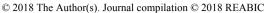


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Special Issue: Transoceanic Dispersal of Marine Life from Japan to North America and the Hawaiian Islands as a Result of the Japanese Earthquake and Tsunami of 2011

Research Article

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).

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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 longdistance 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.

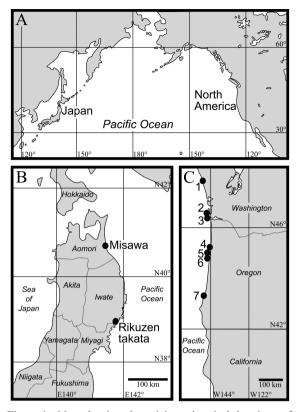


Figure 1. Map showing the origin and arrival locations of Japanese Tsunami Marine Debris (JTMD) material that contained ostracods. Details in Table 1. (A) North Pacific Ocean. (B) Exact origins, Tohoku region, northeast Japan. (C) Arrival locations, west coast of North America 1, Kalaloch; 2, Long Beach; 3, Seaview; 4, Agate Beach; 5, 6, Off Newport; 7, Coos Bay.

Watling (1975) suggested that the Japanese ostracod Spinileberis 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 Aspidoconcha 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.

JTMD-BF-	State	Landing Site	Date	Object Type	Exact origin in northeast Honshu, Japan, if known
1	Oregon	Newport: Agate Beach (44.66455, -124.061158)	5 June 2012	floating dock	Aomori Prefecture: Misawa (40.680544, 141.436141)
40	Washington	Long Beach (46.475511, -124.071969)	22 March 2013	vessel Sai-shō-maru	Iwate Prefecture: Rikuzentakata (38.982067, 141.708677)
207	Oregon	Coos Bay: Charleston (43.345911, -124.321667)	17 May 2014	buoy	()
402	Washington	Seaview (46.336032, -124.069151)	10 May 2015	vessel	
403	Washington	Kalaloch (47.605564, -124.378775)	25 April 2015	buoy	
410, 411	Oregon	floating in open ocean off Newport (44.576869, -124.695656)	10 February 2015	basket	

Table 1. Japanese Tsunami Marine Debris (JTMD)-Biofouling (BF) samples, landing sites, dates, objects types, and origins.

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)

Sclerochilus (Praesclerochilus) verecundus Schornikov, 1981: 112, 116, figures 8*B*, 15*B*, 18*V*, 20*G*, 22*B*, *D*, 24*B*, *V*, *Z*, 37*B*, *V*; pl. 7 (1, 4, 5, 7, 8, 9).

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: Yamane 1998; Irizuki 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 distaldorsal 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°33′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

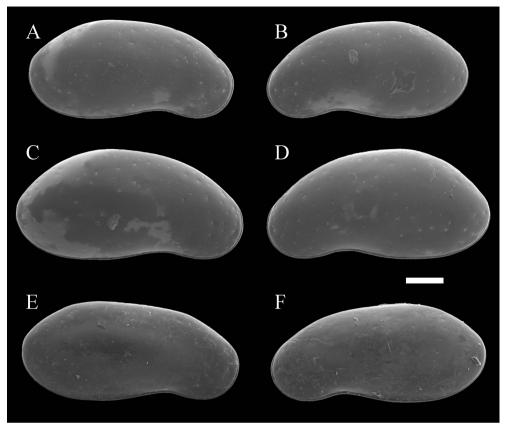


Figure 2. Scanning electron micrographs of external lateral view. (A–D) *Sclerochilus verecundus* from Japanese Tsunami Marine Debris Biofouling Sample 40. (E, F) *Sclerochilus mukaishimensis* from Kure City, Hiroshima Prefecture, Japan. (A) Right valve, male. (B) Left valve, male. (C) Right valve, female. (D) Left valve, female. (E) Right valve, male. (F) Left valve, male. Scale bar is 100 µm.

