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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

Tsunami-generated rafting of foraminifera across the North Pacific Ocean

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Abstract

This is the first report of long-distance transoceanic dispersal of coastal, shallow-water benthic foraminifera by ocean rafting, documenting survival and reproduction for up to four years. Fouling was sampled on rafted items (set adrift by the Tohoku tsunami that struck northeastern Honshu in March 2011) landing in North America and the Hawaiian Islands. Seventeen species of shallow-water benthic foraminifera were recovered from these debris objects. Eleven species are regarded as having been acquired in Japan, while two additional species (*Planogypsina squamiformis* (Chapman, 1901) and *Homotrema rubra* (Lamarck, 1816)) were obtained in the Indo-Pacific as those objects drifted into shallow tropical waters before turning north and east to North America. Four species were acquired after the debris came ashore in Hawaii and in North America. As previously shown for the Japanese species *Trochammina hadai* Uchio, 1962 and the Indo-Pacific species *Amphistegina lobifera* Larsen, 1976, introduced foraminiferal species may rapidly proliferate and disperse, negatively impacting native species. In the geologic past, panoceanic rafting must have been relatively infrequent, as it would have floating pumice and vegetation with relatively limited potential for multiyear survival at sea. In modern times, the ever-increasing abundance of floatable plastic artifacts emplaced along tectonic coastlines provides a greater abundance of more permanent materials for tsunami- and storm-generated rafts that can introduce foraminifera and other marine biota to distant shorelines.

Key words: foraminifera**,** introduced species, Northeast Pacific, rafting, transoceanic dispersal, tsunami-generated debris

Introduction

The Tōhoku earthquake and tsunami of 11 March 2011 resulted in benthic foraminifera being washed inland (Pilarczyk et al. 2012) and displaced by turbidity currents into deep water (Usami et al. 2016). The present study investigates a third mode of foraminiferal transport resulting from this historic seismic event — transoceanic rafting. While ships' ballast water is commonly cited as a vector of marine species (Carlton 1985; Gollasch 2002), including foraminifera (Radziejewska et al. 2006; McGann et al. 2012; McGann 2014a), tsunami-generated debris rafting is now recognized as another means for long-distance transport of benthic coastal-marine species (Carlton et al. 2017). As a result of population growth and coastal development around the Pacific Rim, there is now an abundance of floatable anthropogenic objects that can be dislodged by tsunamis and potentially transport epibenthic organisms across vast distances.

Foraminifera are rhizopodian protists, most no bigger than a sand grain, that are among the most abundant and diverse shelled organisms in the sea. They are low on the marine trophic pyramid, feeding primarily on bacteria and algae. In turn, they are mostly ingested by indiscriminate feeders. Little is known about the ecological impact of the relatively few introduced foraminifera that have been reported around the world. Nevertheless, the potential of introduced foraminifera to change the seascape has been documented in the eastern Mediterranean, where the invasion of the Lessepsian foraminifer *Amphistegina lobifera* Larsen, 1976 has been described as "a very good example to show how much a "harmless" alien species can actually have the potential to destroy an ecosystem" (Streftaris and Zenetos 2006). Indeed, Yokes and Meriç (2009) report that former rocky reefs on the Turkey coast are now covered with thick deposits of *A. lobifera* tests up to 80 cm deep, converting former hard habitat to soft bottoms. They further report that "Waves carry foraminifera tests to the shores where they accumulate in small bays, thus changing gravelly shores to sandy beaches. This extensive deposition of tests is creating an immense ecological problem by changing the whole habitat structure, while definitely altering the species composition of the coastal ecosystem in the long run".

This investigation of foraminifera recovered from Japanese Tsunami Marine Debris (JTMD) that arrived on the Hawaiian and North American coasts represents the first study of transoceanic dispersal of coastal foraminifera by rafting.

Materials and methods

Foraminifera sorted from JTMD samples and preserved in ethanol were sent to this author for study. Samples were recovered between 2012 and 2015 from a wide variety of JTMD objects, ranging from large docks to small buoys that had landed in North America and the Hawaiian Islands (Figure 1; Supplementary material Table S1). Objects are identified as directly related to the March 2011 tsunami through multiple lines of evidence detailed in Carlton et al. (2017). Each object was assigned a unique identification number preceded by JTMD-BF- (Japanese Tsunami Marine Debris - Biofouling).

The tests were transferred to cardboard (micropaleontological) slides for microscopic examination. The relative ages of specimens are recorded as juvenile, subadult, or adult growth (developmental) stages. A dark greenish-brown color of chambers, particularly common among the juvenile specimens, was assumed to be that of protoplasm, indicating specimens that were likely alive when collected.

Published illustrations of Foraminifera from both sides of the North Pacific were compared in an attempt to confirm the origin of JTMD specimens. In foraminiferal literature, however, it is not unusual to encounter different names for the same morphospecies or their ecophenotypic variants in different regions. A bias toward endemism and taxonomic splitting renders some regional studies difficult to integrate with other works. In addition, relatively few studies have focused on restricted embayments and tidal inlets between British Columbia and northern California. In the Systematic Account below, previous records of each species on the Pacific coast of northern Honshu (Nomura 1981, 1997) and from British Columbia to northern California (Culver and Buzas 1985, 1986) are cited. JTMD foraminifera have been deposited in the University of California Museum of Paleontology microfossil collection.

Results

A total of 234 foraminifera were isolated from 30 samples collected from 23 JTMD objects (Table S1): four from Hawaii and 19 from North America (two from the southern part of Vancouver Island, British Columbia, seven from Washington, nine from Oregon, and one from northern California). Seventeen benthic and one planktic (*Globigerina bulloides* d'Orbigny, 1826) species were identified (Figure 2). All of the benthic species were characteristic of very shallow coastal waters. The majority (~ 70%) of specimens are juveniles. Eleven species are regarded from Japan, while two additional species (*Planogypsina squamiformis* (Chapman, 1901) and *Homotrema rubra* (Lamarck, 1816)) were acquired in the Indo-Pacific as those objects drifted into shallow tropical waters before turning north and east to North America. Four species were acquired after the debris came ashore in Hawaii (*Planorbulina acervalis* Brady, 1884; *Amphistegina lobifera* Larsen, 1976) and in North America (*Elphidiella hannai* (Cushman and Grant, 1927); *Glabratella ornatissima* (Cushman, 1925)).

