

Research Article

Species diversity and abundance of shipworms (Mollusca: Bivalvia: Teredinidae) in woody marine debris generated by the Great East Japan Earthquake and Tsunami of 2011

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Abstract

The Tohoku tsunami of March 2011 ejected a vast amount of debris into the Pacific Ocean. Wood boring shipworms (Bivalvia: Teredinidae) were either already present in, or settled on, the wooden fraction of this debris, offering a unique opportunity to study shipworm diversity in rafted wood of a known origin and time of ocean entry. Lumber and other wood began appearing on Central Pacific (Hawaiian Islands) and Eastern Pacific beaches in 2013. Eighty pieces of wood Japanese Tsunami Marine Debris (JTMD) consisting of construction beams, trees, milled logs, and wood from vessels or maritime structures were analyzed. Six shipworm species resident in the coastal waters of Japan were found: *Bankia bipennata* (Turton, 1819), *Bankia carinata* (Gray, 1827), *Teredothyra smithi* (Bartsch, 1927), *Psiloteredo* sp., *Lyrodus takanoshimensis* (Roch, 1929), and *Teredo navalis* Linnaeus, 1758. Two pelagic species, *Teredora princesae* (Sivickis, 1928) and *Uperotus clava* (Gmelin, 1791), were acquired by JTMD wood in the transoceanic voyage. Several of these wood items were discovered soon after stranding and contained live shipworms. Up to five shipworm species were found in any one wooden object. The present work represents the first study of the diversity and abundance of shipworms transported across an ocean basin in a large woody debris field.

Key words: wood borers, North Pacific Ocean, ocean rafting, biodeterioration, dispersal

Introduction

On March 11, 2011, a devastating tsunami along the northeast coast of Honshu, Japan, destroyed the coastal zone over a wide geographic area. The massive amounts of debris swept into the ocean included wood derived from buildings, trees, small vessels, and milled logs, providing a rare opportunity to study the organisms associated with woody debris crossing the North Pacific. Japanese tsunami marine debris (JTMD) traveled a wide variety of paths for many months through the North Pacific (Lebreton and Borrero 2013; Maximenko et al. 2015) before stranding on the shores of the Northeastern Pacific (NEP) and Hawaii commencing in 2013.

Wood departing Japan, if initially present in the sea at the time of the tsunami, left with Japanese coastal organisms, including shipworms, already aboard. Wood from the land and washed into the ocean was susceptible to colonization by coastal species. Both categories of wood, when drifting across the ocean, were available for colonization by oceanic pelagic species on the high seas.

Shipworms are marine bivalves of the family Teredinidae. They are obligate wood-borers with the exception of a few species that bore into mudstone, sediments, rock, and seagrass rhizomes (Turner 1966; Lozouet and Plaziat 2008; Shipway et al. 2016). They live in a wide range of wood substrates, including mangroves, floating seeds and nuts, fixed wooden maritime structures (such as piers and docks), the hulls of wooden ships, sunken wood on the seabed, and floating wood (Turner 1966; Distel 2003; Voight 2015). Shipworms use wood for both food and shelter; boring tunnels with the file-like denticles on their shells. The wood particles generated are digested with the aid of enzymes secreted by endosymbiotic bacteria. These bacteria also fix nitrogen, which is incorporated into the tissues of their host (Lechene et al. 2007; Horak and Montoya 2014).

Amongst the Bivalvia, the Teredinidae are unusual due to a number of morphological adaptations for life within wood. The shell is highly reduced, covering only the anterior end of the body, while the body is elongate and worm-like. Shipworms possess a pair of calcareous structures (pallets), unique to this family, which flank the siphons. When the animal retracts its siphons, the pallets are pushed forward, sealing the tunnel and providing protection from predation and desiccation. Shipworms are identified primarily by the morphology of their pallets, as the shells are highly variable and are not typically useful for identification (Turner 1966).

Although teredinid tunnels are excavated throughout the life of the animal, boring and growth rates vary

with the type of wood, temperature, salinity, food resources, and exposure. Growth rates may further vary between individuals of the same species in the same piece of wood (Nair and Saraswathy 1971; Eckelbarger and Reish 1972; MacIntosh et al. 2014). Body length is variable and thus a poor indicator of the residence time in wood; moreover, shipworms contract when removed from their tunnels, making accurate measurements challenging. Shipworms line the interior surface of their burrow with layers of calcium carbonate that protect the long fragile body. When changing their boring orientation, they will often build calcium carbonate “walls”, sealing off sections of their burrow (Board 1970).

Three modes of reproduction are found in Teredinidae. Of the 72 species, 23 are larviparous, brooding larvae within their gills. Brooding species fall into two categories: short- and long-term brooders. Short-term brooders (STB) retain veliger larvae until what is known as the straight hinge stage. After being released, these planktotrophic larvae can remain in the water column for up to six weeks before settlement, depending on the water temperature. Long-term brooders (LTB) release larvae later in development as pediveligers. Pediveliger larvae spend less than a week in the plankton before they must settle out on wood (Imai et al. 1951; Calloway and Turner 1988; Shipway 2013). A majority of species are oviparous. These broadcast spawners release their gametes into the water, and the resulting planktotrophic larvae have a pelagic period of four to six weeks (Nair and Saraswathy 1971; Turner and Johnson 1971). The timing of reproduction is highly dependent on temperature and salinity (Culliney 1975; Norman 1977; Rayner 1979; MacIntosh et al. 2012). Regardless of reproductive mode, shipworms are highly prolific, although once settled, their ability to degrade wood is dependent on local environmental conditions (Santhakumaran 1984; Borges 2014; Rao et al. 2016).

