BIOGEOGRAPHY

Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography

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The 2011 East Japan earthquake generated a massive tsunami that launched an extraordinary transoceanic biological rafting event with no known historical precedent. We document 289 living Japanese coastal marine species from 16 phyla transported over 6 years on objects that traveled thousands of kilometers across the Pacific Ocean to the shores of North America and Hawai'i. Most of this dispersal occurred on nonbiodegradable objects, resulting in the longest documented transoceanic survival and dispersal of coastal species by rafting. Expanding shoreline infrastructure has increased global sources of plastic materials available for biotic colonization and also interacts with climate change–induced storms of increasing severity to eject debris into the oceans. In turn, increased ocean rafting may intensify species invasions.

Transoceanic rafting is a fundamental feature of marine evolutionary biogeography and ecology, often invoked to explain the origins of global patterns of species distributions (*1*, *2*). Until now, however, there have been no direct observations of rafting episodes transporting diverse living communities of coastal marine organisms long distances from one continental margin to another. On 11 March 2011, an undersea megathrust earthquake measuring 9.0 moment magnitude struck Japan. The earthquake created a tsunami reaching 38.38 m in height on the Tōhoku coast of Honshu (*3*). In the ensuing coastal devastation, millions of objects ranging in size from small plastic fragments to fishing vessels and large docks were carried into the Pacific Ocean. These items (Fig. 1) already supported diverse communities of marine life or were colonized by marine organisms after entering the ocean and were then transported by ocean currents from the Western Pacific to the Central and Eastern Pacific Ocean (fig. S1). Hence, this event provided the opportunity to track and evaluate the fate (destination and species composition) of the biologically rich debris field over multiple years from a single known time and place of origin.

Since 2012, debris with living species originating in Japan has landed on coastlines from Midway Atoll to Hawai'i Island and from south central Alaska to central California. Debris landing in the contiguous United States traveled at least 7000 km from Japan. We assessed the diversity of animal communities on 634 Japanese tsunami marine debris (JTMD) objects (table S1), consisting of vessels, docks, buoys, totes (crates), wood, and many other objects, identified as JTMD by multiple criteria (*4*). Object landings continued across the entire 5-year study period (fig. S1), showing no asymptote, although arrivals of several individual object types have slowed or declined (fig. S3 and fig. S4A).

We documented a minimum of 289 living invertebrate and fish species arriving from Japan (table S2A), none of which were previously reported to have rafted transoceanically between continents (*4*). This biota included macroinvertebrates (235 taxa), fish (2 taxa), microinvertebrates (33 taxa), and protists (19 taxa). Additional species continued to arrive through February 2017, increasing total species richness detected over time (Fig. 2). Microinvertebrates and protists could not be sufficiently preserved and thus were not adequately assessed on most JTMD objects, compared with macrobiota (*4*). For macrobiota, 59.6% of all taxa were detected on vessels, and 24.5% were found only on vessels (Fig. 3A). Moreover, mean species richness was greater on large-sized objects (5 to 12 m in length, including vessels and docks) than small objects (<1 m in length) ($P < 0.01$) (figs. S5 and S6).

Five invertebrate groups (mollusks, annelids, cnidarians, bryozoans, and crustaceans) composed 85% of the species diversity of macrobiota (Fig. 3B) (*5*). Recorded JTMD landings and macrobiotic richness exhibited strong geographical and temporal variation. Landings and richness were concentrated in the Pacific Northwest (Oregon and Washington) between North latitudes 42°03.27' and 47°54.19', a pattern consistent across all object types (figs. S7 and S8). We documented peak richness in 2012 to 2014 for each object type and region (fig. S7 and fig. S4), 2 to 3 years after debris entry into the Western Pacific Ocean. Strong spring pulses were evident for both landings and species accumulation for each year between 2012 and 2016 (Fig. 2 and fig. S2). These pulses were most pronounced in the Pacific Northwest (*5*) and were associated with springtime southwesterly or downwelling-favorable winds.

Temporal analyses of a subset of 110 JTMD objects that were most thoroughly sampled for macrobiota [higher-resolution objects (JTMD-HR) (*4*)] show that mean per capita richness/object did not decline across years (Fig. 4A and fig. S4C). This is best illustrated for vessels, which exhibited relatively high per capita richness (Fig. 4B and fig. S4B) and no significant temporal decline in per capita richness for arrivals to either North America or Hawai'i (Fig. 4C). However, the detection rate of landings has declined since 2015 (figs. S2 and S3A), causing total richness per year for JTMD-HR to also decline from 2012–2014 peaks (fig. S3C).