One to four species of western Pacific foraminifera were found on JTMD objects. The most species (four) were found on a dock (JTMD-BF-1) that departed the Port of Misawa on March 11, 2011 and landed on the central Oregon coast on June 5, 2012, and on a buoy (JTMD-BF-207) that floated into Coos Bay, Oregon, on May 17, 2014.

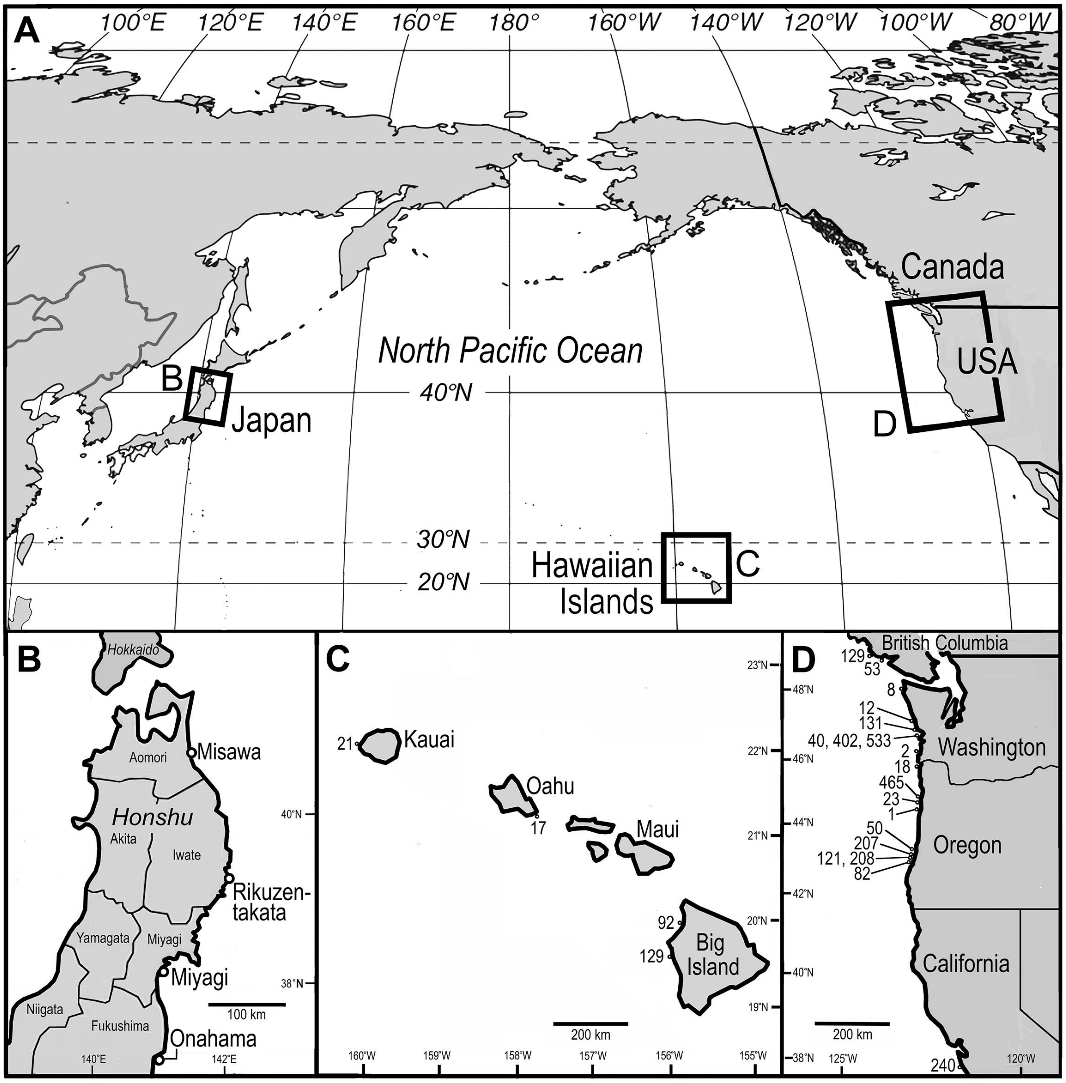

Figure 1. Maps showing the origin and arrival locations of Japanese Tsunami Marine Debris (JTMD) material that contained foraminifera. A, North Pacific; B, Japan; C, Hawaii; D, North America. Details in Table S1.

Systematic Account

Phylum Foraminifera (d'Orbigny, 1826) Lee, 1990
Class Tubothalamea Pawlowski, Holzmann, Tyszka, 2013
Order Miliolida Delage and Hérouard, 1896
Suborder Miliolina Delage and Hérouard, 1896
Superfamily Milioloidea Ehrenberg, 1839
Family Hauerinidae Schwager, 1876
Subfamily Miliolinellinae Vella, 1957
Genus *Miliolinella* Wiesner, 1931

***Miliolinella subrotunda* (Montagu, 1803)**
(Figure 2f)

Vermiculum subrotundum Montagu, 1803: 2, pl. 1, fig. 4.

Material.—JTMD-BF-1, fouling inside floating dock bumper, 1 juvenile; BF-2, among gooseneck barnacle *Lepas*, 1 juvenile; BF-40, inside rim of vessel hold, 1 juvenile; BF-129, on amphipod mud tubes in fouling, 13 juveniles.

Previous records.—Northeastern Honshu: Ujiie and Kusukawa (1969); Oregon: Detling (1958, as *Pateoris hauerinoides* (Rhumbler, 1936)).

Remarks.—This porcelaneous species is represented entirely by juveniles that, like those of many other *Miliolinella*, vary widely before they attain the diagnostic morphology of the adult form. Species of *Miliolinella* are shallow-water clinging epiphytes.

