's, located further south in western Newfoundland and in 2013 several egg-bearing females were collected further north in York Harbour. Accidental transport by ballast water of ships seems the likely vector for transport of Baltic prawn to the Gulf of St. Lawrence from Northern Europe or the Caspian Sea. It is possible that this shrimp has a wider presence in Atlantic Canadian waters but, due to its close resemblance to native shrimp species, it may have been previously misidentified, as occurred with specimens collected from the Magdalen Islands. We further expect that other species of the genus *Palaemon*, including *P. elegans* Rathke, 1837 from the Baltic Sea or northeastern United States, and *P. macrodactylus* Rathbun, 1902 from the northeastern United States, may invade the Gulf of St. Lawrence. We provide an illustrated key for the identification of these exotic *Palaemon* species and to differentiate them from native members of the subfamily Palaemoninae.

Key words: *Palaemon adspersus*, Baltic prawn, new record, northwest Atlantic, Newfoundland, non-indigenous species

Introduction

The growing extent of biological invasions in coastal waters is widely recognised, with new introductions of exotic species resulting from increased human-mediated global dispersal and global warming (Cohen and Carlton 1998; Ruiz et al. 2000; Hiddink et al. 2012). Long distance dispersal of aquatic species facilitated by pathways between particular regions is defined as an invasion corridor (Ricciardi and Mclsaac 2000). Species movement through invasion corridors mainly occur via ballast water transport (Cohen and Carlton 1998; Cristescu et al. 2001). Ballast water management regulations have been considered

ineffective, especially for macroinvertebrates (Ricciardi and Mclsaac 2000; Briski et al. 2012) and are currently under review in Canada (C. H. McKenzie, Dept. of Fisheries and Oceans, St. John's, NL, Canada, pers. com.). In particular, invasion corridors linking Eurasia with the North American Great Lakes have been reported to be delivering organisms at high rates (Ricciardi and Mclsaac 2000). These invasion rates are generally underestimated, as many species may remain undetected or misidentified for years, and therefore detailed histories of these invasions remain unclear. Therefore, early detection of non-indigenous species will enhance our understanding of their invasion histories.

Successful establishment of a non-indigenous species will be largely determined by its biological requirements and the availability of suitable habitat, particularly if they originate from similar latitude (Carlton 1985; Carlton and Cohen 2003; Niimi 2004). Salinity is an important limiting environmental factor on the distribution ranges of most aquatic species (Paavola et al. 2005). Species with high tolerance to salinity changes, including many crustaceans, are potentially better colonizers, and one of the most successful groups of historic invasions around the world (e.g. Ruiz et al. 2000). One such example is the European green crab, *Carcinus maenas* Linnaeus, 1758 (Carlton and Cohen 2003), which due to multiple introductions from different source populations and different genetic lineages, has recently expanded its distribution range northward in coastal waters of eastern Canada (Roman 2006).

The introduction of *Palaemon adspersus* Rathke, 1837 reported here represents the second European species of *Palaemon* detected in coastal North American waters. The first European species detected was the rockpool prawn, *Palaemon elegans* Rathke, 1837, reported from the northeast coast of the United States in 2010 (JT Carlton, Williams College, Mystic, CT, USA, pers. com.). In addition, the oriental shrimp, *Palaemon macrodactylus* Rathbun, 1902, a species originating from Southeast Asia (Newman 1963), that has spread globally (see González-Ortegón et al. 2007), has been observed in the northeastern United States since 2001 (Warkentine and Rachlin 2010).

In the present study, the possible establishment of the Baltic prawn in western Newfoundland is reported and assessed based on sample collections in this area (2009–2014) and the potential vector for this new introduction is discussed. DNA analysis was used to verify the morphological identification of *P. adspersus*. In addition, an illustrated key is provided to facilitate the identification of palaemonid shrimps in northeastern North America that includes the three most recent introductions not included in previous keys (Holthuis 1952; Williams 1984; Squires 1990, 1996).

Materials and methods

Study area and identification of species

As part of an ongoing project investigating the biodiversity and distribution ranges of several marine fishes along the west coast of insular Newfoundland, pole seining has been conducted annually since 2009 (Table S1). A pole seine

(1.4 m H × 10.0 m L, 7 mm stretched mesh) was pulled 60 – 100 m parallel to the shoreline at 0.3 – 1.4 m depths at nine sampling stations (Figure 1). Catches were identified, counted, and measured before being returned alive to seine sites. In addition, shrimp specimens from an eel fisherman (D. Hynes) in St. Andrew's, caught by fyke net, (3 m bag, 20 m leader, 7 mm stretched mesh) were examined.

Specimens not readily identified to species on site were retained and preserved in 5% buffered formalin for later detailed examination and identification. In 2011, 5 specimens of an unidentified shrimp species were retained from Site S2 (Figure 1) near the community of Stephenville Crossing. Additional shrimp specimens from this area were collected for DNA analysis in 2012. Morphological features of live specimens were first examined and photographed before being preserved in anhydrous ethanol. Environmental parameters, including salinity, water temperature, substrate types and associated vegetation were recorded annually at each site, when possible.

Pole seining was not conducted by the authors in 2013. However, preserved shrimp samples collected by beach seine from Stephenville Crossing Site S2 of that year were provided by C. McKenzie (unpubl. data) from aquatic invasive species surveys. A 25 m long beach seine (19 mm stretched mesh in the wings and belly, and 13 mm in the codend) was deployed by boat 55 m from shore and pulled perpendicular to the shore.

Additional shrimp samples from the southern portion of the Magdalen Islands were collected by N. Simard (Dept. of Fisheries and Oceans, Mont-Joli, QC, Canada) with a pole seine in 2011 (Figure 1, Table S1).

