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Research Article

Going global: the introduction of the Asian isopod *Ianiropsis serricaudis* Gurjanova (Crustacea: Peracarida) to North America and Europe

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Abstract

The Asian isopod *Ianiropsis serricaudis* is now well established in fouling communities, often associated with introduced ascidians, throughout the Northern Hemisphere but has gone largely unnoticed because of its diminutive size (typically less than 3 mm in length) and the difficulties of identifying small peracarid crustaceans. Known locations include the northeastern Pacific (Puget Sound, San Francisco Bay, and Monterey Bay), the northwestern Atlantic (from the Gulf of Maine to Barnegat Bay, NJ), and the northeastern Atlantic (England and the Netherlands). We predict that this species is widespread along North America and European coasts, and may already be introduced to cold temperate waters of the Southern Hemisphere as well.

Key words: introduced species, marine, Isopoda, *Ianiropsis serricaudis*, shipping, ballast water, fouling

Introduction

Introductions of small species in marine fouling communities can often go undetected for many years for a variety of reasons, even as they potentially thrive and impact surrounding species (Carlton 2009). While many successful introductions of peracarid crustaceans, particularly benthic and epibenthic amphipods and isopods, are known around the world (Chapman and Carlton 1991; Ashton et al. 2008; Carlton 2011), their often diminutive size makes them easily missed, mis-identified, or even ignored in surveys of marine fouling communities. This, coupled with a lack of taxonomic expertise and at times limited collaboration between experts, makes the reporting of such under-the-radar species spotty at best (Bishop and Hutchings 2011).

In 1977 a janirid isopod was found in marine fouling communities in San Francisco Bay, California. It was not identifiable in local keys (Miller 1975), but because of the prevalence of Atlantic and Japanese species in the Bay, and specifically in the communities in which the isopod was found, examination of the Atlantic and Asian literature (by E. W. Iverson, then with the California Academy of Sciences, San Francisco, pers. comm. 1977) suggested it was *Ianiropsis serricaudis* Gurjanova, 1936, native to the North-west Pacific Ocean. Over subsequent decades, *Ianiropsis* were collected in the Bay but not identified to species, resulting in *I. serricaudis* not being treated as an established invasion in San Francisco Bay by Cohen and Carlton (1995).

In 2000, an *Ianiropsis* was found to be abundant in fouling communities in southern New England (as detailed below; examination of older samples revealed its presence in 1999); no *Ianiropsis* had been previously recorded from the northwest Atlantic Oceanic. Taxonomic work on the material commenced in 2011, with an initial identification (based on Doti and Wilson 2010) by NVH and ELW as the western Pacific species *I. notoensis* Nunomura, 1985. In the summer of 2004, during surveys for non-native species on the south coast of England an unknown janirid was encountered, tentatively identified as juveniles of the native isopod *Janira maculosa* Leach, 1814. In March 2010, one of us (JTC) suggested that an isopod initially identified (as discussed below) as the native Californian species *Ianiropsis tridens* Menzies, 1952 collected in 2002 in estuarine waters in the Monterey Bay (California) region, might instead be *I. serricaudis*, but material was not available at that time for re-identification.

In October, 2011, one of us (JRC) wrote to Carlton, noting that an isopod provisionally identified as *I. notoensis* had been discovered in Puget Sound, and inquiring about the status of the identification of the unknown *Ianiropsis* in New England fouling communities. In December 2011, another one of us (MF) reported an unidentified *Ianiropsis* that had appeared in the Netherlands, but was not identifiable in Doti and Wilson (2010), because while the Dutch population appeared similar to *I. serricaudis*, it did not have the pleotelson characters indicated in that work (Faasse 2007).

In late 2011 we realized that all of the reports of an *Ianiropsis* from California, Washington, New England, and Europe might involve the same species that had been potentially globally distributed by ships. Coincidentally in 2012 and 2013 separate studies (by CSS, RP, and RS, as noted below) collected unidentified *Ianiropsis* from coastal New Jersey fouling and benthic communities.

Methods

As a result of the above reports and discoveries, all parties were contacted to exchange specimens and discuss key morphological characters. What follows is a summary of the different sampling events over the past several decades in different parts of the world.

