

Research Article

Transoceanic rafting of Bryozoa (Cyclostomata, Cheilostomata, and Ctenostomata) across the North Pacific Ocean on Japanese tsunami marine debris

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Abstract

Forty-nine species of Western Pacific coastal bryozoans were found on 317 objects (originating from the Great East Japan Earthquake and Tsunami of 2011) that drifted across the North Pacific Ocean and landed in the Hawaiian Islands and North America. The most common species were *Scruparia ambigua* (d'Orbigny, 1841) and *Callaetia* sp. Of 36 bryozoans identified to species level, 15 are already known from North America, one of which (*Schizoporella japonica* Ortmann, 1890) is an earlier introduction from Japan; 18 species are known only from the Western Pacific, one of which (*Bugula tsunamiensis* McCuller, Carlton and Geller, 2018) is newly described in a companion paper. The 13 additional bryozoans, not taken to species level, are likely derived from the Western Pacific based upon evidence reviewed here; two of these species (*Callaetia* sp. and *Arbocuspis* sp.) are undescribed. Seven warm-water species, *Metroperiella* cf. *biformis* (Zhang and Liu, 1995), *Celleporaria brunnea* (Hincks, 1884), *Drepanophora* cf. *gutta* Tilbrook, Hayward and Gordon, 2001, *Smittoidea spinigera* (Liu, 1990), *Biflustra grandicella* (Canu and Bassler, 1929), *Biflustra irregulata* (Liu, 1991), and *Celleporina* cf. *globosa* Liu, 2001, not known from Japan, may have been acquired by Japanese Tsunami Marine Debris (JTMD) as these objects were carried by ocean currents into more southern waters. Three oceanic bryozoans (*Jellyella tuberculata* (Bosc, 1802), *Jellyella eburnea* (Hincks, 1891), and *Arbopercula angulata* (Levinsen, 1909)) provide insight into the routes that some JTMD items may have taken, and thus the conditions experienced, as they rafted from the Western Pacific to the Central and Eastern Pacific. The cooler-water species *J. tuberculata* and *A. angulata* were found primarily on JTMD objects arriving in the Pacific Northwest, whereas *J. eburnea* was most common on objects landing in the Hawaiian Islands. The most common bryozoan growth forms on these rafted objects were runners (creeping uniserial morphology) and arborescent forms capable of using available surface area provided by other organisms (such as hydroids) on space-limited objects. Species that form flat or mounded encrustations were less frequent, suggesting that they do not fare as well in a potentially space-limited environment.

Key words: amph-Pacific distributions, anthropogenic debris, invasive species, Northeastern Pacific, Western Pacific

Introduction

Bryozoans are a large and diverse group of invertebrates well represented in many marine habitats, including fouling communities. While the ranges of many bryozoan species are restrained due to their lecithotrophic, short-duration larval stage, and thus low planktonic dispersal ability (Johnson et al. 2012), rafting on natural substrates (such as algae, seagrass, or wood) may explain in part the presumably natural widespread distribution of many species, although the taxonomic validity of many putative cosmopolitan species is being increasingly questioned (Hoare et al. 2001; Harmelin et al. 2012; Vieira et al. 2014a, b). Confounding our understanding of the role of natural rafting are the centuries of anthropogenic dispersal of bryozoans in fouling communities on ships' hulls or by the widespread movement of commercial shellfish (Carlton 2009), both of which activities altered the distribution of many species (Watts et al. 1998; Johnson et al. 2012). Adding to the complexities of dispersal mechanisms in modern times has been the introduction of long-lasting plastic debris into the world's oceans, potentially altering species' ranges by providing non-biodegradable rafting substrates of much greater temporal and spatial duration than floating organic objects (Gregory 2009; Kiessling et al. 2015; Carlton et al. 2017).

Bryozoans are sessile, colonial, filter feeders with many species possessing the ability to persist through adverse conditions; consequently, they frequently represent the most abundant and diverse group within regional rafting communities (Winston 1982a; Barnes and Fraser 2003; Kiessling et al. 2015). Bryozoans are also abundantly found in port, harbor, and vessel fouling communities (Connell 2000; Raveendran and Harada 2001; Yakovis et al. 2008). Fouling species colonizing floating materials may be particularly susceptible to both coastal and transoceanic transport (Watts et al. 1998).

The relative dominance of bryozoans in both rafted and fouling communities may also be due in part to their impressive variety of growth forms, each suited for differing substrate microhabitats, environmental conditions, and competitive strategies (Lidgard 1985; Ward and Thorpe 1989; Hageman et al. 2013). Thus, species exhibiting encrusting, one-dimensional planar growth often quickly exploit open space but are poor competitors, whereas arborescent species may rise above potential competitors but may be limited by their ability to withstand damage due to water motion (McKinney and Jackson 1991). Indeed, neustonic encrusting membraniporine bryozoans are among the first colonists on debris that enters the sea in the open ocean (as, for example, trash discards from ships); in

turn, these initially bryozoan-dominated communities may subsequently be dominated by gooseneck barnacles in the genus *Lepas* (Tsikhon-Lukanina et al. 2001).

Increasing concentrations of marine debris, assumed to largely originate from coastal zones, occur worldwide (Moore 2008; Cózar et al. 2014; Eriksen et al. 2014). Concomitantly, studies of rafted communities on this debris are on the rise but often are limited by a lack of information on where and when this debris entered the ocean (Goldstein et al. 2014; Kiessling et al. 2015). Large pulses of anthropogenic debris introduced into the ocean may occur through natural events such as monsoons, hurricanes, and tsunamis, potentially providing vastly increased habitat for biofouling organisms (Thiel and Hays 2006). The 2011 Tōhoku earthquake and tsunami was one such event in which a large debris field was ejected into the North Pacific Ocean (Carlton et al. 2017). Objects from the tsunami, accompanied by living and reproductively viable marine species from Japan, began washing ashore in 2012 in North America and the Hawaiian Islands.

We report here on Western Pacific bryozoans that arrived in the Central and Eastern Pacific Ocean attached to vessels, crates, buoys, ropes, and other Japanese Tsunami Marine Debris (JTMD) objects. Species arrived both dead and alive (the latter with intact polypides or brown bodies, as well as often being reproductively active with ovicells containing embryos). Unlike many free-living organisms that may have been lost after death, bryozoan skeletons often persist and thus provide greater insight into the potential diversity of rafted species, especially given that only a small fraction of the debris field was intercepted and biologically sampled (Carlton et al. 2017). We thus include species that we believe arrived dead (noting that some taxa that we place in this category may have died only after landing), given the possibility that the same species arrived alive on other debris not seen by us.

Materials and methods

Bryozoan samples were obtained from a wide variety of JTMD objects (identified as such through multiple lines of evidence; see Carlton et al. 2017) landing between 2012 and 2017 in North America and the Hawaiian Islands (Supplementary material Table S1). Each object was assigned a unique identification number preceded by JTMD-BF- (Japanese Tsunami Marine Debris-BioFouling-).

Bryozoan specimens (dried or in 95% ethanol) were found loose in samples, or were removed from their substrate with a scalpel, and placed in voucher collections. Images were taken using a Leica EZ4 HD

camera (Leica Microsystems, Wetzlar, Germany) and LAS EZ imaging software (Leica Microsystems, Wetzlar, Germany); measurements of zooidal characters were done using Fiji software (Schindelin et al. 2012). For scanning electron microscopy (SEM), specimens were cleaned in sodium hypochlorite solution, rinsed in tap water, and then placed in ethanol to prevent degradation during transport. Samples were then air dried and coated with Au-Pd using an Anatech USA Hummer 6.6 Sputtering System at 15mA (Anatech, Hayward, California, USA) and viewed under a JEOL JSM-7100FLV field emission scanning electron microscope (JEOL USA Inc., Peabody, Massachusetts, USA) at 5.0kV accelerating voltage. Images were retained as TIFF files. Species selected for SEM imaging included those presenting characters apparently distinct from published descriptions, those not extensively illustrated or well described already in the literature, and those not identified to species.

Voucher specimens were identified as “living” if the majority of zooids contained tissue, if not intact polypides, and note was made of any embryos present (suggesting reproductive activity at the time of death or sample preservation). Degenerated zooids (containing brown bodies) were considered in the context of the colony as a whole; thus, if brown bodies occurred but the majority of zooids were without tissue, the specimens were not counted as alive.

For summary statistics, diversity is defined as the number of species detected per object. Objects were grouped by item type (i.e., vessel, buoy/float, pontoon section, etc.). Species were grouped by growth habit and form after Amini et al. (2004).

Voucher collections will be deposited at the Royal British Columbia Museum (Victoria, Canada), along with the general JTMD archival collections.

Results

Species diversity and frequency

Forty-nine species of bryozoans (10 cyclostomes, 2 ctenostomes, and 37 cheilostomes) (Table 1) were found on 317 JTMD objects (Table S1), totaling 715 individual records. Three oceanic neustonic species (*Jellyella tuberculata* (Bosc, 1802), *Jellyella eburnea* (Hincks, 1891), and *Arbopercula angulata* (Levinsen, 1909)) were acquired in the transoceanic passage. Two species, *Membranipora villosa* Hincks, 1880 and *Pomocellaria californica* (Trask, 1857), were acquired on the Pacific coast of North America and, while treated below, were not included in the statistical summaries relative to the arrival of Western Pacific species in the Central and Eastern Pacific.

Over half of the sampled objects had one species of bryozoan, with few objects having more than 5 species (Figure 1). The majority of bryozoan records were from totes, crates, vessels, buoys, and floats (Table 2). Vessels presented the highest number of bryozoan species ($n = 62$ vessels; range 1 to 11 species; mean \pm SD 2.79 ± 2.26 species) with 40 percent of the vessels having three or more species originating from Japanese coastal waters. Two vessels, JTMD-BF-40 (landing in Washington in 2013) and JTMD-BF-23 (landing in Oregon in 2013), each had 11 species on them. Floating docks originating from Misawa, Japan (JTMD-BF-1 [landing in Oregon in 2012] and JTMD-BF-8 [landing in Washington in 2012]) had 6 and 5 species on them, respectively. Objects with lower species numbers (here shown as mean \pm SD) included miscellanea such as propellers, pots, and rope (45 objects; 1.87 ± 1.10 species); followed by baskets, boxes, crates, and totes (100 objects; 1.54 ± 0.78 species); buoys and floats (57 objects; 1.98 ± 1.69 species), and pontoon sections (5 objects; 2.00 ± 1.73 species). The lowest bryozoan diversity was found on Japanese post-and-beam-wood (9 objects; 1.11 ± 0.33 species). Interestingly, natural substrates in the form of Japanese trees (JTMD-BF-160 [Oregon, 2014], JTMD-BF-264 [Washington, 2014], and JTMD-BF-651 [Oregon, 2016]) and a log (JTMD-BF-42 [Oregon, 2016]) averaged 4.25 ± 3.20 (range 1 to 7) species.

The most common species, occurring on 75 percent and 28 percent of objects, were *Scruparia ambigua* (d'Orbigny, 1841) and those in the family Aeteidae, respectively. *Scruparia ambigua* was the only bryozoan present on 39 percent of objects. *Scruparia* and aeteids were recorded together from 33 objects that supported no other bryozoan species.

Four species (*Scruparia ambigua*, *Callaetia* sp., *Aetea anguina* (Linnaeus, 1758), and *Celleporella hyalina* (Linnaeus, 1767)) were found as epibiota of mobile invertebrates, such as the neustonic crab *Planes marinus* Rathbun, 1914 (JTMD-BF-40, -342), the caprellid amphipod *Caprella andreae* Mayer, 1890 (JTMD-BF-223), and even on the elytra (scales) of a polynoid polychaete (JTMD-BF-241) (Figure 2), indicating active reproduction and settlement was occurring in these bryozoan species.

Biogeography

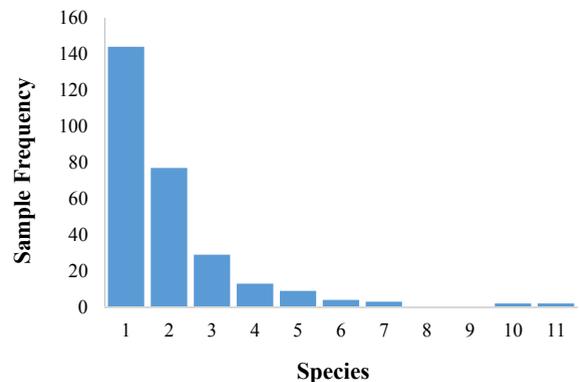
Of the 36 taxa resolved to species level, 18 species are known only from the Western Pacific and 15 are already recorded from North America (Table S2). *Schizoporella japonica* Ortmann, 1890 is regarded as an earlier introduction from Japan. Two species, *Callaetia* sp. and *Arbocuspis* sp. are undescribed. One

Table 1. Northwestern Pacific coastal Bryozoa found on JTMD arriving in the Hawaiian Islands and North America.