It is noteworthy that the frequency of high-richness arrivals (>20 species per object) declined from 2012 to 2016 (Fig. 4A). A large dock (Fig. 1A) arriving in June 2012 with ~80 macroinvertebrate species was followed by another dock (fig. S1) and vessels between late 2012 and spring 2015 with between 20 and 50 species; only one object has arrived since the summer of 2015 with >20 species. This decline in high-richness arrivals may result from the oceanic environment through which JTMD has passed for 6 years, a habitat generally viewed as inhospitable [due to lower trophic resources, increased ultraviolet B exposure, and other stressors (*6*)] for shallow-water coastal species.

Our analyses provide minimum estimates of the biodiversity and landings from the massive debris field launched in 2011. For macrobiota alone, rarefaction curves are far from saturation (figs. S9 and S10), indicating that many more taxa arrived than were detected. This interpretation is supported by the low frequency of species occurrences (fig. S11), where (i) more than 50% of all taxa were detected only once over the 5-year study period and (ii) new species, as noted above, were still being detected on landings in 2017 (Fig. 2 and fig. S4C). Chao richness estimates indicates that total macrobiota taxa approach 357 ± 41 species for all JTMD-HR object types, or an average increase of 63% from observed taxa ($n = 226$) (table S4). Although we surmise that sufficient biofouled debris existed to approach this asymptote, several phenomena prevented sampling the debris field comprehensively (*4*). Although we detected more than 50 microinvertebrate and protist taxa, these are undoubtedly major underestimates of the species pool. Furthermore, most of these measures do not yet evaluate cryptic taxa, symbionts, parasites, and genetic variants.

It is surprising that living species from Japan continue to arrive after nearly 6 years at sea, 4 or more years longer than previous documented

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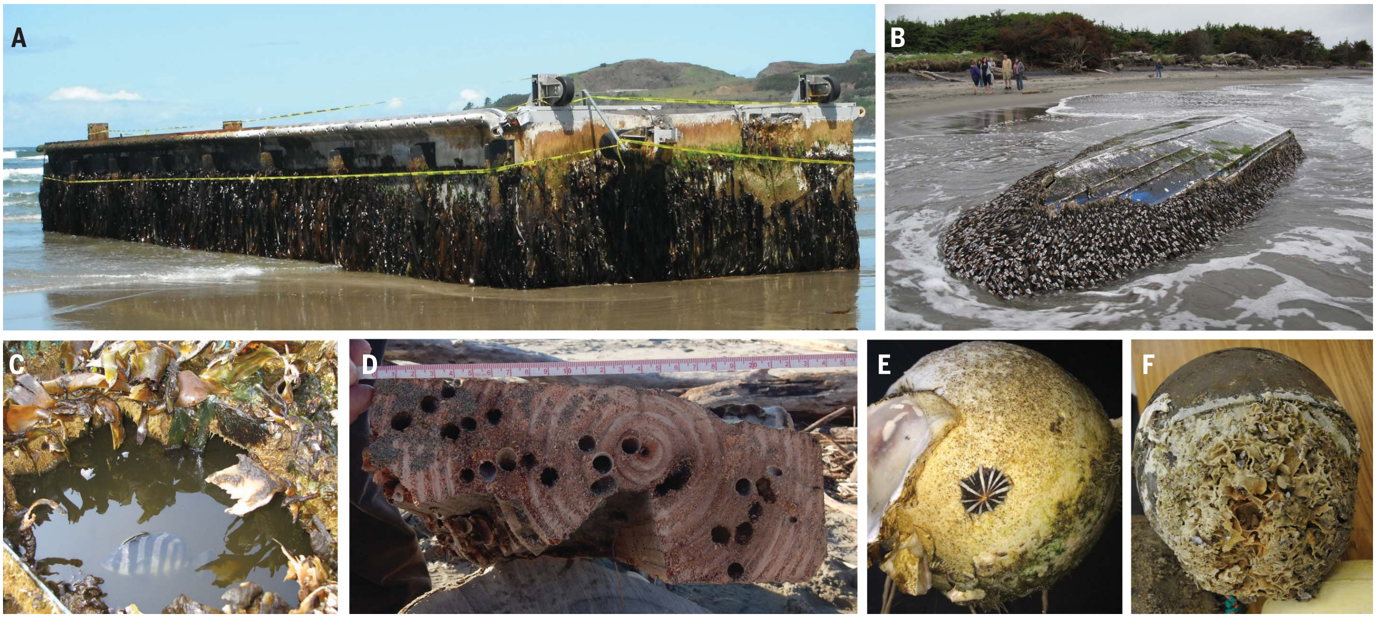