The dependence of shipworms on wood for nutrition and shelter causes extensive damage to maritime wooden structures with costs exceeding a billion dollars annually (Distel et al. 2011). This destruction has led to a long legacy of studies dating back to the 18th century (Borges 2007). In the 20th century, W.F. Clapp Laboratories of Duxbury, Massachusetts, carried out extensive sampling of marine wood-borers around the globe from 1948 to 1959, including offshore sampling along the Atlantic and Pacific coasts of the United States (Wallour 1960). However, few efforts have been made to study shipworms in driftwood rafting in the open ocean. Limited offshore sampling of wood in Hawaiian waters confirmed that some species of shipworms are essentially pelagic, existing

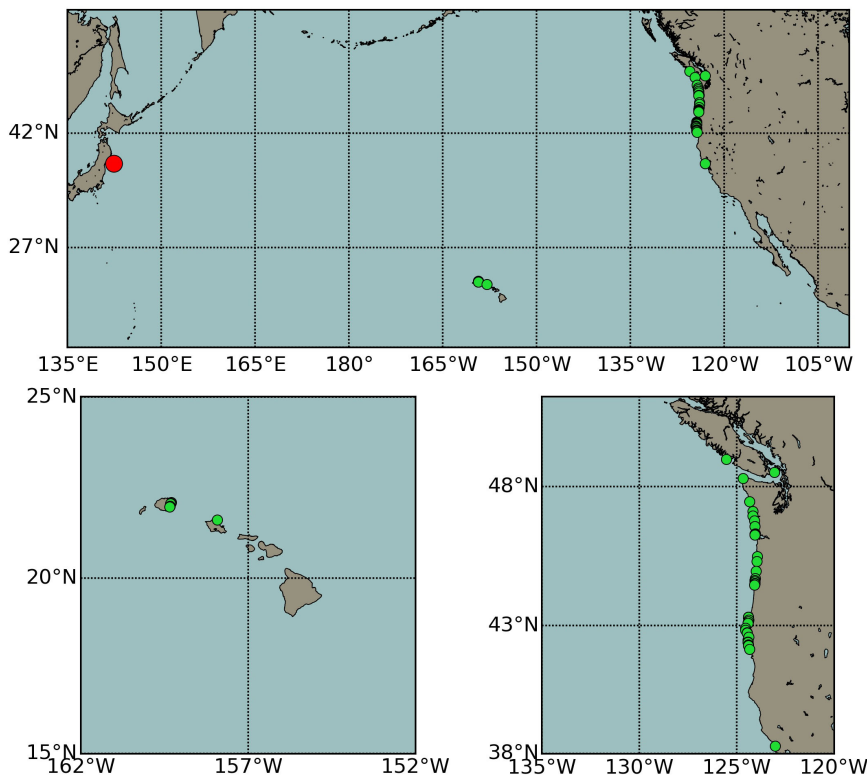


Figure 1. Tsunami epicenter (red circle) and survey locations (green circles) for tsunami wood debris. Locations list in the Supplementary material Table S1. Map by Lucas Merkelbach.

solely in wood floating on the high seas (Edmondson 1962).

We know of no previous opportunity to study the diversity and abundance of shipworms in a large, rafted, woody debris field with a known source and date of entry into the sea. This study presents an annotated synopsis and analysis of the shipworm species found in wood JTMD in North America and Hawaii. We report on wood landing and studied between February 2013 and February 2017.

Materials and methods

Beach surveys were conducted from northern California to British Columbia (38° to 50°N), and along the east shores of Kauai (21.3°) and Oahu (22.1°N), Hawaii, from February 2013 to April 2017 (Figure 1). Surveys were conducted at 37 locations, eight of which were visited on a daily, weekly, or monthly basis (see Supplementary material Table S1). A majority of sites were in Oregon and southern Washington. In general, shore surveys were conducted on foot and ranged from 1.6 to 6.4 km. At one location, vehicle surveys of 8 to 16 km were carried

out on a daily or weekly basis by a volunteer (R. Lewis) throughout the survey period. Additional wooden beams were collected by colleagues and volunteers who mailed cut sections to the authors. Several contributors stockpiled JTMD beams for beachcombing purposes but gave us permission to process some of the wood.

Wooden debris was identified as sourced from the Japanese tsunami by several means, depending upon the type of wood. “Post and beam” construction lumber was identified by mortise and tenon characters unique to Japanese carpentry (Stephen Holland, personal communication, 2013; Figure 2). Vessels with wooden components, milled logs, and other wood were identified by registration marks, names, or stamped insignia, typically combined with the presence of Japanese fouling and boring (shipworm) species. Japanese trees were typically recognized as unique by coastal residents intimately familiar with regional tree species as well as by the presence of Japanese fouling and boring organisms on and in the wood.

Wood from 16 items was presented to the Department of Wood Science and Engineering, College of Forestry, Oregon State University, Corvallis, for thin



Figure 2. Japanese tsunami marine debris wooden beam showing mortise and tenon (post and beam) carpentry (JTMD-BF-248). Photo by NC Treneman.

sectioning and identification to the lowest taxonomic level (family, genus, or species) possible.

Each JTMD object was assigned a unique identification number preceded by JTMD-BF (Japanese Tsunami Marine Debris Biofouling; see Carlton et al. 2017). Items were photographed, and samples were taken of boring and fouling organisms. Smaller wood items were collected whole. If the item was too large to be transported, one or more sections, 30–40 cm in length, were cut from an end (unbroken, if possible). Samples of railings and wood inserts inside fiberglass hulls were collected from JTMD vessels. Processing was carried out in the field and laboratory. Out of the 129 items assessed for shipworm presence and JTMD status, 80 were completely processed, defined as splitting one or more 30–40 cm section into pieces of wood one cm or less in width. A piece of wood from each item was archived (NC Treneman, Oregon Institute of Marine Biology, Charleston, Oregon) in most instances.