Carlton (1979a) reported a newly-discovered introduced isopod as *I. serricaudis* while studying fouling community biodiversity in San Francisco Bay. Cordell et al. (2013) collected janirids while surveying the fouling communities of a number of sites in Puget Sound in Washington State. A team of researchers taking part in a series of Rapid Assessment Surveys of non-indigenous species of New England in 2000, 2003, 2010 and 2013 (Pederson et al. 2005; McIntyre et al. 2013; Wells et al. 2014) collected samples at numerous coastal sites in New England and New York, focused mostly on floating docks, but including some surveys of rocky intertidal sites during 2010 (McIntyre et al. 2013). A similar rapid assessment survey of dock fouling communities conducted in England in 2004 (Arenas et al. 2006) produced janirid isopods of interest. Research along the coast of Netherlands secured another large specimen set while surveying the fouling of floating docks and intertidal sites (Faasse 2007).

We supplemented these surveys with additional sampling specifically for *Ianiropsis* on floating docks and the rocky intertidal, and retrieved numerous specimens in Massachusetts (a salt pond in Woods Hole, and several sites in Salem Sound), in Rhode Island (Narragansett Bay) and Connecticut (at the mouth of the Mystic River). Additionally very large numbers of *Ianiropsis* were collected from settling communities on artificial plastic substrata attached to shallow water wooden docks, as part of an epifouling study in Barnegat Bay, New Jersey in 2012 and 2013.

Specimens from San Francisco Bay will be deposited at the California Academy of Sciences, San Francisco; specimens from New England and New Jersey will be deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. and at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut. Specimens from The Netherlands will be deposited in Naturalis Biodiversity Center, Leiden.

Results

Morphological analysis and identification

With collections in hand from around the Northern Hemisphere, and with a growing network of researchers (the coauthors of this paper), detailed examination of numerous specimens permitted taxonomic resolution of this isopod as the Western

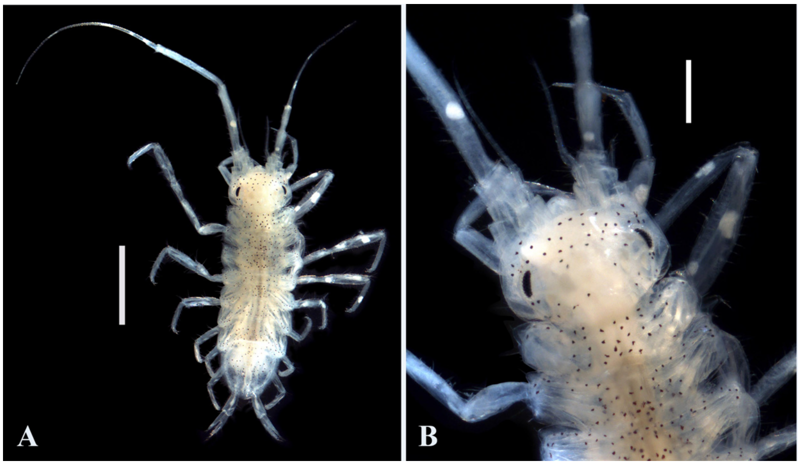

Figure 1. *Ianiropsis serricaudis* from Rhode Island, USA: A - dorsal view, preserved specimen (scale bar 1 mm); B - head showing elongate maxilliped palp (to immediate left of scale bar) and antennal peduncle segments 6 and 7 (overlapping the distal end of the maxilliped) (scale bar 0.25 mm). Photographs by Eric Lazo-Wasem.

Figure 2. *Ianiropsis serricaudis:* juvenile on alga *Ulva lactuca* (scale bar 0.3 mm). Photograph by Eric Lazo-Wasem.

Pacific species *Ianiropsis serricaudis* (Figure 1-A, adult; Figure 2, juvenile). We summarize here the key morphological characters we used in identifying *I. serricaudis* and compare it to similar species (Table 1). We follow Nunomura (1995) and Saito et al. (2000) in treating *Ianiropsis notoensis* as a junior synonym of *I. serricaudis*.

While Kussakin (1962, 1968) noted that males and females are 2.9 mm and 2.7 mm in length respectively, our largest male specimens were 3.2 mm and female specimens 2.4 mm (collections of (males) 13 August 2012 from Point Judith Marina, Snug Harbor, Rhode Island, and (females) 1 October 2012 from Beverly Town Pier, Beverly, Massachusetts).

Gurjanova (1936) described *I. serricaudis* (as *Janiropsis serricaudis*) as possessing 4 or 5 marginal denticles on the pleotelson ("4–5 Zähne an jeder Seite;" the original figure shows 4 minute denticles). Kussakin (1962) stated the range of denticles to be 4 to 7. Jang and Kwon (1990) figure 4 denticles on *I. serricaudis* in their Korean material. Doti and Wilson (2010) key out *I. serricaudis* as one of three species with "5 denticles or more" on the pleotelson margin; 4 species are keyed out as having "up to 4 denticles," but not *serricaudis*. Due to this variability in reported pleotelson spination, we relied on additional characteristics for identification as discussed below.