Fig. 1. Japanese tsunami marine debris rafts and associated biota. (**A**) Fisheries dock (JTMD-BF-1) (*4*) from the Port of Misawa, Aomori Prefecture, washed ashore 5 June 2012 on Agate Beach, near Newport, Lincoln County, Oregon (photograph by J. W. Chapman). (**B**) A fishing vessel (JTMD-BF-2), washed ashore at Ilwaco, Pacific County, Washington, 15 June 2012, heavily covered with the pelagic gooseneck barnacle *Lepas*; living Japanese fauna included barnacles, isopods, amphipods, and mussels (photograph by A. Pleus). (**C**) Japanese barred knifejaw fish *Oplegnathus fasciatus* in the stern well of the fishing vessel 斎勝丸 (*Sai-shō-Maru*) (JTMD-BF-40) from Rikuzen-takata, Iwate Prefecture, washed ashore 22 March 2013, on Long Beach Peninsula, Pacific County, Washington (photograph by A. Pleus). (**D**) Post-and-beam wood (JTMD-BF-297) from Tōhoku coast, Honshu, washed ashore 1 April 2013, at Bandon, Oregon, and heavily bored by the Japanese shipworm *Psiloteredo* sp. (photograph by N. C. Treneman). (**E**) Buoy (JTMD-BF-207), found floating inside the Charleston Boat Basin in Coos Bay, Coos County, Oregon, on 17 May 2014; living Japanese limpet *Siphonaria sirius* in center, next to dead Japanese oyster *Crassostrea gigas* (photograph by L. K. Rasmuson). (**F**) Buoy (JTMD-BF-216), washed ashore at Dunes City, Lane County, Oregon, with large foliaceous living colonies of the Japanese bryozoan *Biflustra grandicella* (photograph by A. Marohl).

instances of the survival of coastal species rafting in the ocean (*7*). Long-term surviving species included the mussel *Mytilus galloprovincialis*, the barnacle *Megabalanus rosa*, limpets, bryozoans, sea anemones, amphipods, isopods, additional bivalves, and other taxa. This at-sea long-term longevity is due in part to (i) the multiyear growth, aging, and unexpectedly long survival of some original individuals departing Japan in 2011 and (ii) self-recruitment by other species via reproductive strategies that produce and maintain multiple generations on these floating islands. Diverse taxa across at least 13 phyla and orders arrived in reproductive condition (table S2A), and population size structure revealed that multiple cohorts were common, indicating that reproduction had occurred during ocean transit. Marine species across many phyla having nonplanktonic propagules or extremely short-term dispersal capacity may thus have been strongly favored (*6*). Plastic debris can persist in the oceans for decades [(*8*) and below], and yet our knowledge of associated biota is strikingly limited, especially relative to the physiological processes involved in the long-term survival of coastal species in an environment (*6*) in which they did not evolve.

Upon arrival on new shores, the establishment of rafting species will depend on the number and frequency of delivery of reproductively viable individuals (*9*, *10*) and the presence of a suitable