Order Cyclostomata	Scrupariidae	Cribrilinidae
Crisiidae	<i>Scruparia ambigua</i>	<i>Cribrilina mutabilis</i>
<i>Crisia cf. serrulata</i>	Electridae	Hippothoidae
<i>Crisia</i> sp.	<i>Arbocuspis</i> sp.	<i>Celleporella hyalina</i>
<i>Crisidia</i> sp.	<i>Conopeum nakanosum</i>	Exochellidae
<i>Filicrisia cf. franciscana</i>	Membraniporidae	<i>Exochella tricuspis</i>
Lichenoporidae	<i>Biflustra grandicella</i>	Lepraliellidae
<i>Disporella cf. novaehollandiae</i>	<i>Biflustra irregulata</i>	<i>Celleporaria brunnea</i>
Entalophoridae	<i>Biflustra cf. arborescens</i>	<i>Drepanophora cf. gutta</i>
? <i>Entalophora</i> sp.	<i>Membranipora villosa</i>	Romancheinidae
Oncosoeciidae	Calloporidae	<i>Escharella hozawai</i>
<i>Proboscina</i> sp.	<i>Callopora craticula</i>	Cryptosulidae
Stomatoporidae	<i>Cauloramphus spinifer</i>	<i>Cryptosula pallasiana</i>
<i>Stomatopora</i> sp.	<i>Cauloramphus</i> sp.	Microporellidae
Tubuliporidae	Bugulidae	<i>Fenestrulina cf. orientalis</i>
<i>Tubulipora misakiensis</i>	<i>Bugula tsunamiensis</i>	<i>Microporella borealis</i>
<i>Tubulipora pulchra</i>	<i>Bugulina stolonifera</i>	<i>Microporella luellae</i>
	Candidae	<i>Microporella neocriboides</i>
	<i>Tricellaria inopinata</i>	Schizoporellidae
Order Ctenostomata	Catenicellidae	<i>Schizoporella japonica</i>
Alcyoniidae	<i>Catenicella</i> sp.	Bitectiporidae
<i>Alcyonidium</i> sp.	Celleporidae	<i>Metroperiella cf. biformis</i>
Walkeriiidae	<i>Celleporina cf. globosa</i>	Smittinidae
<i>Walkeria prorepens</i>	<i>Celleporina porosissima</i>	<i>Smittidea spinigera</i>
	<i>Celleporina</i> sp. A	Watersiporidae
Order Cheilostomata	<i>Celleporina</i> sp. B	<i>Watersipora mawatarii</i>
Aeteidae	Phidoloporidae	<i>Watersipora cf. typica</i>
<i>Aetea anguina</i>	<i>Rhynchozoon</i> sp.	
<i>Callaetea</i> sp.		

species, *Bugula tsunamiensis* McCuller, Carlton and Geller, 2018, was described as a result of JTMD findings (McCuller et al. 2018). We regarded 13 species not taken to species level as from Japan based upon the objects they were on. In addition, no species unique to the Eastern Pacific were on these objects. We note two exceptions, *Pomocellaria californica* and *Membranipora villosa*, which were acquired after the JTMD objects on which they were found entered coastal waters of Western North America. Neither species occurred along with any of the 11 yet-to-be-resolved taxa that we suggest are from the Western Pacific.

Six species, *Conopeum nakanosum* Grischenko, Dick and Mawatari, 2007, *Cribrilina mutabilis* Ito, Onishi and Dick, 2015, *Microporella luellae* Grischenko, Dick and Mawatari, 2007, *M. neocriboides* Dick and Ross, 1988, *Callopora craticula* (Alder, 1856) and *Watersipora mawatarii* Vieira, Spencer Jones and Taylor, 2014, were previously recorded from Hokkaido (and, for *M. neocriboides*, Alaska as well). Virtually all JTMD objects appear to have departed the Tōhoku coast of northeast Honshu by either travelling east or south, rather than moving into colder northern waters (Carlton et al. 2017; N. Maximenko, personal communication, January 2017). Indeed, the objects bearing *C. nakanosum* and *W. mawatarii* also bore warmer-water southern species

**Figure 1.** Frequency distribution of bryozoan species detected on Japanese tsunami marine debris samples.

of other bryozoans. It thus may be that these 5 species occur on the northeast Honshu coast, just south of Hokkaido, or further south. We found one species, the cheilostome *Escharella hozawai* (Okada, 1929), which appears to have been last collected in northernmost Honshu in the 1920s. We newly report *Biflustra cf. arborescens* (Canu and Bassler, 1928) from the Western Pacific Ocean.

Table 2. Bryozoan records on Japanese tsunami marine debris biofouling by object type. Neustonic species (*Jellyella eburnea*, *J. tuberculata*, *Arbopercula angulata*) and Northeast Pacific acquisition species (*Membranipora villosa*, *Pomocellaria californica*) are not included in calculations.

Item type	Number of objects	Number of bryozoan records (all species combined)	Percentage (%)
<i>totes, crates, or other containers</i>	100	154	26.97
<i>vessels</i>	62	173	30.00
<i>buoys, floats</i>	57	112	19.61
<i>other items</i>	45	84	14.71
<i>post and beam wood</i>	9	10	1.75
<i>trees/logs</i>	4	17	2.98
<i>pontoon sections</i>	5	10	1.75
<i>Misawa docks</i>	2	11	1.93
TOTAL	284	571	100%

Seven additional species, *Metroperiella* cf. *biformis* (Zhang and Liu, 1995), *Celleporaria brunnea* (Hincks, 1884), *Drepanophora* cf. *gutta* Tilbrook, Hayward and Gordon, 2001, *Smittoidea spinigera* (Liu, 1990), *Biflustra grandicella* (Canu and Bassler, 1929), *Biflustra irregulata* (Liu, 1991), and *Celleporina* cf. *globosa* Liu, 2001, are not known from Japan. We suggest that these species were acquired by JTMD as these objects were carried south of Japan, and prior to the objects being then transported by ocean currents back north and east to the Central and Eastern Pacific. Alternatively, it may be that with warming climates, some of these species may have moved poleward in recent decades. As we note in Table S2, *Celleporaria brunnea* is regarded as introduced from North America to South Korea. While 3 of the 4 objects upon which *C. brunnea* occurred also supported additional southern species of bryozoans or bivalves, its presence on JTMD may also indicate that it has now spread north to Japanese waters and is yet undetected there as a range expansion.

Growth Form

Over half (56%) of the species observed exhibited encrusting-unilaminar or multilaminar colony growth forms. The remaining species represented erect-flexible (19%), erect-foliose (11%), or creeping (11%) forms. Despite their low diversity, creeping forms comprised the majority (60%) of records, followed by erect-flexible-articulated-branching (12%) and encrusting-unilaminar (10%) forms. One species with erect-rigid-foliose form (*Biflustra grandicella*) developed massive colonies on two objects, a buoy landing in Oregon in 2014 (JTMD-BF-216) and a buoy washing ashore in Oregon in 2016 (JTMD-BF-531; Figure S8F), sized 112.5 cm² and 363.6 cm², respectively.

Live-dead status and reproduction

Many species were represented by mixed live or dead colonies depending upon the particular object

and when and where it landed. Seven species were only represented by living colonies (*Catenicella* sp., *Crisia* sp., *Entalophora* sp., *Fenestrulina* cf. *orientalis* Liu, Liu and Sun, 2003, *Metroperiella* cf. *biformis*, *Watersipora mawatarii*, and *Watersipora* cf. *typica* (Okada and Mawatari, 1937)).

Nineteen species were represented only by dead colonies (*Arbocuspis* sp., *Biflustra irregulata*, *Callopora craticula*, *Cauloramphus spinifer* (Johnston, 1832), *Cauloramphus* sp., *Celleporaria brunnea*, *Celleporina porosissima* Harmer, 1957, *Celleporina* sp. A, *Celleporina* sp. B, *Celleporina* cf. *globosa*, *Conopeum nakanosum*, *Cribrilina mutabilis*, *Crisidia* sp., *Drepanophora* cf. *gutta*, *Membranipora villosa*, *Microporella luellae*, *Microporella neocriboides*, *Rhynchozoon* sp., and *Stomatopora* sp.).

Brooding species that were alive and with embryos included *Bugula tsunamiensis*, *Celleporella hyalina*, *Crisia* sp., *Escharella hozawai*, *Exochella tricuspis* (Hincks, 1881), *Fenestrulina* cf. *orientalis*, *Metroperiella* cf. *biformis*, *Schizoporella japonica*, *Scruparia ambigua* and *Tricellaria inopinata* d'Hondt and Occhipinti Ambrogi, 1985.

Systematic Account

Class Stenolaemata Borg, 1926
Order Cyclostomata Busk, 1852
Suborder Articulina Busk, 1859
Family Crisiidae Johnston, 1838

Crisia cf. *serrulata* Osburn, 1953 (Figure S1A)

Material.—JTMD-BF-208, 423, 667, 677.

Remarks.—This bryozoan resembles the Northeast Pacific *Crisia serrulata* known from British Columbia and south, in having 12–30 alternating zooids per internode merged almost to the aperture, which is turned forward, facing frontally, with a short spinous process on its outer margin (Soule et al. 1995).

A similar species, *Crisia maxima* Robertson, 1910, has zooids connate to a lesser extent and lacking, or without regular appearance, of the short spinous process (Osburn 1953; Soule et al. 1995). Our material consists of a few fragments, internodes averaging 21 zooids, with zooids as described for *C. serrulata*. While no *Crisia* species from the Western Pacific is known to possess internodes with this number of zooids, we presume this species is from Japan. The JTMD objects on which this species occurred bore no evidence of species unique to the Eastern Pacific. As no gonozooids were present in the material in hand, we were hesitant to confidently assign these specimens to a species.

Distribution.—British Columbia to Mexico (Osburn 1953; Soule et al. 1995) and the Galapagos (Osburn 1953).

***Crisia* sp.**

(Figure S1B, C)

Material.—JTMD-BF-538.

Remarks.—These colonies closely match *Crisia operculata* Robertson, 1910, known from British Columbia to Panama. Most notably, our material includes gonozooids with oocystostomes bearing a cap-like projection overarched the aperture, a characteristic of this species. This specimen arrived on a vessel which bore no evidence of other bio-fouling species acquired in the Eastern Pacific; thus, the material in hand may represent a similar species of *Crisia* from the Western Pacific.

***Crisidia* sp.**

Material.—JTMD-BF-208.

Remarks.—Our material was a small fragment consisting of few internodes with one zooid and segmented spine per internode. It is most similar to *Crisidia cornuta* (Linnaeus, 1758), but differs from that species in that new internodes arise laterally, as opposed to dorsally, from the zooids. *C. cornuta*, an almost certain species complex, is reported as a widespread species in Northern Hemisphere waters, including Japan (Mawatari 1981).

***Filicrisia* cf. *franciscana* (Robertson, 1910)**

(Figure S1D)

Material.—JTMD-BF-23, 40, 139, 205, 210, 264, 329.

Remarks.—*Filicrisia franciscana* and *Filicrisia geniculata* (Milne Edwards, 1838) are nearly identical with the exception of the morphology of the oocyst (Osburn 1953), which our material (which may represent two taxa) lacks. Colonies (BF-23, measurements based upon 10 zooids) may form delicate tufts

Figure 2. JTMD species growing on neustonic mobile species. (A) *Callaetia* sp. on leg of neustonic crab *Planes marinus*, JTMD-BF-342. (B) *Scruparia ambigua* on caprellid amphipod *Caprella andreae*, JTMD-BF-223. (C) Two colonies of *Celleporella hyalina* encrusting leg segments of *Planes marinus*, JTMD-BF-40. Photographs by M. I. McCuller.

of long (ca. [mean \pm SD] 0.77 ± 0.13 mm), slender (ca. 0.09 ± 0.01 mm) zooids. Colonies from JTMD-BF-40, based upon measurements of 7 zooids) were

larger in zooid length (ca. 1.01 ± 0.14 mm) and diameter (ca. 0.11 ± 0.02 mm). Colonies from all samples exhibit similar growth patterns, with one zooid per sterile internode, from which originates a branch on either side, and black or dark-brown joints. Japanese literature uses the name *F. franciscana* (Okada 1928; Mawatari 1955). *Filicrisia geniculata*, although reported from British Columbia to southern California, is a North Atlantic species that requires re-assessment as to its presence in the Northeast Pacific (Soule et al. 2007).

