

Research Article

***Grandidierella japonica* Stephensen, 1938 (Amphipoda: Aoridae) in the Northwest Atlantic Ocean**Thomas J. Trott^{1*}, Eric A. Lazo-Wasem² and Claire Enterline¹¹Maine Coastal Program, Department of Marine Resources, 194 McKown Point, West Boothbay Harbor, Maine, USA²Peabody Museum of Natural History, Yale University, 170 Whitney Avenue, New Haven, Connecticut, USAAuthor e-mails: tom.trott@maine.gov (TT), eric.lazo-wasem@yale.edu (ELW), claire.enterline@maine.gov (CE)

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Abstract

The aorid amphipod *Grandidierella japonica* Stephensen, 1938, originally described from northern Japan, is reported for the first time from the Gulf of Maine and Long Island Sound in the Northwest Atlantic Ocean. It was discovered among grab samples of eelgrass (*Zostera marina* Linnaeus, 1753) beds taken in Casco Bay, Maine in summer 2018 and has been found intertidally in Long Island Sound since 2013 along Connecticut shores. It occurs in habitats like its native range but also in rocky areas and tidepools in bedrock. The presence of adults of both sexes, ovigerous females, and immature stages in all collections indicates the species is established. Among males, some morphological characteristics of gnathopod 1 vary with increasing total body length: the number of accessory carpal teeth increases, the carpus shape (length/width ratio) changes, and numbers of stridulating ridges increase. Maine and Connecticut specimens are distinguished from each other by the shape of male gnathopod 1 basis. Morphological variation, temporal differences in discovery, and separation by the biogeographic barrier Cape Cod suggests Maine and Connecticut populations originate from separate introductions.

Key words: introduced species, Peracarida, *Zostera marina*, taxonomy, Long Island Sound, Casco Bay, Gulf of Maine

Introduction

The gammaridean amphipod *Grandidierella japonica* Stephensen, 1938, was discovered during routine sampling of eelgrass (*Zostera marina*) in Casco Bay, Portland, Maine and through intertidal sampling on the Connecticut shores of Long Island Sound. This species was originally described from brackish waters near Hokkaido and Abisiri, northern Japan (Stephensen 1938) and is widely distributed throughout the Pacific (Kudryaschov and Tzvetkova 1975; Myers 1981; Muir 1997; Coles et al. 1999). Its introduction to the Pacific coast of North America, where it ranges from Mexico (Okolodkov et al. 2007) to Canada (Pilgrim et al. 2013), was first noticed in California in 1966 (Chapman and Dorman 1975). In the northeastern Atlantic, *G. japonica* was first reported in England at Southampton Water (Smith et al. 1999) and later in the Orwell

Estuary (Ashelby 2006). It has dispersed more recently along the shores of France (Jourde et al. 2013; Lavesque et al. 2014; Droual et al. 2017) and the Mediterranean (Marchini et al. 2016; Munari et al. 2016). There are no published reports of *G. japonica* in the Northwest Atlantic where the only species of *Grandidierella* found is *G. bonnieroides* from Florida (Heard 1982; LeCroy 2002).

This account provides a brief description of *G. japonica* followed by a preliminary analysis of morphological variation. Potential vectors, pathways for introduction, and the biogeography of the region are briefly discussed to assess the likelihood of separate introductions into the Gulf of Maine and Long Island Sound.

Materials and methods

Eelgrass beds (*Zostera marina*) in Casco Bay, located off Portland (43.6591°N; 70.2568°W) on the southern coast of Maine (Figure 1), were surveyed on 12 September 2018. They were qualitatively sampled at depths of 2.33 to 4.76 meters approximately 2 h after low tide using a 0.05 m² Ponar grab sampler. Samples were sieved at sea on 0.5 mm screen to separate macroinvertebrates from debris.

Several intertidal habitats were also qualitatively surveyed from 2013–2018 on the Connecticut shores of Long Island Sound (Figure 2) as part of routine annual collections in the region made on an *ad hoc* basis beginning well before 2013. Depending on the type of habitat explored, washings from algae or sampled sediments were sieved in the field on 0.5 mm screen to retain macroinvertebrates. In some instances, amphipods were hand-picked from rock crevices and algal holdfasts.

Specimens were sorted from sieved and hand-collected samples in the laboratory within 24 h of collection with the aid of a dissecting microscope (20x) and preserved in 90% ethanol. Some specimens were preserved in formalin to retain color for microphotography. *Grandidierella japonica* from Maine and Connecticut were identified by T. Trott and E. Lazo-Wasem, respectively.

Length of amphipods was measured from rostrum to telson. Measurements were made from live view screen images acquired with a Stemi 2000-CS dissection microscope fitted with a Q Imaging 5.0 Micropublisher RTV digital camera. Multiple distances (Range: 4–5) were measured incrementally along the curvature of the body, from tip of rostrum to base of telson, using a calibrated measurement tool and total length calculated by adding individual distances; more distances were made as necessary to account for a strongly curved individual.