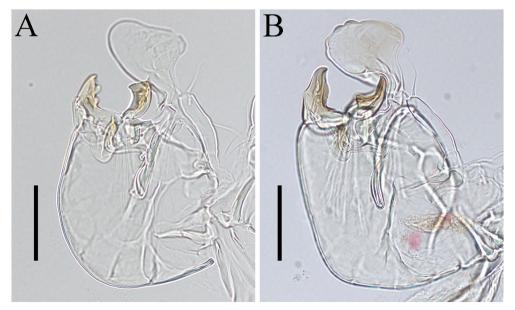


Figure 3. Light micrographs of male copulatory organ. (A) *Sclerochilus verecundus* from Japanese Tsunami Marine Debris Biofouling Sample 40. (B) *Sclerochilus mukaishimensis* from Kure City, Hiroshima Prefecture, Japan. Scale bars are 50 μm.

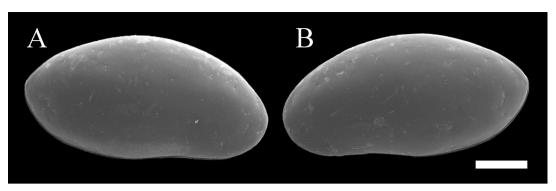


Figure 4. Scanning electron micrographs of external view of *Obesostoma* cf. *setosum* from Japanese Tsunami Marine Debris Biofouling Sample 1, male. (A) Right valve. (B) Left valve. Scale bar is 100 μm.

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. Genuslevel 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* striungulum 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).

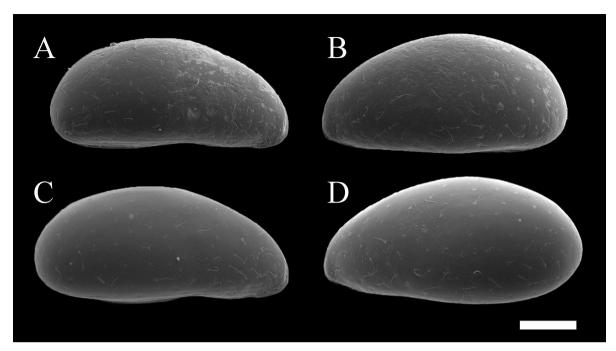


Figure 5. Scanning electron micrographs of external view of *Xestoleberis setouchiensis* from Japanese Tsunami Marine Debris Biofouling Sample 40. (A) Right valve, male. (B) Left valve, male. (C) Right valve, female. (D) Left valve, female. Scale bar is 100 µm.

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 shipmediated 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.

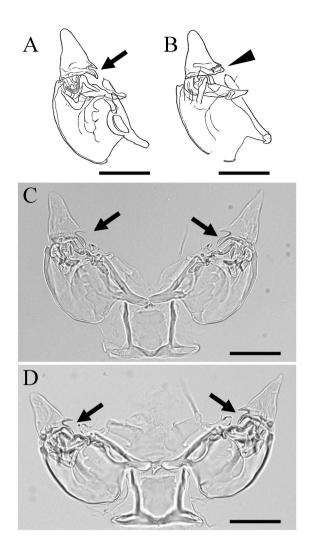


Figure 7. Male copulatory organs of *Xestoleberis setouchiensis*. (A) Right organ of parallelogramatic type redrawn from Okubo (1979). (B) Right organ of spiny type redrawn from Okubo (1979). (C) Specimen from Japanese Tsunami Marine Debris Biofouling Sample 40. (D) Specimen from Kure City, Hiroshima 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 phytophilic 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. Irizuki 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 longdistances 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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References

Aguilar-Alberola JA, Mesquita-Joanes F, López S, Mestre A, Casanova JC, Rueda J (2012) An invaded invader: high prevalence of entocytherid ostracods on the red swamp crayfish *Procambarus clarki* (Girard, 1852) in the Eastern Iberian Peninsula. *Hydrobiologia* 688: 63–73, https://doi.org/10.1007/s10 750-011-0660-1