An unidentified *Filicrisia* species was recorded from North Pacific plastic rafting communities by Goldstein (2014). Osburn (1953) noted that *F. franciscana* can be found as a fouling species in “considerable masses” on pilings and floats. None of the examined objects bore evidence of any additional encrusting invertebrate species having been acquired in the Northeast Pacific, and thus we assume that these colonies originated from the Western Pacific Ocean.

Distribution.—Japan: Mutsu Bay (Okada 1928; Mawatari 1955); Northeast Pacific from Alaska to Baja California (Osburn 1953; Soule 1963).

Suborder Rectangulata
Family Lichenoporidae Smitt, 1867

***Disporella* cf. *novaehollandiae* (d’Orbigny, 1853)**
(Figure S2A–C)

Material.—JTMD-BF-23, 160, 290, 667, 679.

Remarks.—*Disporella novaehollandiae* was redescribed by Gordon and Taylor (2001) from New Zealand in their attempt to resolve taxonomic problems within recent cyclostomes. This species has been recorded in Japan (Ortmann 1890; Sakakura 1935) as *Lichenopora novae-zelandiae* (Busk, 1875), although many Japanese records lack adequate descriptions or illustrations. Our material agrees with the account of Gordon and Taylor (2001) in zooid formation, brood-chamber morphology, and presence of spiny pinhead spinules within autozooid and kenozooid interiors (Figure S2C). Iris-like diaphragms were present in some colonies. A small ledge within the opening of the oeciostome was observed in one of the two mature colonies. In both mature colonies, the oeciostome occurred at the distal end of a brood-chamber lobe situated between autozooidal radii (Figure S2B), a character apparently not typical of this species, but similar to that of the specimen illustrated by Osburn (1953) in which the oeciostome is in the macular center. According to Gordon and Taylor (2001), placement of the oeciostome is adjacent to the central autozooid of a radii. However, they mention Gordon and Parker’s (1991) account of

Disporella victoriensis MacGillivray, 1884 (as *Lichenopora victoriensis*) from Australia, in which the oeciostome is in the same location as the present material, although this character is also not typical of *D. victoriensis*. Despite the location of the oeciostome, presence of the internal ledge suggests our material is *D. novaehollandiae*. More extensive analyses, including genetics work, are likely needed to determine the placement of *D. novaehollandiae*-like specimens with atypical oeciostome location. The variability in size of colonies and their abundance on several JTMD objects suggests that they were of Japanese origin and subsequently produced larvae that settled immediately to form new colonies nearby. Multiple specimens were epizoic on Japanese-origin mussels, *Mytilus galloprovincialis* Lamarck, 1819 along with cheilostomatous and other cyclostomatous bryozoans.

Whether Eastern Tropical Pacific and Hawaiian populations represent the true *D. novaehollandiae* bears further study.

Distribution.—Japan (Ortmann 1890; Sakakura 1935), Indian Ocean, New Zealand and Australia (Gordon and Taylor 2001; Gordon and Mills 2016), southern California to Colombia and the Galapagos Islands (Osburn 1953; Soule 1963); Hawaiian Islands (Soule et al. 1987).

Suborder Tubuliporina
Family Entalophoridae Reuss, 1869

? *Entalophora* sp.
(Figure S3A, B)

Material.—JTMD-BF-667.

Remarks.—As we are uncertain of the generic assignment, we place a question mark in front of the genus name. The encrusting portion is tubuliporine, but rises up to form branches with zooids arranged around the stem. One gonozooid is present at a branch bifurcation, with its oeciostome present at the base of a zooid.

Family Oncousoeciidae Canu, 1918

***Proboscina* sp.**

Material.—JTMD-BF-139, 160, 205.

Remarks.—The encrusting, branching nature of our specimens and the presence of an oecia at the distal end of a branch suggest their placement within *Proboscina*. However, the free portion of zooids is much raised from the zoarium, a character not typically ascribed to this genus, which may be due to the wide range of environmental conditions faced. To that end, we do not feel comfortable proceeding with a species identification pending further material.

Family Stomatoporidae Pergens and Meunier, 1886

***Stomatopora* sp.**
(Figure S3C, D)

Material.—JTMD-BF-667.

Remarks.—Our material is uniserial, consisting of zooids creeping over barnacle and bivalve shells. Growth is similar to the cheilostome genus *Aetea* (below), which has an adnate and erect portion, but is different than that group in the extent of calcification and presence of numerous pseudopores characteristic of cyclostomes. No gonozooids were present in this material.

Family Tubuliporidae Johnston, 1838

***Tubulipora misakiensis* Okada, 1917**
(Figure S4A, C)

Material.—JTMD-BF-23, 197, 210, 449, 661, 667.

Remarks.—The present material matches *Tubulipora misakiensis* on the basis of flabelliform colonies, zooecia length with distal two-thirds or more free, a highly inflated ooecia and vertical or “recurved” ooeciostome (often broken off in our specimens) with a small, circular ooeciopore that was often broken. Primary disks present (in JTMD-BF-23) were circular and smooth.

Distribution.—Japan: Mutsu Bay (Okada 1929) and Hokkaido (Mawatari and Mawatari 1974).

***Tubulipora pulchra* MacGillivray, 1885**
(Figure S4B, C)

Material.—JTMD-BF-23, 160, 425.

Remarks.—*Tubulipora pulchra* was originally described from Australia and has since been recorded worldwide, including Japan. It is most notable for the toothed primary disc and flared ooeciostome, both characters that our material shares with this species. This is doubtless a global species complex.

Distribution.—In the Pacific theater, Japan (Okada 1928; Mawatari and Mawatari 1974), China (Liu et al. 2001), South Korea (Rho and Seo 1986), and British Columbia to Galapagos Islands (Osburn 1953).

Class Gymnolaemata Allman, 1856

Order Ctenostomata Busk, 1852

Suborder Alcyonidiina d'Hondt, 1985

Family Alcyonidiidae Johnston, 1838

***Alcyonidium* sp.**

Material.—JTMD-BF-40, 43, 347, 548, 589, 592, 615.

Description.—Colony rough, encrusting, thin (JTMD-BF-40, 347, 548, 592, 615) or thick and multilaminar (JTMD-BF-43, 589) with a firm chitinous outer

layer. Color unknown in life; in spirit, white/beige (JTMD-BF-43; preserved in formalin) to brown (BF-40, 347; preserved in 95% EtOH). Zooids oval to hexagonal with orifice at distal end of long peristome, polypides with approximately 18 tentacles. Small kenozooids numerous, dispersed across the surface; basal layers composed of large, empty, elongated kenozooids giving the colony an overall spongy texture.

Remarks.—Our material is similar to *Alcyonidium sagamianum* Mawatari, 1953 described from Kanagawa Prefecture in having the central part of the zoarium filled with empty kenozooids. However, in *A. sagamianum* the colony form is erect and branching while our specimens consist of a substantial crust over the stalks and valves of a gooseneck barnacle, *Lepas* sp., or surrounding hydroid stolons (JTMD-BF-43, 589, respectively) or as a unibilaminar sheet (JTMD-BF-40, 347, 548, 589, 615). The long peristome is shared with that of *Alcyonidium mammillatum* Alder, 1857, recorded from Japan by Silén (1941), but is more likely a species restricted to the North Atlantic Ocean. Our specimens do not appear to correspond closely to any species of *Alcyonidium* documented from Japan or the Pacific coast of North America. The genus *Alcyonidium* requires review and revision in the North Pacific (Ryland and Porter 2013).

Suborder Stoloniferina Ehlers, 1876

Family Walkeriidae Hincks, 1880

***Walkeria prorepens* Kubanin, 1992**
(Figure S5)

Material.—JTMD-BF-8, 40, 50, 131, 168, 344, 363, 383, 386, 405, 406, 408, 411, 412, 465, 469, 471, 472, 473, 474, 475, 640, 649.

Remarks.—*Walkeria prorepens* is a delicate, easily overlooked, creeping bryozoan. *Walkeria uva* (Linnaeus, 1758), a global species complex, differs from *W. prorepens* in its zooid budding locations and symmetry: the former has a pair of zooids budding laterally from internodes, while the latter buds one zooid per internode on its dorsal side. In our JTMD samples *W. prorepens* was found growing on substrates amongst filamentous algae, hydroid stolons, and other fouling organisms. Our material closely aligns with that of Kubanin (1992) from the Sea of Japan, although only some colonies were in sufficient condition to permit observations on growth pattern. Material of *W. uva* described and illustrated by Mawatari (1952) from Kii Peninsula may represent *W. prorepens*.

Distribution.—Japan: Kii Peninsula? (Mawatari 1952, as *W. uva*), Japan Sea (Kubanin 1992).

Order Cheilostomata Busk, 1852
Suborder Inovicellina Jullien, 1888
Superfamily Aeteoidea Smitt, 1867

Family Aeteidae Smitt, 1868

Material.—JTMD-BF-139, 156, 168, 196, 198, 201, 202, 209, 210, 212, 216, 222, 223, 224, 240, 253, 304, 329, 333, 337, 338, 340, 344, 352, 353, 366, 367, 379, 382, 383, 384, 386, 389, 391, 398, 406, 408, 413, 414, 422, 435, 437, 449, 463, 495, 532, 533, 534, 536, 538, 555, 574, 625, 626, 636, 637, 645, 659, 667.

Remarks.—We recognized both *Aetea anguina* and *Callaetea* sp. in the above JTMD samples, but did not distinguish between the two species in most of our material.

***Aetea anguina* (Linnaeus, 1758)**

(Figure S6A, B)

Material.—JTMD-BF-18, 23, 40, 82, 226, 668, 670, 679.

Remarks.—Two species of *Aetea*, *A. anguina* and *A. truncata* (Landsborough, 1852), have been recorded from Japan, the former from Kii Peninsula to Mutsu Bay (Okada 1929; Mawatari 1956) and the latter from Tanabe, Wakayama Prefecture and Toyoma Bay (Sakakura 1935; Okada and Mawatari 1938). Our material closely corresponds to that of *A. anguina* based on the delicate, bent zooids that have an annulated erect stalk and a punctate adnate portion; colonies were mostly found creeping along a variety of substrates, but occasionally as epibionts on the carapace of neustonic crabs (*Planes marinus*; JTMD-BF-40). *A. anguina* may represent a global species complex, with the complication that members of this group may also have been dispersed for centuries in ship fouling communities.

Distribution.—Considered “cosmopolitan” in both cold and warm seas (Osburn 1950, and many later workers).

***Callaetea* sp.**

(Figure 2A; Figure S6C, D)

Material.—JTMD-BF-8, 131, 134, 170, 208, 227, 229, 230, 255, 264, 339, 342, 349, 356, 387, 402, 405, 514, 521, 638, 648, 661.

Description.—Colony lightly calcified, delicate, creeping along substrate or rising above to form tangled masses. From narrow kenozooidal stolons bud lateral stolons irregularly and zooids; basal side of zooid may also bud stolons. Zooids scoop-shaped, curved (ca. 0.434 mm ± 0.064 mm long by 0.087 mm ± 0.008 mm wide); frontal membrane elongate (ca. 0.279 mm ± 0.042 mm) and narrow (ca. 0.038 mm ± 0.017 mm), curvature of the zooid orientating the

frontal membrane obliquely in relation to the plane of the stolon.

Remarks.—The only previously reported species of *Callaetea* Winston, 2008 occur in the Mediterranean Sea. Our specimens match this genus in having zooids budded from delicate kenozooidal stolons, but differ from *Callaetea lileacea* Winston, 2008 in the extent of the frontal membrane and in the direction of the frontal membrane. Additionally, while still very delicate, our specimens appear to be more highly calcified than *C. lileacea*. In that species, SEM photos were not possible as drying the specimens caused them to fall apart (Winston 2008). We also observed zooids that budded kenozooidal stolons from the basal side, not noted in the description of *C. lileacea*. These differences suggest a new species of *Callaetea*. We are grateful to L. M. Vieira for pointing out to us that our material more closely matches (and represents a new taxon in) *Callaetea*, rather than *Aetea truncata*.