Using morphological and molecular evidence De Grave and Ashelby (2013) have recently indicated that the genus *Palaemonetes* is a junior synonym of *Palaemon*. As such, they suggested the transfer of all *Palaemonetes* species to the genus *Palaemon*. Thus, *Palaemonetes intermedius*, *P. pugio*, and *P. vulgaris* should be within the genus *Palaemon*. Here we have adopted this change using *Palaemon* (= *Palaemonetes*) for these three species. Also, in keeping with De Grave and Ashelby (2013), we use *Palaemon mundusnovus* as a replacement name for the North American *Palaemonetes intermedius* that is a homonymy with an earlier-named Australian species of the same name.

Key morphological and meristic characters are presented to differentiate the exotic species

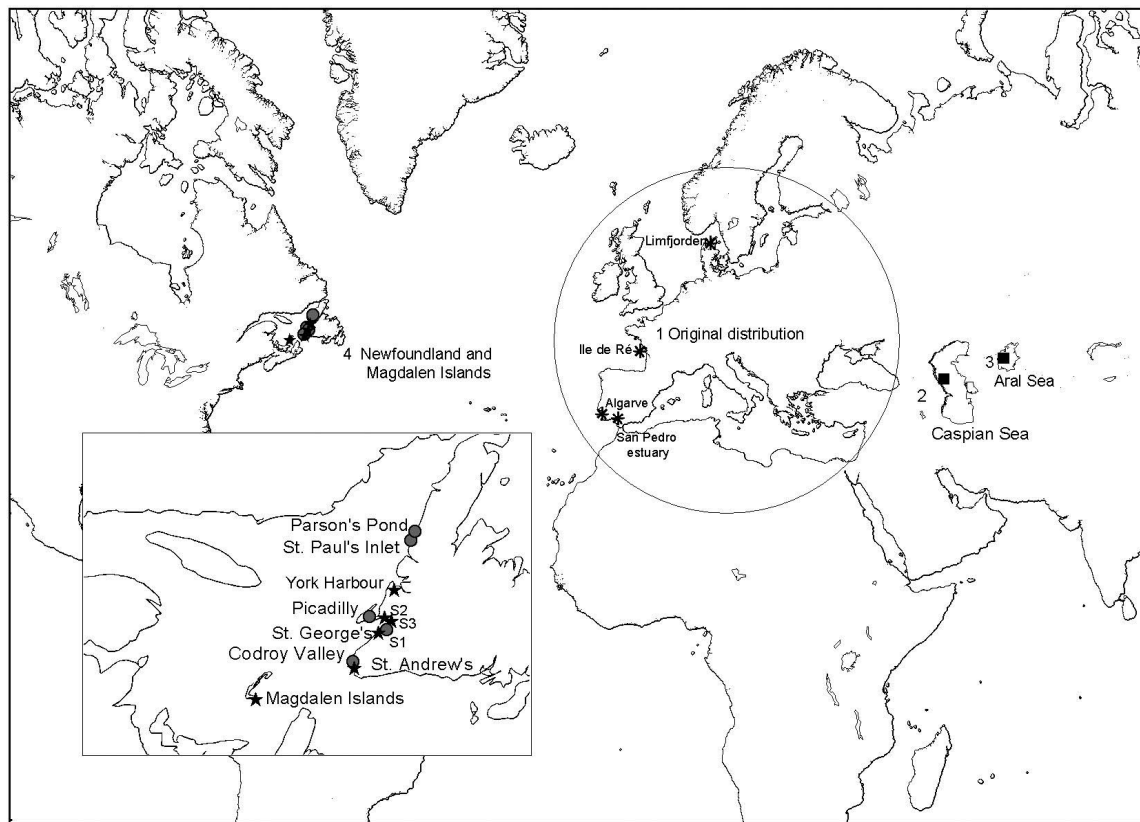


Figure 1. Worldwide distribution of *Palaemon adspersus* Rathke, 1837, and a magnification of the study area in Newfoundland and Magdalen Island (inset); 1. Original distribution; 2. Caspian Sea; 3. Aral Sea; 4. Newfoundland and Magdalen Islands, Gulf of St. Lawrence (Canada): Sampling sites in the western Newfoundland (S1, S2, and S3 are Stephenville Crossing Site 1, Site 2, and Site 3, respectively). Black stars and dark grey points indicate sites where *P. adspersus* have been detected and not detected, respectively in this study. See Table S1 for further details about the sampling sites in the study area. * European locations from which *P. adspersus* 16S DNA sequences were compared with Stephenville Crossing (Canada) sequences.

Palaemon adspersus, *P. elegans*, and *P. macrodactylus* from indigenous species of the subfamily Palaemoninae from New Jersey (US) to Atlantic Canada: *Leander tenuicornis* Say, 1818; *Palaemon* (= *Palaemonetes*) *mundusnovus* Holthuis, 1949; *P. pugio* Holthuis, 1949; *P. vulgaris* Say, 1818; and *Macrobrachium* spp.

Information summarized in the key was adapted from Holthuis (1952), Williams (1984), Squires (1990), and González-Ortegón and Cuesta (2006). In addition, information on colour, habitat, environmental tolerance, and distribution of each exotic species is provided. Specimens of *Palaemon adspersus* from Newfoundland and the Magdalen Islands have been deposited at the Atlantic Reference Centre of the Huntsman Marine Science Centre (Canada) under catalog numbers 79205, 79281, 79282, 79284, and 79285.