The number and size of the burrows in a cross-section of 30–40 cm from the end of a piece of wood (unbroken if possible) were recorded and used as an estimate of overall abundance and wood degradation. Teredinid burrows were exposed using an axe and hammer to cut along the length of 30–40 cm sections. Pallets, shells, tissue, and tunnel linings were collected, photographed, counted and measured. Age classes within a species were determined by accessing pallet morphology and size. Tissue was preserved in 95% ethanol for molecular studies. The pallets and/or shells from a single individual shipworm were sometimes found *in situ*, allowing for a match between species, shells, pallets, and a specific tunnel; however, this was a rare occurrence because gaining access to the wood interior destroys tunnel connections. Items with high shipworm abundance were sometimes so degraded that they crumbled during processing.

Wood JTMD items, with rare exceptions, were discovered long after the shipworms had died; consequently, body measurements were possible in only a few items. Tunnel length (including side galleries) was determined by molding a wire along the tunnel. The diameter of the anterior end of the tunnel was measured as an indicator of the size of the animal. Total body length was measured from the anterior foot to the end of the siphons. All measurements were used to estimate abundance, frequency, and age classes of the species present.

Stranding dates consist of either direct observation of a fresh arrival (i.e., an object not known to be on a shore in the previous 24–48 hours) or an estimated landing date, determined by the condition of an item, depth of burial, and the degraded nature of the biological community. Some items, particularly post-and-beam wood, were discovered one, two, or more years after landing. The length of time an item was in the ocean was calculated as months from the tsunami (TM), with March 2011 designated as TM 1 (given that March 11 is early in the month), *versus* the estimated time of landing.

Specimens were identified independently by N. Treneman, L. Borges, and R. Shipway using identification keys (Turner 1966, 1971). Photographs of multiple specimens of each species were shared and discussed by the authors. Pallets of some species were subjected to slow chemical digestion by vinegar to expose the underlying structure. T. Haga (National Museum of Nature and Science, Tsukuba, Japan) and A. Nishimoto (National Research Institute of Fisheries Science, Yokohama, Japan) provided pallets of *Psiloteredo* sp. and *Bankia bipennata* (Turton, 1819) from Japanese waters for comparison. Specimens in the Teredinidae collections at the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts and the Bernice Pauahi

Bishop Museum in Honolulu, Hawaii, were compared to JTMD specimens.

Results

Wood identity and delivery history

Construction beams comprised 63 of the 80 processed items (Figure 3), with the remainder consisting of trees, milled logs, boat components, and housing elements. The smallest wood studied was a vessel insert of 0.00027 m³. JTMD beam-wood volume ranged from 0.002 to 0.42 m³, with lengths of 63 to 754 cm. Tree-wood volume ranged from 0.17 to 2.02 m³. Wood species identified were Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco, 1950), pine (*Pinus* sp.), spruce (*Picea* sp. A), Japanese cedar or Sugi (*Cryptomeria japonica* (Thunb. ex L.f.) D. Don, 1839), fir (*Abies* sp.), Japanese chinquapin (*Castanopsis uraiana* (Hayata) Kaneh. & Hatus., 1939), and an unidentified species of mahogany, all of which contained shipworms. Trees had an average TM of 47 months, compared to 45 for boats, 31 for beams, and 26 for milled logs.

The first wood JTMD on a NEP beach was observed at TM 25 (2 years); this date can be used as the minimum period of transoceanic transit and arrival. JTMD wood items observed on NEP beaches at TM 26, 27, 37, 38, 46, 62, and 65 contained living specimens of Japanese oviparous species in different combinations (as discussed in more detail, below). The survival of a transoceanic crossing by oviparous coastal species from Japan to NEP shores suggests that these species have a life span of at least two and possibly up to five years. The last observed wood JTMD item in this study was a tree (JTMD-BF-651) stranded at Newport, Oregon, on TM 65, in July 2016. This beam contained live *Bankia carinata* (Gray, 1827), *Psiloteredo* sp. and *Teredora princesae* (Sivickis, 1928).

Shipworm diversity

Nine species of shipworms were found in JTMD. Six are coastal or shallow continental shelf species resident in Japan (Tsunoda 1979; Haga 2017): *Bankia bipennata* (Turton, 1819), *Bankia carinata* (Gray, 1827), *Teredothyra smithi* (Bartsch, 1927), *Lyrodus takano-shimensis* (Roch, 1929), *Teredo navalis* Linnaeus, 1758, and *Psiloteredo* sp. (Table 1). Two pelagic species, known to colonize drift wood on the high seas, *Teredora princesae* (Sivickis, 1928) and *Uperotus clava* (Gmelin, 1791), were also found. One specimen of *Bankia setacea* (Tryon, 1863), acquired in the Northeast Pacific, was found in a JTMD tree stranded in February 2016.

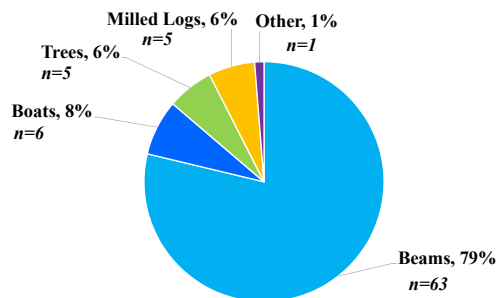


Figure 3. Proportion of wood Japanese Tsunami Marine Debris sampled for shipworms. “Other”: housing components, such as door frames.

The average number of Japanese species was 1.7 per item, with a maximum of five species in one item (Table S2). Diversity was highest in trees (n = 5), with an average (a) of 3.2 Japanese species, compared to boats (n = 6, a = 2.3), milled logs (n = 5, a = 1.8) and beams (n = 63, a = 1.4).

Systematic Account

Order Myida Stoliczka, 1870
 Superfamily Pholadoidea Lamarck, 1809
 Family Teredinidae Rafinesque, 1815
 Subfamily Teredininae Rafinesque, 1815

Material Examined: Individual items, their identity, location, date of landing and a summary of species present in each item, are shown in Table S2. JTMD-BF-numbers are further provided in the text for certain items of particular interest.