Suborder Scrupariina Silén, 1941
Superfamily Scruparioidea Gray, 1848
Family Scrupariidae Busk, 1852

***Scruparia ambigua* (d’Orbigny, 1841)**

(Figure 2B; Figure S6E, F)

Material.—JTMD-BF-1, 2, 6, 8, 12, 17, 18, 23, 28, 29, 30, 31, 36, 38, 39, 40, 42, 43, 50, 53, 58, 71, 80, 82, 129, 131, 134, 135, 139, 142, 149, 154, 168, 170, 171, 176, 177, 188, 196, 198, 199, 201, 202, 205, 208, 210, 211, 215, 216, 222, 223, 224, 225, 226, 227, 228, 229, 230, 232, 233, 240, 241, 242, 250, 253, 254, 255, 264, 277, 282, 283, 288, 304, 305, 306, 328, 329, 331, 334, 337, 338, 339, 340, 342, 343, 344, 348, 349, 352, 353, 354, 356, 361, 363, 365, 366, 367, 369, 372, 377, 379, 380, 382, 383, 384, 387, 388, 389, 390, 391, 393, 396, 398, 400, 402, 404, 405, 406, 408, 409, 410, 412, 413, 414, 415, 417, 422, 425, 426, 427, 428, 429, 435, 436, 437, 447, 455, 457, 458, 460, 463, 464, 465, 466, 469, 470, 471, 472, 474, 475, 476, 495, 498, 503, 504, 505, 508, 514, 515, 518, 521, 526, 529, 531, 532, 533, 534, 538, 546, 547, 548, 549, 551, 553, 555, 563, 564, 565, 567, 569, 570, 571, 572, 573, 574, 575, 576, 577, 578, 579, 580, 581, 582, 583, 585, 586, 587, 588, 589, 590, 591, 594, 595, 596, 597, 599, 604, 605, 607, 614, 616, 617, 623, 625, 626, 628, 631, 632, 634, 635, 636, 637, 640, 645, 648, 649, 651, 652, 653, 657, 659, 661, 663, 668, 671, 677, 679, 699.

Remarks.—*Scruparia ambigua* is the most frequent and abundant bryozoan on JTMD. While considerable variation in size occurs in our material, all specimens have branches which arise from recumbent, creeping zooids and ovicells that occur on a slightly-reduced

opesia, in contrast to a similar species, *Scruparia chelata* (Linnaeus, 1758), a species with stolons and an ovicell with a much-reduced opesia (Osburn 1950). *Scruparia* broods few short-lived lecithotrophic larvae, which suggests localized recruitment and thus may explain their abundance in JTMD samples (Raffert 1994; Banta et al. 1995). Creeping zooids were found covering hydroid stolons and other bryozoans, producing erect zooid chains. Additionally, as noted earlier, *S. ambigua* was encountered growing on mobile species such as the neustonic crab *Planes marinus* (JTMD-BF-40, 342), caprellid amphipods (JTMD-BF-223; Figure 2B), and the elytra of polynoid worms (JTMD-BF-241), suggesting that it may not be as space-limited as other bryozoan species.

Scruparia ambigua was described from the Falkland Islands in the South Atlantic Ocean in the first half of the 19th century; the name has since been applied, ambiguously, to *Scruparia* populations in almost all oceans (Osburn 1950; Orensanz et al. 2002; Floerl et al. 2009). *S. ambigua* thus likely represents a global complex requiring genetic insight, and North Pacific populations may prove to require a distinct name. Although known as a fouling organism on buoys (McCauley et al. 1971; Relini et al. 2000) and other substrates (Haderlie 1969; Gordon and Mawatari 1992; Ferreira et al. 2006), and while clearly capable of ocean rafting as a biofouler (present study), it is rarely reported from ship hull fouling (WHOI 1952) although it may be frequently overlooked in such communities where larger macrobiota are often the focus.

The often extensive colonies of *Scruparia* on JTMD (typically too abundant to have both colonized and grown robustly in the short time after debris appeared to arrive and reside in North American waters prior to shore landing), its nearly ubiquitous nature, its occurrence on many JTMD objects that bore no evidence of having been colonized by any other Eastern Pacific species, and its apparently rare presence (below) in the Pacific Northwest all suggest that the *Scruparia* originated from Japan. Moreover, we have examined a number of marine debris items that washed ashore in Oregon after being adrift in the nearshore ocean (as evidenced by *Lepas* sp. colonization) that indicate (by their identification marks and by their other biofouling) that they originated in the Pacific Northwest. None of these were found to bear *Scruparia*.

Distribution.—Reported worldwide, as noted above. Recorded from Honshu, Japan by Mawatari (1973). At the time of Osburn's (1950) monographic review of anascan bryozoans of the Pacific Coast of North America, *S. ambigua* was reported in the temperate northeast Pacific only from Vancouver Island and southern California, such that it was omitted both

from Soule et al.'s (2007) treatment of the intertidal and shallow water Bryozoa from Point Conception to the Oregon coast, as well as Bergey and Denning's (1996) summary of Bryozoa of the Pacific Northwest. However, *S. ambigua* was found to be a member of the fouling community (to a depth of 46 m) on an oceanographic monitoring buoy anchored 55 km off the coast of northern Oregon (McCauley et al. 1971), and on fouling panels deployed in shallow water of Monterey Harbor, in Monterey Bay, central California (Haderlie 1969), as well as being reported from fouling communities in San Francisco Bay (California Academy of Sciences Invertebrate Zoology collections, online database accessed December 2016). The rare report of *S. ambigua* (if correctly identified) on a buoy in Oregon, given its short-term larvae, is of interest; it may have been able to arrive offshore via algal rafting (McCauley et al. 1971).

Suborder Malacostegina Levinsen, 1902
Superfamily Membraniporoidea Busk, 1854
Family Electridae d'Orbigny, 1851

***Arbocuspis* sp.**
(Figure S7A–D)

Material.—JTMD-BF-173, 207, 216, 237, 239, 338, 481, 567, 586.

Description.—Zoarium lightly calcified, growing directly on plastic (JTMD-BF-239) or on shells. Zooids small (ca. 0.39 mm long and 0.18 mm wide) with regular, quincuxal arrangement; teardrop-shaped, widest at distal ends. Opesia occupies one third to one half of zooid length. Membrane covering the entire frontal area, thus the frontal calcification is cryptocystal in nature, smooth, approximately 1/3 zooid length proximally, with one to three robust spines projecting out over opesia. The single proximal spine occasionally elongated with a bifurcated tip as if two small spines merged together (Figure S7D); however, branched tips were not evident in the current material. Descending portion of cryptocyst pustulose, extending around entire opesia, widest proximally, forming a median process, and steeply sloping inwards. Basal edge of lateral walls with three small multiporous plates and transverse walls with many uniporous septula along the basal edge (Figure S7C).

Remarks.—JTMD material agrees with Liu et al.'s (2001) description of *Arbocuspis bellula* (Hincks, 1881) (as *Electra bellula*, based on Chinese populations). Leandro Vieira has kindly confirmed our suspicion that Liu's material (and thus our JTMD populations) represent an undescribed species (L. M. Vieira, personal communication, 2017). *A. bellula*, described from Australia and subsequently reported

throughout the Indian, Pacific, and Atlantic Oceans (Winston 1982b; Gordon et al. 2007) is a widespread tropical and subtropical species complex (Vieira et al. 2016).

Distribution.—South China Sea (Liu et al. 2001 as *A. bellula*).

***Arbopercula angulata* (Levinsen, 1909)**
(Figure S7E, F)

Material.—JTMD-BF-8, 23, 207, 240, 304, 338, 341, 362, 371, 374, 375, 379, 380, 391, 400, 406, 414, 425, 428, 523, 530, 553, 571, 586, 587, 653, 687.

Remarks.—Skeletal characteristics of our material agree with the description of *Arbopercula angulata* by Mawatari (1953, as *Electra angulata*). We follow Tilbrook et al. (2001) in referring Pacific populations to *A. angulata* rather than the Atlantic *Arbopercula tenella* (Hincks, 1880), the latter name also used for Japanese populations by Mawatari (1974) and Kubota and Mawatari (1985). Mawatari (1952) earlier noted that the ancestrula and operculum of *A. angulata* differ from that of *A. tenella*. The descriptions of Japanese populations align most closely with those of Levinsen (1909) and Harmer (1926) for *A. angulata* rather than those of Hincks (1880) for *A. tenella*.

Distribution.—Thailand (Levinsen 1909); Japan (Mawatari 1953; Long and Rucker 1969); South Korea (Seo and Min 2009); North Pacific rafting communities (Tsikhon-Lukanina et al. 2001; Goldstein et al. 2014).

***Conopeum nakanosum* Grischenko, Dick, and Mawatari, 2007**
(Figure S8A, B)

Material.—JTMD-BF-338.

Remarks.—Characteristics of a small, dead colony fragment agree with *Conopeum nakanosum* in possessing a pair of distal kenozooids. Our specimen was found in association with Aeteidae, *Arbocuspis* sp., *Biflustra grandicella*, and *Arbopercula angulata* on a pallet. This *Conopeum* colony was overgrown by the southern species *Biflustra grandicella*.

Distribution.—Japan: Hokkaido (Grischenko et al. 2007).

Family Membraniporidae Busk, 1852

***Biflustra grandicella* (Canu and Bassler, 1929)**
(Figure S8C–F)

Material.—JTMD-BF-18, 160, 173, 208, 216, 241, 318, 338, 404, 512, 531, 567.

Remarks.—While large multilaminar colonies were present on some JTMD material, *B. grandicella*

occurred primarily as smaller portions of colonies. The largest masses measured 112.5 cm² and 363.6 cm² on JTMD-BF-216 (a buoy) and JTMD-BF-531 (a buoy; Figure S8F), respectively. This is a relatively easily recognized species due to the large zooids and the row of uniporous septula that runs along the midline of transverse walls. Colonies were composed of zooids with both granular and smooth cryptocysts depending on the extent of calcification. Some JTMD specimens had spines projecting into the opesia as noted by Liu et al. (2001). Two samples, JTMD-BF-208 and 216, had specimens with a proximomedian process or spines similar to that of *Biflustra savartii* (Audouin, 1826) or *Biflustra conjunctiva* (Zhang and Liu, 1995), but the septula on the transverse and lateral walls align more closely with those of *B. grandicella*.

Distribution.—South China Sea (Liu 1992; Liu et al. 2001); recently reported as an invasion in New Zealand and Australia (Tilbrook 2012) and in Brazil (Almeida et al. 2017).

***Biflustra irregularata* (Liu, 1991)**
(Figure S9A, B)

Material.—JTMD-BF-215, 237, 239, 240, 264, 378, 533.

Remarks.—While most of our material was dead with little remaining tissue, colony and zooid morphology (in particular distinctive irregularly-shaped zooids) most closely resemble *Biflustra irregularata*. Present in all specimens were distinct brown chitinous lines running through the interzooidal grooves, as noted by Liu (1992) and Seo and Min (2009); this character is also present in *Biflustra arborescens* (Canu and Bassler, 1928) (Almeida et al. 2017), which, however, has oval-rectangular zooids and a beaded mural rim. One characteristic of *B. irregularata* not observed was chitinous spines on the frontal membrane; Taylor and Tan (2015)'s Malaysian material also lacked spines. This species has been observed encrusting a wide variety of substrates, including mollusk shells, gorgonians, corals, stones, and plastic (Liu 1992; Seo and Min 2009), but may also foul buoys, cables, nets, and cages (Liu et al. 2001). Powell (1971, below) found it on wharf pilings, floats, navigation buoys, and rocks; Taylor and Tan (2015) report it from oyster rafts and gastropod shells.

Reports of *B. arborescens* from the tropical Eastern Pacific likely represent *B. irregularata*. Banta and Carson (1977) described their material from Costa Rica as possessing “about 30 cuticular spinules” on the frontal membrane, zooids “sometimes distorted in shape”, and zooids surrounded by brown lines,

characteristics which, combined, are those of *B. irregulata*, not *B. arborescens*. *Biflustra irregulata* was not described when Banta and Carson (1977) and, earlier, Powell (1971), both studying material from the Pacific coast of Panama, were considering potential membraniporid candidates.

Distribution.—Central Indo-Pacific: Bohai Bay (Yellow Sea) and South Korea through the East China Sea and the South China Sea (Liu 1992; Liu et al. 2001; Seo and Min 2009); Indian Ocean: Penang, Malaysia (Taylor and Tan 2015) and Cox's Bazaar, Bangladesh, Bay of Bengal (Gordon et al. 2007). Vieira et al. (2016) questioned Taylor and Tan's identification of *B. cf. irregulata* from Malaysia, but Almeida et al. (2017) restored and accepted the identification. Eastern Pacific: Costa Rica (Banta and Carson 1977, as *Membranipora arborescens*); Panama (Powell 1971, as *M. arborescens*), and the Galapagos (Banta and Redden 1990, as *M. arborescens*, citing Banta and Carson 1977). Southwest Atlantic: Bahia State, Brazil (Almeida et al. 2007).