For male gnathopod 1, the presence of accessory carpal teeth among all specimens (N = 14) was noted and their number counted. To test the hypothesis that the development of accessory carpal teeth is allometric, the

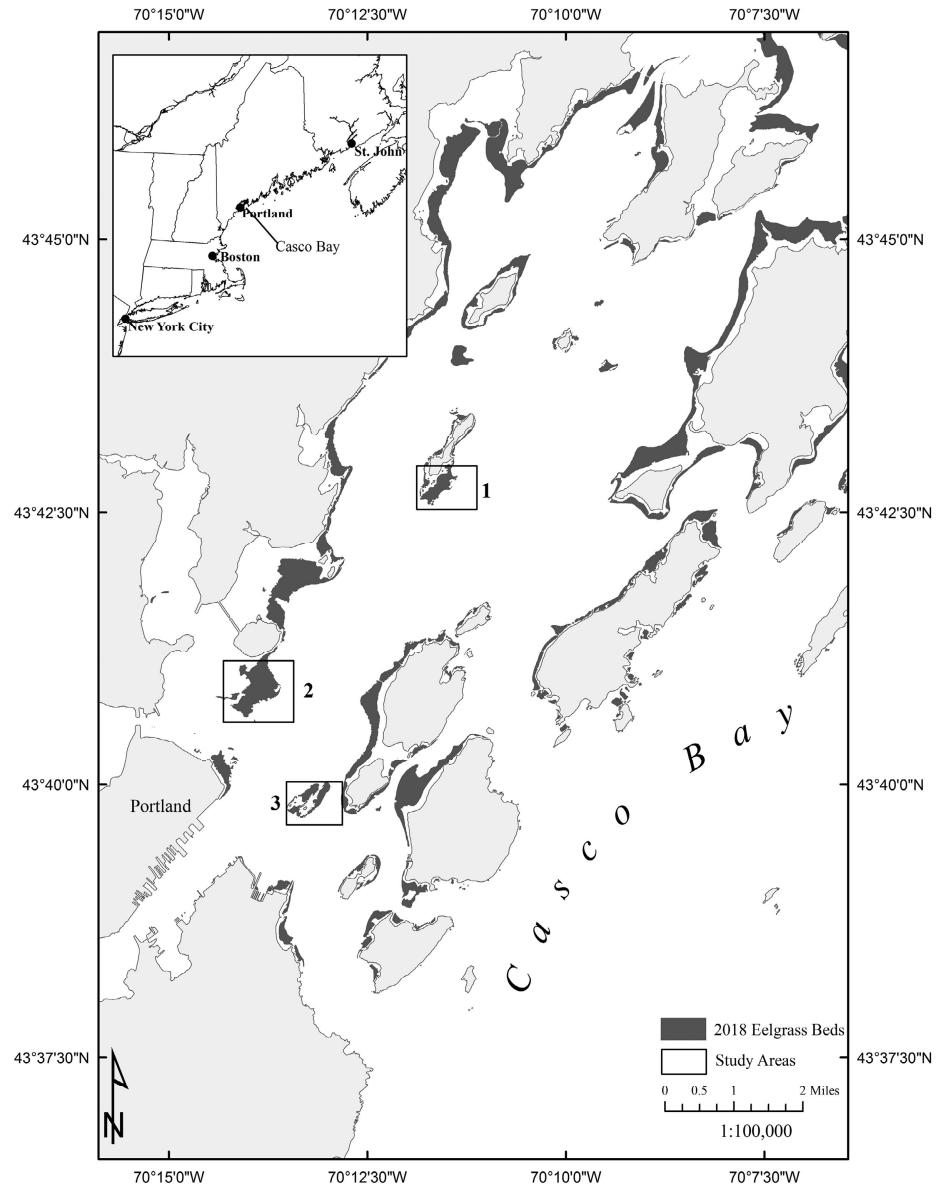


Figure 1. Casco Bay, Maine, U.S.A. showing locations of sampled eelgrass (*Zostera marina*) beds. *Grandidierella japonica* was collected at locations 2 and 3. Inset illustrates Casco Bay in relation to the Gulf of Maine. Locations: 1, Clapboard Island; 2, Mackworth Island; 3, Hog Island Ledge. Map by C. Enterline.

difference between the average total length of males with either one ($N = 4$) or two ($N = 10$) accessory carpal teeth was tested for significance ($P < 0.05$) using a one-tailed t-test assuming unequal variances.

Voucher specimens from Maine and Connecticut were deposited in the Yale Peabody Museum. Maine specimens: YPM IZ 105148, 1 ♂, Macworth Island, and YPM IZ 105149, 1 ♀, Macworth Island. Additional voucher specimens from Maine were deposited in the National Museum of Natural History: USNM 1594816, 1 ♂, Hog Island Ledge; USNM 1594817, 3 ♀♀, Hog Island Ledge; USNM 1594818, 2 ♀♀, Hog Island Ledge. Catalogue numbers for Connecticut specimens can be found by querying the publicly accessible Peabody Museum collections portal (YPM 2020).