Teredothyra smithi (Bartsch, 1927)

This species was found in 10% of the JTMD items examined. Abundance ranged from 2 to 14%, except for one beam (JTMD-BF-244) where it was the dominant species (50% of recovered pallets) (Table 1). Most of the pallets recovered had juvenile morphology, with a thin, very light brown periostracum split at the posterior edge covering two calcareous projections.

Mature pallets (Figure 4E) had a pointed calcareous blade divided by a median distal division covered with a dark, reddish-brown periostracal cap. Mature forms were rare and always found in beams with a majority of the juvenile type. Two tunnels, 37 and 50 mm long, were measured in items stranded at TM 38 (JTMD-BF-171) and 25 (JTMD-BF-244), respectively. A total of seven tissues samples were recovered from two items stranded on TM 37 (JTMD-BF-128)

Table 1. Measurements and ecological characteristics of Japanese Tsunami Marine Debris (JTMD) shipworms. ^aTurner 1966; Nair and Saraswathy 1971; Okutani et al. 2009, ^bEdmondson 1962, ^cCalloway and Turner 1988.

Species	Geographic Distribution ^a	Habitat ^{a,b}	Frequency in Wood JTMD	Tunnel Length (mm)	Body Length (mm)	Reproductive Strategy ^{a,c}
<i>Teredothyra smithi</i>	Indo West Pacific, Indian Ocean subtropical tropical	coastal and continental shelf	10%	37, 50 <i>n</i> = 2	40, 45, 60 <i>n</i> = 3	oviparous
<i>Teredora princesae</i>	Indo-Pacific Indian Ocean North Pacific subtropical tropical	pelagic	40%	1–320 <i>n</i> = 35	15–30 <i>n</i> = 4	oviparous
<i>Uperotus clava</i>	Southern Indo-Pacific Indian Ocean tropical	pelagic (mostly in drifting nuts and seeds)	1%			oviparous
<i>Psiloteredo</i> sp.	NW Pacific cold northern	continental shelf	91%	37–1187 <i>n</i> = 34	45–432 <i>n</i> = 9	oviparous
<i>Teredo navalis</i>	cold to warm pantemperate	coastal and estuarine	1%			short term brooder
<i>Lyrodus takanoshimensis</i>	Atlantic, Pacific, Indian Ocean warm temperate subtropical tropical	coastal and estuarine	4%			short term brooder
<i>Bankia bipennata</i>	pansubtropical pantropical	coastal and estuarine	10%	50, 150 <i>n</i> = 2		oviparous
<i>Bankia carinata</i>	pansubtropical pantropical	coastal	49%	8–255 <i>n</i> = 18		oviparous

and 38 (JTMD-BF-171). Of these seven, three were complete specimens (body lengths of 40, 45 and 65 mm) and all contained mature gonads.

Teredothyra smithi is regarded as a species widely distributed through subtropical and tropical waters of the Indo-West Pacific (Turner 1966). The northern limit of this species along the coast of Japan is at 36.5°N latitude, 141°W longitude in sunken wood taken from 95 to 115 m (Haga 2001).

Teredora princesae (Sivickis, 1928)

Teredora princesae was present in 40% of the wood items examined, where it was often the dominant species, with pallet frequencies ranging from 11% to 98% (Table 1). It was especially abundant in beams landing in Hawaii; a 30 cm section of one beam (JTMD-BF-315; Kauai, November 2013) contained hundreds of shells and pallets across multiple age classes, with tunnels from a few millimeters to over 100 mm in length. Hawaiian JTMD wood comprised 9 of the 45 items with multiple species (including pelagic species). *Teredora princesae* was the most abundant in all the 9 items, being dominant in only 6 of the remaining 36 items with multiple species.

Pallet morphology (Figure 4G) was highly variable. General characteristics included a thumbnail-like depression, which at times ended with a small anterior pocket, and a short, pointed, translucent stalk. The

internal layers of the pallet were built up much like a layer cake, as seen in the North Atlantic *Psiloteredo megotara* (Hanley, 1848) (Borges 2015). These were often visible in the thumbnail, which in some cases had longitudinal ridges. Shells had the characteristic upturned posterior slope typical of this species (Turner 1966). Tunnels ranged in length from 1 to 320 mm, with entrance holes found along the entire length of wood items, rather than being concentrated at the ends. A ridged calcareous pad was deposited at the entrance on top of the tunnel lining that the pallets rested upon and to which they were often stuck.

Living *Teredora princesae*, with body lengths ranging from 15 to 30 mm, were recovered from a beam arriving on TM 38 (JTMD-BF-171). These animals started ejecting eggs from their exhalant siphons upon extraction. Items with arrival dates of 27, 37, 38, 46, 60, 62, and 65 TM (JTMD-BF-165, 128, 171, 264, 501, 542, 651) also contained living or freshly dead animals. No larvae were observed in the gills of any specimens, confirming that this species is oviparous. The bodies of this species were short and wide. This morphology was reflected in the tunnel shape, which widened close to the entrance.