1.Maxilliped Palp Size (Figures 1-B and 4). The size of the maxilliped palp in terminal males is pronounced enough to be seen easily from a dorsal view of the cephalon. This character is found in three species: *I. serricaudis,* the southern hemisphere *I. palpalis,* and the northeastern Pacific *I. epilittoralis* (Wilson and Wägele 1994). Only the latter species has denticles present on the pleotelson comparable to *I. serricaudis*.

2.Antennal Peduncle Segments (Figure 1-B). Peduncle segments 6 and 7 of the antennae of *Ianiropsis serricaudis* terminal males are particularly elongate relative to the overall length of the antennae, together being as long or longer than

Table 1. Key characteristics distinguishing selected *Ianiropsis* species (Gurjanova 1936; Kussakin 1962; Schultz 1969; Nunomura 1985; Jang and Kwon 1990; Wilson and Wägele 1994; Hayward and Ryland 1995; Doti and Wilson 2010; Golovan and Malyutina 2010).

Ianiropsis species	Denticles on lateral margin of pleotelson	Maxilliped palp elongate, visible in dorsal view	Combined length of antennal peduncle segments 6 and 7	Number of claws on dactyli of pereopods 1 and 7.
I. serricaudis Gurjanova, 1936 (= ***I. notoensis*** Nunomura, 1985) [NWP; introduced in North America and Europe]	THREE or FOUR, sometimes to seven, along posterior 1/2 of margin	YES, elongate	ELONGATE, ~ ½ main body length	TWO claws on 1, TWO-THREE claws on 7
I. koreaensis Jang and Kwon, 1980 [NWP]	THREE or fewer	NO, truncate	ELONGATE, ~ ½ main body length	TWO claws on 1, THREE claws on 7
I. epilittoralis Menzies, 1952 [NEP]	TWO, sometimes to four along posterior 1/3 of margin	YES, elongate	SHORT, ~ ¼ main body length	TWO claws on 1, THREE claws on 7
I. tridens Menzies, 1952 [NEP]	THREE, sometimes four along posterior 1/3 of margin	NO, truncate	SHORT, ~ ¼ main body length	TWO claws on 1, THREE claws on 7
I. analoga Menzies, 1952 [NEP]	FOUR to seven, along posterior 2/3 of margin	NO, truncate	SHORT, ~ ¼ main body length	TWO claws on 1, THREE claws on 7
I. breviremis (Sars, 1883) [NEA]	FIVE or more	NO, truncate	ELONGATE, ~ ½ main body length	TWO claws on 1, THREE claws on 7
I. palpalis Barnard, 1914 [South Africa]	NONE	YES, elongate	(not available)	TWO claws on 1, THREE claws on 7

NWP: Northwest Pacific Ocean; **NEP,** Northeast Pacific Ocean; **NEA**, Northeast Atlantic Ocean

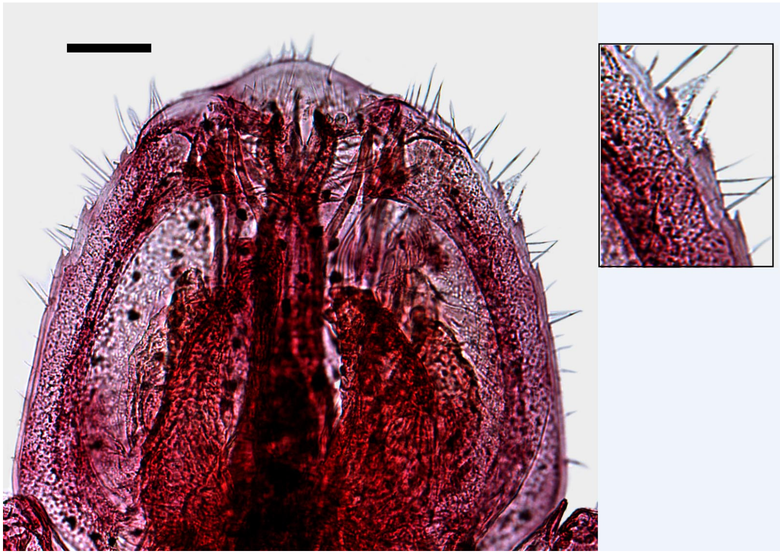

Figure 3. *Ianiropsis serricaudis:* pleotelson, showing 3 marginal spines (inset) (scale bar 0.1 mm). Photograph by Eric Lazo-Wasem.