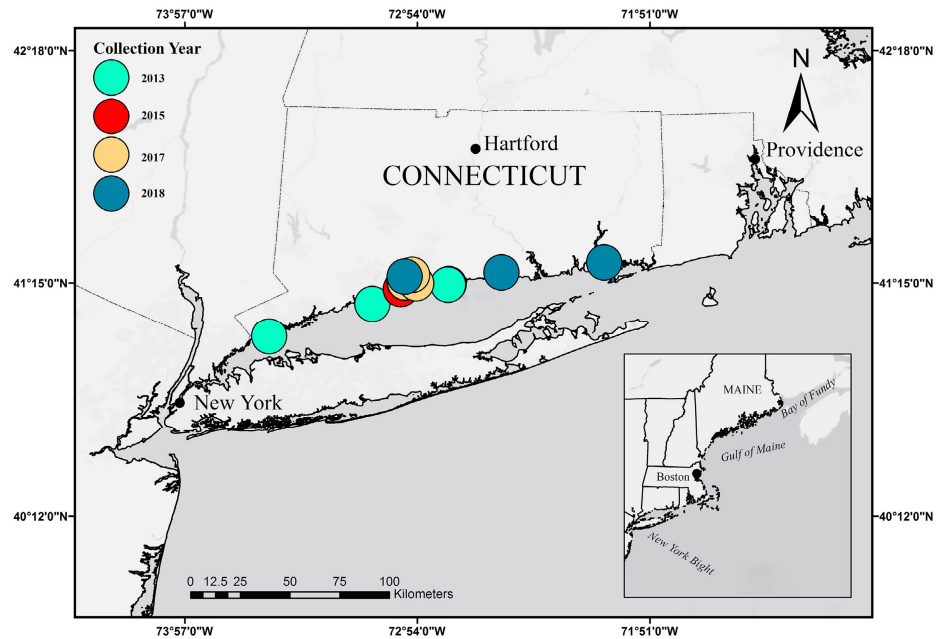


Figure 2. Long Island Sound, U.S.A. showing location and year where *Grandidierella japonica* was collected along the shoreline of Connecticut. Inset illustrates Long Island Sound in relation to the U.S. North Atlantic coast. Map by T. Trott.

Results

Grandidierella japonica was collected from eelgrass growing in sandy mud sediments near Hog Island Ledge (1 ♂, length = 7.11 mm; 8 ♀♀, 3 ovigerous, maximum length = 6.17 mm) and Macworth Island (1 ♂, length = 7.12 mm; 3 ♀♀, 1 ovigerous, length = 6.16 mm), Casco Bay, Maine (Figure 3A, B). In Long Island Sound, males (N = 17, maximum length = 7.67 mm) and females (N = 27, maximum length = 13.38 mm) were found in a variety of habitats distributed along the Connecticut shoreline (Figure 3C, D; Table 1). The discovery of *G. japonica* proceeded from west to east from 2013 to 2015, respectively (Figure 2). Ovigerous females (N = 18) were present among these collections. These data for Long Island Sound are from kept specimens; not all captured amphipods were saved.

Among males, some morphological characteristics of gnathopod 1 were variable. The shape of the basis of gnathopod 1 appeared oval-oblong in Maine specimens (Figures 3A, 4B) but oval in Connecticut (Figures 3B, 4A). This difference did not correspond with total body length. However, the shape of the carpus (length to width ratio) changed with size as the carpus elongates with age, trending to 2.5:1 for Connecticut specimens (Figure 4A) and 3:1 for ones from Maine (Figure 4B). Comparing all male amphipods, the number of accessory teeth on the inner surface near the posterior margin of the carpus and number of stridulating ridges on the anterior margin of the carpus changed with body length. Smaller amphipods possessed only one accessory tooth with the second accessory tooth appearing near the carpal tooth in larger animals (Figures 4C, D; 5A). Accessory teeth were completely lacking in two very small males (≤ 5.04 mm).

