Transoceanic transport of living marine Ostracoda (Crustacea) on tsunami debris from the 2011 Great East Japan Earthquake

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Abstract
We report the first direct evidence for the transoceanic transport of living marine Ostracoda. Seven benthic, phytal species, Sclerochilus verecundus Schornikov, 1981, Sclerochilus sp. 1, Sclerochilus sp. 2, Obesostoma cf. setosum (Okubo, 1977), Obesostoma sp., Paradoxostomatidae sp., and Xestoleberis setouchiensis Okubo, 1979, were transported in tsunami debris that departed the Japanese coast in March 2011 amongst the biofouling on docks, vessels, and buoys that subsequently landed on the Pacific coast of North America. Remarkably, X. setouchiensis survived more than four years rafting through the North Pacific, with a living specimen still arriving in April 2015. Marine debris in general, and tsunami debris specifically, adds to the long list of vectors by which species may be transported globally.

Key words: trans-Pacific dispersal, biofouling, Japan, phytal species, meiofauna, USA Pacific Northwest

Introduction
On 11 March 2011 the Great East Japan Earthquake and the subsequent tsunami struck the Tohoku coast of Honshu of northeast Japan, seriously destroying not only human settlements but also coastal environments (Goto et al. 2012; Kanaya et al. 2012; Seike et al. 2013). The tsunami flushed out a vast amount anthropogenic debris that began to wash ashore on the Pacific coast of North America and the Hawaiian Islands in 2012 (Choong and Calder 2013; Calder et al. 2014; Carlton et al. 2017). This debris field carried hundreds of species of Japanese marine animals and plants eastward across the North Pacific Ocean. We report here on the Ostracoda found on the Japanese tsunami debris arriving in North America (Figure 1). Ostracods are small bivalved crustaceans and are one of the most speciose and ecologically diverse groups of marine invertebrates. Ostracods exhibit direct development and have no nauplius larva stage (Rodriguez-Lazaro et al. 2012; Yasuhara et al. 2017).
Nevertheless, long-distance dispersal has been well studied in freshwater species, many of which produce resting or dry-resistant eggs (McKenzie and Moroni 1986; Martens 1994; Horne and Martens 1998; Meisch 2000; Karanovic 2012) that can be transported by fish, birds, amphibians, and reptiles (e.g. Kornicker and Sohn 1971; Lopez et al. 1999, 2005) as well as, unfortunately, by scientists (Valls et al. 2014). Several species of ectoparasitic freshwater ostracods (Entocytheridae), together with their host North American crayfish, have invaded Hawaii (Hart and Hart 1974), Hokkaido (Smith and Kamiya 2001), the Iberian Peninsula (Aguilar-Alberola et al. 2012), and other regions.

In contrast, long-distance dispersal of marine ostracods is not well understood, although a number of studies have discussed the potential for passive dispersal with rafting seaweeds (McKenzie 1977; Danielopol and Bonaduce 1990; Danielopol et al. 1994). Ingólfsson (1995) found the ostracod Philomedes globosus (Lilljeborg, 1853) on drifting seaweeds 58 to 118 km off the Iceland coast. However, since P. globosus is a nektobenthic myodocopid ostracod and can swim freely, it is doubtful whether this species depends on drifting algae for long-distance dispersal. Kiessling et al. (2015) listed “Cypris sp.” in error as a marine ostracod on rafting debris based on the report of Astudillo et al. (2009), who reported the cypris larvae of the pelagic barnacle (Lepas spp.).

The potential for intercontinental, transoceanic transport of marine ostracods has been touched upon by only a few authors (Teeter 1973; Witte and van Harten 1991; Witte 1993), despite the long-history of both global shipping (moving fouling and ballast communities) and mariculture (transporting live shellfish, such as often heavily biofouled commercial oysters, around the world) (Carlton 2009). Although ostracods have been recorded from vessel fouling (Carlton and Hodder 1995), ballast water (Gollasch et al. 2002; David et al. 2007; Zvyagintsev et al. 2009 [the report by Carlton and Geller 1993 involves the oceanic ostracod Conchoecia; J. T. Carlton, personal observation]), ballast sediments (Gruszka et al. 2013) and algae transported with bait worms (Haska et al. 2011; Fowler et al. 2016), few actual colonization events have been reported.

Kornicker (1975) documented the introduction of the myodocopid Eusarsiella zostericola (Cushman, 1906) from the northwest Atlantic Ocean to the Pacific coast of North America and to England through the transplanting of the Atlantic coast oyster Crassostrea virginica (Gmelin, 1791). Faasse (2013) updated the British records and newly reported E. zostericola from mainland Europe, suggesting that it was transported with shellfish from England to the Netherlands.