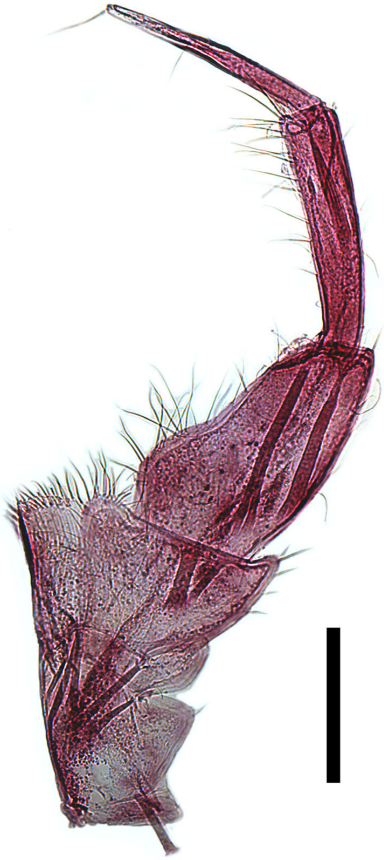

Figure 4. *Ianiropsis serricaudis*: Maxilliped showing elongate palp (scale bar 0.3mm). Photograph by Eric Lazo-Wasem.

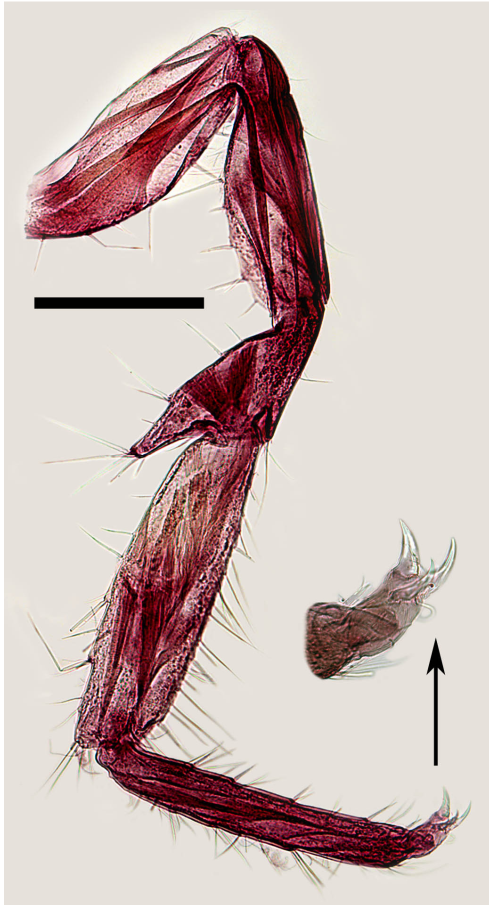

Figure 5. *Ianiropsis serricaudis:* Pereopod 1 showing two terminal claws on dactylus (scale bar 0.3mm). Photograph by Eric Lazo-Wasem.

half the body length. In a population of *I. serricaudis* from Toyama Bay, Japan (Nunomura, 1985, as *I. notoensis*), however, the two antennae peduncular segments are only a quarter of the overall body length.

3.Pleotelson Spination (Figure 3). The pleotelson commonly has four, but variably 3 to 7 small clear denticles along the posterior lateral margins; the denticles do not extend along the lateral margin more than one-half of the way along the posterior-most edge. Nearly all larger specimens collected in New England, Puget Sound, and The Netherlands have four denticles, with smaller individuals often having three denticles. The more narrow range of denticle counts in introduced populations (3 to 4, as opposed to up to 7 as reported from native regions) on the pleotelson may reflect a founder effect, not unexpected in non-native populations. Six species of *Ianiropsis* are known to have denticles on the pleotelson (Doti and Wilson 2010), with some degree of variability, so this feature must be used with care. *Ianiropsis palpalis* lacks denticles entirely. *Ianiropsis analoga* as described by Kussakin (1962) has a comparable number of denticles but is easily distinguished because the anterior-most serrations of the denticles reach the middle of the pleotelson lateral margin. As also noted above, Doti and Wilson (2010) describe *I. analoga* as having typically 5 or more denticles.

4.Pereopod Dactyl Claws (Figure 5). The dactyli of pereopod 1 have two claws; the dactyli of pereopod 7 have three claws. Nunomura (1985) describes the Toyama Bay (Japan) population of *I. serricaudis* as having two such claws on both pereopods 1 and 7.

5.Uropods. Specimens from both New England and the Netherlands have pronounced uropods, matching descriptions for *I. serricaudis*. Doti and Wilson (2010) utilize the length of the uropod as a distinguishing character for this species, being long relative to most other *Ianiropsis* species.