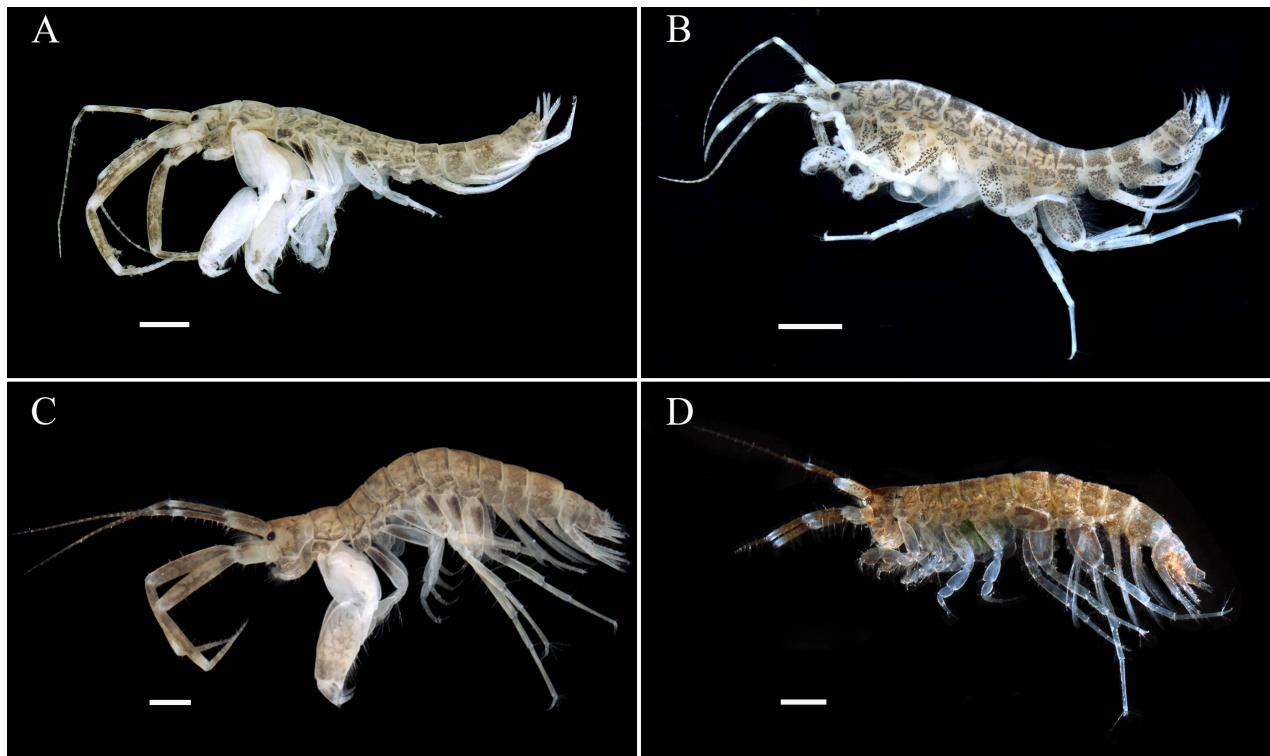


Figure 3. *Grandidierella japonica* from the Northwest Atlantic, U.S.A. (A) Male, Macworth Island, Maine. (B) Female, Macworth Island, Maine. (C) Male, Savin Rock, Connecticut. (D) Female, Thimble Islands, Connecticut. Photos are light micrographs of specimens preserved in: 90% ethanol: A, B; Formalin: C, D. Catalogue numbers: YPM IZ 105148, A; YPM IZ 105149, B; YPM IZ 076900, C; YPM IZ 067820, D. Scale: A, B, C and D = 1 mm. Photos by E. Lazo-Wasem.

Table 1. Long Island Sound collections of the amphipod *Grandidierella japonica* from different habitats located along the shore of Connecticut, USA.

Year	Month/Day	Lat/Long	Place Name	Intertidal Habitat	N ^a
2013	Jul 25	41.155°; -73.103°	Stratford Point	sandy cobble	1
	Aug 14	41.244°; -72.758°	Horse Island	bedrock	9
	Sep 11	41.242°; -72.761°	Outer Island	bedrock: seaweed and tidepool	1
	Nov 03	41.059°; -73.637°	Greenwich Point	rocky	4
2015	Jul 22	41.252°; -72.957°	Bradley Point	bedrock: tidepools	1
	Aug 03	41.249°; -72.959°	Twin Rocks	muddy sand	5
2017	Jun 21	41.252°; -72.957°	Bradley Point	bedrock: tidepools	3
	Jun 30	41.252°; -72.956°	Savin Rock	rocky	1
	Jul 11	41.248°; -72.904°	Lighthouse Point	muddy sand	1
	Jul 12	41.248°; -72.905°	Lighthouse Point	muddy sand, bedrock	2
	Jul 18	41.286°; -72.923°	Vietnam Memorial	marsh: freshwater drainage area	10
2018	Jun 01	41.270°; -72.520°	Clinton Town Beach	sandbar	2
	Jul 16	41.251°; -72.957°	Bradley Rocks	rocky, muddy coarse sand mix	3
	Aug 25	41.314°; -72.056°	Pine Island	rocky	1

N^a is the number of individuals.

Conceding the total number of specimens with only one accessory carpus tooth was small, the average lengths of specimens with one versus two accessory teeth (Figure 5B) was significantly different ($t = 4.06$, $df = 8$, $P < 0.004$). The number of stridulating ridges also increased with body length. Large individuals with two accessory teeth on the carpus had > 40 ridges, while smaller amphipods with one accessory tooth had ≤ 25 – 30 (Figure 4C, E).