Watling (1975) suggested that the Japanese ostracod Spiniileberis quadriaculeata (Brady, 1880) had been introduced with the Pacific oyster Crassostrea gigas (Thunberg, 1793) to California, and that he had inadvertently redescribed it as a new species S. hyalina Watling, 1970. Carlton (1979) suggested the ostracods Aspidococoncha limnoriae De Vos, 1953 and Redekea californica De Vos and Stock, 1956, were both introduced to the Pacific coast of North America (despite the name of the latter) with their non-native isopod Limnoria hosts. Carlton and Eldredge (2015) suggest that Paravargula trifax Kornicker, 1991 (known from the Marshall and Samoan islands) is cryptogenic in the Hawaiian Islands, where it is only found in harbor and port environments that host numerous Indo-Pacific species introduced by ship fouling and ballast.

This present paper provides the first direct evidence for the transoceanic transportation of marine Ostracoda on rafted anthropogenic materials. We provide taxonomic accounts for seven species.
Table 1. Japanese Tsunami Marine Debris (JTMD)-Biofouling (BF) samples, landing sites, dates, objects types, and origins.

<table>
<thead>
<tr>
<th>JTMD-BF-</th>
<th>State</th>
<th>Landing Site</th>
<th>Date</th>
<th>Object Type</th>
<th>Exact origin in northeast Honshu, Japan, if known</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Oregon</td>
<td>Newport: Agate Beach (44.66455, -124.061158)</td>
<td>5 June 2012</td>
<td>floating dock</td>
<td>Aomori Prefecture: Misawa (40.680544, 141.436141)</td>
</tr>
<tr>
<td>40</td>
<td>Oregon</td>
<td>Coos Bay: Charleston (43.345911, -124.321667)</td>
<td>17 May 2014</td>
<td>buoy</td>
<td>Iwate Prefecture: Rikuzentakata (38.982067, 141.708677)</td>
</tr>
<tr>
<td>402, 411</td>
<td>Oregon</td>
<td>floating in open ocean off Newport (44.576869, -124.695656)</td>
<td>10 February 2015</td>
<td>basket</td>
<td></td>
</tr>
</tbody>
</table>

Materials and methods

Ostracod specimens were collected from seven debris items landing between 2012 and 2015 in Oregon and Washington (Table 1; Figure 1). Each object was assigned a unique identification number preceded by JTMD-BF- (Japanese Tsunami Marine Debris - Biofouling - ; see Carlton et al. 2017).

The soft parts of the ostracod specimens were separated from the valves and dissected using fine needles under a stereo-binocular microscope (SZ-60, OLYMPUS, Japan). The valves were preserved on a cardboard cell slide and the soft parts mounted in a gum-chloral medium, Neo-Shigaral (Shiga Konchu Fukyusha, Japan), on glass slides. The specimens were then observed using a transmitted-light binocular microscope (BX-53, OLYMPUS, Japan) with a differential interference contrast system. The valves were washed with distilled water and gold-coated by an Ion sputtering device (JFC-1100, JEOL, Japan). The specimens were then observed by SEM (JSM-6510LV, JEOL, Japan).

 JTMD specimens have been deposited in the collections of the National Museum of Nature and Science, Tokyo (NSMT).

Systematic Account

Order Podocopida Sars, 1866
Superfamily Cytheroidea Baird, 1850
Family Bythocytheridae Sars, 1866
Genus Sclerochilus Sars, 1866

Sclerochilus verecundus Schornikov, 1981
(Figures 2, 3)


Material.—JTMD-BF-1, from fouling community (4 specimens); JTMD-BF-40, from fouling community (48 specimens).