DNA extraction, amplification, and sequencing

DNA extractions were obtained from abdominal muscle tissue using the NucleoSpin Tissue kit (Macherey-Nagel and Co, Düren, Germany). The mitochondrial 16S ribosomal rDNA gene (16S rDNA) was amplified with the primers 1472 (5'-agatagaaaccaactgg-3', Crandall and Fitzpatrick 1996), and 16L2 (5'-tgctgtttatcaaaaacat-3', Schubart et al. 2002). PCRs were carried out in a BIORAD MyCycler thermocycler in a volume of 25 µL containing ~25 ng genomic DNA, 200 µM of each dNTP (Roche Diagnostics, Mannheim, Germany), 0.5 µM of each primer, 0.625 U Taq DNA polymerase (Roche Diagnostics), and the buffer recommended by the polymerase supplier. Thermocycling conditions were as follows: 2 min at 95°C, 35 cycles of 20 s at 95°C, 20 s at 48°C,

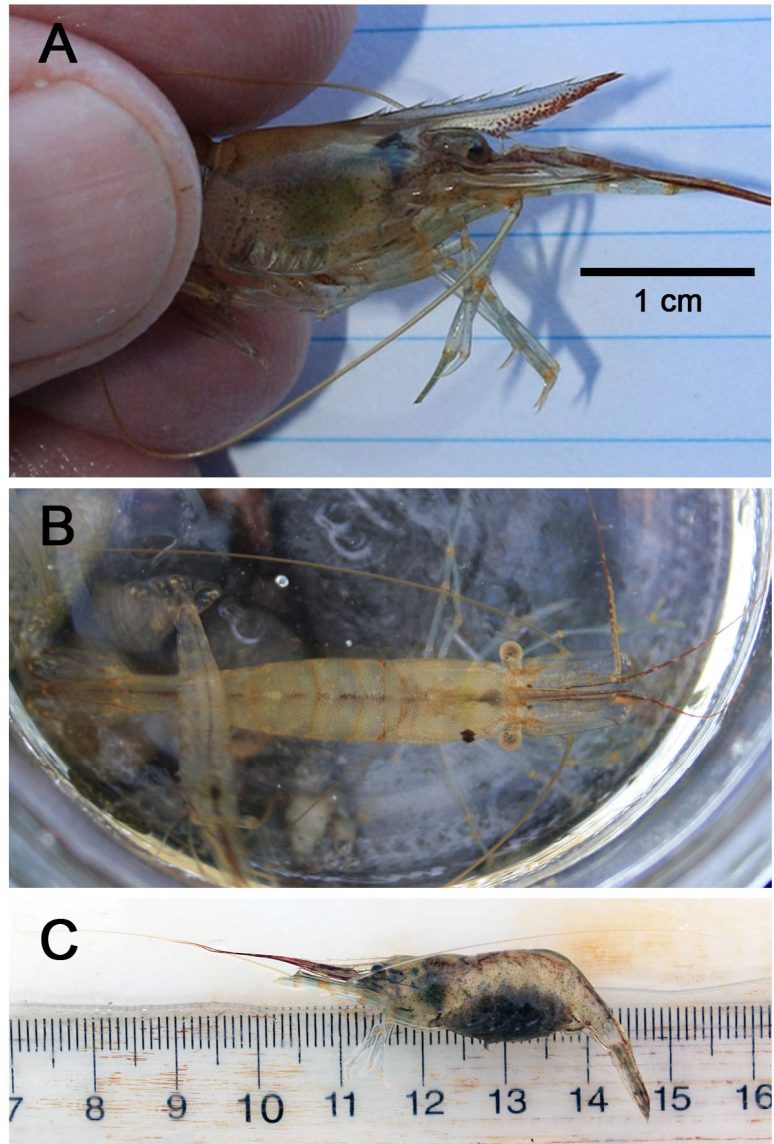


Figure 2. Photographs of *Palaemon adspersus* specimens collected in western Newfoundland, Canada. A – specimen showing red spots on rostrum and yellow bands at the joints of the pereopods; B – specimen showing yellow bands along edges of abdomen segments, and red pigmentation on antennules; C – berried female from York Harbour. Photographs A and B by V. Ramírez-Luna and photograph C by P. Sargent.

45 s at 72°C, and a final 5 min extension at 72°C. The PCR products were resolved in 1.5% agarose gels, and visualized with RedSafe (Ecogen, Barcelona, Spain) staining and ultra-violet transillumination. PCR products were purified using ExoSAP-IT (USB, Cleveland, OH, USA) and sequenced in both directions using PCR primers in a capillary DNA sequencer CEQ 8000 Genetic Analysis System (Beckman Coulter, Fullerton, CA, USA). We sequenced the 16S DNA region of eight specimens from Stephenville Crossing (GenBank accession numbers HF970342-HF970345 and HG971751-HG971754) and five European

specimens (four from Limfjorden, Denmark, accession numbers HG971755-HG971758, and one from Île de Ré, France, accession number HG971759).

To verify the morphological identification of *P. adspersus*, 16S rDNA sequences were obtained from GenBank (Table S2); one from San Pedro River, Spain (accession number JN674330) and one from Algarve, Portugal (accession number JQ042293). We used the 16S rDNA based method to compare sequences between the non-native Stephenville Crossing population and the European population published in GenBank.

Between 477 and 524 base pairs in length were aligned in CLUSTALX v.2.01.12 (Larkin et al. 2007). Phylogenetic and molecular evolutionary analyses were conducted using MEGA version 6 (Tamura et al. 2013).

Results

Field collections and morphology-based identification of P. adspersus

In September 2011, five specimens of an unidentified shrimp species were collected just west of Stephenville Crossing, Newfoundland, Canada (Site S2; Figure 1). Morphological characteristics of these specimens were inconsistent with those of native palaemonids in Atlantic Canada and consistent with those of the European species, *Palaemon adspersus*. Specimens exhibited red spots along the lower edge of the rostrum, yellow bands on the joints of the pereopods (Figure 2A), and antennules with strong red pigmentation (Figure 2B). Further, total length of these five specimens ranged from 49.0 – 53.8 mm, such that all but one specimen exceeded the approximate maximum total length previously recorded for native Palaemonidae species (Anderson 1985; Squires 1990). Substrate and environmental conditions at this collection site (Table S1) were also consistent with known habitat for *P. adspersus* (Berglund 1980; Cuesta et al. 2006; Janas et al. 2013).

The presence of *P. adspersus* was not detected in earlier surveys (2009 to 2011) at other sites along the west coast of Newfoundland, including a site just south of Stephenville Crossing (Site S1; Figure 1). At Site S1, the only crustacean species collected were mysids *Mysis* sp., sand shrimp, *Crangon septemspinosa* Say, 1818, and green crab, *Carcinus maenas*.