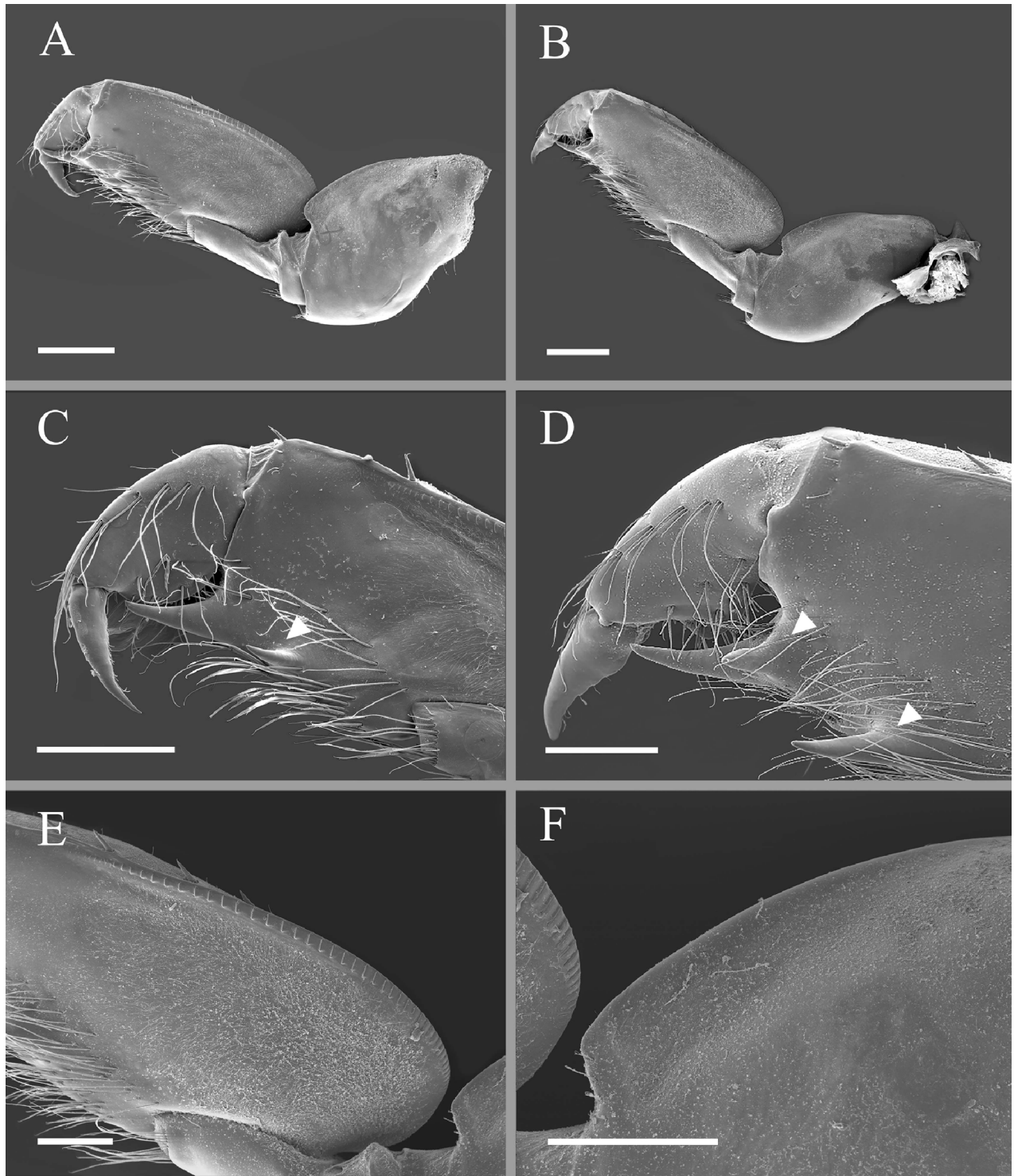


Figure 4. *Grandidierella japonica* from the Northwest Atlantic, U.S.A. (A) Mature male, gnathopod 1 (Savin Rock, Connecticut, USA). (B) Mature male, gnathopod 1 (Macworth Island, Maine, USA). (C) Close-up of immature male gnathopod 1 showing single carpal spine (arrowhead). (D) Close-up of Fig. 4B showing two carpal spines (arrowheads). (E). Close-up of carpal stridulating ridge shown in Fig. 4B. (F) Close-up of edge of basis complementing stridulating ridge shown in Figure 4E. Catalogue numbers: YPM IZ 105148: A; YPM IZ 076900: B, D, E, F; YPM IZ 105413: C. Scale: A and B = 500 μ m; C to F = 250 μ m. Scanning electron micrographs by L. Rojas.

Diagnosis

In general, morphological features of specimens matched well with the descriptions and drawings of *Grandidierella japonica* (Stephensen 1938;

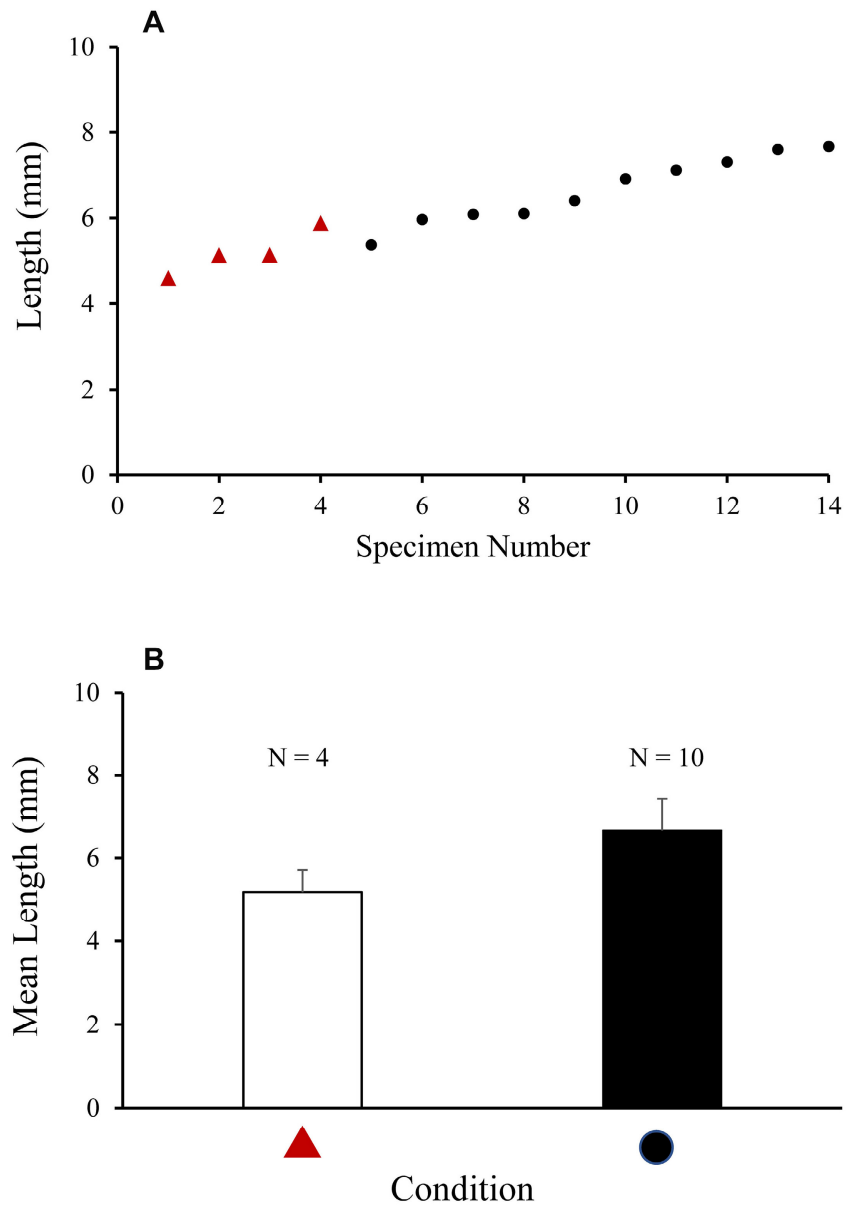


Figure 5. Development of accessory teeth on the carpus of gnathopod 1 of male *Grandidierella japonica* from New England. A. Range of total body length where accessory teeth are present as one (▲) or two teeth (●). B. Mean total body length \pm standard deviation of males with one (▲) or two (●) accessory teeth.