Color Variation. Gurjanova (1936) described live specimens of *I. serricaudis* as having black eyes with small black pigment spots across the body, giving individuals a light grey cast. Many of our live specimens collected in New England and The Netherlands show color variation, often having dark red pigmented eyes, and red-brown pigment spots across an otherwise translucent body, with particularly pronounced pigmentation associated with the alimentary canal. In the Mystic River Estuary, Connecticut, *I. serricaudis* in samples from the green-brown bryozoan *Amathia* occasionally exhibited a green tint, those from the yellow sponge *Halichondria* were at times yellow, and some specimens from the red sponge *Clathria* were rust-colored (C. Dempsey, Williams College, Williamstown, Massachusetts, pers. comm. 2012).

Native range, ecology, and biology in the Northwestern Pacific

Ianiropsis serricaudis is found in Japan, Korea, and Russia, from the Sea of Okhotsk to the Sea of Japan. Gurjanova (1936) reported the habitat as on the undersurface of rocks, and on sponges, ascidians, and the coralline alga *Amphiroa* from the shore to 2 meters. Kussakin (1962, 1968) reported that it occurs from the intertidal zone to 7 meters, in water temperatures ranging from -1.8ºC in the winter to 24ºC in the summer, and added the coralline algae *Pachyarthron cretaceum* (Postels and Ruprecht) Manza 1937, the rhizoids of the kelp *Laminaria*, and brown algae such as *Desmarestia* as additional habitats. Kussakin (1988) reported that ovigerous females were found in August and October, with eggs ranging in number from 7–32 (averaging 18). We have not found abundance data in the Western Pacific literature.

Introduced range, ecology, and biology in North America and Europe

We summarize here the history of the detection and collection of *Ianiropsis serricaudis* outside of Asia (Table 2). In Table 2 we also summarize habitat data for each location.

San Francisco Bay, California: *Ianiropsis serricaudis* was first identified outside of Asia by Ernest W. Iverson, from San Francisco Bay, based upon specimens collected by Carlton, Chapman, and Iverson in March 1977 in float fouling communities in the warm and brackish water of the Oakland Estuary. It was collected, along with the Japanese isopod *Dynoides dentisinus* Shen, 1929, among the introduced ascidians *Ciona intestinalis* (Linnaeus, 1767) (from the North Atlantic) and *Styela clava* Herdman, 1881 (from Japan). Carlton (1979a) speculated that it may have been transported to San Francisco Bay in shipping associated with the Vietnam War, many of which vessels came out of the Western Pacific theater of operations, including Japan. The 1977 San Francisco Bay record was previously noted by Carlton (1979b, 1987), Chapman (2000, Table 2, as *I. serricatus*), and Ruiz et al. (2000, Appendix 1).

Ianiropsis were subsequently collected in fouling surveys in San Francisco Bay in the 1990s and 2000s. These specimens have now been confirmed as *I. serricaudis*, including material from a marina on Treasure Island in the Central Bay (October 1993; J. T. Carlton and Andrew N. Cohen [Center for Research on Aquatic Bioinvasions, Richmond, California], collectors) and from a marina (water temperature 18.7ºC; salinity 28.3) at Richmond, on the east shore of the Bay and the Presidio Yacht Club, Fort Baker, Sausalito (May, 2004; J. T. Carlton, J. W. Chapman and A. N. Cohen, collectors). The Richmond collections include ovigerous females.

Moss Landing, California: Heiman and Micheli (2010) reported *Ianiropsis serricaudis* as rare (3 specimens) in mudflats near reefs of the introduced Australian serpulid polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) in brackish water in Elkhorn Slough, Moss Landing, Monterey County, approximately 160 km south of San Francisco Bay. Samples were collected in 2002. The material had been initially identified in manuscript as the native species *I. tridens*, but one of us (JTC) suggested in correspondence (March 2010) with K. Heiman (Muhlenberg College, Allentown, Pennsylvania) that the estuarine habitat was more suggestive of the introduced species *I. serricaudis*, earlier known from San Francisco Bay. The name was then changed for publication, but the specimens were not re-examined at the time. K. Heiman kindly provided (April 2013) preserved specimens of this material to us, and we were able to confirm the identification as *I. serricaudis*. Although soft sediment is an unusual micro-environment for this species, we suspect the specimens in question may represent individuals that had strayed from more structured habitats: a number of additional species strongly associated with tubeworm reefs were also found in nearby

Table 2. Introduced Range and Habitats of *Ianiropsis serricaudis*.