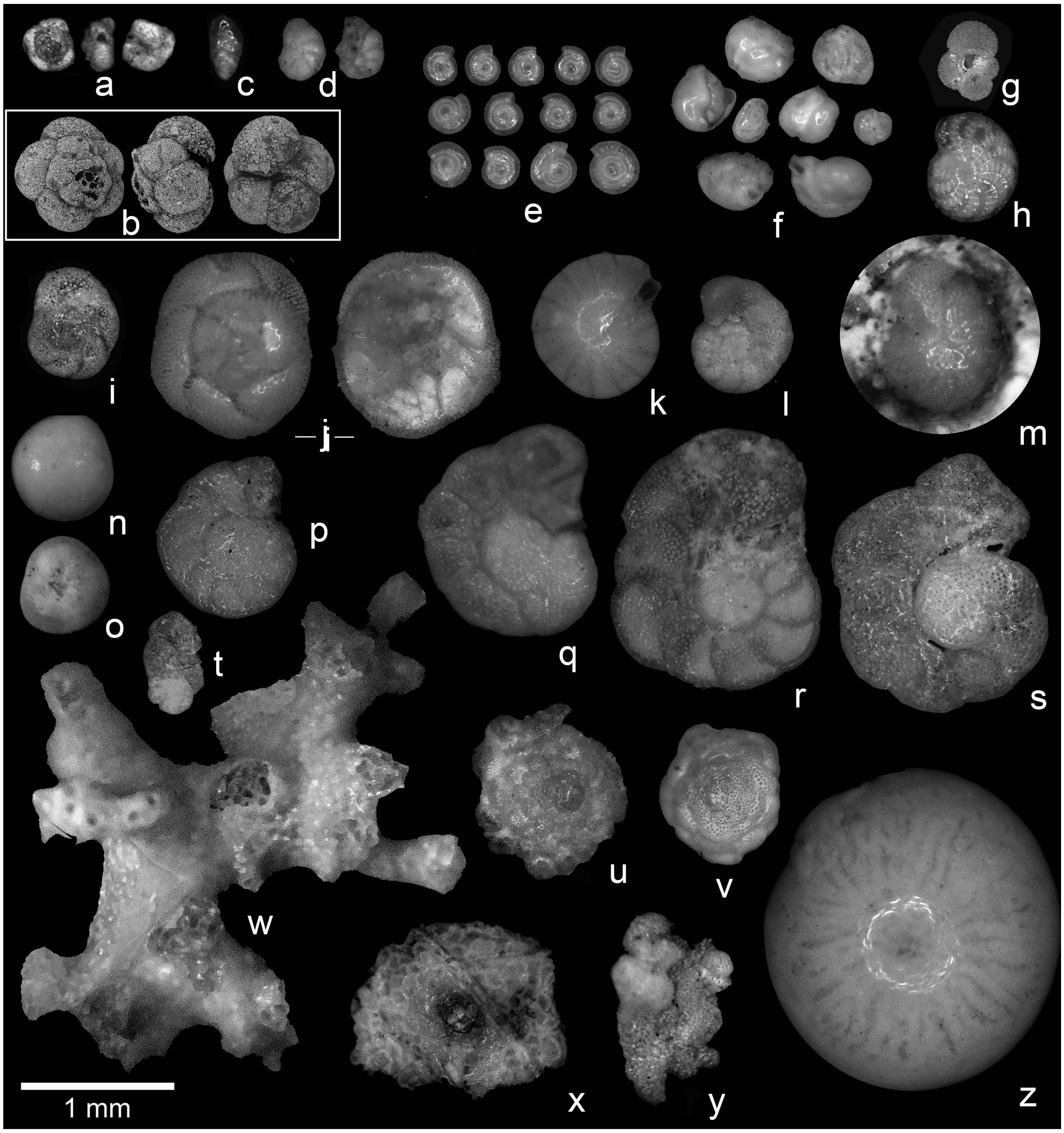

Figure 2. Foraminifera. (a) *Trochammina* sp.: three views of juvenile, UCMP 16400, loc. JTMD-BF-207. (b) *Trochammina hadai* Uchio from San Francisco Bay, shown here for comparison with figure a. (c) *Bolivina* cf. *B. seminuda* Cushman: lateral view of juvenile, UCMP 16401, JTMD-BF-12. (d) *Nonionella stella* Cushman: spiral views of two juveniles, UCMP 16402, loc. JTMD-BF-121. (e) *Cornuspira involvens* Reuss: lateral views of 13 juveniles, UCMP 16403, loc. JTMD-BF-131. (f) *Miliolinella subrotunda* (Montagu): lateral views of 8 juveniles, UCMP 16404, loc. JTMD- BF-129. (g) *Globigerina bulloides* d'Orbigny: umbilical view of subadult, UCMP 16405, loc. JTMD-BF-1. (h) *Elphidium crispum* Linnaeus: lateral view, UCMP 16406, loc. JTMD-BF-1. (i–j) *Rosalina globularis* d'Orbigny: i, spiral view of juvenile, UCMP 16407, loc. JTMD-BF-207; j, spiral and umbilical views of adult, UCMP 16408, loc. JTMD-BF-1. (k) *Elphidiella hannai* (Cushman and Grant): lateral view, UCMP 16409, loc. JTMD-BF-8. (l–m) *Cibicidoides lobatulus* (Walker and Jacob): l, spiral view of juvenile, UCMP 16410, loc. JTMD-BF-402; m, umbilical view of subadult attached to barnacle shell, UCMP 16411, loc. JTMD-BF-82; o, spiral view of subadult, UCMP 16412, loc. JTMD-BF-131. (n–o) *Glabratella ornatissima* (Cushman), separated plasmogamic pair, UCMP 16417, loc. JTMD-BF-1. (p–s) *Cibicidoides lobatulus*: p, spiral view of subadult, UCMP 16413, loc. JTMD-BF-1; q, spiral view of adult, UCMP 16414, loc. JTMD-BF-131; r, spiral view of large adult, UCMP 16415, loc. JTMD-BF-1; s, spiral view of large adult with pseudo-retral processes resulting from ultimate spire being slightly evolute, UCMP 16416, loc. JTMD-BF-207. (t) *Dyocibicides perforata* Cushman and Valentine: dorsal view of juvenile, UCMP 16418, loc. JTMD-BF-8. (u) *Planorbulina acervalis* Brady: dorsal view, UCMP 16419, loc. JTMD-BF-92. (v) *Planorbulina mediterranensis* d'Orbigny, dorsal view, UCMP 16420, loc. JTMD-BF-402. (w) *Homotrema rubra* (Lamarck), lateral view UCMP loc.16424, loc. JTMD-BF-533. (x) *Planogypsina squamiformis* (Chapman): ventral view of partial specimen, UCMP 16421, loc. JTMD-BF-240. (y) *Acervulina inhaerens* Schultze: dorsal view of partial specimen, UCMP 16422, loc. JTMD-BF-207. (z) *Amphistegina lobifera* Larsen, lateral view of weathered test from Hawaiian beach, UCMP 16423, loc. JTMD-BF-17.