Chapman and Dorman 1975; Ariyama 1996). Diagnosis was based on: (1) uropod 3 uniramous (Figure 6), (2) mature male gnathopod 1 carpochele (Figure 4A–D), (3) transverse stridulating ridges on the upper (anterior) carpus margin in males (Figure 4E), and (4) two accessory teeth on the inner carpus surface (Figure 4D). At least five species of *Grandidierella* have transverse carpal ridges (Ariyama 1996; Hou and Li 2002), but males of *G. japonica* have two accessory teeth on the inner carpus in combination with ridges. Stephensen (1938), Chapman and Dorman (1975) and Ariyama (1996) consider these accessory carpal teeth as diagnostic for *G. japonica*. This key characteristic will be discussed in the context of observations reported in this paper.

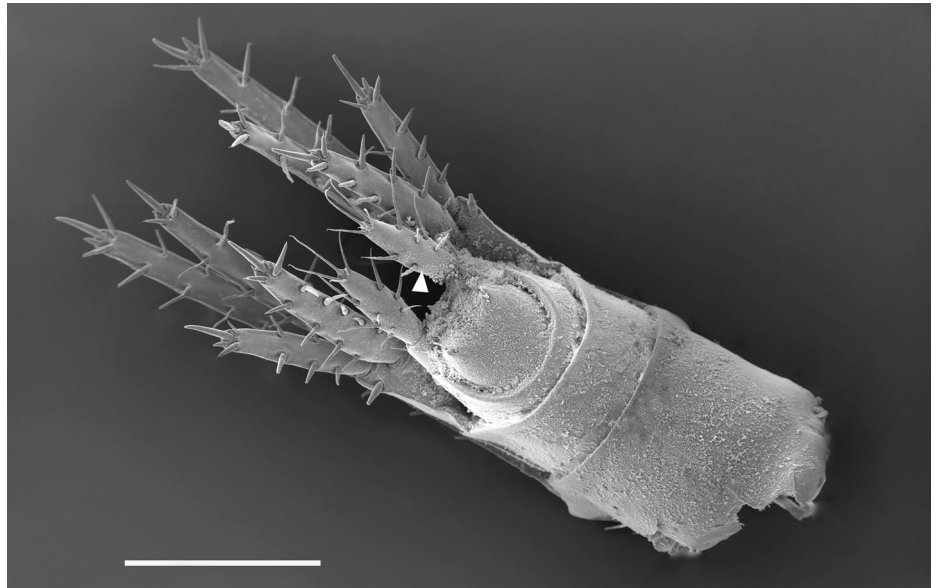


Figure 6. *Grandidierella japonica* from the Northwest Atlantic, U.S.A. Urosome of male in Figure 3C (YPM IZ 076900) showing uniramous uropod 3 (arrowhead). Scale: 500 μ m. Scanning electron micrograph by L. Rojas.

Remarks

As a matter of importance for identification, Bousfield (1973) and Chapman and Dorman (1975) describe gnathopod 1 differently. Among the aorids of New England, Bousfield (1973) described gnathopod 1 as subchelate and often complexly subchelate in males. Chapman and Dorman (1975) describe gnathopod 1 of *Grandidierella japonica* as carpochelate. We acknowledge that these authors were concerned with different taxonomic levels, family versus species, but point out that their inconsistency in terminology might pose difficulties for identifications depending on which taxonomic reference is used.

There are no known native species of *Grandidierella* in New England, although Bousfield (1973) includes this genus in his key to the Atlantic genera of Aoridae. That said, the only other western Atlantic aorid genera which have uropod 3 uniramous are *Neohela*, *Unciola*, and *Pseudunciola*. At the time of this writing only *Unciola* and *Pseudunciola* are represented in shallow New England waters; *Neohela* inhabits cold deep waters (Bousfield 1973; Dickinson et al. 1980). Using Bousfield (1973) terminology, a complexly subchelate gnathopod 1 is common to *Grandidierella*, *Unciola*, and *Pseudunciola*, but present only in males of *Grandidierella*; it is present in both sexes for *Unciola* and *Pseudunciola*. At the level of species, males of *G. japonica* are distinguished from those of *Unciola* and *Pseudunciola* by having two accessory teeth on the inner surface near the posterior margin of the gnathopod 1 carpus (Figure 4C). Furthermore, male *G. japonica* have distinctive transverse ridges on the upper anterior margin of male gnathopod 1 carpus (Figure 4E), a feature absent among species of *Unciola* and *Pseudunciola*.

Superficially, *G. japonica* resembles New England species of Corophiidae since they also have uropod 3 uniramous, but that is where the similarity ends. No males among genera in that family have accessory teeth on the gnathopod 1 carpus, and stridulating ridges are lacking as well. Lastly, confusion with New England species of *Microdeutopus* is possible based on overall appearance, but none have uropod 3 uniramous, or accessory carpal teeth on male gnathopod 1.