***Biflustra cf. arborescens* (Canu and Bassler, 1928)**

(Figure S9C–F)

Material.—JTMD-BF-80, 131, 369, 380, 543.

Description.—Colony encrusting, uni- to multi-laminar. Zooids rectangular, slightly rounded at the distal end, arranged in quincunx, separated by slightly raised, thin lateral walls and a brown chitinous line. Opesia elongate, narrower at the proximal end, occupying majority of frontal surface; mural rim pustulose; cryptocyst narrow, granular, sometimes forming triangular tubercles at the proximal corners; gymnocyst lacking. Two opercula: primary operculum longer than wide, brown and chitinous; secondary operculum smaller, longer than wide, pointing proximally and slightly overlapping primary operculum. Basal side of transverse wall with two large multiporous septula; lateral walls with four large multiporous septula.

Remarks.—Our specimens closely align with that of *Biflustra arborescens* (L.M. Vieira, personal communication, 2017), but have four large multiporous septula (Figure S9F) while *B. arborescens* is described as having two multiporous septula (Almeida et al. 2017). One unique characteristic observed in the present material is the presence of a secondary operculum, distal to the primary operculum and pointed proximally, its tip just overlapping the primary operculum's distal edge.

Distribution.—West Atlantic: New England to Florida (Winston 1982b; Winston and Hayward 2012) and Brazil (Almeida et al. 2017); East Atlantic: Portugal (Souto et al. 2014).

***Jellyella eburnea* (Hincks, 1891)**

(Figure S10A, B)

Material.—JTMD-BF-17, 35, 49, 96, 144, 145, 207, 209, 212, 223, 226, 227, 253, 304, 329, 339, 341, 363, 367, 383, 392, 408, 410, 411, 413, 415, 428, 524, 527, 530, 533, 536, 555, 556, 557, 558, 566, 570, 572, 574, 581, 583, 585, 590, 598, 645, 649, 652, 653, 659, 668, 669, 670, 671, 672.

Remarks.—*Jellyella eburnea* is a neustonic species typically found on plastic marine debris (Thiel and Gutow 2005; Goldstein et al. 2014), on floating algae, and on the shells of bubble-rafting *Janthina* snails or the dead shells of *Spirula* squid (Taylor and Monks 1997). Colonies occurred commonly on buoys and other plastic JTMD items, as well as being a member of the epibiota of the common JTMD mussel *Mytilus galloprovincialis*. Our material shows considerable variation in the gymnocystal structures, ranging from a low-lying ruffled shelf to a high shield of tubercle or spine-like processes. Occasionally the gymnocyst resembles that of congener *Jellyella tuberculata*. Some reports of *J. tuberculata* in tropical locales may represent *J. eburnea*.

Distribution.—A warmer-water species widely distributed, as expected for an open ocean neustonic species, but whether consisting of multiple isolated clades that may in fact compose cryptic species is not known. Australasia, Indo-Pacific (Gordon et al. 2007), Northwest Pacific, Malaysia (Taylor and Tan 2015); South Africa (Taylor and Monks 1997); West Atlantic: Florida (Winston 1982b, as *Membranipora* sp.).

***Jellyella tuberculata* (Bosc, 1802)**

(Figure S10C, D)

Material.—JTMD-BF-1, 5, 8, 13, 40, 94, 134, 196, 199, 203, 207, 227, 240, 251, 290, 328, 330, 336, 356, 413, 455, 512, 513, 528, 533, 580, 587, 638, 639, 652, 654, 659.

Remarks.—Widespread neustonic species primarily epiphytic on floating *Sargassum* in the Atlantic Ocean, but also found on shells, buoys, and other plastic materials worldwide (Liu 1992; Thiel and Gutow 2005; Goldstein et al. 2014). Characteristic of this species is branched spinules, hooks, or paired wings projecting into the opesia (Figure S10D). Colonies from JTMD were found overgrowing the original coastal fouling community as well as growing over other pelagic acquisitions such as the goose neck barnacle *Lepas* sp. *Jellyella tuberculata* appears to be a cooler water species than *J. eburnea*, with earlier records of *J. tuberculata* in tropical and subtropical waters (as noted above) requiring verification.

Additional material of *J. eburnea* or *J. tuberculata* is in hand (JTMD-BF-39, 42, 149, 154, 156, 224,

236, 349, 390, 391, 420, 422, 442, 455, 504, 515, 518, 527, 546, 578, 579, 640, 661), but colonies were too fragmentary to assign to species.

Distribution.—Temperate reports include Japan (Mawatari 1974), California (Soule et al. 1995), New England to Florida (Osburn 1912, as *Membranipora tehuelcha* d’Orbigny, 1839; Winston 1982b), and South Africa (Florence et al. 2007). Warmer water reports in the Pacific and Indo-Pacific theaters include South Korea (Seo and Min 2009), Bangladesh (Gordon et al. 2007), Vanuatu (Tilbrook et al. 2001), Costa Rica (Banta and Carson 1977), and the Galapagos Islands (Chiriboga et al. 2012), and in the Atlantic, Colombian Caribbean (Montoya-Cadavid 2007) and Brazil (Vieira et al. 2016).

Membranipora villosa Hincks, 1880

Material.—JTMD-BF-349, 370, 383, 384, 405, 408, 410.

Remarks.—Three morphologically-similar *Membranipora*, *M. membranacea*, *M. serrilamella* and *M. villosa*, in the North Pacific were thought to be differentiated by the development and serration of the cryptocyst and the presence or absence of cuticular spines (Osburn 1950): *M. villosa* with a finely serrated cryptocyst with cuticular spines on the frontal wall and at zooidal margins, *M. serrilamella* with a heavily denticulate cryptocyst with longer spinules and no cuticular spines, and *M. membranacea* with a narrow, smooth cryptocyst and lacking frontal cuticular spines. Yoshioka (1982) argued that these morphologies represented ecophenotypes induced by nudibranch predation, placing *M. serrilamella* and *M. villosa* in the synonymy of the older name *M. membranacea*. Dick et al. (2005), after reviewing the systematic and nomenclatural complexities since Yoshioka’s work, resurrected *M. villosa*, placed *M. serrilamella* in synonymy with *M. villosa*, and restricted *M. membranacea* to the Atlantic Ocean.

Dick et al. (2005) noted that only the *serrilamella* morphology, lacking cuticular spines, had been reported from Japan (Mawatari 1974; Liu et al. 2001; as well as Seo and Min 2009), rather than the *villosa* morphology, and speculated that the absence of the latter morphology might be due to the introduction of *M. serrilamella* from North America to Japan, “in which case Japanese populations of nominal *M. serrilamella* might not exhibit a defensive response to chemical cues from species of nudibranch predators native to Japan” (Dick et al. 2005 also note that “an introduction would also explain the low genetic divergence between Japanese specimens and one of the clades at Friday Harbour, Washington”).

We follow Dick et al. (2005) in using the name *villosa* for our Japanese material, which while lacking cuticular spines on the frontal wall (in concert with the *serrilamella*-morph), displays cuticular spines at the zooid margins, a feature also attributed to *M. villosa*, as well as the *villosa*-like cryptocyst. Tower cells, indicative of the *membranacea*-morph, were not observed. While most colonies arrived without tissue, a few (on JTMD-BF-405, 408, 410) small colonies, growing on algae, possessed tissue. All three of these objects also bore light signatures of newly settled Northeast Pacific species (such as nepionic barnacles and newly settled crabs); moreover, colonies of *M. villosa* on JTMD-BF-408 were found overgrowing *Jellyella eburnea*. Colonies of *M. villosa* on these objects may represent Eastern Pacific acquisition.

Distribution.—Japan (Mawatari 1956, 1974), South Korea: South and Yellow Seas (Seo and Min 2009), Alaska: Ketchikan (Dick et al. 2005); Alaska to California (Grischenko et al. 2007).

Suborder Flustrina Smitt, 1868
Superfamily Calloporoidea Norman, 1903
Family Calloporidae Norman, 1903

Callopora craticula (Alder, 1856)

(Figure S11)

Material.—JTMD-BF-139, 205.

Remarks.—Although material consisted of skeletal remains with spine bases only, characteristics agree most closely with the recent description of this species by Grischenko et al. (2007) from Akkeshi Bay, Hokkaido, Japan.

Distribution.—Widespread Arctic-Boreal species. Japan: Hokkaido (Grischenko et al. 2007), northern Sea of Japan (Kluge 1975), Saint Lawrence Island (Grischenko 2002), Alaska (Osburn 1950; Dick et al. 2005), Arctic Ocean: Spitsbergen (Kuklinski 2002), France (Prenant and Bobin 1926), Britain and Scotland (Hayward and Ryland 1998).

Cauloramphus spinifer (Johnston, 1832)

(Figure S12A, B)

Material.—JTMD-BF-391.

Remarks.—Our specimen matches *Cauloramphus spinifer* with its 3 orificial spines and 5–10 opesial spines. This species may be circumboreal, as it was originally described from Europe and subsequently recorded in the Pacific, or it may consist of cryptic sibling species.

Distribution.—Japan (Mawatari 1956; Grischenko et al. 2007), Barents Sea (Kluge 1975), Svalbard (Gontar et al. 2001).

***Cauloramphus* sp.**
(Figure S12C–F)

Material.—JTMD-BF-160.

Remarks.—A colony fragment in hand is too poor to assign to species level. Kenozooidal ovicells forming a crescentic hood and an extensive frontal membrane suggest placement in *Cauloramphus*. Up to three pairs of spines or spine bases were located laterally around the zooid margin. No orificial spines were present and it is unclear whether the process on the ovicells represents a pore or the base of an orificial spine (Figure S12C, E). No avicularia were observed, although there appear to be bases of pedunculate avicularia just proximal to the distal-most pair of lateral spines (Figure S12F). Our specimen is similar to *Cauloramphus korensis* Seo, 2001 in the lack of distal spines and the large kenozooidal ovicell, but does not have brown or violet spines.

Superfamily Buguloidea Gray, 1848
Family Bugulidae Gray, 1848

***Bugula tsunamiensis* McCuller, Carlton and Geller, 2018**
(Figure S13)

Material.—JTMD-BF-23, 131, 134, 168, 196, 210, 212, 223, 226, 240, 241, 250, 253, 254, 264, 290, 304, 339, 352, 353, 356, 390, 398, 402, 410, 413, 414, 415, 471, 526, 530, 531, 532, 533, 555, 578, 626, 652, 668, 669, 670, 671, 672.

Remarks.—This distinctive species in the *Bugula uniserialis* Hincks, 1884-group (Vieira et al. 2012; Fehlauer-Ale et al. 2015) does not match any previous descriptions of *Bugula* species in the North Pacific Ocean (McCuller et al. 2018) or elsewhere in the world (L.M. Vieira, personal communication, 2017). Combined with molecular evidence, this Western Pacific bugulid is described as a new species in an accompanying paper (McCuller et al. 2018).

***Bugulina stolonifera* (Ryland, 1960)**

Material.—JTMD-BF-1.

Remarks.—We report this well-known fouling species (long known as *Bugula stolonifera*) on the basis of its detection in a metagenomic analysis of a fouling community sample from the “Misawa 1” (JTMD-BF-1) dock that landed in central Oregon in June 2012. A sequence from these samples was 100% identical to a sequence of *B. stolonifera* from

a fouling community in Galizia, Spain (Fehlauer-Ale et al. 2015; Genbank KC129849-1; Jonathan Geller, personal communication, 2017). The sequence also matched sequences of specimens identified as *B. stolonifera* from San Francisco Bay and from Matsushima Bay, Honshu (noted below) (J. Geller, personal communication). While we have no morphological vouchers of *B. stolonifera* from JTMD-BF-1, the massive “Misawa 1” dock, from the Port of Misawa, Aomori Prefecture, presented a rich, complex community, which continued to reveal previously undetected taxa in studies of additional archived samples over several years, and it is thus not surprising that no voucher specimens are in hand.

Distribution.—Reported from harbors and bays world-wide, the original home of this species, obscured by global shipping, has yet to be determined (Carlton and Eldredge 2009; Winston and Hayward 2012). A curiously late arrival in Japan, it was first found in 1997 in the Port of Nagoya (Scholz et al. 2003), and by 2013 had extended north to Tokyo Bay (Lutaenko et al. 2013). Material in hand provided and identified by Dr. Michio Otani is from fouling panels set out in 2015 north of Tokyo in Shiogama, Matsushima Bay, Miyagi Prefecture on the Tōhoku coast.