Superfamily Cornuspiroidea Schultze, 1854
Family Cornuspiridae Schultze, 1854
Subfamily Cornuspirinae Schultze, 1854
Genus *Cornuspira* Schultze, 1854

***Cornuspira involvens* Reuss, 1850**
(Figure 2e)

Operculina involvens Reuss, 1850: 370, pl. 46, fig. 20.

Material.—JTMD-BF-131, cluster of 104 juveniles; BF-208, 1 subadult.
Previous records.—Northeastern Honshu: Asano (1939), Uchio (1952), Takayanagi (1955), Matoba (1970, as *Cyclogyra planorbis* Schultze,1854), Ikeya (1977, as *Cornuspira planorbis* Schultze, 1854); British Columbia: Cushman (1925); Washington: Cushman and Todd (1947, as *Cornuspira planorbis*); Oregon: Detling (1958); Northern California: Cushman (1917), Hanna and Church (1927), Cushman and Valentine (1930), Cooper (1961), Maurer (1968), Lankford and Phleger (1973, as *Cyclogyra involvens*), McCormick et al. (1994, as *Cyclogyra involvens*).
Remarks.—The clustered juveniles of this cosmopolitan species are prime evidence of foraminiferal reproduction during transoceanic rafting, which in this case must have occurred more than a year after the skiff had been dislodged and sent adrift. These specimens may represent the most recent of multiple generations produced in transit.

Class Globothalamea Pawlowski, Holzmann, Tyszka, 2013
Order Rotaliida Delage and Hérouard, 1896
Superfamily Globigerinoidea Carpenter, Parker, Jones, 1862
Family Globigerinidae Carpenter, Parker, Jones, 1862
Subfamily Globigerininae Carpenter, Parker, Jones, 1862
Genus *Globigerina* d'Orbigny, 1826

***Globigerina bulloides* d'Orbigny, 1826**
(Figure 2g)

Globigerina bulloides.—d'Orbigny, 1826: 277, modèle no. 17; Matoba, 1970: 55, pl. 7, fig. 15.

Material.—JTMD-BF-1, on barnacles and in fouling on dock, 1 subadult; BF-23, 1 adult.
Remarks.—This species inhabits the surface waters of all oceans and is one of the most common species of planktic foraminifera. The specimens could have come aboard anytime during the voyage of the JTMD, but most likely did so on the open ocean where the species is most abundant. The only other planktic specimens were two tiny and unidentifiable juveniles among the clustered *Cornuspira involvens*.

Superfamily Acervulinoidea Schultze, 1854
Family Acervulinidae Schultze, 1854
Genus *Acervulina* Schultze, 1854

***Acervulina inhaerens* Schultze, 1854**
(Figure 2y)

Acervulina inhaerens Schultze, 1854, p. 68, pl. 6, fig. 12.

Material.—JTMD-BF-207, on buoy, 1 adult.
Previous records.—Northeastern Honshu: Asano (1937), Takayanagi (1955), Uchio (1968).
Remarks.—This encrusting species was originally described from the Pleistocene of southern California. Its northernmost record in the modern Northeast Pacific is that of Natland (1933) in the San Pedro Channel off southern California (Culver and Buzas 1986). Winston et al. (1997) reported that in Florida waters *Acervulina* sp. is one of the first species to settle on plastic drift items.

Genus *Planogypsina* Bermúdez, 1952

***Planogypsina squamiformis* (Chapman, 1901)**
(Figure 2x)

Gypsina vesicularis var. *squamiformis* Chapman, 1901: 200, pl. 19, fig. 15.

Material.—JTMD-BF-240, in fouling, 1 adult.
Previous records.—Indo-Pacific: Chapman (1901, as *Gypsina vesicularis* var. *squamiformis* n. sp.).
Remarks.—This is a shallow-water encrusting species originally described from Funafuti Atoll (Tuvalu); it appears to be restricted to the Indo-Pacific. JTMD-BF-240 represents a sample from a vessel that landed just south of San Francisco, California, and thus this vessel must have been carried south of Honshu's Tohoku coast and encountered very shallow water in the tropics before being acquired by ocean currents and transported northeast to North America. Also aboard BF-240 were species of subtropical and tropical invertebrates, including bryozoans and bivalves (Carlton et al. 2017, supplementary online material).

Family Homotrematidae Cushman, 1927
Genus *Homotrema* Hickson, 1911

***Homotrema rubra* (Lamarck, 1816)**
(Figure 2w)

Millepora rubra Lamarck, 1816: 202; type-fig. not given.

Material.—JTMD-BF-533, 9 adults; BF-645, 1 adult.
Previous records.—The genus *Homotrema* is cosmopolitan in warm waters (Loeblich and Tappan 1987), such as those of the Indo-Pacific region. Winston et al. (1997) recorded it on plastics that had washed up on a beach in New Zealand.
Remarks.—This shallow-water attached species typically has its northernmost occurrences in the

Pacific in the tropical Caroline Islands (Makled and Langer 2011) and Moorea, although there are isolated reports in Japan from central Honshu and south (but not north of Tokyo). Hence, the objects that brought *H. rubra* to the coasts of Oregon and Washington likely had stopovers in the Indo-Pacific region. Similar to *Planogypsina squamiformis* and vessel BF-240 (above), both of the items with *H. rubra* also supported subtropical and tropical invertebrates (Carlton et al. 2017, supplementary online material).