This pelagic species is found in driftwood on the beaches of Hawaii and islands of the subtropical and tropical Indo-Pacific, as well as in the Indian Ocean (Edmondson 1962; Nair and Saraswathy 1971). However, this species is rarely recovered from test panels deployed



Figure 4. Pallets of JTMD shipworms. Left side: outer face; right side: inner face. A: *Bankia bipennata* (JTMD-BF-171); B: mature *Bankia carinata* (BF-651); C: immature *B. carinata* (BF-123); D: *Lyrodus takanoshimensis* (BF-160); E: mature *Teredothyra smithi* (BF-128); F: *Teredo navalis* (BF-356); G: *Teredora princeasae*, from Hawaii JTMD; H: *Psiloteredo* sp. (BF-416); I: *Uperotus clava* (BF-495). bl: blade, st: stalk. Scale bars: A = 6 mm; B–H = 2 mm. Photographs by NC Treneman.

in coastal waters of the same regions (Tsunoda 1979; Rayner 1983; Raveendran and Wagh 1991). The lack of other common pelagic species (Edmondson 1962) in JTMD and the high abundance of *Teredora princesae* in Hawaiian JTMD support the conclusion that *T. princesae* is the dominant species of pelagic shipworm in the North Pacific and further indicates that this species is a pelagic specialist, adapted to the unpredictable and generally low availability of wood in the open ocean (Edmondson 1962; Turner 1966).

***Uperotus clava* (Gmelin, 1791)**

One pair of *Uperotus clava* pallets was recovered from a section of boat wood (JTMD-BF-495) washed ashore in southern Oregon in May 2014 (TM 39). No tissue, shells, or tunnels were associated with the pallets, which were stained from the metal fastenings attached to the wood. The pallets were 6.5 mm in length; the blades 4 mm tall and 2.19 mm wide, with characteristic ribs radiating out from a central point on the upper half of the blade (Figure 4I). The ribs extended beyond the distal edge of the blade, giving the rim a toothed appearance. The lower half of the blade was smooth, and did not form a sheath around the stalk. The extension of the stalk into the blade was visible on the smooth inner face of the pallet. The thick, blunt-tipped stalk was slightly translucent compared to the opaque blade. Turner's (1966) drawing (plate 23A) of *Teredo nucivorus* (Spengler, 1792), synonymized by Turner with *U. clava*, is the best match for our pallets.

This species, reported in the Indian Ocean and the southern Indo-Pacific, is also known as a pelagic specialist most commonly found in drifting coconuts and mangrove seeds (Iredale 1936; Roch 1961; Edmondson 1962; Cragg 2007). While two Pacific species, *Uperotus clava* and *U. rehderi* (Nair, 1956), remain reported in the literature, Turner (1966) and others have regarded these as ecophenotypes, one boring into floating seeds (*U. clava*) and one (*U. rehderi*) into timber (Rayner 1983; Higo et al. 1999). The presence of *U. clava* in JTMD boat wood indicates the passage of this item along a route south of Hawaii into tropical waters.

***Psiloteredo* sp.**

Psiloteredo sp. was found in 91% of the examined items, and sole occupant of 56%, with a high frequency but generally low abundance in JTMD. Twenty pallets or less of this species were collected (per item) from 80% of processed items containing *Psiloteredo* sp. Beams with less than five holes in a cross section were common; in these cases, fewer than 11 pallets were recovered.

The pallets (Figure 4H) were built up in horizontal layers of calcium carbonate that become successively larger from the outer to the inner face. These were covered with layers of periostracum (see Borges 2015). The blades were slightly asymmetrical, with the two sides attached to the stalk at different distances from the tip. Layer lines were often exposed in the thumbnail, a depression in the outer distal face. Grooves in the proximal outer face along the sides of the stalk were often present, one usually deeper than the other. The end of the stalk was generally pointed, sometimes with small longitudinal ridges at the tip. Tunnels frequently penetrated into the center of the wood, after which they followed the grain. The tunnel entrance was ringed with successive ridges of calcium carbonate (concamerations). *Psiloteredo* sp. is the largest JTMD shipworm, with a maximum body length of 432 mm and maximum tunnel length of 1187 mm (Table 1). Specimens had mature gonads and no larvae were found in the gills.

The high frequency of this species in JTMD suggests that *Psiloteredo* sp. larvae were present in large quantities in coastal Tohoku waters at the time of the tsunami. Okutani et al. (2009) found *Psiloteredo* sp. (identified as the North Atlantic *Psiloteredo megotara* (Hanley, 1848)) in sunken wood dredged from 250 to 450 meters along the continental shelf of the Pacific side of Hokkaido. It is likely that the beams solely occupied by *Psiloteredo* sp. moved rapidly out to the open ocean, while those containing warm-water Japanese species were swept south or lagged behind. If *Psiloteredo* sp. has a similar reproductive capacity as *P. megotara*, it would be capable of producing millions of gametes (Sigerfoos 1908). The tsunami may have induced spawning in this species and/or March may be a breeding season for *Psiloteredo* sp.

While almost identical in gross anatomy to *Psiloteredo megotara*, genetic analyses reveal that this North Pacific species is distinct (Treneman et al. 2018). The identity of this Japanese *Psiloteredo* will be treated in a separate paper.

***Teredo navalis* Linnaeus, 1758**

Five *Teredo navalis* pallets were found in the upper deck wood of a boat (JTMD-BF-356) that arrived on the Oregon coast in April 2015 (Table 1). The boat had originated from the Iwate Prefecture of northeast Honshu (Craig et al. 2018; Carlton et al. 2017). The densely packed, twisted tunnels were degraded and occupied by a number of invertebrates, including bryozoans, crabs, polychaetes and sponges.

The pallets (Figure 4F) were 5 to 6 mm in height, with the periostracum worn away, exposing the calcium carbonate section beneath. The posterior edge was concave on both sides, slightly less so on the inner face. The anterior portion was an inverted triangle with a short sheath at the top of the stalk. The sides of the pallet were parallel in the upper portion and rise to lateral horns with rounded tips. The outer face was more rounded, the inner face flatter. The blade was made of an opaque, tan material and the stalk was translucent, slightly irregular in shape and pointed at the end. The calcium carbonate in several pallets was chalky and the stalks opaque and thicker. No tissue was present, and no match between pallets and tunnels was possible.