In September 2012, 9 and 64 specimens of *P. adspersus*, of which 30 were retained for DNA analysis, were collected at Sites S2 and S3, respectively, near Stephenville Crossing (Figure 1; Table S1). In addition, 107 sand shrimp were collected at Site S3. However, as in the previous years (2009 and 2010), the only crustacean species collected at Site S1 were mysids, sand shrimp, and green crab.

In August 2012, one additional *P. adspersus* specimen was collected in St. Andrew's by eel fisherman D. Hynes (Figure 1). Earlier observations by D. Hynes suggested this species had been present for several years in this area. Additional pole seining in September 2012 adjacent to this

area (Table S1) did not result in the collection of any Baltic prawn but mysids and sand shrimp were collected.

In July 2013, four Baltic prawn specimens, along with sand shrimp and green crab, were retained from a beach seine hauled at Site S2 while sampling for aquatic invasive species (C. H. McKenzie et al., unpubl. data).

In August 2013, three berried female Baltic prawn specimens (Figure 2C) were collected in minnow traps while surveying for banded killifish *Fundulus diaphanous* Lesueur, 1817, in York Harbour, Newfoundland (Figure 1, Table S1). This observation was the first indication that reproduction of Baltic prawn in the Gulf of St. Lawrence could be occurring.

In August 2014, while pole seining, sand shrimp and green crab were collected at Site S2 but no Baltic prawns were detected. However, five Baltic prawn specimens were collected at St. George's, Newfoundland (Figure 1, Table S1), while sand shrimp and green crab were not collected.

A re-examination of a shrimp collection provided by N. Simard from the Magdalen Islands, Quebec, in 2011 (Figure 1, Table S1), showed two specimens originally identified as *Palaemon* (= *Palaemonetes*) *pugio* were actually *P. adspersus*, providing the first record of Baltic prawn in the southern Gulf of St. Lawrence.

16S ribosomal DNA-based identification of P. adspersus

The 16S rDNA region of eight specimens from Stephenville Crossing, four from Limfjorden (Denmark), one from Île de Ré (France) were sequenced and two GenBank sequences of *P. adspersus*, from Spain and Portugal, were used to confirm the morphological identification of *P. adspersus*. These 15 16S rDNA sequences were aligned with 66 16S DNA sequences of 22 species of the genus *Palaemon* and three other 16S DNA sequences from three species of the genus *Macrobrachium* available from GenBank (Table S2). The topology of the maximum-likelihood tree is consistent with a maximum parsimony tree reconstructed from the same data set. That is, the best selected model consistently clustered all sequenced samples of *Palaemon* specimens from Stephenville Crossing within the *P. adspersus* clade (Figure 3). This result strongly supports the conclusion that the specimens collected from Stephenville Crossing belong to *P. adspersus*.