Superfamily Serioidea Holzmann and Pawlowski, 2017
Family Bolivinidae Glaessner, 1937
Genus *Bolivina* d'Orbigny, 1839

***Bolivina* cf. *B. seminuda* Cushman, 1911**
(Figure 2c)

Bolivina seminuda Cushman, 1911: 34, text-fig. 35.

Material.—JTMD-BF-12, 1 juvenile; BF-50, 1 juvenile; BF-1, fouling, 1 juvenile.
Previous records.—Northeastern Honshu: Hada (1931), Matoba (1970, as *Bolivina* cf. *seminuda*).
Remarks.—None of these three juvenile specimens clearly display the "seminude" chambers characteristic of Cushman's species, but all other aspects of their morphology are similar to it. In the eastern Pacific, the northernmost occurrence of *Bolivina seminuda* is the Santa Barbara Basin, southern California (Resig 1956; Culver and Buzas 1986).

Superfamily Discorboidea Ehrenberg, 1838
Family Rosalinidae Reiss, 1963
Genus *Rosalina* d'Orbigny, 1826

***Rosalina globularis* d'Orbigny, 1826**
(Figures 2i–j)

Rosalina globularis d'Orbigny, 1826: 271, pl. 13, figs. 1–4; modèle no. 69.

Material.— JTMD-BF-1, in fouling inside bumper, 1 adult, 3 subadults, 4 juveniles; BF-2, 2 juveniles; BF-12, in fouling, 2 juveniles; BF-18, 1 juvenile; BF-23, 1 juvenile; BF-53, on shell fragment on wood, 1 juvenile; BF-82, in external groove on the barnacle *Megabalanus rosa* Pilsbry, 1916, 1 adult; BF-121, on barnacle *Semibalanus cariosus* (Pallas, 1788) attached to wood, 27 early-stage juveniles; BF-129, embedded in amphipod mud tubes in hull fouling, 1 adult; BF-207, 1 adult; BF-329, fouling, 3 juveniles; BF-402, fouling, 1 subadult.
Previous records.—Northeastern Honshu: Matoba (1970); Ikeya (1977); British Columbia: Cushman (1925, as *Discorbis columbiensis*), Cockbain (1963), Blais-Stevens and Patterson (1998, as *D. columbiensis*), Vásquez Riveiros and Patterson (2008); Washington: Echols (1969, as *R. columbiensis*), Lankford and Phleger (1973); Oregon: Detling (1958), Lankford and Phleger (1973); Northern California: Myers (1943, as *Discorbis* sp.), Cushman (1943, as *Tretomphalus myersi* n. sp.), Maurer (1968, as *D. columbiensis*), Lankford and Phleger (1973), Steinker (1976), Erskian and Lipps (1977), McCormick et al. (1994, as *R. columbiensis*), McGann (2002, 2014b), Anima et al. (2008).
Remarks.—*Rosalina* species are shallow-water epiphytes, clinging to plants but still motile (Murray 2006). The morphologic variability and life cycle of *R. globularis* have probably received more attention than any other benthic foraminiferal species because live specimens are easily obtained and workers have been fascinated by its temporary pelagic mode that involves the formation of a large float chamber. Those globular forms were described by d'Orbigny (1839) as *Tretomphalus bulloides*, but Myers' (1943) culturing of California specimens revealed it to be the sexual reproductive stage of *R. globularis*, which was confirmed by Douglas and Sliter (1965) and Sliter (1965). They found that asexual reproduction, which is the more common mode, produces microspheric agamonts that have the typical compressed form of *Rosalina* with a small proloculus. At temperatures > 18 °C, they observed the species morphing into the bulbous pelagic form, which reproduces sexually and produces megalospheric gamonts characterized by more-inflated chambers and a larger "prolocus. This apparent relation between the pelagic form and temperature was challenged by Saraswat et al. (2011), who cultured *R. globularis* from Goa, India, and found that temperatures between 20° and 35 °C resulted in only agamonts with maximum growth at 30 °C and reproduction at 27 °C. In temperate regions that have yielded both the benthic and pelagic stages, the benthic gamont has often been referred to as *R. columbiensis* (e.g., Douglas and Sliter 1965; Sliter 1965). Thus, each of the three morphologies of *R. globularis* that had been described as a unique taxon were later synonymized as a single species. Nevertheless, Matoba (1970) continued to recognize all three binomina. Complicating the issue is Matoba's (1976) later listing of just one species of *Rosalina* in Sendai Bay, *R. vilardeboana* d'Orbigny, 1839, which he did not accompany with a taxonomic comment or illustration.

Superfamily Glabratelloidea Loeblich and Tappan, 1964
Family Glabratellidae Loeblich and Tappan, 1964
Genus *Glabratella* Doreen, 1948

***Glabratella ornatissima* (Cushman, 1925)**
(Figures 2n–o)

Discorbis ornatissima Cushman, 1925, p. 42, pl. 6, figs. 11, 12.

Material.—JTMD-BF-1, 1 plastogamous pair of adults.
Previous records.—Oregon: Detling (1958), Echols (1969); Northern California: Lipps and Erskian (1969), Erskian and Lipps (1977, 1987), Quinterno and Gardner (1987), McCormick et al. (1994), Anima et al. (2008).
Remarks.—This species often dominates the shallow turbulent coastal zone from central California to the Arctic Ocean, where it is commonly found plastogamously paired for sexual reproduction (Lankford and Phleger 1973; Lipps and Erskian 1969; Erskian and Lipps 1977, 1987). It appears to have been acquired as this large dock from Misawa came ashore on the Oregon coast.

Superfamily Planorbulinoidea Schwager, 1877
("Clade" 3 of Holzmann and Pawlowski 2017)
Family Cibicididae Cushman, 1927
Subfamily Cibicidinae Cushman, 1927
Genus *Cibicidoides* Thalmann, 1939

Cibicidoides lobatulus (Walker and Jacob *in* Kanmacher, 1798)

(Figures 2l–m; p-s)

Nautilus lobatulus.—Walker and Jacob, *in* Kanmacher, 1798: 20, pl. 3, fig. 71. 3.