Teredo navalis is the most infamous shipworm treated here, having been recognized since the 1700s for its destructive repertoire (Hill and Kofoed 1927; Ryabchikov et al. 1961). Capable of tolerating a wide range of ecological conditions (Borges et al. 2014), it is found throughout the Japanese coast (Tsunoda and Nishimoto 1978; Tsunoda 1979). As we note below, *T. navalis* is already established in the Northeast Pacific Ocean, where it is regarded as an introduced species.

***Lyrodus takanoshimensis* (Roch, 1929)**

Lyrodus takanoshimensis pallets were found in three JTMD items, two trees (JTMD-BF-160 and JTMD-BF-264) and one boat (JTMD-BF-356, which as noted above originated from Iwate Prefecture) (Table 1). Their pallets were small (1–3 mm, Figure 4D), with a dark brown periostracal cap on top of a calcareous, flattened base. The cap was concave along the distal edge, with a shallow cavity in the middle. The stalk was approximately of the same length as the blade, slightly translucent, and thicker in the middle. The end of the stalk was rounded. No living individuals or tissue were recovered.

This poorly known presumptive Japanese species is reported from isolated populations around the world (Tsunoda 1979; Mead et al. 2011; Rao et al. 2016). A population of *Lyrodus takanoshimensis* was reported by Popham (1983) in Ladysmith Harbor, British Columbia, probably introduced in wooden crates used to transport commercial oysters from Japan.

***Bankia carinata* (Gray, 1827)**

Bankia carinata occurred in 49% of the items), was present in 87% of the items with more than one species, and in 100% of the items with four or more species (Table 1). Mature pallets had the typical cone-in-cone construction of the genus *Bankia* (Figure 4B). The cones were yellow brown with a smooth, opaque

stalk. When fresh, the stalk was covered with an ochre periostracum. The tips of the periostracum extended beyond the sides of the cones forming short awns. The periostracal edge of each cone was smooth and had no fringe. Immature pallets had a dark brown periostracal cap covering most of the blade (Figure 4C). Cone segmentation could often be clearly seen through the periostracum on the inner face, and the underlying segmented calcium carbonate base was often exposed. Immature pallets bore a close resemblance to *Lyrodus pedicellatus* (Quatrefages, 1849) (Turner 1966; personal observation), however, immature *B. carinata* pallets exhibited visible segmentation on the inner face and had a shorter periostracal cap with lateral points, separating them from those of *L. pedicellatus*. Immature pallets were often found in large numbers compared to mature ones.

The tunnels were long and slender, with a range of 8–255 mm in length. Entrances were commonly at the ends of an item or in a mortise. The tunnel lining was brown and almost papery, often with a slight red stain. Bodies were very fragile, and only a few partial bodies attached to pallets were obtained. The posterior adductor muscles were bright red, and the mantle a yellow-brown, and sometimes translucent when freshly dead.

This subtropical and tropical species has successfully invaded various regions worldwide (Nair and Saraswathy 1971; Borges et al. 2014). The high frequency of this species in JTMD suggests that it is abundant in Japan. *Bankia carinata* is known in the Eastern Pacific Ocean from San Diego, California to Posorja, and Guayas, Ecuador (Coan and Valentich-Scott 2012).

***Bankia bipennata* (Turton, 1819)**

Specimens of *Bankia bipennata* were present in 10% of items (Table 1), and in low numbers in all the items it occupied. The pallets were very fragile and broke into pieces during the wood's exposure on the beach, making abundance estimates difficult. In the six items where the specimens were freshly dead and the pallets still flexible, the frequency of *B. bipennata* pallets was between 3–9%. The long pallets (Figure 4A and 5) ranged from 50 to 130 mm in length; milky yellow and flexible when fresh. The long stalk was granular under a periostracal cover. The outer periostracal fringe of the cones had short, blunt, square serrations; the inner fringe had long pointed serrations (Figure 5). The awns had a short, pointed serrations. The entrance point in wood was generally at the end of a beam, root, or in a mortise. Like *B. carinata*, the bodies of this species were easily damaged during processing and no complete individuals were collected.

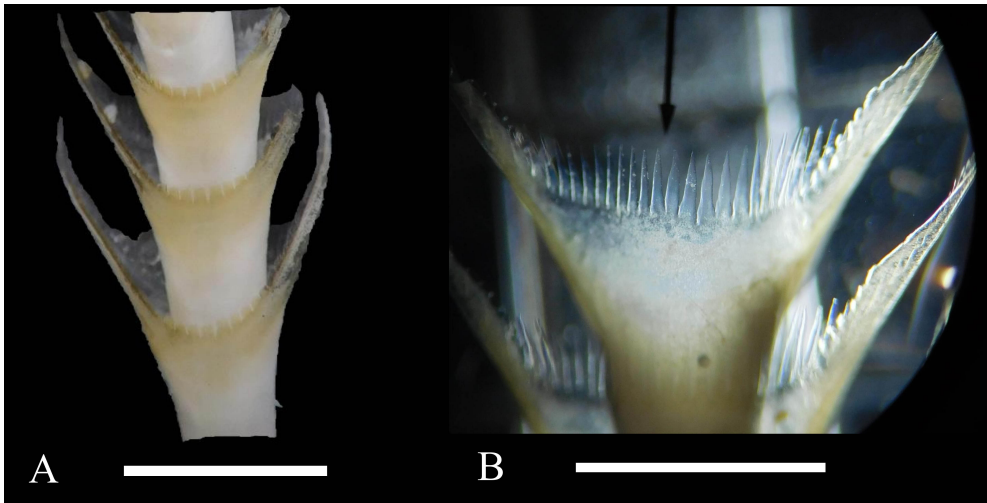


Figure 5. Pallets of *Bankia bipennata* (JTMD BF-171). A: outer face; B: inner face, arrow at the top is pointing to inner fringe. Scale bars: 2 mm. Photo by NC Treneman.