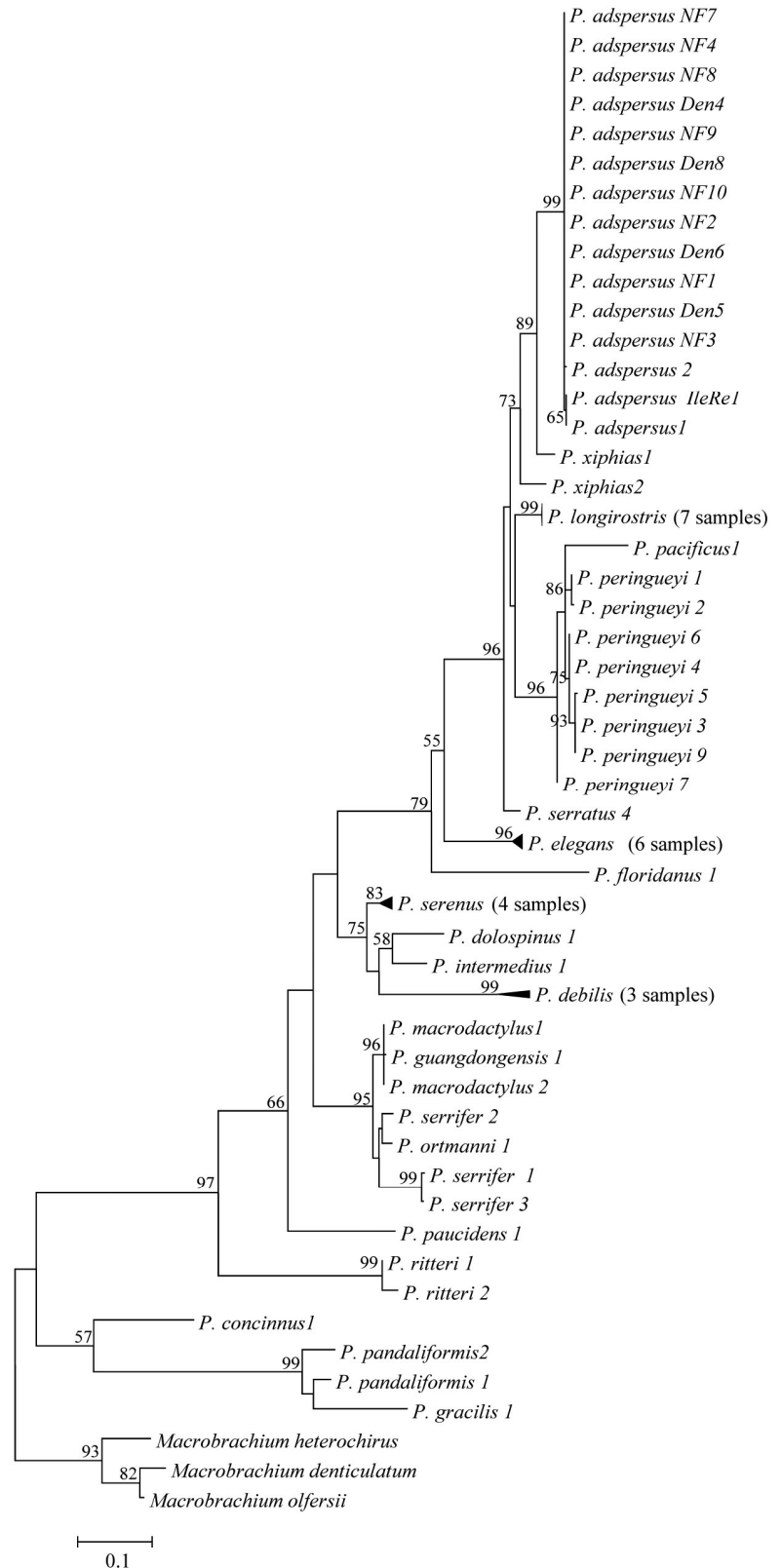


Figure 3. Maximum likelihood phylogenetic relationships based on the 16S DNA sequences of *Palaemon* spp. and *Macrobrachium* spp., which were used as the outgroup. Nucleotide substitution model: TN93+G. All *P. adspersus* sequences cluster into a single clade with high support. The topology of the tree is consistent with a maximum parsimony tree reconstructed from the same data set (not shown).

An illustrated key to identification of the Palaemoninae species in northwest Atlantic waters from New Jersey (US) to Canada (adapted from Holthuis 1952; Williams 1984; Squires 1990)

Family Palaemonidae: Caridea having first 2 pairs of legs chelate, second pair usually larger than first, carpus of second pair not subdivided. Rostrum usually armed with non-movable teeth. Mandibles usually with an incisor process. Subfamily Palaemoninae: Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male, appendix interna on second pleopod of female. Pleurobranch present on third maxilliped segment. Posterior margin of telson with 2 pairs of spines and 1 or more pairs of setae (Holthuis 1952). The technical terms used in the key are illustrated in Figures 4A and 5. Morphological differences among these species are further summarized in Table S3.

1. Hepatic spine present, branchiostegal spine absent; chelate second pereopods enlarged and greatly elongated.....*Macrobrachium* sp.*
 - Hepatic spine absent, branchiostegal spine present (Figure 4B-I); second pereopods not greatly enlarged.....2
2. Cephalothorax without branchiostegal groove; branchiostegal spine originating clearly behind anterior margin of cephalothorax (Figure 4B, C); endopod of first pleopod of male with appendix interna.....*Leander tenuicornis*
 - Cephalothorax with branchiostegal groove; branchiostegal spine slightly displaced from or situated on anterior margin of cephalothorax (Figure 4D-I); endopod of first pleopod of male without appendix interna *Palaemon* spp.3
3. Rostrum usually with 1 dorsal tooth on cephalothorax behind posterior margin of orbit (Figure 4D-F)4
 - Rostrum usually with 2 dorsal teeth on cephalothorax behind posterior margin of orbit (Figure 4G)6
 - Rostrum usually with 3 dorsal teeth on cephalothorax behind posterior margin of orbit (Figure 4H-I)7
4. Rostrum with 5 to 7 dorsal teeth, usually 5 and 1 postorbital tooth; inferior half of rostrum with dark red spots (Figures 2A, 4D); body with a uniform yellowish grey colour and yellow bands at the joints of the pereopods; mandible with palp (Figure 5A)*Palaemon adspersus*
 - Rostrum with 7 to 10 dorsal teeth, usually 8 to 9 (including the postorbital tooth); rostrum without dark red spots on its lower half (Figure 4E-I); body generally almost colourless and translucent; mandible without palp (Figure 5B)5
5. Lower margin of rostrum with 2 to 4 teeth, generally 3; upper margin straight, with dagger-shaped rostrum (Figure 4E); dactylus and fixed finger of second pereopod without teeth on the cutting edge (Figure 5C).....*Palaemon* (= *Palaemonetes*) *pugio***
 - Lower margin of rostrum with 4 or 5 teeth, seldom 3; upper margin concave, tip of rostrum gradually curved upwards (Figure 4F); dactylus of second pereopod with one distinct tooth proximally on cutting edge and fixed finger of second pereopod without teeth on cutting edge (Figure 5D).....*Palaemon mundusnovus* (= *Palaemonetes intermedius*)**
6. Branchiostegal spine on anterior margin of cephalothorax (Figure 4G); colour translucent; mandible without palp (Figure 5B)7
 - Branchiostegal spine slightly displaced from or situated on anterior margin of cephalothorax (Figure 4H-I); cephalothorax and abdomen pigmented; mandible with palp (Figure 5A)8
7. Number of teeth on dactylus/fixed finger is usually 2/1 (Figure 5F); 2 terminal setae extend beyond movable spines*Palaemon* (= *Palaemonetes*) *vulgaris***
 - Number of teeth on dactylus/fixed finger are usually 0/0 or 1/0 (Figure 5C, D); 2 terminal setae do not extend beyond movable spines5
8. Rostrum strongly expanded ventrally, to the greatest extent at the level of the first ventral tooth, dorsally with 7 to 9 teeth (including postorbital teeth but not the apical cleft tooth) and a single row of setae on ventral margin (Figure 4H); dactylus and fixed finger of second pereopod without teeth on cutting edge (Figure 5E); shorter ramus of the outer flagellum of antennule fused for about 50-60 % of its length to longer ramus (Figure 5G); with a protuberance just above the posterolateral marginal spine of the sixth abdominal segment (Figure 5I); cephalothorax and abdomen usually with a black transverse striped pattern, without a whitish longitudinal stripe running along the entire back*Palaemon elegans*
 - Rostrum without a strong ventral expansion, with 9 to 15 dorsal teeth (including postorbital teeth but not the apical cleft tooth) and a double row of setae on ventral margin (Figure 4I); dactylus of second pereopod with 2 teeth proximally, fixed finger with 1 tooth proximally on the cutting edge (Figure 5F); shorter ramus of the outer flagellum of antennule fused for about 20 % of its length to longer ramus (Figure 5H); without a protuberance above spine of the posterolateral margin of the sixth abdominal segment (Figure 5J); lateral view of cephalothorax with few oblique transverse stripes and abdomen translucent or pigmented with reddish spots without striped pattern, with a whitish longitudinal stripe running along the entire back.....*Palaemon macrodactylus*

*see Williams (1984) and Holthuis (1952) for identification of *Macrobrachium* spp.; Squires (1990) identified a single record of *Macrobrachium* sp. just inside Atlantic Canadian waters in the Gulf of Maine.