Region	Location	First Collection Record(s)	Habitat	Reference
Eastern Pacific	California: San Francisco Bay	1977	Among introduced ascidians (*Ciona intestinalis*, *Styela clava*) and in general fouling communities	Carlton 1979a, b; herein
	California: Monterey Bay: Elkhorn Slough	2002	In mudflats near reefs of introduced serpulid *Ficopomatus enigmaticus* (see text)	Heiman and Micheli (2010); herein
	Washington: Puget Sound	2010	Among introduced ascidians (*Didemnum vexillum*)	Cordell et al. 2013
Western Atlantic	Connecticut: Long Island Sound: Mystic River	1999	Among native bryozoan *Amathia dichotoma*; in mixed algal - invertebrate epibenthos; on native sponges *Halichondria bowerbanki, Clathria prolifera* and introduced ascidian *Botrylloides violaceus,* and in general fouling communities	Herein
	Maine to Connecticut	2000 - 2010	With native algae *Ulva* spp., *Chondrus crispus*, and introduced alga *Grateloupia turuturu*; among introduced ascidians *Didemnum vexillum, Botrylloides violaceus*, among introduced bryozoans *Tricellaria inopinata,* and in general fouling communities	Pederson et al. 2005; McIntyre 2013; Janiak and Whitlatch 2012; McIntyre et al. 2014; Wells et al. 2014; herein
	New Jersey: Barnegat Bay	2012-2013	Among the introduced ascidian *Botryllus schlosseri*, on cryptogenic alga *Ulva lactuca*, and on native bryozoans *Einhornia crustulenta, Schizoporella* sp.	Herein
Eastern Atlantic	Netherlands	2000	With filamentous red algae, and on the introduced ascidians *Botrylloides violaceus, Didemnum vexillum*, and cryptogenic ascidian *Diplosoma listerianum*	Faasse 2007
	England: Southampton	2004	On the introduced ascidian *Styela clava,* and in general fouling communities	Herein

mudflats; conversely, species characteristic of mudflats were occasionally found in the reef habitat (Heiman and Micheli 2010).

Puget Sound, Washington: *Ianiropsis serricaudis* was first collected in Puget Sound between June and October 2010 (Cordell et al. 2013). While abundant at one study site - a mussel aquaculture farm in Totten Inlet in the southern part of Puget Sound - no specimens were collected at nine other sites around the Sound. This site was also one of the most inland of all the sites sampled, with an annual monthly mean salinity between 26.5–29, as well as an average temperature range between 6–17ºC. The isopods were strongly associated with the introduced Japanese compound ascidian *Didemnum vexillum* Kott, 2002: average densities were nearly 20,000/m^3 with *D. vexillum*, and about 1000/m^3 in non-ascidian habitats (Cordell et al. 2013).

New England: The first specimens of *Ianiropsis serricaudis* from the Northwestern Atlantic Ocean were collected (JTC) in November 1999 in the Mystic River estuary in Mystic, Connecticut, at the eastern end of Long Island Sound (but not identified as such until 2012). The isopods were amongst the native bryozoan *Amathia dichotoma* (Verrill, 1873) in a pier fouling community. *Ianiropsis serricaudis* was subsequently found throughout the following decade to be abundant in shallow-water fouling communities in the Estuary. Specimens were also collected in mixed algae-invertebrate epibenthos collections trawled at 3 meters depth at Ram Island, at the mouth of the Mystic River, in August 2008 (specimens identified April 2013).

Ianiropsis serricaudis now ranges widely across New England, with records in hand from Maine to Connecticut (Pederson et al. 2005;

McIntyre et al. 2013; Wells et al. 2014). The first indication of the fuller range of this species came from a Rapid Assessment Survey (RAS) for non-indigenous species on floating dock sites in southern New England in the summer of 2000, when it was found in dock fouling at a few sites in estuarine Rhode Island waters. In 2003, an expanded RAS collected *I. serricaudis* from marina float fouling in Massachusetts in Buzzards Bay on the south shore of Cape Cod, as well as additional sites in Connecticut and Rhode Island (Pederson et al. 2005). In 2010, another Rapid Assessment Survey of New England waters found *I. serricaudis* to be common residents at floating dock and intertidal sites from Rhode Island to Maine (McIntyre et al. 2013) with no clear preference for habitat types, i.e., they were found at brackish or estuarine sheltered floating docks, as well as wave-exposed rocky intertidal marine sites. Specimens were typically associated with the green alga *Ulva* spp., and compound ascidians, particularly the Japanese species *Didemnum vexillum* and *Botrylloides violaceus* Oka, 1927.