Remarks.—Sclerochilus verecundus was originally described from the Pacific coast of Shikotan Island, which lies off Japan’s northernmost prefecture of Hokkaido (Schornikov 1981). This species has been reported from various sites in the Sea of Japan along the Russian maritime province (Schornikov and Zenina 2007, 2014), along the east coast of South Korea (Lee et al. 2000), and the southern Kuril Islands (Schornikov 1981). Of interest is that this species has never been found from the Tohoku region of Honshu, the source of the present material. However, one quite similar species, Sclerochilus mukaishimensis Okubo, 1977 (Figure 2E, F), is reported from Japanese waters by various authors (Yajima 1987; Iwamori et al. 2008). Schornikov (1981) examined the morphology of S. mukaishimensis based on additional specimens (collected by I. Okubo) from Shiju-shima Island (Seto Inland Sea, Onomichi City, Hiroshima Prefecture). Schornikov (1981) noted differences in soft-parts morphologies between S. mukaishimensis and S. verecundus, e.g., the distal-dorsal region of the tip of the male copulatory organ is narrowly rounded and smooth in S. mukaishimensis, but broadly rounded and wavy in S. verecundus. We observed the same difference in the male copulatory organs (Figure 3) based on comparisons between specimens of S. mukaishimensis from Kure City, Hiroshima Prefecture (34°10’21.7”N, 132°23’28.8”E) and S. verecundus of the present JTMD samples. Unfortunately it is difficult to distinguish these two species based on the carapace morphology due to an absence of surface ornamentation and a similar carapace outline (Figure 2). From Schornikov (1981) onward, S. mukaishimensis has been identified
Figure 2. Scanning electron micrographs of external lateral view. (A–D) Sclerochilus verecundus from Japanese Tsunami Marine Debris Biofouling Sample 40. (E, F) Sclerochilus mukaishimensis from Kure City, Hiroshima Prefecture, Japan. (A) Right valve, male. (B) Left valve, male. (C) Right valve, female. (D) Left valve, female. (E) Right valve, male. (F) Left valve, male. Scale bar is 100 μm.

Figure 3. Light micrographs of male copulatory organ. (A) Sclerochilus verecundus from Japanese Tsunami Marine Debris Biofouling Sample 40. (B) Sclerochilus mukaishimensis from Kure City, Hiroshima Prefecture, Japan. Scale bars are 50 μm.
based on the carapace shape only (e.g. Yajima 1982, 1987; Yamane 1998; Masuma and Yamada 2014), and we therefore suspect that *S. mukaishimensis* in the previous studies may have in fact included *S. verecundus*.

*Sclerochilus verecundus* is not reported from the Northeast Pacific Ocean. *Sclerochilus contortellus* Swain, 1967 from the west coast of North and Central America (Swain 1967, 1969; Swain and Gilby 1974) is similar in carapace shape to *S. verecundus*, but no soft-part description is available for *S. contortellus*. We regard our identification of JTMD material as *S. verecundus* to be confirmed based on the male copulatory organ morphology.

### Sclerochilus sp. 1

**Material.**—JTMD-BF-207, two juvenile specimens.  
**Remarks.**—The specimen was placed in the genus *Sclerochilus* based on the oblong reniform carapace outline and vertical row of five adductor muscle scars but, in the absence of the male copulatory organ, specific identification was not possible.

### Sclerochilus sp. 2

**Material.**—JTMD-BF-402, from fouling community (6 specimens).  
**Remarks.**—As with *Sclerochilus* sp. 1, these specimens were placed in the genus *Sclerochilus* based upon the oblong reniform carapace outline and five adductor muscle scars. The character of the male copulatory organ in this material suggests this is an undescribed species.

Family Paradoxostomatidae Brady and Norman, 1889  
Subfamily Paradoxostomatinae Brady and Norman, 1889; emend Schornikov, 1993  
Genus *Obesostoma* Schornikov, 1993

### Obesostoma cf. setosum (Okubo, 1977)

(Figure 4)

*Paradoxostoma setosum* Okubo, 1977: 104, figure 4f-h; 106, figure 6f; 127–129, figure 19

**Material.**—JTMD-BF-1, one adult male.  
**Remarks.**—The Paradoxostomatinae possess certain characters, such as the elongate tube-shaped mandibular coxa and oral cone with a sucker, that make it relatively easy to identify this subfamily. Genus-level identification is largely dependent on the carapace and soft part morphologies of adult males (Schornikov 1993; Schornikov and Keyser 2004). This JTMD specimen was tentatively recognized as *Obesostoma setosum* by the carapace shape (Figure 4) and the morphologies of antenna, mandible, maxillula, and walking legs. The specimen has a brush-shaped organ, which is a specific structure of the adult male of cytheroidean ostracods. Unfortunately, the male copulatory organ was not preserved in this specimen; therefore, the species identification remains tentative.

*Obesostoma setosum* is reported from the Seto Inland Sea (Okubo 1977, 1980) and east coast of South Korea (Lee et al. 2000). The genus *Obesostoma* includes six species (Brandão 2014) from temperate, subtropical and tropical waters of the Kuril and Japanese Islands, the Red Sea, and the Black Sea as well as possibly the Mediterranean and the Baltic Sea (Schornikov 1993). We note that *Paradoxostoma striangulum* Smith, 1952 from Vancouver Island, Canada, has a very similar carapace and appendage morphologies to *Obesostoma*; however, no formal taxonomic reconsideration of this species has been carried out. Therefore, the genus *Obesostoma* remains unknown from the Eastern Pacific.