- Astudillo JC, Bravo M, Dumont CP, Thiel M (2009) Detached aquaculture buoys in the SE Pacific: potential dispersal vehicles for associated organisms. *Aquatic Biology* 5: 219–231, https://doi.org/10.3354/ab00151
- Athersuch J (1976) The genus *Xestoleberis* (Crustacea: Ostracoda) with particular reference to Recent Mediterranean species. *Pubblicazioni della Stazione zoological di Napoli* 40: 282–343
- Benson RH (1964) Recent marine podocopid and platycopid ostracodes of the Pacific. *Pubblicazioni della Stazione zoological di Napoli* 33: 387–420
- Brandão SN (2014) *Obesostoma* Schornikov, 1993. In: Brandão SN, Angel MV, Karanovic I, Parker A, Perrier V, Yasuhara M (eds), World Ostracoda Database. http://www.marinespecies.org/ostracoda/aphia.php?p=taxdetails&id=459754 (accessed on 27 June 2016)
- Calder DR, Choong HHC, Carlton JT, Chapman JW, Miller JA, Geller J (2014) Hydroids (Cnidaria: Hydrozoa) from Japanese tsunami marine debris washing ashore in the northwestern United States. Aquatic Invasions 9: 425–440, https://doi.org/10. 3391/ai.2014.9.4.02
- Carlton JT (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation, University of California, Davis, 904 pp
- Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261: 78–82, https://doi.org/10.1126/science.261.5117.78
- Carlton JT, Hodder J (1995) Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16thcentury sailing vessel. *Marine Biology* 121: 721–730, https://doi. org/10.1007/BF00349308
- Carlton JT (2007) Ballast. In: Hattendorf JB (ed), The Oxford Encyclopedia of Maritime History. Oxford University Press. Volume 1, pp 249–251
- Carlton JT (2009) Deep invasion ecology and the assembly of communities in historical time. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems. Springer-Verlag, Berlin, pp 13–56, https://doi.org/10.1007/978-3-540-79236-9 2
- Carlton JT, Eldredge LG (2015) Update and Revision of The Marine Bioinvasions of Hawai'i: The Introduced and Cryptogenic Marine and Estuarine Animals and Plants of the Hawaiian Archipelago. In: Evenhuis NL, Carlton JT (eds), Lucius G. Eldredge III Memorial Volume: Tribute to a Polymath. Bishop Museum Bulletin Zoology 9, pp 25–47
- Carlton JT, Chapman JWC, Geller JB, Miller JA, Carlton DA, McCuller MI, Treneman N, Steves BP, Ruiz GM (2017) Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. *Science* 357 (6358): 1402–1406, https://doi.org/10.1126/science.aao1498
- Choong HHC, Calder DR (2013) Sertularella mutsuensis Stechow, 1931 (Cnidaria: Hydrozoa: Sertulariidae) from Japanese tsunami debris: systematics and evidence for transoceanic dispersal. BioInvasions Records 2: 33–38, https://doi.org/10.3391/bir.2013.2.1.05
- Cronin TM (1983) Bathyal ostracodes from the Florida-Hatteras slope, the Straits of Florida, and the Blake Plateau. Marine Micropaleontology 8: 89–119, https://doi.org/10.1016/0377-8398(83)90007-5
- Danielopol DL, Bonaduce G (1990) Origin and distribution of the interstitial species group Xestoleberis arcturi Triebel (Ostracoda: Crustacea). Courier Forschungsinstitut Senckenberg 123: 69–86
- Danielopol DL, Marmonier P, Boulton AJ, Bonaduce G (1994) World subterranean ostracod biogeography: dispersal or vicariance. *Hydrobiologia* 287: 119–129, https://doi.org/10.1007/BF00006901
- David M, Gollasch S, Cabrini M, Perkovic M, Bosnjak D, Virgilio D (2007) Results from the first ballast water sampling study in the Mediterranean Sea the Port of Koper study. *Marine Pollution Bulletin* 54: 53–65, https://doi.org/10.1016/j.marpolbul.2006.08.041
- Dingle RV (2002) Insular endemism in Recent Southern Ocean benthic Ostracoda from Marion Island: Palaeozoogeographical and evolutionary implications. Revista Española de Micropaleontología 34(2): 215–233