**recent evidence (De Grave and Ashelby 2013) indicates that the genus *Palaemonetes* is a junior synonym of *Palaemon* resulting in the transfer of all *Palaemonetes* species in the present study to *Palaemon*; also *Palaemonetes intermedius* has been renamed *Palaemon mundusnovus* as the North American name (*Palaemonetes intermedius*) fell to homonymy with an earlier-named Australian species of the same name.

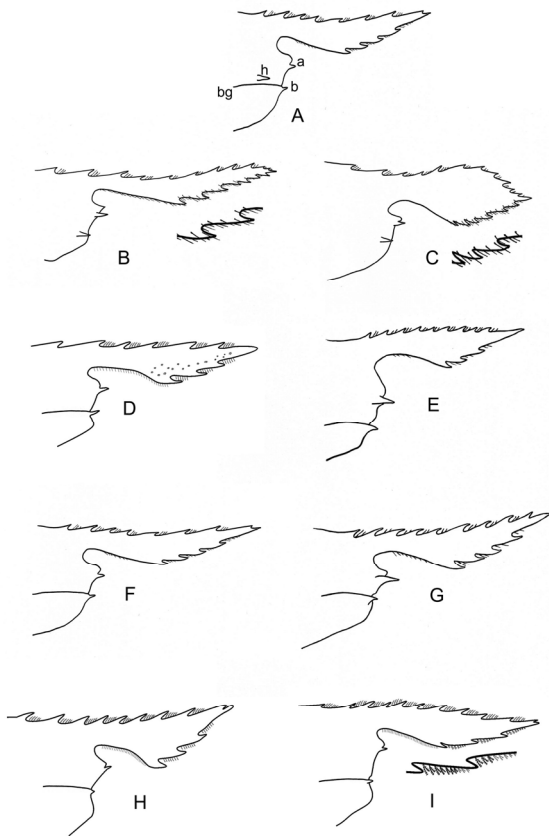


Figure 4. Anterior part of cephalothorax in lateral view of Palaemoninae species in northeastern North America. (A) Technical terms used in the identification key: a – antennal spine, b – branchiostegal spine, h – hepatic spine, bg – branchiostegal groove; (B) *Leander tenuicornis* (male) and (C) *L. tenuicornis* (female) (after Holthuis 1952); (D) *Palaemon adspersus*; (E) *Palaemon* (= *Palaemonetes*) *pugio* (after Holthuis 1952); (F) *Palaemon mundusnovus* (= *Palaemonetes intermedius*) (after Holthuis 1952); (G) *Palaemon* (= *Palaemonetes*) *vulgaris* (after Holthuis 1952); (H) *Palaemon elegans* (after González-Ortegón and Cuesta 2006); (I) *Palaemon macrodactylus* (after González-Ortegón and Cuesta 2006).

Taxonomic and ecological accounts of non-indigenous Palaemon species

***Palaemon adspersus* Rathke, 1837**

Colour: Body with a uniform yellowish grey colour with yellow bands at the joints of the pereopods. The lower half of the rostrum is covered with chromatophores in the form of red spots. The long flagella and the peduncle of the antennules bear strong red pigmentation.

Habitat: Sheltered, brackish waters in lagoons, bays and estuaries. Commonly associated with seagrasses and algae (Berglund 1980).

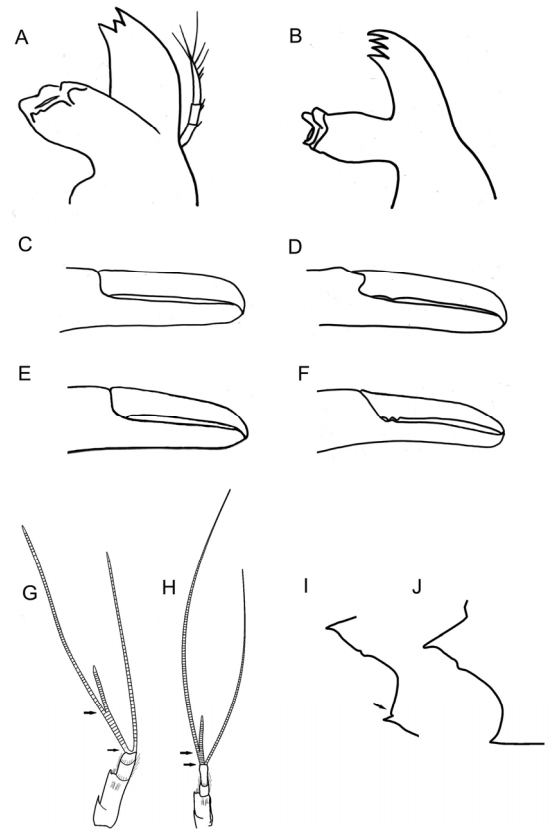


Figure 5. Morphological characteristics used to distinguish shrimp species of the subfamily Palaemoninae: (A, B) mandible; (C - F) chela of second pereopod; (G, H) antennule; (I, J) posterolateral view of sixth abdominal segment. (A) *Palaemon adspersus*; (B) *Palaemon* (= *Palaemonetes*) *vulgaris* (after Squires 1990); (C) *Palaemon* (= *Palaemonetes*) *pugio* (after Holthuis 1952); (D) *Palaemon mundusnovus* (= *Palaemonetes intermedius*) (after Holthuis 1952); (E, G, I) *Palaemon elegans* (after González-Ortegón and Cuesta 2006); (F, H, J) *Palaemon macrodactylus* (after González-Ortegón and Cuesta 2006).