A comparison of JTMD *Bankia bipennata* to specimens from Hokkaido, Japan (provided by T. Haga) revealed slight differences. The serrations along the outer face in the Japanese specimen was more pointed (a cone instead of the blunt teeth in the JTMD specimens) and the serrations on the awns were more numerous and shorter, unlike the near lack of serrations on the JTMD awns. Examination of specimens at the MCZ, including the holotype of *Bankia fosteri* (Clench and Turner, 1946), indicate that the descriptions of *B. bipennata* and species morphologically similar (Turner 1971) need to be revised. In summary, specimens designated as *B. bipennata* at the MCZ vary in several key characteristics including stalk granulation, shape of the serrations, and gross shell morphology. We use the name *B. bipennata* for this JTMD species, based upon Turner (1971), but further studies are required to clarify this species group.

Bankia bipennata is reported from the tropical Atlantic, the Indo-Pacific, India, and Japan. Coan and Valentich-Scott (2012) note a record from Salinas, Guayas, Ecuador.

***Bankia setacea* (Tryon, 1863)**

We found one set of *Bankia setacea* pallets 11 mm long in a tree (JTMD-BF-501) washed ashore at Long Beach, Washington, in February 2016. Their size indicates an age of approximately 1–2 months (Quayle 1992), suggesting that this individual settled after the tree drifted into the Eastern Pacific. We thus regard this as a local North American acquisition, despite the fact that *B. setacea* is also known from Hokkaido (Hill and Kofoid 1927; Tsunoda and Nishimoto 1978).

Discussion

Circulation, rafting and wood colonization history

The 2011 tsunami generated millions of pieces of wood available for shipworm settlement, making it possible to establish that living, reproductively viable shipworms travelled from the Western Pacific to the Eastern Pacific Ocean. Rafts of natural material such as kelp, pumice, and wood have been shown to carry living species for 100s to 1000s of kilometers (Thiel and Haye 2006; Fraser et al. 2011; Saunders 2014), however, we know of no previous reports of trans-oceanic continent-to-continent transport and subsequent landings over the distances and time periods involved in this study.

The geography and currents along the eastern Japanese coast produce a division between cold and warm water ecological provinces at approximately 36°N (Tsunoda 1979). The warmer Kuroshio Current travels north along the southern coast of Japan, and merges with the cold Arctic Oyashio current. These currents are deflected east at approximately the same latitude (38.3°N) at which the tsunami occurred. The speed and complex eddies and meanders of these currents as they leave the coast of Japan allow for multiple pathways and unpredictable transit time to NEP and Hawaiian shores (Niiler et al. 2003; Lebreton and Borrero 2013; Maximenko et al. 2015). Warm patches of water occur within a few hundred km of the Japanese coast (N. A. Maximenko, University of Hawaii, Honolulu, HI, personal communication, 2016), making it possible for larvae of the tropical and subtropical species to survive and settle on wood JTMD many kilometers from the coastline.

Bankia bipennata, *Bankia carinata*, and *Teredothyra smithi* have been reported south of 36°N along the Pacific coast of Japan and are considered to be warm water species (Tsunoda 1979; Higo et al. 1999; Haga 2001). Tsunoda (1979) reported *Teredo navalis* is a resident throughout the Japanese coastline and *Lyrodus takanoshimensis* resident south of 38°N, on the Pacific side. *B. bipennata*, *B. carinata* and *T. smithi* are oviparous, and *T. navalis* and *L. takanoshimensis* are short-term brooders (STB) (Calloway and Turner 1988). Shipworm larvae from coastal Japanese species may have been carried by the Kuroshio Current to the open ocean where they settled on wood JTMD. However, it is equally possible that these species colonized JTMD as the wood circulated along the southern coast of Japan. *T. navalis* and *L. takanoshimensis* are widespread euryhaline species typically found in ports and estuaries (Ryabchikov 1957; Paalvast and van der Velde 2011; Borges et al. 2014). The presence of these species in an item may indicate that it spent more time in the nearshore waters of Japan.

The date of settlement cannot be fixed for JTMD shipworms because the amount of time each item spent near Japan is unknown. It may also be that cross inoculation occurred between wood JTMD items in the open ocean. Growth and boring rates can vary within and between items, as noted earlier, making it difficult to ascertain if multiple generations were present. However, in several instances the large range in pallet, shell, and tunnel sizes indicated multiple generations of *Psiloteredo* sp., *Bankia carinata*, *Teredothyra smithi*, and the oceanic *Teredora princesae*. It is likely that *T. princesae* settled on JTMD circulating in the subtropical convergence zone (SCZ) north of Hawaii (Howell et al. 2012).

Reproductive biology and JTMD shipworm diversity

JTMD contained six of the 25 species of shipworms reported as resident in Japan by Tsunoda (1979). Of these six, no long-term brooding (LTB) species were found, which is not surprising considering the life history strategies of these species. Once released, competent pediveliger larvae are capable of settling on wood immediately and can recruit to the same timber in which their parent resides (Turner and Johnson 1971). Thus, any items which become colonized by a LTB species would have been heavily infested, rapidly degraded, and would likely sink. Further, due to this brief free-swimming period, LTB species have a short settlement window and limited distribution range (MacIntosh et al. 2012, 2014); therefore, any wood escaping the coastal region of Japan would likely pass beyond the dispersal range of these species.

Short-term brooding species have a median distribution range, with larvae typically spending around two weeks developing in the plankton before settlement. However, only two species with an STB strategy were found in wood JTMD and neither of these was found alive. The highly degraded wood in which *Teredo navalis* was found reached NEP shores only because the wood was attached to a large vessel. Laboratory studies indicate that these species have a lifespan of 2 years or less, and are capable of destroying wood with great rapidity (Hill and Kofoid 1927; Culliney 1975; Mann and Gallagher 1985). It may be that both STB and LTB species are not well suited for long-term transits at sea, suggesting that dispersal for centuries by wooden ships may be more responsible for the now world-wide distribution of species such as *Teredo navalis* (Carlton 1999, 2009) rather than *via* drifting wood, as long invoked in the shipworm literature.