Family Candidae d’Orbigny, 1851

***Pomocellaria californica* (Trask, 1857)**
(Figure S14A, B)

Material.—JTMD-BF-208, 417, 569.

Remarks.—Our material consists of only small fragments of a few zooids each lacking ovicells. Zooids appear to closely match *Pomocellaria californica* based on the single axial vibracula, small paddle-shaped avicularia, transverse setal grooves, and long distal spines. While only BF-569 showed a trace of colonization by other Northeast Pacific species (including nepionic echinoids and decapods), these colonies may represent newly-settled *P. californica*.

Distribution.—British Columbia to southern California (Osburn 1950, as *Scrupocellaria californica*).

***Tricellaria inopinata* d’Hondt and Occhipinti Ambrogi, 1985**
(Figure S14C, D)

Material.—JTMD-BF-1, 8, 12, 18, 23, 40, 58, 121, 131, 139, 168, 177, 205, 210, 237, 331, 336, 657.

Remarks.—Considerable variation occurs within and between colonies of *Tricellaria inopinata*, resulting in confusion between it and the Eastern Pacific *Tricellaria occidentalis* (Trask, 1857). Historically, *T. occidentalis* and *T. occidentalis* var. *catalinensis* (Robertson, 1905) were recorded from Japan

(Mawatari 1951). Dyrinda et al. (2000) suggest that Japanese species recorded as *T. occidentalis* are likely *T. inopinata* (described from the Mediterranean, but believed to be native to Japan), due to the species' extensive morphological variation, and further provide evidence that the two species are distinguishable. Grischenko et al. (2007) report specimens from Akkeshi Bay that had purported characters of both species within the same colonies. As no type material of *T. occidentalis* appears to be available, and as only older material was used by Dyrinda et al. (2000) to distinguish *T. occidentalis*, Grischenko et al. (2007) maintain use of the name *T. occidentalis* in Japan until the two species are more thoroughly delineated.

We note that colony form, although not previously discussed, may aid in distinguishing the two species. *T. occidentalis* grows in bushy tufts formed of curved branches which roll inward (Osburn 1950; Mawatari 1951; Grischenko et al. 2007). In comparison, the bushy colonies of *T. inopinata* have branches that are only slightly rolled inward, or are straight or rolled slightly outward (D'Hondt and Occhipinti-Ambrogi 1985; De Blauwe and Faasse 1998; Johnson et al. 2012). This difference may be due to the average number of zooids per internodes: 3 (most common) to 5 in *T. occidentalis* (as in Figure S14C) and 3 to 19 for *T. inopinata* (as in Figure S14D).

JTMD material contains some specimens that appear most closely aligned with *T. occidentalis* (JTMD-BF-40) and others that were closer to *T. inopinata* (JTMD-BF-58). As the majority of our material is similar to introduced populations of *T. inopinata* that we have studied in New England, USA, we treat the present specimens as representing this species.

Distribution.—Japan (Okada 1929; Mawatari 1951); North West Atlantic (Johnson et al. 2012); Northeast Atlantic (Occhipinti-Ambrogi and D'Hondt 1994).

Superfamily Catenicelloidea Busk, 1852
Family Catenicellidae Busk, 1852

***Catenicella* sp.**
(Figure S14E, F)

Material.—JTMD-BF-538, 555, 667.

Description.—Delicate, branching, arborescent colonies. Internodes of one or two zooids. Zooids with few pseudopores scattered over the frontal wall; vittae mostly frontal with one row of small pores within; scapular chambers elongate, without avicularia. No ovicells observed.

Remarks.—This material resembles populations of *Catenicella contei* (Audouin, 1826) from Brazil (Ramalho et al. 2014) in the structure of the scapular chambers and vittae, and in the absence of

avicularia. However, as ovicells are an important character for identification of catenicellids, our identification remains at the genus level, pending further material. One species, *Catenicella elegans* Busk, 1852, is reported from Japan (Okada 1921), but that species has paired avicularia.

Superfamily Celleporoidea Johnston, 1838
Family Celleporidae Johnston, 1838

Four *Celleporina* species occur on JTMD. Additional material of *Celleporina* is in hand from JTMD-BF-76, 105, 150, 336, and 455, as very small fragments in poor condition not assignable to species.

***Celleporina* cf. *globosa* Liu, 2001**
(Figure S15A, B)

Material.—JTMD-BF-23.

Remarks.—Two small colonies without vicarious avicularia were most similar to *Celleporina globosa* described by Liu et al. (2001) from China. While similar in appearance to *Celleporina fusiforma* (Ikezawa and Mawatari, 1993) from Hokkaido, the adventitious avicularia of that species are directed obliquely distally outwards and lack serrations.

Distribution.—China: coastal waters of Qingdao (Liu et al. 2001).

***Celleporina porosissima* Harmer, 1957**
(Figure S15C, D)

Material.—JTMD-BF-215, 667.

Remarks.—Two small colony fragments bear zooid characteristics agreeing with the original description of *Celleporina porosissima* and a subsequent redescription by Ikezawa and Mawatari (1993). This species differs from both of our other JTMD *Celleporina* species primarily in the spinous processes within the zooidal chamber and the morphology of distally budded zooids.

Distribution.—Japan: Hokkaido (Ikezawa and Mawatari 1993; Grischenko et al. 2007), Shimoda (Okada 1934), South Korea (Seo and Min 2009).

***Celleporina* sp. A**
(Figure S15E, F)

Material.—JTMD-BF-18, 40.

Description.—Colony encrusting, forming small nodules or domes. Peristome high; primary orifice longer than wide with a narrow U-shaped sinus; paired adventitious avicularia on either side, directed disto-laterally, with slightly serrated distal edges. Young, frontally-budded zooids with a single series of large pores around the entire orifice. Brooding zooids with hemispherical ovicells; tabula large, covering the entire frontal area. No vicarious

avicularia observed. No spinules within zooidal chambers observed.

Remarks.—A species which shares similar characters is *Celleporina serrirostrata* Liu, 2001 from the coast of Guangdong Province in the South China Sea. However, our specimens do not appear to have spinous processes within the chambers of frontally-budded zooids as does *C. serrirostrata*.

Celleporina sp. B

Material.—JTMD-BF-679.

Description.—Colony encrusting, multilaminar and raised. Orifice ovoid with U-shaped sinus; small paired adventitious avicularia on either side, facing centrally. Vicarious avicularia small, shoe-shaped, numerous, with complete crossbar. Ovicells with large tabula covering the entire frontal surface with many slit-like pores radially arranged. No frontally budded zooids observed. No spinules within zooidal chambers observed.

Remarks.—This specimen is distinct from other JTMD *Celleporina* in having abundant vicarious avicularia and inconspicuous adventitious avicularia. The specimen arrived in our hands too late for imaging.

Family Phidoloporidae Gabb and Horn, 1862

Rhynchozoon sp. (Figure S16)

Material.—JTMD-BF-290.

Description.—Colony unilaminar to multilaminar. Zooids hexagonal, separated by interzooidal grooves, arranged quincuncially; frontally-budded zooids subcircular, irregularly arranged. Orifice nearly circular, about as long as wide, rim serrated, condyles rounded, with U-shaped proximal sinus. No orificial spines. Sub-orificial avicularia often present, triangular tip, pointing laterally. Frontal wall inflated, surrounded by approximately 20 small marginal pores from which may be robust ridges in new peripheral zooids. No frontal or vicarious avicularia observed. No ovicells observed.

Remarks.—Considering their diversity, *Rhynchozoon* species are curiously species-poor in Japan with only three species recorded: *R. larreyi* (Audouin, 1826), *R. tubulosum* (Hincks, 1880), and *R. verruculatum* (Smitt, 1873) (Mawatari 1987; Kaselowsky 2004). Material examined here differs from those species most notably in the number of marginal pores; the aforementioned species have few large pores, while our specimen has many small pores. The sinus is also a deep U-shape, differentiating it from the broad, shallow sinuses of both *R. tubulosum* and *R. verruculatum*.

Superfamily Cribrilinoidea Hincks, 1879
Family Cribrilinidae Hincks, 1879

Cribrilina mutabilis Ito, Onishi and Dick, 2015 (Figure S17)

Material.—JTMD-BF-597.

Remarks.—This single colony fits the recently described *Cribrilina mutabilis*. As reported in Ito et al. (2015), this species has 3 different zooid types: R, I, and S. Our colony has a mixture of both R and I types with approximately 8–10 costae fused at the midline (R type), with or without intercostal pores (I type). *C. mutabilis* has previously been reported as growing on seagrass or algae blades; our specimen was found on a mussel shell (*Mytilus galloprovincialis*) in the process of being overgrown by *Scruparia ambigua*.

Distribution.—Japan: Hokkaido (Ito et al. 2015).

Superfamily Hippothooidea Busk, 1859
Family Hippothoidae Busk, 1859

Celleporella hyalina (Linnaeus, 1767) (Figure 2C)

Material.—JTMD-BF-40, 90, 129, 168, 210, 215, 241, 264, 293, 383, 413, 651, 657, 679.

Remarks.—Reported as a widespread Arctic-Boreal taxon that is a likely species complex as noted by Grischenko et al. (2007), based on differences in number of pores on the ovicell. JTMD material matches the description of *Celleporella hyalina* from Hokkaido, Japan by Grischenko et al. (2007), but also present some differences. Autozooid orifices were much smaller (ca. 0.10 mm long by 0.09 mm wide) and male zooids were approximately one-third to one-half the size of autozooids. Ovicells were also much smaller (ca. 0.13 mm long by 0.18 mm wide) than that of typical *C. hyalina*. These discrepancies may be due to the wide variety of temperatures the colonies likely experienced over the course of their rafts' journeys. Molecular studies on *C. hyalina* colonies collected in the Atlantic basin and the Pacific coast of Chile confirm that subgroups (or distinct species) exist and that differences are reflected in zooid morphology, life history, and ecology (Hoare et al. 2001). In JTMD material, *C. hyalina* is primarily found on the Japanese mussel *Mytilus galloprovincialis*, the Japanese acorn barnacle *Megabalanus rosa* Pilsbry, 1916, and the neustonic crab *Planes marinus* (JTMD-BF-40; Figure 2C). Some colonies, such as those present on JTMD-BF-40, were alive with ovicells and embryos at the time of preservation, suggesting that this species is capable of reproduction after rafting long distances.

Distribution.—Widely reported from the North and South Atlantic Oceans. Western Pacific records include Japan (Okada 1929; Mawatari 1956; Grischenko et al. 2007), Sea of Japan (Grischenko and Zvyagintsev 2012), South China Seas (Liu et al. 2001), while in the Eastern Pacific it has been reported from Alaska to the Galapagos Islands (Osburn 1952; Dick et al. 2005; Soule et al. 1995), largely under its well-known older name *Hippothoa hyalina*.

Superfamily Lepralielloidea Vigneaux, 1949

Family Exochellidae Bassler, 1935

***Exochella tricuspis* (Hincks, 1881)**

(Figure S18A)

Material.—JTMD-BF-40, 160, 210, 305, 449, 667.

Remarks.—Our specimens were consistent with *Exochella tricuspis*. Okada and Mawatari (1937) described *Exochella areolata* from northern Honshu, Japan, which Seo and Min (2009) synonymized with *E. tricuspis*.

Distribution.—Japan: Honshu (Okada and Mawatari 1937), South Korea (Seo and Min 2009); Australia (Gordon 2007); New Zealand (Levinsen 1909).

Family Lepraliellidae Vigneaux, 1949

***Celleporaria brunnea* (Hincks, 1884)**

(Figure S18B)

Material.—JTMD-BF-27, 197, 212, 397.

Remarks.—Material from JTMD agrees entirely with the description of *Celleporaria brunnea* by Canning-Clode et al. (2013) and with other standard treatments of the species. *C. brunnea* is native to and widespread throughout the Northeastern Pacific Ocean, but has recently begun to appear in other regions of the world (due presumably to transport by shipping) including South Korea in 2004 (Seo and Min 2009), Turkey in 2004 (Koçak 2007) and Portugal in 2012 (Canning-Clode et al. 2013). Remarkably, our four collections of this species were all from the same type of object—small pontoon sections—landing in Hawai'i in 2013 (JTMD-BF-27), in Washington in 2013 and 2014 (JTMD-BF-197, 397), and in Oregon in 2014 (JTMD-BF-212). None of these objects reveal any trace of settlement of North American or Hawaiian invertebrates, and, in turn, the present colonies were too large to have settled in local coastal waters before these small docks washed ashore. Colonies were found on the lower side of a valve of Japanese oysters (JTMD-BF-197, 212) or on the underside of a Japanese barnacle (JTMD-BF-27) indicating that settlement occurred in the Western Pacific before the barnacles or oysters settled.