Environmental Tolerance: Tolerates wide ranges of salinity (1–35) and temperature (2–25°C), optimal conditions being higher salinity (7–35) and low temperature (2°C) (Cuesta et al. 2006; Janas et al. 2013).

Original distribution: East Atlantic, from Norway (up to 60°N) to Morocco (Lagardère 1971) and the Baltic (Jazdzewski and Konopacka 1993), Mediterranean, and Black Seas (Holthuis 1980).

Introduced in: Caspian and Aral Seas (Zenkevich 1963; Holthuis 1980); Atlantic Canada (present study).

***Palaemon elegans* Rathke, 1837**

Colour: Cephalothorax and abdomen with a black striped pattern. The pereopod joints are marked by yellow bands and the palms of the chela on the second pereopods are blue. However, such colouration may be different in specimens living in turbid waters, in which the stripes may be almost completely faded away.

Habitat: Common in tidal rockpools, and in *Zostera*, *Posidonia* and *Cymodocea* seagrasses. Also, it can be found in slightly brackish water close to river mouths (Lagardère 1971).

Environmental Tolerance: Tolerates wide ranges of salinity (1–35) and temperature (2–30°C) (Janas et al. 2013). It is particularly a strong oxyregulator under hyperoxic and hypoxic conditions (Morris and Taylor 1985).

Original distribution: East Atlantic, from western Norway (Bergen) to Namibia. Azores, Madeira, Canary, and Cape Verde Islands, the Mediterranean and Black Seas (d’Udekem d’Acoz 1999).

Introduced in: Baltic Sea (Janas et al. 2004; Reuschel et al. 2010; Kotta and Kuprijanov 2012); Aral and Caspian Seas (Zenkevich 1963); Salem, Massachusetts, USA in 2010 and is presently distributed from Kennebunk, Maine to Sandwich, Massachusetts, USA (J. Carlton pers. com.).

***Palaemon macrodactylus* Rathbun, 1902**

Colour: Translucent, with reddish spots covering the entire body surface, pereopod joints are marked by yellow bands, the rostrum covered with chromatophores in the form of red blotches and a very distinctive dorsal colourless stripe running along its cephalothorax and abdomen. This colour pattern is sometimes stronger in females.

Habitat: Estuaries, protected harbours, bays, ponds, tidal creeks. This species tolerates a very broad range of ecological conditions (Newman 1963).

Environmental Tolerance: Tolerates wide ranges of salinity (1–35) and temperature (10–25°C) and is particularly tolerant of hypoxic conditions (González-Ortegón et al. 2006; 2013).

Original distribution: North coast of China, Korea, and Japan (Holthuis 1980).

Introduced in: Pacific coast of North America, (California: San Francisco Bay, Santa Monica Bay, Los Angeles Harbour, Humboldt Bay, Tijuana estuary; Oregon: Coos Bay: Ashelby et al. 2013), British Columbia, Canada (Ashelby et al. 2013), Atlantic coast of North America (New York City

estuary: Warkentine and Rachlin 2010; northern New Jersey to Boston, Massachusetts: J. Carlton pers. com.), Australia (d’Udekem d’Acoz et al. 2005), Argentina (Mar del Plata Harbour and Buenos Aires Province: Spivak et al. 2006; Martorelli et al. 2012), and Europe: U.K. (Worsfold and Ashelby 2008), Iberian Peninsula (Guadalquivir, Guadalete and Guadiana estuaries, San Pedro and Salado rivers: Cuesta et al. 2004; Chicharro et al. 2009; González-Ortegón et al. 2010), France (Gironde estuary: Béguyer et al. 2007), Germany (Geeste estuary: González-Ortegón et al. 2007), Belgium (yacht harbour of Zeebrugge and Ostend sluice dock: d’Udekem d’Acoz et al. 2005), Bulgaria (Varna Lake: Raykov et al. 2010), The Netherlands (Westerschelde estuary and IJmuiden: d’Udekem d’Acoz et al. 2005), Mediterranean Sea (Balearic Islands: Torres et al. 2012; North Adriatic: Cuesta et al. 2014) and the Black Sea (Micu and Niță 2009).

Discussion

The euryhaline species *Palaemon adspersus* Rathke 1837, native in European waters from the Baltic Sea to Mediterranean Sea (González-Ortegón and Cuesta 2006), was collected in eastern Canadian waters along ca. 200 km of the western Newfoundland coast. DNA analysis verified the morphological identification of this non-native species and this introduction represents the first record of the Baltic prawn in North American waters. Previous records of this species outside Europe were from Eurasian waters: the Caspian Sea in the 1930s and 1980s and the Aral Sea in the 1950s (Zenkevich 1963; Holthuis 1980).

The detection of Baltic prawn along the west coast of Newfoundland for four consecutive years (2011 to 2014), a species with longevity estimated at < 3 years (Bilgin et al. 2009), along with berried females, and detection in the Magdalen Islands suggest this European species is established in Atlantic Canadian waters. However, given the extent of commercial shipping within the Laurentian Channel, the presence of this non-native species in Canadian waters from repeated ship ballast water discharges cannot be excluded.

Accidental transport in ballast water of ships from the Caspian Sea or northern European waters seems to be the most likely vector for this first documentation of *P. adspersus* in Canadian waters. A series of invasions have been reported in the North American Great Lakes by euryhaline species originating from the Caspian Sea via

possible invasion corridors through the Baltic, North, or Mediterranean Seas (Ricciardi and MacIsaac 2000; Cristescu et al. 2001). Freighters from the Ponto-Caspian region bound for ports along the Great Lakes often take on ballast water near St. Petersburg in the Baltic Sea (Sprules et al. 1990). A clear example of this phenomenon is the cladoceran *Cercopagis pengoi* Ostroumov, 1891, which has extended its range over the past decade from the Ponto-Caspian basin into the Baltic Sea and the North American Great Lakes (Cristescu et al. 2001). Northern European waters have also been reported as the most likely source of a cryptic secondary introduction event of the European green crab, *Carcinus maenas*, to Canada (Roman 2006). This conclusion was based on frequent cargo vessel traffic from the North Sea to the Strait of Canso, one of the largest ice-free harbours in northeastern North America (Roman 2006). As well, considering that most successful introductions originate from regions with similar latitudes and climates (Carlton 1985), northern European populations of *P. adspersus* are a more likely candidate to establish in Canadian waters than southern European populations as the former should be more tolerant to low water temperatures of western Newfoundland.