### Obesostoma sp.

**Material.**—JTMD-BF-410, from fouling community (18 specimens).
Figure 5. Scanning electron micrographs of external view of *Xestoleberis setouchiensis* from Japanese Tsunami Marine Debris Biofouling Sample 40. (A) Right valve, male. (B) Left valve, male. (C) Right valve, female. (D) Left valve, female. Scale bar is 100 μm.

Remarks.—Specimens were placed in the genus *Obesostoma* based on the carapace shape and the morphologies of antenna, mandible, maxillula, and walking legs. The character of the male copulatory organ suggests that this may be an undescribed species.

**Paradoxostomatidae sp.**

Material.—JTMD-BF-411, from fouling community (2 specimens).

Remarks.—The specimens were placed in the family Paradoxostomatidae based on the elongate tube-shaped mandibular coxa but, as only juveniles were found, generic identification is not possible.

Family Xestoleberididae Sars, 1928  
Genus *Xestoleberis* Sars, 1866  
*Xestoleberis setouchiensis* Okubo, 1979  
(Figures 5–7)

*Xestoleberis setouchiensis* Okubo, 1979: 10–14, figures 2, 3; pl. 1

Material.—JTMD-BF-40 (14 specimens), BF-403 (16 specimens)

Remarks.—Okubo (1979) described *Xestoleberis setouchiensis* from the Seto Inland Sea. *Xestoleberis setouchiensis* is a widely distributed species in Japanese waters; from the cold temperate northeastern coast of Hokkaido to the subtropical Yakushima and Tanegashima Islands (Sato and Kamiya 2007).

Figure 6. Light micrograph of ventral view of *Xestoleberis setouchiensis* from Japanese Tsunami Marine Debris Biofouling Sample 40. Arrowhead indicates eggs. Scale bar is 100 μm.

This species has a dorsoventrally compressed carapace (Figures 5, 6) and includes two morphotypes relative to the basal part of the distal lobe of the male copulatory organ (Okubo 1979), i.e., a parallelogra-
matic type (Figure 7A, D) and a spiny type (Figure 7B). The JTMD specimens belong to parallelogramatic type (Figure 7C).

*Xestoleberis setouchiensis* is not known from the Pacific coast of North America; however, some species that have a dorsoventrally compressed carapace reminiscent of *X. setouchiensis* have been recorded, including *X. cf. setigera* Brady, 1880 from the Gulf of California (Swain et al. 1964) and *X. depressa* Sars, 1866 from the San Diego region (Juday 1907) and Vancouver Island (Lucas 1931). No soft-part information is available for either species, preventing further detailed comparison with *X. setouchiensis*. Holden (1976) reported *X. cf. briggsi* McKenzie, 1967 as a Lower Miocene fossil from Midway Island, in the central Pacific. Gottwald (1983) described *Xestoleberis arcturi darwini* as a new subspecies from the Galapagos Islands. Remarkably, this subspecies shows almost identical characters of carapace shape and size and of soft parts (including the male copulatory organ) with *X. setouchiensis*. The male copulatory organ of *X. arcturi darwini* can be further identified as the parallelogramatic type of *X. setouchiensis*. We thus suppose that *X. arcturi darwini* and *X. setouchiensis* are identical. Sand ballast, easily contaminated with small pieces of seaweed and detritus, was widely used as late as the early 20th century by sailing ships (Carlton 2007), and this, or another ship-mediated vector, may explain the presence of this species on either side of the Pacific Ocean.

Discussion

Seven ostracod taxa (three identified to species level) were found in the biofouling of Japanese tsunami marine debris. *Sclerochilus verecundus, Obesostoma cf. setosum* and *Xestoleberis setouchiensis* are not known from the Pacific coast of North America. Since these species are only found in Japan, the east coast of South Korea, the Russian maritime province, and the Kuril Islands, we concluded that they were transported on the debris and were not acquired in the Eastern Pacific Ocean, nor were the other four taxa, none of which bear close resemblance to Northeast Pacific taxa.

Remarkably, *X. setouchiensis* survived more than four years rafting through the North Pacific, presumably having gone through multiple generations, with a living specimen arriving in April 2015. While JTMD with living Japanese biota continued to arrive in North America and the Hawaiian Islands as of March 2017, samples are not yet in hand to determine if living Western Pacific ostracods are aboard.