Caution is advised in using the number of accessory teeth on gnathopod 1 carpus as diagnostic when dealing with small individuals shown to lack the second accessory tooth. This would be especially important when specimens in question originated from the southwestern Pacific, where five species of *Grandidierella*, all possessing stridulating ridges, are sympatric. These congeners are *G. japonica* Stephensen, 1938, *Grandidierella perlata* Schellenberg, 1938, *Grandidierella taihuensis* Morino and Dai, 1990, *Grandidierella vietnamica* Dang, 1968, and *Grandidierella chaohuensis* Hou and Li, 2002. The two accessory teeth of *G. japonica* were considered diagnostic by Stephensen (1938), Chapman and Dorman (1975) and Ariyama (1996). Given the present findings, this would be true only for large individuals. The absence of both accessory teeth for the smallest New England males complicates further diagnosis based on these features.

Discussion

The discoveries of *Grandidierella japonica* in Casco Bay, Maine and at several locations along the Connecticut shoreline are the first for the Northwest Atlantic Ocean. Aside from these records, no species of *Grandidierella* occur in either the Acadian or Virginian Biogeographic Provinces, notwithstanding the listing of the genus by Bousfield (1973) for New England gammarids. A search of the Yale Peabody Museum database shows 2600 samples for amphipods from Maine south to New Jersey, 1860's to present, but *Grandidierella* is never reported before 2013 (YPM 2018). This database includes large 19th century holdings of the U.S. Fish Commission and the vast Massachusetts Bay samples collected by the Systematic Ecology Program of the Marine Biological Laboratory in the 1960s. All these collections referenced were identified by specialists E.L. Mills, E.L. Bousfield, and E.A. Lazo-Wasem. Moreover, a search of the National Museum of Natural History database shows 4,000 records for amphipods and *G. japonica* is not among them (NMNH 2019).

Recruitment within sampled populations of *G. japonica* is verified by the presence of ovigerous females and immature stages. That fact and the time span of collections from Connecticut make clear that occurrence of this species among locations is not by chance due to the coincidence of sampling with a sporadic introduction event. Instead, the spread of this species is chronicled from west to east along the Connecticut shore (Figure 2),

likely originating in New York and continuing to Rhode Island, places where *G. japonica* has recently been found in fouling communities (Trott *unpublished data*). In addition, recent summer 2019 collections of males and ovigerous females in Casco Bay suggest that *G. japonica* is established there (Trott *unpublished data*).

The shape of the basis of gnathopod 1 was noticeably different according to whether males were from Connecticut or Maine. The appearance of the basis is not related to total body length and therefore tied with maturity in males. Instead, basis shape seems to be characteristic of different populations. The same dichotomy, oval versus oval-oblong, is reported for native and introduced populations elsewhere. With few exceptions, the oval-oblong shape is common among Japanese populations (Nagata 1960, 1965; Hirayama 1984; Ariyama 1996) and the oval shape common among introduced populations (Chapman and Dorman 1975; Jourde et al. 2013; Marchini et al. 2016; Munari et al. 2016; Droual et al. 2017). Outliers of this relationship are specimens collected from brackish waters in Japan with an oval shaped basis (Stephensen 1938) and the oval-oblong basis shape for specimens collected from full-strength sea water in Maine (this study), and estuarine waters in Southampton, England (Smith et al. 1999). These morphological differences might be linked with phenotypic variation, although salinity is an unlikely contributing factor. Moreover, Connecticut collection locations ranged from 27 to 35 ppt at the Vietnam Memorial and Bradley Point, respectively, but the basis appeared consistently oval-shaped among all specimens. Since the association of basis shape with native versus introduced populations is not perfect, future studies should include descriptions to help clarify the strength of such correspondence.

The number of accessory teeth on the carpus of male gnathopod 1 increases with body size. The smallest of individuals (≤ 5.04 mm) lacked accessory teeth, as also shown for the 4.6 mm male collected from the Orwell Estuary, England (Ashelby 2006). Marchini et al. (2016) remarked about the variation among native and introduced populations and suggested this characteristic might be associated with maturity. We show such variation with average total body length to be statistically significant for northwestern Atlantic populations of *G. japonica*. The size where accessory teeth are fully developed is expected to vary among populations, given the considerable range in maximum size of males reported from different localities with two accessory teeth (6.2 mm, Marchini et al. 2016; 7.5 mm, Droual et al. 2017; ~ 7.5 mm, Jourde et al. 2013; 7.67 mm, present study; 8–9.5 mm, Ariyama 1996; 9.9 mm, Munari et al. 2016; 22 mm, Chapman and Dorman 1975). Of course, the minimum size where two accessory teeth are fully developed would be more relevant in this instance, but such measurements have yet to be reported.

Grandidierella japonica is sexually dimorphic, particularly in the size and shape of gnathopod 1. Furthermore, males have distinctive transverse

Table 2. Environmental conditions ($\bar{x} \pm \text{SD}$) at eelgrass (*Zostera marina*) beds sampled on 12 September 2018 in Casco Bay, Maine, U.S.A. where *Grandidierella japonica* was collected.

Bed No. ^a	Sample	Lat/Long	Temp (°C)	Salinity (psu)	Depth (m)	N ^b
2	EG005	43.6785°; -70.2354°	16.71 ± 0	34.24 ± 0.01	2.55	63
3	EG010	43.6648°; -70.2233°	16.36 ± 0	34.69 ± 0	3.76	256
3	EG012	43.6656°; -70.2206°	16.28 ± 0	34.81 ± 0	4.76	217

^a Bed number corresponds to locations shown in Figure 1.