Local vessel traffic from other Atlantic Canadian ports may be another means for *Palaemon adspersus* to have reached the west coast of Newfoundland, as was reported for European green crab, *Carcinus maenas*, first detected in Placentia Bay, southeast Newfoundland, in 2007 (Blakeslee et al. 2010). Placentia Bay is an area heavily used by ballast-carrying commercial vessels (Klassen and Locke 2007) and is where numerous non-native species have been recently found (McKenzie et al. 2010; Matheson 2013; Sargent et al. 2013). On the west coast of Newfoundland, green crab was detected near Stephenville in 2008 (DFO 2011), but it is yet undetermined whether green crab was introduced there by means of local vessel traffic or by larval dispersal from a neighbouring location. For the Baltic prawn to have been transported from elsewhere in Atlantic Canada would require it to have been established somewhere else before 2011. While there is presently no evidence for this scenario, the possibility cannot be discounted. Failure to detect *P. adspersus* in other Atlantic Canadian regions could be the result of a combination of factors including: 1) general unawareness of this species, resulting in no one looking for it; 2) similar appearance to native Palaemoninae

species, so that it may have been misidentified; 3) sampling methods may have been inappropriate to collect specimens; and 4) the preferred habitat of this species may not have been sampled. Misidentification of *P. adspersus* as *Palaemon* (= *Palaemonetes*) *pugio* in the Magdalen Islands and lack of sampling of Sites S2 and S3 before 2011 could support the hypothesis that this species was present elsewhere in Atlantic Canada prior to 2011.

The occurrence of *P. adspersus* in Newfoundland waters suggests the possibility of introductions of additional shrimp species to the Gulf of St. Lawrence. Recent introductions of *Palaemon macrodactylus*, and *P. elegans* in the northeastern United States (Warkentine and Rachlin 2010; J. Carlton, pers. com.) and warming water temperatures may facilitate the spread of these and other non-indigenous decapod crustaceans northward into Gulf of St. Lawrence waters (Jamieson 2000; Stachowicz et al. 2002). Other European palaemonid shrimp species recently found colonizing new regions, such as *P. longirostris* H. Milne Edwards, 1837 (Grabowski 2006; Sezgin et al. 2007), *P. serratus* (Pennant, 1777) (Gönlügür-Demirci 2006) and *Palaemon* (= *Palaemonetes*) *varians* (Leach, 1814) (Grabowski 2006), may follow the same invasion corridor as *P. adspersus* and establish populations in the Gulf of St. Lawrence.

The recent introduction of Baltic prawn reported here underlines the need for reconsideration of ballast water management practices as previously suggested by Miller et al. (2005) and Roman (2006). Currently, mid-ocean ballast water exchange regulations for transoceanic and coastal vessels arriving at ports on the Atlantic coast of Canada are ineffective for controlling introductions of macroinvertebrates (Briski et al. 2012). Existing Canadian regulations state that all vessels entering Canadian waters exchange or treat their ballast 200 nautical miles from shore and in at least 2000 m of water before discharging, except under exceptional circumstances (Transport Canada 2007). Due to safety considerations (e.g. during storms), however, vessels may exchange their ballast in alternative ballast water exchange zones, one of which is located within the Laurentian Channel in the Gulf of St. Lawrence (DFO 2009). At such times, vessels may release propagules of non-indigenous species directly into the Gulf of St. Lawrence; most of these vessels originate from the northeastern United States and Europe (Simard and Hardy 2004; McKenzie et al. 2010; Lo et al. 2012). In addition,

vessels operating exclusively within waters of Canadian jurisdiction are exempt from ballast water exchange regulations (Canada Shipping Act 2006; Transport Canada 2007). Thus, such vessels travelling between Canadian ports may facilitate the secondary introduction of non-indigenous species. Interregional vessel transportation is a potentially important vector (Lavoie et al. 1999; Simkanin et al. 2009) of secondary spread and is a growing concern as a means for the spread of invasive species, especially to Newfoundland (Blakeslee et al. 2010; McKenzie et al. 2010). The recent detection of *P. adspersus* in the present study provides additional evidence of the ineffectiveness of Canada's current ballast water regulations (Smith et al. 2014). Consequently, the spread of non-indigenous species is likely to increase unless changes are made to current regulations regarding ballast water discharge and vessel movement between ports (Lambert and Lambert 1998).

Currently, the Baltic prawn appears merely as a non-indigenous species in Atlantic Canada and does not appear to be invasive. Further research on the introduction of *P. adspersus* in Atlantic Canada should include efforts to determine the initial area of introduction and current distribution Atlantic Canada, the European source population, and an assessment of its ecological interaction with native species. The determination of the source population location and the point of initial introduction of *P. adspersus* is of considerable importance, as this information may both aid in predicting future species invasions from the same region(s) and reveal the invasion corridor and transmission vector through which this non-indigenous species was transported. Finally, potential interactions between Baltic prawn and those congeners native to Atlantic Canada (e. g. *P. pugio* and *P. vulgaris*) inhabiting similar habitats (Köhn and Gosselek 1989; this study), should be examined to ascertain whether *P. adspersus* will persist to become another problematic invasive species in this region, or will integrate within the ecosystem to enrich biodiversity.

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The following supplementary material is available for this article:

Table S1. Locations and environmental conditions of survey sites conducted along the west coast in Newfoundland and the Magdalen Islands between 2009 and 2014

Table S2. Species name and GenBank number.

Table S3. Morphological differences between species of the subfamily Palaemoninae from northwest Atlantic waters (New Jersey, US to Canada).

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