- Faasse M (2013) The North American ostracode *Eusarsiella* zostericola (Cushman, 1906) arrives in mainland Europe. *BioInvasions Records* 2: 47–50, https://doi.org/10.3391/bir.2013.2.1.08
- Fowler AE, Blakeslee AMH, Canning-Clode J, Repetto M, Phillip AM, Carlton JT, Moser FC, Ruiz GA, Miller AW (2016) Opening Pandora's bait box: a potent vector for biological invasions of marine species. *Diversity and Distributions* 22: 30–42, https://doi. org/10.1111/ddi.12376
- Frame K, Hunt G, Roy K (2007) Intertidal meiofaunal biodiversity with respect to different algal habitats: a test using phytal ostracodes from Southern California. *Hydrobiologia* 586: 331–342, https://doi.org/10.1007/s10750-007-0707-5
- Gollasch S, MacDonald E, Belson S, Botnen H, Christensen JT, Hamer JP, Houvenaghel G, Jelmert A, Masson D, McCollin T, Olenin S, Persson A, Wallentinus I, Wetsteyn LPMJ, Wittling T (2002) Life in ballast tanks. In: Leppakoski E (ed), Invasive Aquatic Species of Europe. Kluwer Academic Publishers, Netherlands, pp 217–231, https://doi.org/10.1007/978-94-015-9956-6_23
- Goto K, Chagué-Goff C, Goff J, Jaffe B (2012) The future of tsunami research following the 2011 Tohoku-oki event. Sedimentary Geology 282: 1–13, https://doi.org/10.1016/j.sedgeo.2012.08.003
- Gottwald J (1983) Interstitielle Fauna von Galapagos (XXX). Podocopida 1 (Ostracoda). *Mikrofauna Meeresboden* 90: 1–187
- Gruszka P, Rokicka-Praxmajer J, Cupak J, Radziejewska T, Wolska M (2013) Unintended "biological cargo" of ships entering the River Odra estuary: assemblages of organisms in ballast tanks. Scientific Journals. Maritime University of Szczecin 33: 22–29
- Hart DG, Hart CW (1974) The ostracod family Entocytheridae. Monograph 18, the Academy of Natural Sciences of Philadelphia 19th and the parkway. Philadelphia, Pennsylvania, USA, pp 239
- Hartmann G (1988) Distribution and dispersal of littoral Pacific island Ostracoda. In: Hanai T, Ikeya N, Ishizaki K (eds), Evolutionary biology on Ostracoda, Proceedings of the ninth international symposium on Ostracoda. Kodansha Ltd, Tokyo, pp 787–795, https://doi.org/10.1016/S0920-5446(08)70221-8
- Haska CL, Yarish C, Kraemer G, Blaschik N, Whitlatch R, Zhang H, Lin S (2011) Bait worm packaging as a potential vector of invasive species. *Biological Invasions* 14: 481–493, https://doi.org/ 10.1007/s10530-011-0091-y
- Holden JC (1976) Late Cenozoic Ostracoda from Midway island drill holes. Geological Survey Professional Paper 680F: 1–43
- Horne DJ (2003) Key events in the ecological radiation of the Ostracoda. Paleontological Society Papers 9: 181–201
- Horne DJ, Martens K (1998) An assessment of the importance of resting eggs for the evolutionary success of Mesozoic nonmarine cypridoidean Ostracoda (Crustacea). Archiv für Hydrobiologie Special Issues in Advanced Limnology 52: 549–561
- Horne DJ, Whittaker JE (1985) A revision of the genus *Paradoxostoma* Fischer (Crustacea; Ostracoda) in British waters. *Zoological Journal of the Linnean Society* 85: 131–203, https://doi.org/10.1111/j.1096-3642.1985.tb01502.x
- Ikeya N, Kato M (2000) The life history and culturing of Xestoleberis hanaii (Crustacea, Ostracoda). Hydrobiologia 419: 149–159, https://doi.org/10.1023/A:1003931901501
- Ingólfsson A (1995) Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. Marine Biology 122: 13–21, https://doi.org/10.1007/BF00349273
- Irizuki T, Seto K, Nomura R (2008) The impact of fish farming and bank construction on Ostracoda in Uranouchi Bay on the Pacific coast of southwest Japan—Faunal changes between 1954 and 2002/2005. Palaeontological Research 12: 283–302, https://doi. org/10.2517/1342-8144-12.3.283
- Juday C (1907) Ostracoda of the San Diego region, II. Littoral forms. University of California Publications in Zoology 3: 135–156
- Kanaya G, Suzuki T, Maki H, Nakamura Y, Miyajima Y, Kikuchi E (2012) Effects of the 2011 tsunami on the topography, vegetation, and microbenthic fauna in Gamo Lagoon, Japan. *Japanese Journal of Benthology* 67: 20–32 [In Japanese with English abstract], https://doi.org/10.5179/benthos.67.20