Figure 7. Male copulatory organs of *Xestoleberis setouchiensis*. (A) Right organ of parallelogramatic type redrawn from Okubo (1979). (B) Right organ of spiny type redrawn from Okubo (1979). (C) Specimen from Japanese Tsunami Marine Debris Biofouling Sample 40. (D) Specimen from Kure City, Hiroshima Prefecture, Japan. Arrows indicate basal part of distal lobe. Scale bars are 50 μm.

The JTMD biofouling assemblages are composed of algae, hydroids, bryozoans, barnacles, and many other species (Carlton et al. 2017). The genera *Sclerochilus, Obesostoma, and Xestoleberis* are predominantly phytal ostracods (Schornikov 1980; Horne and Whittaker 1985; Horne 2003) and some authors have noted their close association with biofouling (Maddocks 1979; Schornikov 1981). Thus it is not surprising that these ostracods are members of rafting communities. Schornikov (1980) indicated that the floating seaweed *Sargassum* and ship fouling could mediate the wide geographical distribution and
spread of phytotrophic species of *Sclerochilus*, *Xestoleberis*, and *Paradoxostoma*. Schornikov and Zenina (2014) found more than 500 living specimens of *Sclerochilus verecundus* in fouling assemblages (mostly *Mytilus* mussels and a small amount of barnacles, hydroids, and sponges) on a floating dock. Izuzuki et al. (2008) reported many living individuals of *Sclerochilus mukaishimensis* and *Xestoleberis setouchiensis* from seaweed on artificial rafts used for fish farming.

Our results support the hypothesis that phytal marine ostracod species can disperse for long-distances as members of the biofouling assemblages on man-made objects. The lack of nauplius larva stages facilitates in situ recruitment permitting the potential for long-term species endurance on drifting materials. Moreover, the species reported here, or their congeners, are known to tolerate highly stressed environmental conditions, attributes that may further enhance their ability to survive long distance dispersal. *Sclerochilus verecundus* has been reported from the heavily polluted environment of the port of Vladivostok (Schornikov 2000). *Obesostoma obesum* Schornikov, 1993, a congener of *O. setosum*, was found in ship fouling at the Zolotoy Rog (Golden Horn) in Vladivostok and a number of other heavily polluted sites of Russian maritime provinces (Schornikov and Zenina 2014). Sato and Kamiya (2007) note that *Xestoleberis setouchiensis* is an ecological generalist that can live in subtropical, warm to cool-temperate, and even subarctic climates. Moreover, the females of *Xestoleberis* lay eggs in the posterior brood space of the carapace (Figure 6) and early instars remain in this space (Müller 1894; Athersuch 1976; Okubo 1984; Ikeya and Kato 2000). The eggs and juveniles in the brooding chamber might be protected from predators (Athersuch 1976) or from drying. These adaptive characteristics likely contribute to the trans-Pacific survival of the JTMD ostracods.

The lack of previous recognition of the long-distance ocean transport of ostracods by any vector may be linked to their small size, to the few workers specializing in marine living ostracods, and to the historical difficulties in distinguishing many species. Ostracod researchers have historically focused primarily on shell (carapace) morphology, as this is a taxonomic character that can be used by both paleontologists and biologists. However, a number of workers (e.g. Benson 1964; Cronin 1983; Frame et al. 2007) have noted that the species level identification of *Sclerochilus*, *Xestoleberis*, and *Paradoxostomatidae* including *Obesostoma*, is almost impossible based on carapace morphology alone, due to their smooth surfaces and minimal intra-specific difference in outline. Regardless of carapace similarity, if species show widely separated geographical distributions, it is possible that they may be discriminated as distinct based on only small differences.

Our results also suggest that the long-distance dispersal of marine ostracods has occurred far more frequently than reported, as implied in previous studies on oceanic island ostracods (Hartmann 1988; Titterton and Whatley 1988; Dingle 2002). Comprehensive studies on the taxonomy and biogeography of ostracods based not only on carapace and soft part morphologies, but also on molecular phylogenetic approaches (e.g. Nigro et al. 2016; Tanaka and Ohtsuka 2016; Tanaka et al. 2016) are clearly needed.

Tsunami debris adds to the long list of anthropogenic-associated vectors that have the potential to transport ostracods across otherwise usually insurmountable barriers. Catastrophic disasters like the Tohoku earthquake and tsunami occur in other tectonically-active regions of the Indo-Pacific region (such as the 2004 Indian Ocean tsunami and the 2010 Chilean tsunami). The increased availability of plastic and other materials on densely populated coastlines may make future tsunami-generated debris, and marine debris overall, increasingly significant in the dispersal and potential introduction of many marine species.

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Transoceanic dispersal of marine Ostracoda


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