Broadcast spawning (i.e., oviparous) species dominated wood JTMD, demonstrating the advantages of a reproductive strategy maximizing fecundity and broad larval distribution range (MacIntosh et al. 2014). Their presence in wood JTMD may indicate that they are resident further off shore than other coastal Japanese shipworms. The extended pelagic larval lifespan of these species may confer an advantage in the open ocean where wood is typically at a low density (Matsumura and Nasu 1997) with seasonal influx from terrestrial sources (Hägglöblom 1982).

Risk of invasion

The presence of reproductive shipworms in wood rafted from the Northwestern Pacific to NEP and Hawaiian coastlines creates the potential for the establishment of invasive populations. While reproductive success is unlikely in the NEP for the warm-water species *Bankia bipennata*, *B. carinata* or *Teredothyra smithi*, they might be capable of survival and reproduction in Hawaiian waters, where they are not yet reported (Edmondson 1942; Turner 1966; NCT, personal observation).

We suggest that *Psiloteredo* sp. is capable of surviving and reproducing in the NEP. Durski et al. (2015) reports seawater temperatures ranging from 6 to 18 °C along the US Pacific coast for the years 2008 to 2011. Surface waters off the Pacific coast of Hokkaido are 5–17 °C, with ocean floor temperatures of 2.8–15.2 °C (Okutani et al. 2009). Thus, NEP temperatures fall within the range of temperatures of the native waters of *Psiloteredo* sp. Detecting established populations of *Psiloteredo* sp. on the Pacific coast of North America may depend on surveys of continental shelf and offshore waters rather than

ports and harbors, if the Japanese species' habitat is similar to that of the Atlantic *P. megotara* (Brown 1953; Norman 1976; Santhakumaran 1984; Borges et al. 2014).

Lyrodus takanoshimensis and *Teredo navalis* are already established in the NEP. The most northern populations known to date where successful spawning occurs are in two estuaries in British Columbia: *L. takanoshimensis* in Ladysmith Harbor (Popham 1983) and *T. navalis* in Pendrell Sound (Quayle 1964). Water temperatures in these locations rise to 18 to 25 °C for a few months of the year (Quayle 1964). *Teredo navalis* and *L. takanoshimensis* are absent from Hawaiian waters (Edmondson 1942; NCT, personal observation).

Wood and shipworm longevity across the ocean

The events described here, in terms of the arrival of allochthonous wood on the shores of the Pacific coast of North America and the Hawaiian Islands, commenced in the spring of 2013 and largely subsided (with the exceptions noted below) by the spring of 2014. The majority of wood JTMD, having departed Japan in 2011 with their shipworm cargos, was likely biodeteriorated by borers and sank. Some of this wood, after enduring a minimum of two, and, as of this publication, a maximum of five years at sea, stranded on the shores of the NEP and Hawaii with living shipworms.

During the years of 2015 and 2016, only six wood JTMD items with living shipworms, or at least with fresh shipworm tissue, were retrieved. Three fiberglass vessels, with wooden inserts for trim or other purposes, arrived in the spring and early summer of 2015 on the coasts of Oregon and Washington (JTMD-BF-356, 402, and 420). These vessels acted as a longer-lasting wood transport mechanism, essentially securing the wood (which would have long since deteriorated if free-floating) in place, embedded in a fiberglass frame. Two post-and-beam pieces arrived with living shipworms in the spring of 2016, one in Washington (BF-542) and another in Hawaii (BF-627), two to three years after all other post-and-beam wood had expired. The circulation history of these late wood beams is problematic as it is expected that shipworms would destroy housing beams within two or three years. It may be that later arriving wood beams became stranded on beaches in the Western Pacific for some years and were eventually refloated due to storm activity. More research on the circuitous fate of wood at sea is needed to understand how these relatively smaller wood items arrived on NEP shores 5 years after the tsunami.

Finally, two Japanese trees with shipworms arrived in 2016 in the Pacific Northwest, having been at sea for 5 years. This is perhaps not surprising, given the far more massive and thus enduring nature of trees *versus* wood construction framing or vessel wood strips. The first tree (BF-501, a spruce, *Picea* sp.) landed in February 2016 in Washington and was 2.4 m long by 0.3 m wide. The second tree (BF-651, a pine, *Pinus* sp.), landing in July 2016 in Oregon, was 13.3 m in length by a maximum of 0.6 m in diameter. Recognized upon their landing as likely from Honshu based upon their marine biofouling (including Japanese species of mussels, clams, and barnacles), both trees proved to carry an identical complement of shipworm species (*Psiloteredo* sp., *Bankia carinata*, and *Teredora princesae*). Trees as transoceanic vectors for marine species may be more reflective of natural events, albeit exceedingly rare ones (we know of no previous reports). We predict that some of the trees from the coastal forests of Honshu obliterated by the tsunami are still at sea, and that additional landings will occur on the coast of North America, with living shipworms from the Western Pacific.

The massive amounts of woody debris swept into the North Pacific Ocean by the tragic events of March 2011 ferried a vast diversity of Japanese species to the Central and Eastern Pacific (Carlton et al. 2017), including the shipworm fauna discussed here. Living Asian shipworms landed in wood (ranging from less than one meter in size to trees over 13 meters in length) in North America commencing two years after the tsunami, and continued to arrive as of 2016, providing a unique opportunity to understand the long-term survival of teredinids transported transoceanically in a large woody debris field with a known source and date of entry in the sea.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Survey locations for wood Japanese tsunami marine debris.

Table S2. Wood JTMD items processed for shipworms: stranding location, date, and species presence.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_JTMD_Treneman_etal_SupplementaryTables.xlsx