- Karanovic I (2012) Recent freshwater Ostracoda of the world. Springer-Verlag, Berlin, pp 608, https://doi.org/10.1007/978-3-642-21810-1
- Kiessling T, Gutow L, Thiel M (2015) Marine litter as habitat and dispersal vector. In: Bergmann M, Gutow L, Klages M (eds), Marine Anthropogenic Litter. Springer International Publishing, Gewerbestrasse, Switzerland, pp 141–181, https://doi.org/10.1007/ 978-3-319-16510-3 6
- Kornicker (1975) Spread of ostracodes to exotic environs on transported oysters. Bulletins of American Paleontology 65: 129–139
- Kornicker LS, Sohn IG (1971) Viability of ostracode eggs egested by fish and effect of digestive fluids on ostracode shells— ecologic and paleoecologic implications. In: Oertli HJ (ed), Paléoécologie des Ostracodes. Bulletin du Centre de Recherche de Pau, SNPA 5 (supplement), pp 125–135
- Lee EH, Huh M, Schornikov E (2000) Ostracod fauna from East Sea coast of Korea and their distribution—preliminary study on Ostracoda as an indicator of water pollution. *Journal of the Geological Society of Korea* 36: 435–472 [In Korean with English abstract]
- Lopez LCS, Rodorigues PJFP, Rios RI (1999) Frogs and snakes as phoretic dispersal agents of bromeliad ostracods (Limnocytheridae: *Elipidium*) and annelids (Naididae: *Dero*). *Biotropica* 31: 705–708, https://doi.org/10.1111/j.1744-7429.1999.tb00421.x
- Lopez LCZ, Filizola B, Deiss I, Rios RI (2005) Phoretic behaviour of bromeliad annelids (*Dero*) and ostracods (*Elpidium*) using frogs and lizards as dispersal vectors. *Hydrobiologia* 549: 15–22, https://doi.org/10.1007/s10750-005-1701-4
- Lucas VZ (1931) Some ostracods of the Vancouver Island region. Contributions to Canadian Biology 6: 399–410
- Maddocks RF (1979) Two new examples of symbiosis or parasitism in cypridacean Ostracoda. Crustaceana 37: 1–12, https://doi.org/ 10.1163/156854079X00816
- Martens K (1994) Ostracod speciation in ancient lakes: a review. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie 44: 203–222.
- Masuma T, Yamada K (2014) Recent ostracode distributions in Kumihama Bay (brackish lake) in the northern part of Kyoto Prefecture, central Japan. *Laguna* 21: 1–14 [In Japanese with English abstract]
- McKenzie KG (1977) La faune terrestre de l'île de Sainte-Hélène, 3. Ostracoda. Koninklijk Museum voor Midden-Afrika, Tervuren, België: Annalen-Reeks in-8°-Zoologische Wetenschappen 220: 444–451
- McKenzie KG, Moroni A (1986) Man as an agent of crustacean dispersal via useful plants—exemplified by Ostracoda ospiti esteri of the Italian ricefields ecosystem: and implications arising therefrom. *Journal of Crustacean Biology* 6: 181–198, https://doi.org/10.2307/1547979
- Meisch C (2000) Freshwater Ostracoda of western and central Europe. In: Schwoerbel J, Zwick P (eds), Suesswasserfauna von Mitteleuropa 8/3. Spektrum Akademischer Verlag, Berlin, pp 1– 387
- Müller GW (1894) Die Ostracoden Golfes von Neapel und der Angrenzenden Meeresabschnitte. Herausgegben von der Zoologischen Station zu Neapel 21: 1–404
- Nigro LM, Angel MV, Blachowiak-Samolyk K, Hopcroft RR, Bucklin A (2016) Identification, discrimination, and discovery of species of marine planktonic ostracods using DNA barcodes. PLoS ONE 11: e0146327, https://doi.org/10.1371/journal.pone.0146327
- Okubo I (1977) A new species of Sclerochilus (Ostracoda) from the Inland Sea of Japan. Proceedings of the Japanese Society of Systematic Zoology 13: 59–65
- Okubo I (1979) Three species of Xestoleberis (Ostracoda) from the Inland Sea of Japan. Proceedings of the Japanese Society of Systematic Zoology 16: 9–17
- Okubo I (1980) Taxonomic studies on Recent marine podocopid Ostracoda from the Inland Sea of Seto. *Publications of the Seto Marine Biological Laboratory* 22: 1–30