Material.—JTMD-BF-1, in fouling inside bumper, 2 adults, 1 subadult; BF-12, 2 adults, juvenile; BF-21, 1 juvenile; BF-40-4, fouling, 3 adults; BF-82, in groove on barnacle, 1 adult; BF-121, on barnacle *Semibalanus cariosus*, 1 adult; BF-131, fouling, 3 adults; BF-207, 1 large adult; BF-240, 1 adult, 4 subadults; BF-402, fouling on vessel, 5 adults.
Previous records.—Northeastern Honshu: Matoba (1970); Indo-Pacific: Todd (1965); British Columbia: Cockbain (1963), Vásquez Riveiros and Patterson (2008); Washington: Cushman (1943, as *Tretomphalus myersi*), Cushman and Todd (1947), Echols (1969), McGann et al. (2012); Oregon: Detling (1958), Cooper (1961); Northern California: Hanna and Church (1927), Bandy (1953), Cooper (1961), Lankford and Phleger (1973), McCormick et al. (1994), McGann (2002, 2014b), Anima et al. (2008).
Remarks.—This common cold-water epibiotic species often attaches to firm substrates (i.e., rocks, plants, invertebrates, artifacts) and tends to be highly variable in form, ranging from the normal planoconvex test where growth is unrestricted to the aberrant forms of those that encrust uneven surfaces or restricted spaces. Most often ascribed to *Cibicides* because of its planoconvexity, Schweizer et al. (2009) reassigned this species to *Cibicidoides* based upon rDNA evidence.

Subfamily Stichocibicidinae Saidova, 1981
Genus Dyocibicides Cushman and Valentine, 1930

Dyocibicides perforata Cushman and Valentine, 1930

(Figure 2r)

Dyocibicides perforata Cushman and Valentine, 1930: 31, pl. 10. fig. 3.

Material.—JTMD-BF-8, 1 subadult.
Previous records.—Northeastern Honshu: Matoba (1970); California: Cushman and Valentine (1930, n. sp.), Lankford and Phleger (1973).
Remarks.—All species of *Dyocibides* are sessile and inhabit shallow water. This species is distinguished from the more commonly reported *D. biserialis* Cushman and Valentine, 1930 by its distinct perforations.

Superfamily Planorbulinoidea Schwager, 1877
Family Panorbulinidae Schwager, 1877
Subfamily Planorbulininae Schwager, 1877
Genus *Planorbulina* d'Orbigny, 1826

Planorbulina acervalis Brady, 1884

(Figure 2u)

Planorbulina acervalis Brady, 1884: 657, pl. 92, fig. 54.

Material.—JTMD-BF-92, from beach sediment on a styrofoam buoy, 1 adult.
Previous records.—Northeastern Honshu: Uchio (1962), Aoki (1967), Uchio (1968); Oregon: Detling (1958); California: Lankford and Phleger (1973).
Remarks.—This species primarily occurs in warm waters and is exceedingly rare above 33ºN. Lankford and Phleger (1973) examined the foraminiferal fauna from the southern tip of Baja California to northern Washington and found it at numerous localities along Baja California, but only at a single locality to the north, off La Jolla, southern California. The only records of it at higher latitudes are those of Detling (1958) and Cooper (1961), both of who reported it as rare in tide pools along the coast of central Oregon.

Planorbulina acervalis forms irregular encrustments displaying coarsely perforate subspherical chambers. This JTMD specimen collected in Hawaii shows chambers that appear to have protoplasm. Although *P. acervalis* is considered a rafting species (Winston 2012, who notes that it "is one of the first species to settle on plastic drift items") we presume that this specimen was inadvertently acquired from local Hawaiian beach sands.

Planorbulina mediterranensis d'Orbigny, 1826

(Figure 2v)

Planorbulina mediterranensis d'Orbigny, 1826: 280, pl. 4, figs. 4–6.

Material.—JTMD-BF-402, fouling, 1 adult.

Previous records.—Northeastern Honshu: Asano (1937), Fukuta (1951), Uchio (1952), Takayanagi (1953), Uchio (1962); Oregon: Cooper (1961).
Remarks.—Cooper (1961) recorded this cosmopolitan species in tidepools and at beaches at numerous localities from Baja California and California, but its rare occurrence at one locality along the southern Oregon coast was his only record of it among his 26 localities north of the Monterey Peninsula.

Superfamily Astigerinoidea d'Orbigny, 1839
Family Amphisteginidae Cushman, 1927
Genus *Amphistegina* d'Orbigny, 1826

Amphistegina lobifera Larsen, 1976
(Figure 2z)

Amphistegina lobifera Larsen, 1976, 4, pl. 3, figs. 1–5; pl. 7, fig. 3; pl. 8, fig. 3.

Material.—JTMD-BF-17, from sand in Hanauma Bay, 5 adults; BF-92, from beach sediment on styrofoam buoy, 2 adults.
Previous records.—Indo-Pacific (Resig 2004).
Remarks.—Two of the four Hawaiian assemblages were readily distinguished by the presence of *Amphistegina lobifera.* As with other genera of larger foraminifera, *Amphistegina* is characterized by a robust, thick-walled calcareous test bearing endosymbiotic algae. *Amphistegina* species prefer the warm, clear, shallow water (< 30 m) between the coastline and offshore reefs, and are often a significant component of adjacent beach sands. None of the specimens show evidence of protoplasm, which is not surprising considering that *Amphistegina* tests are the major component of those beach sands, possibly hundreds of years old (Resig 2004). Larsen (1976) noted that this form had previously been assigned to *A. lessonii* d'Orbigny (1826), and stated "Though *A. lobifera* is reminiscent of *A. lessonii* in its gross morphology it is well distinguished from the latter species. The most obvious morphological difference is the densely lobate sutures of *A. lobifera* as compared with the simple sutures of *A. lessonii*."

In Japan, specimens identified as *A. lessonii* only occur south of Honshu (Shuto 1953, 1965; Uchio 1962, 1968); some of those specimens may be *A. lobifera*. I assume that the specimens in the present study were likely inadvertently acquired from the Hawaiian beach as samples from these JTMD objects were being collected.

Superfamily Nonionoidea Schultze, 1854
Family Nonionidae Schultze, 1854
Subfamily Nonioninae Schultze, 1854
Genus *Nonionella* Voloshinova, 1958

Nonionella stella Cushman and Moyer, 1930
(Figure 2d)

Nonionella miocenica var. *stella* Cushman and Moyer, 1930: 56, pl. 30, fig. 17.