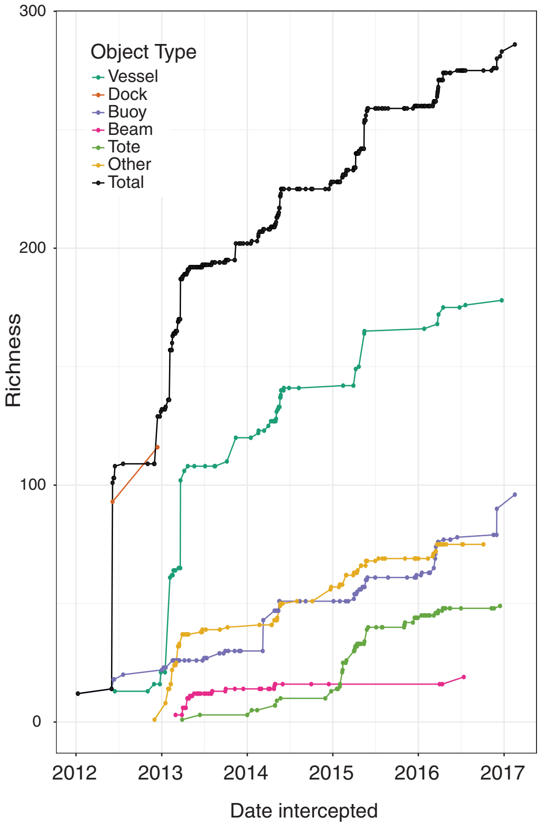

Fig. 2. Cumulative Japanese living protist, invertebrate, and fish species richness by date and object type. Species accumulation for 289 taxa detected from Alaska to California and Hawai'i from June 2012 to February 2017 by object type (table S1 and fig. S2): Vessels are primarily skiffs ranging from 4 to 11.5 m in length; docks are JTMD-BF-1 and JTMD-BF-8, landing in central Oregon (June 2012) and northern Washington (December 2012), respectively (fig. S1); buoys are anchored or attached floats used in aquaculture, small harbors, and navigation; beams are post-and-beam timber (mortise-and-tenon construction) of standard Japanese dimensions; totes include crates, boxes, and cases used in fisheries and for domestic purposes; "other" includes pallets, pontoon sections, ropes, trays, propane tanks, carboys, items associated with the aquaculture and fisheries industries, and many other objects. Post-and-beam pieces detected in 2016 may represent redrift (washed back out to sea after earlier landings), rather than being at sea since 2011. JTMD spring landing concentrations are evident in all years.

environment, among other factors. At least 35% of JTMD species were previously known to occur on the Pacific coast of North America (Fig. 3B), largely due to presumed natural amphi-Pacific ranges. These preoccurring species indicate a climatic match as well as a broad range of matching habitats. In addition, 82 invertebrate species from Japan have previously become established on the Pacific coast in historical time (before the JTMD phenomenon), introduced by multiple vectors (*11*, *12*). Of these, only seven species were represented in the JTMD fauna (*5*). The robustness of a wide phyletic range of species in this rafted fleet, as manifested in their multiyear at-sea longevity and production of multiple generations, also underscores a physiological and reproductive plasticity often linked to invasion success (*13*). Further, arrival in the northeast Pacific during spring (above) provides potentially highly conducive environmental conditions, including increased productivity and warming waters, for reproduction and possible recruitment of rafted species. Introductions related to JTMD arrival have not yet been detected. However, lag times

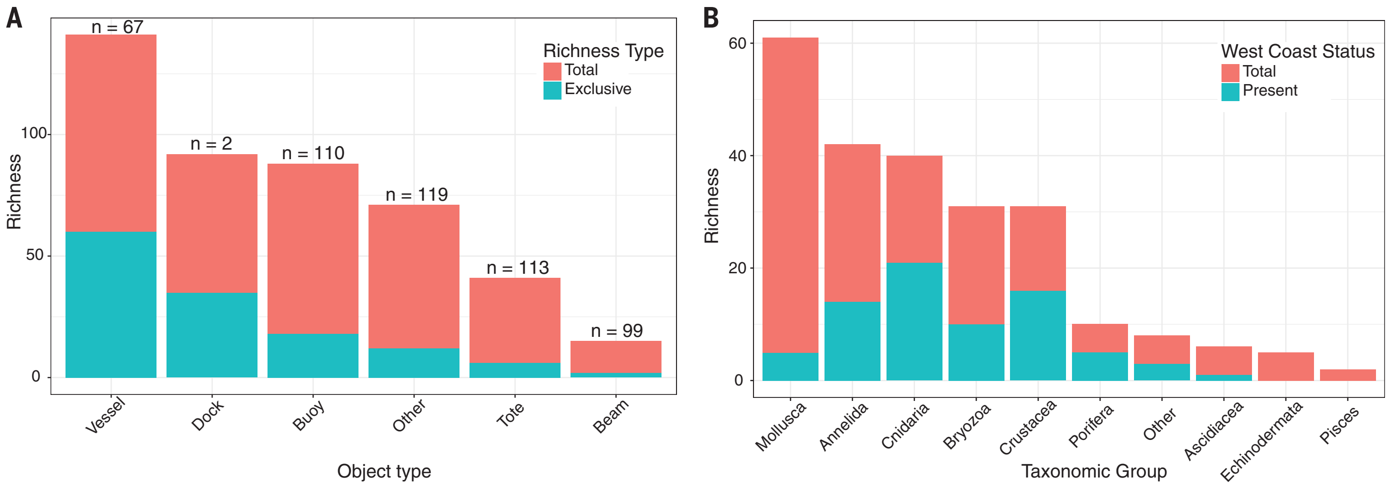

Fig. 3. Living Japanese macroinvertebrate and fish species richness by object type and taxonomic group. (**A**) Total richness by object type landing from Alaska to California and Hawai'i, as described in Fig. 2; number of species exclusive (unique) to a given object type are in blue; "n" is the number of objects in each category of the total 510 items (excluding 124 items on which only dead individuals or algae were documented). (**B**) Species diversity by taxonomic group. Number of species already present (due to natural distribution or previous introductions) on the west (Pacific) coast of North America is in blue. "Other" taxa are Nemertea, Sipuncula, Insecta (Diptera), Pycnogonida, Acarina, and Kamptozoa.