- Okubo I (1984) On the life history and the size of *Xestoleberis* hanaii. Research Bulletin of Shujitsu Women's College and Junior College 14: 19–43
- Rodriguez-Lazaro J, Ruiz-Muñoz F, Viehberg FA (2012) A general introduction to ostracods: morphology, distribution, fossil record and applications. In: Horne DJ, Holmes JA, Rodriguez-Lazaro J (eds), Ostracoda as proxies for Quaternary climate change. Elsevier, Netherlands, pp 1–14, https://doi.org/10.1016/b978-0-444-53636-5.00001-9
- Sato T, Kamiya T (2007) Taxonomy and geographical distribution of recent Xestoleberis species (Cytheroidea, Ostracoda, Crustacea) from Japan. Paleontological Research 11: 183–227, https://doi.org/ 10.2517/1342-8144(2007)11[183:TAGDOR]2.0.CO;2
- Schornikov EI (1980) New ostracods species of coral reefs of the Red Sea and Adan's Bay. In: Preobrazhenskij BV, Krasnov EV (eds), Biology of coral reefs, morphology, systematics, ecology. Akademiya Nauk SSSR, Moscow, pp 131–157 [In Russian]
- Schornikov EI (1981) Ostracoda Bythocytheridae of the Far-Eastern Seas. Nauka, Moscow, 199 pp [In Russian]
- Schomikov EI (1993) Systematic problems of the ostracods of family Paradoxostomatidae and reclassification of *Paradoxo-stoma s.l.* from Peter the Great Bay (Sea of Japan). In: Kafanov AI (ed), Ecosystems research: Costal communities of Peter the Great Bay. Far East Branch, Academy Sciences USSR, Vladivostok, pp 153–166 [In Russian]
- Schornikov EI (2000) Ostracoda as indicators of conditions and dynamics of water ecosystems. In: Martin RE (ed), Environmental Micropaleontology, Topics in Geobiology 15. Springer US, New York, pp 181–187, https://doi.org/10.1007/978-1-4615-4167-7 9
- Schornikov EI, Keyser D (2004) The morphology and classification of Paradoxostomatinae (Ostracoda) from the nearshore zone of Madeira and Canary Islands. Revista Española de Micropaleontología 36: 57–74
- Schornikov EI, Zenina MA (2007) Buried ostracods collected at the location of a nuclear submarine accident in the Chazhma Cove (Peter the Great Bay, Sea of Japan). Russian Journal of Marine Biology 33: 200–203, https://doi.org/10.1134/S1063074007030108
- Schornikov EI, Zenina MA (2014) Ostracods as indicators of conditions and dynamics of water ecosystems (on the example of Peter the Great Bay, Sea of Japan). Dalnauka, Vladivostok, Russia, 333 pp [In Russian]
- Seike K, Shirai K, Kogure Y (2013) Disturbance of shallow marine soft-bottom environments and megabenthos assemblages by a huge tsunami induced by the 2011 M9.0 Tohoku-Oki Earthquake. PLoS ONE 8: e65417, https://doi.org/10.1371/journal. pone.0065417
- Smith RJ, Kamiya T (2001) The first record of an entocytherid ostracod (Crustacea: Cytheroidea) from Japan. Benthos Research 56: 57–61, https://doi.org/10.5179/benthos1996.56.2_57
- Swain FM (1967) Ostracoda from the Gulf of California. The Geological Society of America, Memoir 101: 1–139, https://doi.org/ 10.1130/MEM101-p1
- Swain FM (1969) Taxonomy and ecology of near-shore Ostracoda from the Pacific coast of north and central America. In: Neale JW (ed), The taxonomy, morphology and ecology of Recent Ostracoda. Oliver and Boyd, Edinburgh, UK, pp 423–474
- Swain FM, Gilby JM (1974) Marine Holocene Ostracoda from the Pacific coast of north and central America. *Micropaleontology* 20: 257–353, https://doi.org/10.2307/1484940
- Swain FM, Miller PL, Mandelbaum EC (1964) Ostracoda from Gulf of California. The American Association of Petroleum Geologists, pp 395–397
- Tanaka H, Le DD, Higashi R, Tsukagoshi A (2016) A new interstitial ostracod species of the genus *Paracobanocythere* from Vietnam, with mitochondrial CO1 sequence data of three Asian species. *ZooKeys* 559: 17–33, https://doi.org/10.3897/zoo keys.559.6751
- Tanaka H, Ohtsuka S (2016) Historical biogeography of the genus Polycopissa (Ostracoda: Myodocopa: Cladocopina), with the