In the fall of 2011, samples from Eel Pond (JTC) in Woods Hole, Massachusetts, revealed a large number of *Ianiropsis serricaudis* (including ovigerous females) among thick mats of the arborescent Japanese bryozoan, *Tricellaria inopinata* d'Hondt and Occhipinti Ambrogi, 1985, another introduction recently reported (Johnson et al. 2012). Additionally, monthly surveys (NVH) of three floating dock sites in Narragansett Bay and Rhode Island Sound, and two in Salem Sound, Massachusetts, conducted from the summer of 2011 to the fall of 2012 found common to abundant numbers of *I. serricaudis*, with no clear sign of significant die-back over the unusually warm 2011–2012 winter season. At sites studied in Narragansett Bay salinities range from 24–32 (Kremer and Nixon 1978), and temperatures range from a mean of 4ºC (-0.5ºC at lowest) in winter to 19.5ºC (24ºC at highest) in summer (Nixon et al. 2003).

In March-April 2012, *Ianiropsis* populations in the Mystic River, Mystic, Connecticut were sampled on a wide variety of substrates, all of which supported isopod populations (C. Dempsey, pers. comm. 2012). These substrates included the bryozoan *Amathia dichotoma*, the native sponges *Halichondria bowerbanki* Burton, 1930 and *Clathria prolifera* (Ellis and Solander, 1786), and the ascidian *Botrylloides violaceus*. Temperature ranged from 9.5 to 13.8ºC, with salinities ranging from 16.9 to 29.8. Isopods occurred by the tens of thousands on the bryozoan *Amathia*, with lower densities on the sponge *Halichondria* and *Clathria*, and infrequent occurrence on the ascidian *Botrylloides*. Ovigerous females typically held 16–32 eggs.

Specimens were also recovered from Long Island Sound, in Waterford, Connecticut (24 km south of the Mystic River Estuary) on the native red alga *Chondrus crispus* and the introduced Japanese alga *Grateloupia turuturu* Yamada, 1941 in 2006–2007 (Janiak and Whitlatch 2012, in supplementary online material).

Barnegat Bay, New Jersey: Large populations of *Ianiropsis serricaudis* were found at four locations within Barnegat Bay, NJ from June 2012 to October 2013. The largest population was found on artificial vinyl substratum attached to dock pilings in August and October of 2013 (CSS). Of the 2,373 specimens collected from this location in August, with a density of approximately 7000/m^2, size ranged from 0.5 mm to 3.2 mm total length, and the population contained 11.6% ovigerous females, 8.5% terminal males, and a large juvenile population. An additional 7,242 specimens were collected in October (over 20,000/m^2) with 10.6% ovigerous females and 6.4% terminal males. Based on the equivalent proportion of brooding females from August through October, it is likely that *I. serricaudis* has a prolonged brooding period extending at least from summer through early fall (consistent with Kussakin 1988). Moreover, it is likely that the three-fold population growth from August to October can be attributed to not only continued recruitment but also the maturation of juveniles from late summer broods. Similar intertidal janirid isopods, such as *Jaera albifrons* Leach, 1814, have shown comparable reproductive strategies and brood maturation rates (Jones et al. 1971; Sjöberg 1970). The tidal range at this location is approximately 18 cm; at the highest tide during this sampling period the top of the highest settlement strip was 11 cm below the surface water. Salinity ranged from 24–29.

Specimens of *I. serricaudis* were found primarily in association with three encrusting invertebrates: the introduced ascidian *Botryllus schlosseri* (Pallas, 1766), and the native bryozoans *Einhornia crustulenta* (Pallas, 1766) and *Schizoporella* sp., as well as the green alga *Ulva lactuca* Linnaeus, 1753. In these samples, other dominant and associated amphipods included *Jassa falcata* (Montagu, 1808), *Elasmopus levis* (S. I. Smith, 1873), *Caprella carina* Mayer, 1903 and *Monocorophium acherusicum* (Costa, 1853).

Specimens from three other locations within Barnegat Bay were recovered in July 2012 and 2013 by Gary Taghon from the Rutgers University Marine Science Department. Of 100 stations sampled within the bay using a van Veen grab, specimens of *Ianiropsis serricaudis* were found at only three. In total, 21 individuals were recovered, with 18 of those found at one 2012 sampling station.

Southampton, England: A September 2004 Rapid Assessment Survey for introduced marine species along the south coast of England (Arenas et al. 2006) recovered a small number of janirid isopods, initially identified as the native *Janira maculosa*, from a fouling community on a pontoon float in Hamble Point Marina in Southampton, Hampshire. The specimens were found by John Bishop on a specimen of the introduced ascidian *Styela clava*. We examined these specimens (in the collection of J. T. Carlton) in 2012 and found the smaller specimens to be *I. serricaudis*; the larger specimens were *J. maculosa*. Additional specimens were found at Queen Anne's Battery marina in Plymouth in the same survey, and were also likely *I. serricaudis* (John D. D. Bishop, Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, UK, personal communication).