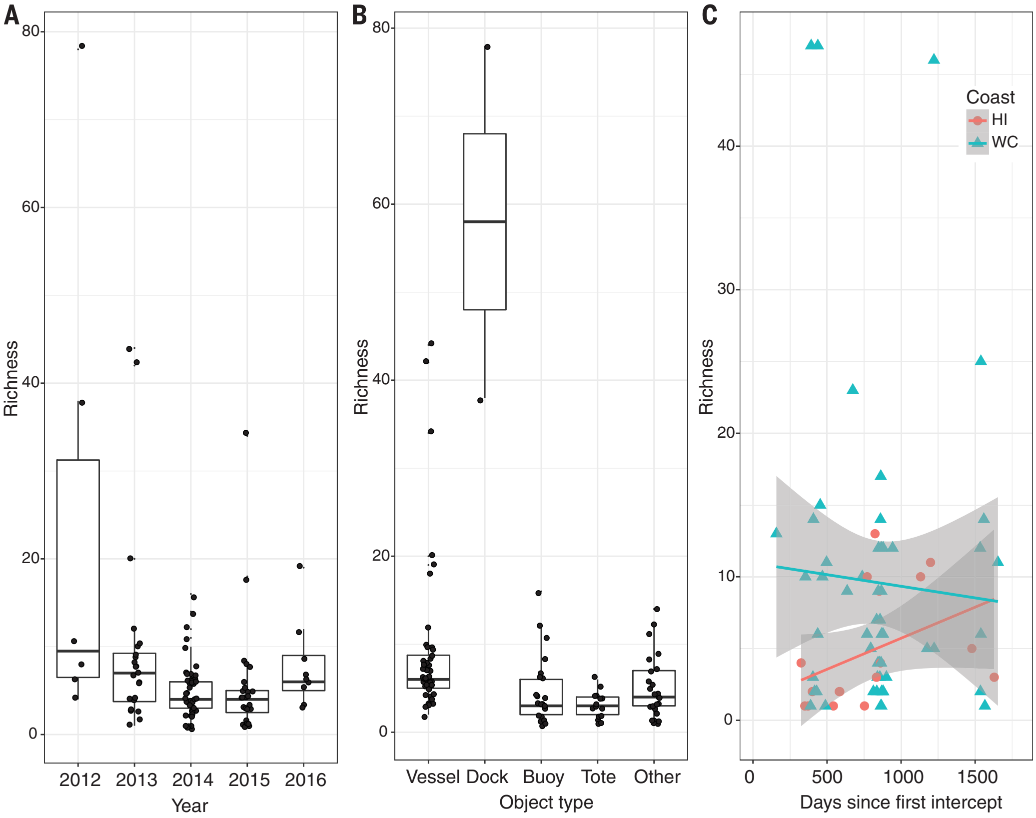

Fig. 4. JTMD richness per object and time. (**A**) Quartile plot of richness by year, based on 110 JTMD-HR (higher-resolution) objects (see text and supplementary materials). Peak per capita richness occurred in 2012 to 2013, with richness falling below 20 species per object since 2015. There was a significant decline in high-richness objects over time (r^2 = 0.2357; $P < 0.05$), based on the upper quartile of each year. (**B**) Quartile plot of richness by object type, based on 110 JTMD-HR objects; two docks in 2012 and vessels (regardless of year) account for all high (>20 species) richness items (Fig. 3A and fig. S4B). (**C**) Linear regression of per capita JTMD richness (as days since first interception) for HR vessels alone; shaded areas are the 95% confidence intervals around the linear model (slope and *y* intercept) parameters. Although outlier high-richness events decline (A) there is no significant decline (C) in per capita richness over time for the west coast of North America (WC) (r^2 = 0.0039; P = 0.6537) or Hawai'i (HI) (r^2 = 0.1518; P = 0.1221).

in the growth of non-native species populations are widely recognized (*14*), such that detection of new invasions may not occur for years or decades.