Material.— JTMD-BF-121, on barnacle *Semibalanus cariosus*, 2 juveniles.
Previous records.—Northeastern Honshu: Morishima (1955, as *N. miocenica* var. *stella*), Matoba (1970, as *N. miocenica* var. *stella*); British Columbia: Cockbain (1963), Patterson et al. (1998), Vásquez Riveiros and Patterson (2008); Washington: Cushman and McCulloch (1940), Cushman and Todd (1947, as *N. miocenica* var. *stella*), Echols (1969, as *N. miocenica* var. *stella*); Oregon: Detling (1958, as *N. miocenica* var. *stella*); Northern California: Cushman and McCulloch (1940, as *N. miocenica* var. *stella*), Bandy (1953, as *N. miocenica* var. *stella*), Cooper (1961, as *N. miocenica* var. *stella*), Lankford and Phleger (1973), Erskian and Lipps (1977), Steinker (1976), McCormick et al. (1994), McGann (2002, 2014b), Anima et al. (2008).
Remarks.—Both specimens are broken and missing the characteristically lobed last chamber, but the low trochospire and other aspects of the tests match those of *N. stella*, which was originally described from southern California. Cushman and McCulloch (1940) note that *N. stella* is distributed along the entire west coast of North America from Alaska (at depth of 2–6 m) to Mexico (below 100 m depth).

Superfamily Rotaloidea Ehrenberg, 1839
Family Elphiididae Galloway, 1933
Subfamily Elphiidielliinae Holzmann and Pawlowski, 2017
Genus *Elphidiella* Cushman, 1936

Elphidiella hannai (Cushman and Grant, 1927) emend. Angell, 1975
(Figure 2k)

Elphidium hannai Cushman and Grant, 1927: 77, pl. 8, fig. 1; emend. Angell, 1975: 85: pl. 1, figs. 1–9.

Material.—JTMD-BF-8, on alga in fouling, 1 adult.
Previous records.—British Columbia: Cushman and McCulloch (1940), Patterson et al. (1998), Vásquez Riveiros and Patterson (2008); Washington: Cushman and Todd (1947), Echols (1969), Lankford and Phleger (1973), Scott (1974), McGann et al. (2012); Oregon: Cushman and Todd (1947), Detling (1958, as *Elphidiella nitida* Cushman, 1941); Northern California: Bush (1930, as *E. hannai*), McDonald and Diedeker (1930, as *E. hannai*), Martin (1936, as *E. hannai*), Cushman and McCulloch (1940), Bandy (1953), Cooper (1961), Lankford and Phleger (1973), Angell (1975), Steinker (1976), Erskian and Lipps (1977), Arnal et al. (1980), Quinterno and Gardner

(1987), McCormick et al. (1994), McGann (2002, 2014b), Anima et al. (2008).
Remarks.—This robust elphiidid inhabits the inner shelf of the Northeast Pacific margin from Point Dume (Malibu) in southern California to Alaska (Angell 1975; Resig 1964; Culver and Buzas 1985, 1986). The type specimens were collected off the Farallon Islands, west of San Francisco. It has not been reported from Japan. Its occurrence on a piece of alga found on the floating dock indicates that both were derived from the coastal waters of Washington where a wave washed it onto the dock.

Genus *Elphidium* Montfort, 1808

***Elphidium crispum* (Linnaeus, 1758)**
(Figure 2h)

Nautilus crispus Linnaeus, 1758, p. 709.

Material.—JTMD-BF-1, on barnacles among fouling, 1 juvenile.
Previous records.—Northeastern Honshu: Asano (1937, 1939), Fukuta (1951), Nagahama (1954), Aoki (1967), Ujiie and Kusukawa (1969), Matoba (1970); British Columbia: Cockbain (1963); Washington: Cushman and Todd (1947); Northern California: Cushman and Grant (1927), Bush (1930), Cushman and Valentine, 1930), Martin (1936), Cushman and McCulloch (1940), Nicol (1944), Cooper (1961), Steinker (1976), Erskian and Lipps (1977), Arnal et al. (1980), McGann (2002).
Remarks.—This widely distributed shallow-water species is distinguished from other *Elphidium* by its compression, acute periphery, and well-developed retral processes.

Subclass Textulariia Mikhalevich, 1980
Order Lituolida Ehrenberg, 1839
Suborder Trochamminina Saidova, 1981
Superfamily Trochamminoidea Schwager, 1877
Family Trochamminidae Schwager, 1877
Subfamily Trochammininae Schwager, 1877
Genus *Trochammina* Parker and Jones, 1859

***Trochammina* sp.**
(Figure 2a)

Material.—JTMD-BF-207, 1 juvenile.
Remarks.—This juvenile specimen does not match well with any of the *Trochammina* species recorded from the Northeast and Northwest Pacific margins. Of the three species of *Trochammina* that Matoba (1970) identified in Matsushima Bay, the test recovered from the JTMD is markedly different from the forms he illustrated as *Trochammina* cf. *japonica* Ishiwada, 1950, *T. hadai* Uchio, 1962, and *T. pacifica* Cushman, 1925. The primary differences between this specimen and the other species are the relative height and pointed apex of its spire and the shape of its chambers, particularly in the first spiral.

Of particular interest is this specimen's relationship to *Trochammina hadai*, which has recently established itself along the northeastern Pacific seaboard. The first report of introduced *T. hadai* was by McGann and Sloan (1996), who found it in San Francisco Bay and attributed its arrival to the discharge of ballast water. McGann et al. (2000) later searched for it in 404 samples collected in that estuary between 1930 and 1981, finding its earliest occurrence as 12 specimens (1.5% of assemblage) in a sample taken in 1983; by 2000 it had proliferated throughout most of the estuary, apparently at the expense of *Elphidium excavatum* (Terquem, 1875). Subsequent studies have recorded *T. hadai* at multiple locations between San Diego Bay, California and Prince William Sound, Alaska (McGann et al. 2000), but not (as of 2000) in Coos Bay, Oregon, where this object (BF-207) was found.