Distribution.—British Columbia to Galapagos Islands (Osburn 1953; Powell 1971; Soule et al. 2007 (in error as “Oregon to Ecuador”). Introduced to South Korea and southern Europe (above). Carlton and Eldredge (2015) note that it was mistakenly reported earlier as established in Hawai'i; however, in 2006 it was observed in Hawai'i (Ruiz et al., unpublished fouling panel survey 2006) and in 2016 it was recovered from panels on Oahu (L. McCann, personal communications, 2017) (Table S2).

***Drepanophora cf. gutta* Tilbrook, Hayward and Gordon, 2001**

(Figure S18C, D)

Material.—JTMD-BF-425.

Remarks.—Two small colonies encrusting a plastic toy (bearing Japanese serpulids and other bryozoans) closely resembles the description of *Drepanophora gutta* from Port Vila Harbour, Efate, Vanuatu in having 1 or 2 distal spines (observed as spine bases only) on non-ovicellate zooids and an anvil-shaped lyrula (Figure S18D). However, JTMD material does not appear to have the long peristome as described by both Tilbrook et al. (2001) and Gluhak et al. (2007), although both colonies were highly calcified which may obscure this character. *Rhamphostomella rogickae* (Brown, 1958) reported by Kaselowsky (2004) from Okinawa may represent this species.

Distribution.—Vanuatu (Tilbrook et al. 2001), Taiwan: Green Island (Gluhak et al. 2007).

Family Romancheinidae Jullien, 1888

***Escharella hozawai* (Okada, 1929)**

(Figure S19)

Material.—JTMD-BF-205, 362, 367, 389, 425, 616.

Description.—Colony uni- or multilaminar. Zooids distinct, typically hexagonal, 0.55 mm ± 0.07 mm long, 0.33 mm ± 0.04 mm wide. Frontal wall granulated, regularly perforated except for the suboral area (Figure S19A). Suboral area with heterozoid chamber, raised to form a high arch, smooth at its peak, with median cavity. Orifice higher than wide, separated by condyles (Figure S19E). Peristome low, surrounding the orifice and appearing as a curved lip on heterozoid chamber margin and proximal edge of ovicell (Figure S19B, C). Ovicell hyperstomial, prominent, more finely granular, imperforate except at the distal margin, often with central umbo and a pair of proximo-lateral spines that curve inwards (Figure S19B, C). Four large multiporous septula on lateral walls (Figure S19D). Ancestrula tatiform, gymnocyst extensive, 4 pairs of spines surrounding sub-circular opesia, budding one distal and two disto-lateral zooids (Figure S19F).

Remarks.—*Escharella hozawai* was described (as *Mucronella hozawai*) from Mutsu Bay (in Kawauchi and off Tozawa) Aomori Prefecture (Okada 1929), and appears to have not been recorded since. *E. hozawai* differs from a morphologically similar Japanese species, *Pacifincola perforata* (Okada and Mawatari, 1937), in the presence of paired curved spines on either side of the lower margin of the ovicell, and a tatiform ancestrula with 8 spines that buds three zooids around its distal end, as opposed to the cribriform ancestrula with four spines that buds four zooids in *P. perforata* (Grischenko et al. 2007). Our material showed considerable variation in spine presence on the ovicell. Paired spines were absent in some parts of the colony, but long and distinct in other parts. *E. hozawai* appears closely allied to *Pacifincola*; further study may suggest eventual placement in that genus.

Material from two objects, a plastic can fragment (JTMD-BF-616) and a plastic tote (JTMD-BF-362), were composed of an encrusting base of *E. hozawai* overgrown by hydroids. Okada (1929) reported this species as growing on seagrasses such as *Zostera marina* Linnaeus, 1753; our material consists of fouling colonies on fiberglass and plastic.

Distribution.—Japan: Mutsu Bay, Honshu (Okada 1929).

Superfamily Schizoporelloidea Jullien, 1883

Family Cryptosulidae Vigneaux, 1949

***Cryptosula pallasiana* (Moll, 1803)**

Material.—JTMD-BF-1, 8, 12, 20, 37, 130, 212, 329, 356, 391, 425, 538.

Remarks.—*Cryptosula pallasiana* is an easily recognizable common fouling organism on floating docks; four objects fouled by *C. pallasiana* were dock or pontoon sections; another three were vessels.

Distribution.—Widespread in the Northern Hemisphere, suggesting a potential species complex, transport and introduction by shipping or the commercial oyster industry, perhaps for centuries, or a combination of both. In the Pacific Ocean reported from Japan (Mawatari 1956; Long and Rucker 1969; Grischenko et al. 2007), South Korea (Seo and Min 2009), New Zealand (Gordon 1968), and the Bering Sea and Alaska to Mexico (Osburn 1952; Grischenko 2002; Dick et al. 2005). Widely reported throughout the North Atlantic, including the Mediterranean Sea (Hayward and Ryland 1999; Abdel-salam and Ramadan 2008; Koçak 2007), as well as from Brazil (Vieira et al. 2008), South Africa (Florence et al. 2007), and the Red Sea (Ostrovsky et al. 2011). Of interest is that Osburn (1952) noted that many earlier workers did not mention this distinctive species from

the Pacific coast of North America, leading Carlton (1979) to suggest that it may have been more recently introduced to the Northeastern Pacific Ocean.

Family Microporellidae Hincks, 1879

***Fenestrulina cf. orientalis* Liu, Liu and Sun, 2003**
(Figure S20)

Material.—JTMD-BF-1, 40.

Description.—Colony encrusting, unilaminar, delicate with light calcification. Zooids separated by deep grooves. Frontal wall slightly convex, surrounded entirely by a single or double marginal row of stellate pores. One or two, rarely three, rows of pores situated between orifice and ascopore. Ascopore crescentic, slightly denticulate. Orifice semicircular with rounded proximolateral corners. Periancestrular zooids with five spines present distal to orifice, non-ovicellate zooids with three spines, and ovicellate zooids with 2 spines. Ancestrula oval with nine or ten spines surrounding orifice.

Remarks.—We tentatively assign the present material to *Fenestrulina orientalis*. Our specimens developed from the tatiform, unmodified version of the ancestrula (Grischenko et al. 2007). A similar species is *Fenestrulina delicia* Winston, Hayward and Craig, 2000 from the Atlantic, but that species has a ridged ovicell and an ascophore with stronger denticulations. On JTMD objects it was found to be encrusting the mussel *Mytilus galloprovincialis* in association with *Scruparia ambigua*, *Exochella tricuspis*, and hydroids. Most zooids in populations on JTMD-BF-40 contained polypides and many were reproductively active. Grischenko et al. (2007) suggests that records from historical Japanese literature of *Microporella malusii* (Okada, 1929) and *Fenestrulina malusii* (Audouin, 1826) (Huang et al. 1990) may represent *F. orientalis*.

Distribution.—Japan: Hokkaido (Grischenko et al. 2007), China (Liu et al. 2001, 2003).

***Microporella borealis* Suwa and Mawatari, 1998**
(Figure S21A, B)

Material.—JTMD-BF-23, 160.

Remarks.—Many species of *Microporella* occur on the Japanese coast. Our material agrees with *Microporella borealis* in possessing four to five oral spines, orifice with a denticulate proximal rim, denticulate crescentic ascopore, and a lanceolate avicularian mandible with paired hooks. However, *M. borealis* has two spines that occur proximal to the ovicell which our specimens were lacking, perhaps due to extensive calcification.

Distribution.—Japan: Hokkaido (Suwa and Mawatari 1998) and Shimoda (Kaselowsky 2004), South Korea (Seo and Min 2009).

***Microporella luellae* Grischenko, Dick and Mawatari, 2007**
(Figure S21C, D)

Material.—JTMD-BF-391.

Remarks.—Our specimen aligns most closely with *Microporella luellae* in possessing 2 widely-spaced orificial spines, a single avicularia, and a crescentic, denticulate ascopore, but differs in that the orificial spines were present in reproductively mature, as well as immature, zooids. This may represent phenotypic variation due to the wide range of conditions experienced by the rafted colony. A similar species is *M. neocriboides* (below), which has an ascopore covered with a cribriform plate.

Distribution.—Japan: Hokkaido (Grischenko et al. 2007).

***Microporella neocriboides* Dick and Ross, 1988**
(Figure S21E, F)

Material.—JTMD-BF-657.

Remarks.—This specimen agrees well with *Microporella neocriboides* as described by Suwa and Mawatari (1998) and Dick et al. (2005), but differs in avicular characters. Whereas *M. neocriboides* usually has one or no avicularia, zooids within our specimen typically have two avicularia, and occasionally one or three (Figure S21E); those with two avicularia were often paired laterally to the aperture, although sometimes both avicularia occur on one side. *Microporella inermis* Liu and Liu, 2001 is similar, but lacks the cribriform plate underneath the pseudopores which was present in our material (Figure S21F).

Distribution.—Japan: Hokkaido (Grischenko et al. 2007), Alaska (Dick and Ross 1988).

Family Schizoporellidae Jullien, 1883

***Schizoporella japonica* Ortmann, 1890**
(Figure S22A, B)

Material.—JTMD-BF-215, 589.

Remarks.—JTMD specimens occur as both uni- and multi-laminar growths of mature zooids with prominent ridged and porous ovicells. Zooids typically lacking oral avicularia or had one or rarely a pair. Raised, frontal avicularia were sometimes present. Top layers (in this case, those flush with an oyster shell on a buoy (JTMD-BF-215)) often had a small conical umbo on the frontal wall proximal to the orifice; umbos on layers beneath were quite

robust, extending far above the zooidal plane (Figure S22A). These characters agree with those of *Schizoporella japonica* (Grischenko et al. 2007). Additional material of *Schizoporella* is in hand from JTMD-BF-131, 164, and 264, but consist of few or heavily abraded zooids. While these are likely to be *S. japonica*, we demure from identifying these colonies to species level.

Distribution.—Hokkaido to China (Grischenko et al. 2007). It was introduced long ago to the Pacific coast of North America on Pacific oysters (*Crassostrea gigas* (Thunberg, 1793)), and was recently recognized in Western Europe (Ryland et al. 2014).

Superfamily Smittinoidea Levinsen, 1909
Family Bitectiporidae MacGillivray, 1895

***Metroperiella* cf. *biformis* (Zhang and Liu, 1995)**
(Figure S22C–F)

Material.—JTMD-BF-210.

Remarks.—Our specimen has a bilaminar growth form, a lepralioid aperture, and large spatulated median avicularia, consistent with that of *Metroperiella biformis*. Two congeners, *Metroperiella montferandii* (Audouin, 1826) and *Metroperiella spatulata* (Okada and Mawatari, 1936), are also recorded from Japan, as *Codonella acuta* (Ortmann, 1890) and *Codonella spatulata*, respectively (Okada and Mawatari 1936). The former species is differentiated from *M. biformis* by its acute avicularia. *M. spatulata* is similar to our species but has an orbicular aperture. We tentatively identify JTMD material as *M. biformis*, which was originally described from the East China Sea as a fouling organism on aquaculture cages, ship bottoms, and buoys, pending more detailed descriptions of *M. spatulata*. Our material is from a vessel's hull along with *Bugula tsunamiensis*, *Exochella tricuspis*, *Filicrisia* cf. *franciscana*, *Scruparia ambigua*, *Smittoidea spinigera*, and *Tricellaria inopinata*. Many zooids contained polypides and while a majority were ovicellate, only a portion were with embryos.

Distribution.—East China Sea (Liu et al. 2001).

Family Smittinidae Levinsen, 1909

***Smittoidea spinigera* (Liu, 1990)**
(Figure S23)

Material.—JTMD-BF-23, 27, 32, 197, 210, 667.

Remarks.—Very few species of *Smittoidea* have been recorded from Northwest Pacific and their identities remain doubtful (De Blauwe and Faasse 2004). *Smittoidea reticulata* (MacGillivray, 1842) identified from Japan by Okada and Mawatari (1936) is described as having an acute avicularian mandible.

Smittoidea prolifica Osburn, 1952 has large avicularia with a rounded mandible, but 2–4 spines are present only within the zone of astogenetic change. Our material most closely corresponds to that of *Smittoidea spinigera*, described from Bohai Bay to the coastal waters of Guangdong, China, in having 3–6 distal spines present even outside the zone of astogenetic change and a rounded avicularian mandible with a triangular projection on the crossbar (Figure S23E).