^b N^b: number of iterations each parameter was measured at depth (m) approximately 2 h after low tide.

stridulating ridges on the upper anterior margin of gnathopod 1 carpus (Figure 4E). The ridges are thought to function in sound production as noted by Stephensen (1938) who first proposed these are stridulating organs. There is no definitive evidence that these ridges are used to create sound, but they have the appearance of the stridulating organs of many crustaceans (Dumortier 1963). The most suggestive evidence is the observation of Chapman and Dorman (1975) of males in aquaria rapidly scraping gnathopod 1 carpus against the corresponding basis, which has a blade-like upper margin (Figure 4F). Since only males possess stridulating organs, and ridges are added as amphipods mature, sound production is most likely used for mating purposes. Information presented by Marchini et al. (2016) suggests the correspondence between the number of ridges and body size occurs among native populations and ones introduced elsewhere. We show this relationship holds for amphipods collected from Maine and Connecticut.

The habitats and environmental conditions where *G. japonica* is found match well with where this amphipod lives within its putative native range and in other introduced locations. Intertidal muddy and muddy-sand sediments are the most common types of substratum occupied where salinities range from brackish to full strength sea water (Tables 1, 2). In Casco Bay, amphipods occupy subtidal eelgrass beds, as in Japan (Nagata 1960) and France (Lavesque et al. 2014). However in Connecticut, rocky intertidal areas and tidepools in bedrock represent new habitat types. In contrast, surveys of rocky intertidal, salt marsh creeks, mud flats and sandy shores around Casco Bay and its vicinity, which were conducted over the same time frame as Connecticut surveys, did not detect *G. japonica* (Trott unpublished data). It is somewhat surprising that there are no published records from where this species has been introduced which report *G. japonica* living among inland freshwater lakes, as do some populations in China (Hou and Li 2002). Lastly, widgeon grass *Ruppia maritima* L. and fouling communities are suspected habitats based on discoveries in California (Chapman and Dorman 1975) and Europe (Marchini et al. 2016), respectively. These habitats are currently being explored for *G. japonica* in Casco Bay.

The potential for successful introductions is high, since *G. japonica* is a eurytopic species physiologically adapted to tolerate a wide range of salinities (Kikuchi and Matsumata 1997). For brooding peracarids without

larval dispersal, invasion rate is largely vector dependent and coupled to invasion success. Wherever this amphipod is discovered, it spreads rather quickly once populations become established. The invasion history is best known on the west coast of the United States. The 20-year chronicle shows invasion rate accelerating from the mid-1990s following phases of establishment in regions north and south of the site of first introduction (Pilgrim et al. 2013). Based on collection records, the first discovery of *G. japonica* on the Atlantic shore of France (Jourde et al. 2013) is followed roughly three years afterwards by the first record in the Mediterranean (Marchini et al. 2016). In the New England region, this species successfully colonized the Connecticut shoreline and formed established populations along Long Island Sound within at least five years. The fate of this species in Casco Bay, Maine should be monitored closely to see if *G. japonica* remains established and, if so, its pace of dispersal along the Gulf of Maine coast.

Transport into the northwestern Atlantic through shipping is the most probable means of introduction to Casco Bay and Long Island Sound. This idea is supported by the fact that non-native populations of *G. japonica* become established near international shipping ports (Coles et al. 1999; Smith et al. 1999; Ashelby 2006). The seaports of New York city and Portland, Maine are major international shipping centers. Situated on the shore of Casco Bay, Portland is the largest tonnage seaport in New England, a major U.S. east coast seaport, and the largest foreign inbound transit tonnage port in the United States (Acheson and Acheson 2016). Amphipods may have arrived in Casco Bay through commerce via container ships originating from the North Sea (McGuire 2019), where introduced populations are established. This shipping route is the suggested mechanism for the introduction of the encrusting bryozoan *Cribrilina (Juxtacribrilina) mutabilis* (Ito, Onishi and Dick, 2015) that was discovered concurrently with *G. japonica* among the same eelgrass beds (Trott and Enterline 2019). The chronology of discovery of amphipods in Long Island Sound suggests a similar scenario, with the introduction of amphipods to the New York city seaport followed by dispersal within Long Island Sound. Dispersal could have been facilitated by commercial shipping to New Haven, Connecticut, the busiest seaport on Long Island Sound (Benson et al. 2018) that receives domestic and international cargo ships headed to and from New York city (Richason and Yacher 1981). In other parts of the world, importation of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) for aquaculture is a suspected vector for *G. japonica* introductions (Chapman and Dorman 1975; Myers 1981; Jourde et al. 2013; Lavesque et al. 2014; Munari et al. 2016; Droual et al. 2017). However in New England, this mode of introduction is very unlikely, because Pacific oysters are not grown commercially or otherwise.

The source populations where New England *G. japonica* originated are most likely in the Northeast Atlantic, where it is established in the North and Mediterranean Seas. Considering that Long Island Sound and the Gulf

of Maine are separated by the biogeographic barrier of Cape Cod (Hale 2010), separate introductions seem likely instead of a northerly dispersal from Long Island Sound. This pathway would rely on transport through the Cape Cod Canal as the shortest route into the Gulf of Maine, thereby avoiding the obstruction of the Cape Cod peninsula and its associated oceanography. However, there is little net flow through the canal (Anraku 1964) and it is not a significant dispersal pathway into the Gulf of Maine (Jennings et al. 2009), although transport by recreational boating (Marchini et al. 2016) is conceivable. The temporal variation in discovery between Casco Bay and Connecticut shores suggests that the Long Island Sound and Casco Bay populations stem from separate introductions. Molecular analysis now underway may help reveal one or more source populations for Maine and Long Island Sound.

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