Oosterschelde, The Netherlands: *Ianiropsis serricaudis* was first observed in 2000 on the island of Neeltje Jans at the entrance of the inlet Oosterschelde (Faasse 2007, as *Ianiropsis* sp.), an estuary along the southern coast of the Netherlands much used for shellfish aquaculture. In 2006 it was also found at a site near the port of Rotterdam, 40 km to the north. It has since been recorded at more than 21 different shallow subtidal, rocky intertidal, and floating dock study sites in the region. It is typically found associated with finely fruticose red algae as well as sessile invertebrates, particularly the compound ascidians *Botrylloides violaceus*, *Didemnum vexillum*, and *Diplosoma listerianum* (Milne-Edwards, 1841). Populations vary considerably according to substrate and seasonality, but are generally abundant overall across the region.

Physical data in the Netherlands again indicate a tolerance for variable conditions. Salinity in the Oosterschelde area ranges from 27.5 to 35 (Hydro Meteo Centrum Zeeland, http://hmcz.nl, accessed 14 January 2012), and possibly even lower in other Dutch sites where *I. serricaudis* is found. Water temperatures in the area vary from about 3ºC (exceptionally 0ºC) to about 20ºC (exceptionally 25ºC) (Wolff 1973).

Discussion

Ianiropsis serricaudis is now a common if not abundant member of shallow water marine habitats on the Atlantic coast from Maine to New Jersey, in several bays and estuaries on the Pacific coast from Washington to California, and in Europe in England and the Netherlands. This isopod survives over the wide temperature ranges (0 to 24–25ºC) typical of species evolving in continental climatic regimes, but is generally restricted to higher salinity regimes (24–35) with occasional, and perhaps transient exceptions, such as in Long Island Sound USA (where some populations were found in salinities as low as 16.9).

The most likely vector of introduction for *I. serricaudis* is global ship transport. Given their nature as a fouling species on hard surfaces, their wide temperature tolerance, and their common presence in ports and harbors, dispersal by both ballast water and hull fouling is probable. Once introduced to a new region, secondary transport is likely mediated by coastal vessel traffic, and perhaps by drifting on fouled substrates dislodged from pilings and floats. Of no small interest is the presence of *I. serricaudis* on marine debris generated by the Tōhoku Earthquake and Tsunami of 11 March 2011, that rafted across the North Pacific Ocean, and washing ashore on the Pacific coast of North America (see Calder et al. 2014). Specimens in our possession (JTC) were collected (by J. W. Chapman and J. A. Miller) on a dock lost in March 2011 from the Port of Misawa, Aomori Prefecture, northern Honshu, that washed ashore near Newport, Oregon in June 2012, and again on a Japanese skiff (originating from northern Honshu) that washed ashore in Gleneden Beach, Oregon in February 2013. We do not include these Oregon records in Table 2, because the specimens were collected solely on arriving debris and do not, to our knowledge, represent established populations at the landing sites.

Cordell et al. (2013) found that populations of *Ianiropsis serricaudis* were more abundant in the presence of introduced ascidians. The large populations of *Ianiropsis serricaudis* found in Barnegat Bay and other sites identified here were also often associated with a number of species of non-native ascidians, including *Botryllus schlosseri*, *Botrylloides violaceus, Didemnum vexillum, Diplosoma listerianum,* and *Styela clava*, and occasionally with other introduced species such as the bryozoan *Tricellaria inopinata,* suggesting a broader interspecific relationship among introduced epibionts. This is consistent with

Chapman and Carlton (1991), who suggest that introduced species tend to have associations or dependencies on other non-native species. This said, *I. serricaudis* was also commonly found with native fouling organisms (Table 2), indicating an ecological plasticity (and thus habitat expansion) also often characteristic of non-native species.

It is highly probable that *I. serricaudis* is much more widespread both in North America and in Europe, and may already be established in fouling communities in temperate waters of the Southern Hemisphere. It is worth noting that despite the widespread global distribution of the genus *Ianiropsis*, including *I. breviremis* in European waters, *I. serricaudis* is at present the only known member of the genus on the Atlantic coast of the United States. As with many successful introductions around the world, *Ianiropsis serricaudis* remains poorly studied in its native range. Likewise, despite numerous habitat descriptions (Table 2), nothing is known about the ecological role of *I. serricaudis* in its introduced range. Given that this isopod can occur in prodigious numbers (often in the millions of individuals) in fouling communities, studies of its role both as competitor and prey will be of great value.

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