Marine debris as effective long-distance oceanic rafts for the transport of coastal species is distinct mechanistically, temporally, and spatially from other, better-known anthropogenic vectors of non-native species. Rafts are slow-moving (1 to 2 knots) compared with commercial vessels (20 to 25 or more knots) (*15*), speeds that influence the development, adhesion, retention, and self-recruitment of sessile fouling species (*16*). Further, rafts provide potential acclimatization time for attached biota to adjust to changing environmental conditions during long transits. Megarafts of marine debris deliver substantial communities of adult organisms capable of reproduction [as compared with planktonic stages of benthic species arriving in ballast water (*17*)]. Rafts are one-way arrival and deposition events (as opposed to transient biofouled vessels entering and then departing ports and harbors in hours or days), such that adult rafted communities, drifting in coastal waters or after landing, may benefit from extended periods of residence time permitting species' reproduction. Notably, marine debris landings may also expose a vastly greater diversity of coastal habitats, and thus communities, to novel biotas, beyond the harbors and ports receiving international vessel traffic.

Rafted anthropogenic debris also differs strikingly from natural rafts. Natural long-distance ocean rafting consists of largely ephemeral, dissolvable, or decomposable materials, including biodegradable terrestrial vegetation (trees, root masses, and seeds) (*7*, *18*) and pumice (*5*, *19*), all with far shorter at-sea half-lives than fiberglass, polystyrene, and polyvinyl chloride–based objects (*8*). Despite the tsunami-induced loss of large expanses of forests on the northeast Honshu coast (*3*), few stranded Japanese trees, typically with few attached species, were observed in North America or Hawaiʻi (*5*). Most trees may have stayed on land or washed ashore in Japan, or may have sunk before undergoing or completing ocean transit. Further, building wood, which had commenced arrival in large quantities in 2013 (also with relatively few species) (Fig. 3A), largely tapered off by 2014 (Fig. 2 and fig. S2). This highly constrained, largely 2- to 3-year (2011 to 2014) at-sea existence of wooden JTMD is due in large part to destruction by wood-destroying teredinid mollusks (shipworms) [(*5*) and Fig. 1D]. Perhaps not surprisingly, then, before 2012 there are no reports of Western Pacific vegetation or wood arriving with communities of living Japanese species in either the Hawaiian Islands or North America, despite >150 years of shore observations by scientists, suggesting that such events are rare.

The recent and increasing availability and use of plastic materials in the latter half of the 20th century (*20*), and their ability to sustain rafting integrity for the lengths of time required for frequent transoceanic dispersal, may thus explain the apparent failure of debris from previous tsunamis to be detected in the North Pacific Ocean. Earthquakes and their resulting tsunamis in the Tōhoku region of northeast Honshu have been recorded for more than 1000 years (*21*). The two most recent events before 2011 of comparable magnitude and wave height occurred in 1896 (the Meiji-Sanriku earthquake) and 1933 (the Sanriku earthquake) (*21*). Before the 1930s to 1940s, these coastal plains of Tōhoku were more rural than urban (*22*), and appreciable amounts of plastic-based material were not present. Fiberglass (of which much of the present debris is composed, especially the many vessels) was not available until 1936 (*23*), and extruded polystyrene foam (a critical component of the Misawa docks, and present in much other debris) was not marketed until the 1940s (*24*), with neither widely used until after the 1950s. Despite the growing cities and expanding coastal populations and fishing communities of the Pacific Northwest of the late 19th and early 20th centuries, we have found no reports of Japanese debris arriving in North America after the 1896 and 1933 tsunamis (*4*). In contrast, long-lasting, nonbiodegradable debris has been added in the late 20th century to the world's oceans. That Western Pacific coastal species survived for, to date, nearly 6 years drifting to the Central and Eastern Pacific indicates that shallow-water species can undergo long-term transoceanic dispersal events if provided permanent rafts.

Most of the world's megacities are in the coastal zone and will continue to be so (*25*), greatly increasing the quantity of nonbiodegradable material available to be swept from watersheds and off of coasts. Large storms also inject debris fields into the ocean (*26*, *27*); in turn, cyclones (hurricanes and typhoons) and other storm activities are increasing due to global climate change (*28*, *29*). Human-mediated amplification of marine debris provides new opportunities for species to surmount historic ocean barriers (*30*–*33*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S11
Tables S1 to S6
References (*34*–*55*)

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