- description and DNA barcode of the second Indo-Pacific species from the Seto Inland Sea. *Marine Biodiversity* 46: 625–640, https://doi.org/10.1007/s12526-015-0412-y
- Teeter JW (1973) Geographic distribution and dispersal of some Recent shallow-water marine Ostracoda. The Ohio Journal of Science 73: 46–54
- Titterton R, Whatley RC (1988) The provincial distribution of shallow water Indo-Pacific marine Ostracoda: origins, antiquity, dispersal routes and mechanisms. In: Hanai T, Ikeya N, Ishizaki K (eds), Evolutionary Biology on Ostracoda, Proceedings of the ninth international symposium on Ostracoda, Kodansha Ltd., Tokyo, Japan, pp 759–786, https://doi.org/10.1016/S0920-5446(08)70220-6
- Valls L, Mestre A, Gil-Delgado JA, Mesquita-Joanes F (2014) The shoemaker's son always goes barefoot: intercontinental dispersal of Ostracoda (Crustacea) by scientists attending an IBS excursion. Frontiers of Biogeography 6: 89–91
- Watling L (1975) Remarks, in, L. Kornicker. Spread of ostracodes to exotic environs on transported oysters. *Bulletins of American Paleontology* 65: 129–139
- Witte L (1993) Taxonomy and biogeography of West African beach ostracods. Geological Survey of the Netherlands, Haarlem, Netherlands, 84 pp
- Witte L, van Harten D (1991) Polymorphism, biogeography and systematics of Kotoracythere inconspicua (Brady, 1880) (Ostracoda: Pectocytheridae). Journal of Biogeography 18: 427– 436, https://doi.org/10.2307/2845484

- Yajima M (1982) Late Pleistocene Ostracoda from the Boso Peninsula, central Japan. The University Museum, the University of Tokyo, Bulletin 20: 141–227
- Yajima M (1987) Pleistocene Ostracoda from the Atsumi Peninsula, central Japan. Transactions and Proceedings of the Palaeontological Society of Japan 146: 49–76
- Yamane K (1998) Recent ostracode assemblages from Hiuchi-nada Bay, Seto Inland Sea of Japan. *Bulletin of Ehime Prefectural Science Museum* 3: 19–59 [In Japanese with English abstract]
- Yasuhara M, Tittensor DP, Hillebrand H, Worm B (2017) Combining marine macroecology and palaeoecology in understanding biodiversity: microfossils as a model. *Biological Reviews* 92: 199–215, https://doi.org/10.1111/brv.12223
- Zvyagintsev AY, Ivin VV, Kashin IA, Orlova TYu, Selina MS, Kasyan VV, Korn OM, Kornienko ES, Kulikova VA, Bezverbnaya IP, Zvereva LV, Radashevsky VI, Belogurova LS, Begun AA, Gordokov AN (2009) Acclimation and introduction of hydrobionts ships' ballast water organisms in the Port of Vladivostok. Russian Journal of Marine Biology 35: 41–52, https://doi.org/10.1134/S1063074009010076