McGann et al. (2012) later examined cores from Padilla Bay, Washington, from which they determined *T. hadai* arrived there sometime between 1876 and 1971, preceding its invasion of San Francisco Bay. They suggested that previous records of *T. advena* Cushman, 1922, in British Columbia (Williams 1989) and *T. pacifica* Cushman in British Columbia (Patterson 1990) and Washington (Scott 1974; Jones and Ross 1979) may be of specimens that more closely resemble *T. hadai*. McGann et al. (2012) specifically argued that Scott's (1974) identification of *T. pacifica* from Padilla Bay, Washington, was almost certainly *T. hadai*, as the former is a continental shelf species not found on intertidal mudflats.

The form of this juvenile specimen has not been seen among the many *T. hadai* juveniles examined by M. McGann (U. S. Geological Survey, Menlo Park CA, personal communication, 2017). It may simply be an aberrant juvenile *T. hadai* (for comparison, see figure 2b of an adult specimen from Lake Merritt, Oakland, a tidal lagoon off San Francisco Bay, California).

Discussion

Biogeography, diversity, and abundance

The JTMD foraminiferal assemblage consists entirely of shallow-water (coastal but not transitional) species, most known to occur naturally on both sides of the North Pacific Ocean, with the exception of *Homotrema rubra* and *Planogypsina squamiformis*, which were acquired by tsunami objects as they passed through the Indo-Pacific on their way to North America.

Virtually all JTMD objects appear to have departed the tsunami-stricken coast of northeast Honshu by either traveling east or south, the latter arriving at least as far as the South China Sea before being re-engaged by the Kuroshio Current (Carlton et al. 2017). The discovery of tropical foraminifera on JTMD thus fits in with this pattern.

The most abundant species on the JTMD that arrived along the North American coast are *Rosalina globularis*, *Cibicidoides lobatulus,* and *Miliolinella subrotunda*, all of which typically cling or attach to firm substrates in shallow-water, wave-dominated environments. Juveniles account for approximately two-thirds of the specimens recovered from the JTMD. Noteworthy is the absence of the genera *Ammonia* and *Quinqueloculina*, which were the dominant foraminiferal genera that Pilarczyk et al. (2012) found inland in sediments that had been transported by the tsunami from coastal beaches and dunes. Their absence on the JTMD is attributed to their inability to firmly attach themselves.

Origin of JTMD foraminifera

If the two Indo-Pacific species are the only foraminifera here clearly recognizable as "exotic" additions to the rafted JTMD, how can we justify assigning a Japanese lineage to the specimens that belong to bicoastal species? There are several lines of evidence that support this deduction:

1. *Acervulina inhaerens, Dyocibicides perforata, Miliolinella subrotunda*, and *Planorbulina mediterranensis*, recorded off Honshu but not previously recorded north of Oregon, were collected from the JTMD that reached the Washington coast; thus, this is prima facie evidence that they, or their recent ancestors, were not acquired in the eastern Pacific.
2. If acquisition of eastern Pacific shallow-water species (other than species acquired on shore landing) was occurring regularly, it would appear improbable that the sole species to do would be those species also occurring in Japan.
3. JTMD objects, after reaching neritic waters off North America, came ashore quickly, as evidenced by the rare settlement of native North American invertebrates, none of which were more than a few days old (Carlton et al. 2017). The adult foraminifera reported here are thus unlikely to have been acquired from the eastern Pacific.
4. All of the recovered benthic foraminifera are shallow-water species. The chances of any surface floating object acquiring a shallow-water benthic foraminifera while on the open ocean is highly improbable. The adult specimens, particularly of species that attach or cling, were likely on the Japanese objects prior to being set adrift, whereas the juveniles represent generations produced in transit. The smallest and most abundant juvenile specimens are of *Rosalina globularis, Miliolinella subrotunda*, and *Cornuspira involvens*, the latter of which was represented primarily by a cluster of more than 100 juvenile specimens. All three species include very tiny juvenile specimens that are evidence of their recent births, which would have occurred in the Northeast Pacific, perhaps only days before their rafts landed. While their identifications do not reveal if they are the progeny of indigenous or exotic specimens (because they are fairly cosmopolitan taxa), the crossing of the Pacific consumed multiple years and thus individuals displaced from Japan would have had sufficient time to produce one or more generations of offspring.
5. Some of the tests of *Rosalina globularis* and *Cibicidoides lobatulus* are noticeably deformed, which is evidence of a sessile life mode, while those with normal tests, as well as *Miliolinella subrotundum,* may have retained motility but live mostly as clingers on hard substrates (Murray 1973, 2006). The ability to cling or firmly attach is advantageous in environments subjected to water motion (as in ocean rafting), and it enabled specimens of these three species, as well as some that are less common, to maintain their grasp during and after the tsunami, for the duration of their subsequent rafting.
6. *Rosalina globularis* or *Cibicidoides lobatulus* were present on 14 of the 19 JTMD objects that arrived on the North American coast, and one or both of those species were usually dominant. Considering the diversity of coastal environments between Vancouver Island and northern California, and that much of the JTMD washed ashore on sandy beaches, their relative frequency and various levels of test deformation on the JTMD suggests that they were derived from similar environments within the same marine province where they had been attached to firm substrates that could float.

Conclusions

This report is the first to document tsunami-generated rafting as a means of dispersing living benthic foraminifera over long distances and thus the survival and reproduction of shallow-water foraminifera on floats while in transit for up to four years.

As previously shown for *Trochammina hadai* and *Amphistegina lobifera*, introduced foraminiferal species may rapidly proliferate and disperse, which can negatively impact native species. Prior to coastal occupation and development by humans, natural substrates (e.g., vegetation and pumice) were the floating vectors of dispersal. It is now evident that the ever-increasing abundance of floatable and largely plastic artifacts emplaced along tectonic coastlines is a plentiful source for tsunami- and storm-generated rafts that can introduce foraminifera and other marine biota to distant shorelines.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Japanese Tsunami Marine Debris (JTMD) objects—landing sites, biofouling (BF) samples, dates, objects types, and origins and recorded foraminiferal species and census counts.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2018/Supplements/AI_2018_JTMD_Finger_Table_S1.xlsx