Distribution.—Northern China: Bohai Bay to Guangdong (Liu 1990; Liu et al. 2001).

Family Watersiporidae Vigneaux, 1949

We report two species of *Watersipora* from JTMD material. Additional *Watersipora* specimens from BF-20, 197, and 290 were in hand, but consist of too few zooids or were in too poor condition to permit species identification.

Watersipora mawatarii Vieira, Spencer Jones and Taylor, 2014 (Figure S24A, B)

Material.—JTMD-BF-1, 212.

Description.—Colonies encrusting in brown to black uni- or bilaminar sheets on serpulid tubes. Zooids subrectangular, about twice as long (ca. 0.90 mm \pm 0.07 mm) as wide (ca. 0.44 mm \pm 0.05 mm), widest proximal to the orifice, pseudopores small (ca. 15 μ m \pm 3 μ m) and covering the entire frontal wall except in the suborificial area. Frontal wall granular. A pair of intrazooidal septula containing 2–5 small pores present on either side, proximolateral to the orifice and near the lateral margin. Orifice large, wider than high, with a broad U-shaped sinus. Orificial rim slightly raised, thin. Condyles bar-shaped, often inconspicuous. Operculum black with distinct, biconcave, broad central band that narrows distally. Lucidae present.

Remarks.—Our material closely matches *Watersipora mawatarii*. While similar to *Watersipora* cf. *typica* described below, the present material differs in its lack of pseudopores in the sub-orificial region and by having smaller pseudopores covering the frontal wall.

Distribution.—Japan: Hokkaido (Vieira et al. 2014a).

Watersipora cf. *typica* (Okada and Mawatari, 1937) (Figure S24C, D)

Material.—JTMD-BF-40.

Description.—Encrusting, uni- or bilaminar colonies, deep reddish-purple in color. Zooids rectangular, about twice as long (ca. 0.85 mm \pm 0.17 mm) as wide (ca. 0.48 mm \pm 0.04 mm); small pseudopores

(ca. 22 μ m \pm 3 μ m) covering the entire surface of the frontal wall; a pair of intrazooidal septula, each with about 5–6 pores, present laterally to either side of the orifice. Orifice large, wider than high, with a broad U-shaped sinus. Orificial rim much raised, thick, especially on either side of sinus. Condyles bar-shaped. Operculum brick red with dark central, parallel-sided band and lighter area at distal end. Lucidae absent.

Remarks.—Similar to *Watersipora subatra* (Ortmann, 1890) as recently described by Vieira et al. (2014a), but that species does not have a light band at the distal end of the orifice as does *W. typica*. Okada and Mawatari (1937) describe this species as having a thin circular area at the distal portion of the operculum; ours has only a thin band at the distal edge of the operculum.

Distribution.—Japan: Honshu (Okada and Mawatari 1937).

Discussion

Prior records of ocean rafting

Almost none of the 49 species of coastal bryozoans recorded here have been reported previously from open ocean rafting (Table S2). While a number of bryozoans are reported from rafting communities (Winston et al. 1996; Astudillo et al. 2009; Kiessling et al. 2015), these are largely from local, inshore, coastal waters, records that do not establish the potential of these species for long-distance trans-oceanic rafting. Goldstein et al. (2014) are among the first to report Bryozoa from the open ocean of the North Pacific. They reported the three neustonic species we record here (*Jellyella eburnea*, *J. tuberculata*, and *Arbopercula angulata* (as *Membranipora tenella*)), as well as *Bugula* spp., *Filicrisia* spp., *Stomatopora* spp. and *Tubulipora* spp. (none identified to species). We found representatives of the last four genera in our JTMD samples. In addition, Goldstein et al. (2014) reported *Bowerbankia* spp., which may be our *Walkeria prorepens*, as well as *Victorella* spp., a genus-species group normally associated with estuarine, brackish systems. *Aetea anguina* has been reported in the open Atlantic Ocean in the Sargasso Sea (Table S2), although *A. "anguina"* of Pacific and Atlantic waters may be different species. We have tentatively equated (Table S2) our records of *Filicrisia* and *Tubulipora* with genus-level records of Goldstein et al. (2014), but species-level confirmation will require examination of the material collected by Goldstein and colleagues.

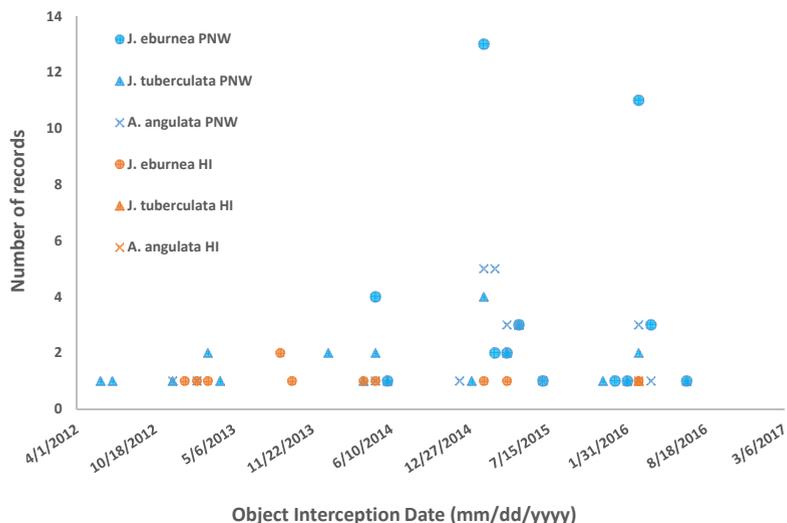


Figure 3. Change in frequency of intercepted objects containing neustonic species (*Jellyella eburnea*, *Jellyella tuberculata*, and *Arbopercula angulata*) based on location and date. PNW = Pacific Northwest, HI = Hawaii

Bryozoa as tracers of marine debris routes

The three oceanic (neustonic) bryozoans, *Jellyella eburnea*, *J. tuberculata*, and *Arbopercula angulata*, provide insight into the routes that certain JTMD items may have taken, and thus the conditions experienced, as they rafted from the Western Pacific to the Central and Eastern Pacific. The cooler-water species *J. tuberculata* and *A. angulata* may be more common in waters north of the 20 °C isotherm, whereas *J. eburnea* may recruit in larger numbers in warmer, subtropical and tropical waters. In turn, *J. tuberculata* and *A. angulata* were found primarily on JTMD objects arriving in the Pacific Northwest, whereas *J. eburnea* was most common on objects landing in the Hawaiian Islands. Indeed, both of the former species were found only once each in Hawai'i (on BF-654 and BF-653, respectively, both landing in 2016). These two objects thus took a higher latitude route through the North Pacific, before turning south and west back to the Central Pacific.

With rare exception, *J. eburnea* did not appear on items landing on the North American Pacific coast until 2015. Records increased thereafter, suggesting that an increasing number of objects (as noted earlier in Results) spent more time on longer and more circuitous routes in lower latitudes (Figure 3). For example, in a 7-week period between 3 March and 18 April 2016, 12 objects were found in Oregon and Washington with *J. eburnea* aboard (along with other southern invertebrate species), whereas it was found on only two objects arriving in the same region in the previous 6 months. Of interest then are the records of objects (such as BF-227, 413, and 659) arriving in the Pacific Northwest with both *J. eburnea*

and *J. tuberculata* attached, or both *J. eburnea* and *A. angulata* (such as BF-304, 341, and 428), or all three species (BF-207), suggesting that these objects had travelled through lower latitudes before being acquired by ocean currents that then took them north and east to North America.

Colony morphology and potential to survive long-distance rafting

All specimens within the Calloporidae (3 species) and Celleporidae (4 species), as well as 4 of the 6 species within the Electridae and Membraniporidae, were represented only by dead colonies. While the potential exists for these species to have arrived alive on objects not intercepted, this and the high diversity but low frequency of the unilaminar encrusting morphology suggests that this growth form is not well-suited to the open ocean.

Creeping-uniserial and erect-flexible-articulated-branching were the most frequently occurring and abundant growth forms found on JTMD, followed by encrusting-uniserial and -multiserial forms. The adaptive significance of such morphologies has been long discussed (Stach 1936; Jackson 1979; Hageman et al. 1998, 2013; Amini et al. 2004). Creeping uniserial forms (or “runners”) have high directionality, in which the acquisition of preferable spatial refuges is maximized, with the caveat that unsuitable habitat patches will also be encountered. Flexible-articulated-branching-forms (arborescent forms or “trees”) are structured to rise above the substrate (away from spatial competitors below them) and into the water column where food availability may be higher, albeit at the cost of fewer attachment points and increased

susceptibility of breakage from water velocity (Jackson 1979; McKinney and Jackson 1991). Indeed, *Scruparia ambigua*, the species found most frequently on JTMD, sends out uniserial encrusting runners, which then undergo frontal budding to form erect branches and thus may maximize the benefits of both runner and arborescent forms on potentially space-limited, slow-moving rafts.

Another group of creeping species are composed of zooids with encrusting and erect portions (*Aetea anguina*) or short, erect, tubular zooids connected by a thin stolon (*Callaetea* sp.); the lophophore is somewhat extended from the substrate and may have better access to food than strictly encrusting species. Of interest is that *Callaetea* sp. was identified on JTMD more frequently and in a wider variety of microhabitats than *A. anguina*, perhaps explained in part by the more delicate stolon of *Callaetea* sp. that does not need to adhere directly to the substrate as does the adnate portion of *A. anguina*. *Callaetea* sp. could be considered more of a “vine” but with reduced ability to extend into the water column in an arborescent manner (Jackson 1979). Likewise, Hageman et al. (2013) found that *Aetea truncata*, a species similar to *Callaetea* sp., was more abundant and widely distributed within microhabitats than *Aetea sica* (Couch, 1844), which adheres to the substrate in a manner similar to *A. anguina*.

Overall, species of *Aetea*, *Callaetea*, *Scruparia*, *Tricellaria*, and *Bugula* tended to be relatively abundant on JTMD. As noted above, the adaptive significance of an arborescent growth form includes increased access to food, increased rates of feeding and thus reproduction, and refuge from competition and predation (McKinney and Jackson 1991). The species in these genera have flexible colonies apparently capable of withstanding drag forces endured by water motion over slow-moving rafts. Hydroids, another erect colonial organism, were similarly often found in high abundance (Calder et al. 2014). In the absence of free primary space afforded by floating debris, especially once *Lepas* barnacles begin to settle and grow, erect species may hold the advantage over encrusting forms on long-lived anthropogenic rafts. For example, *Scruparia* (and occasionally *Aetea*) were observed growing up hydroid stolons, which thus provided additional surface area. In contrast, encrusting species grew on the object itself or occurred as epibionts on algae, bivalves, barnacles (including *Lepas*), and even the neustonic crab *Planes*, but in turn were regularly overgrown by hydroids, bivalves, sponges, and other bryozoans.

Further potentially contributing to rafting survival may be larval type, at least in the arborescent species.

Scruparia ambigua and Aeteidae brood lecithotrophic, non-feeding, coronate larvae that settle hours after release. Of the two, *S. ambigua* was more common and abundant than the Aeteidae, which is likely due to the number of brooded embryos per ovicelled zooid: up to 7 and 1–2, respectively (Mawatari 1973; Cook 1977). *Tricellaria inopinata* was often also abundant, its ovicelled zooids producing 1 coronate larva at a time.

Invasion potential

As noted earlier, only a small fraction of the JTMD field was intercepted and analyzed (Carlton et al. 2017). Thus it is likely that more species arrived than we have reported here. Many Western Pacific species of bryozoans, ranging from the major strike zone of the tsunami of the colder water Tōhoku coast of northeast Honshu to warmer waters south of the Boso Peninsula – and perhaps as far south as the South China Sea where JTMD may have drifted – would find a strong climatic match along the North American Pacific coast and in the Hawaiian Archipelago. Long-term monitoring of bryozoan diversity in these regions will be required to determine if this vast field of debris has led to the introduction of novel species in these regions.

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Supplementary material

The following supplementary material is available for this article:

Table S1. JTMD Objects and Bryozoan Diversity various locations in North America and Hawai'i.

Table S2. North Pacific ranges and biogeographic status of coastal Japanese bryozoan taxa identified to previously described species occurring on Japanese Tsunami Marine Debris.

Figures S1-S24. Photographs of coastal Japanese bryozoan taxa various locations from North America and Hawai'i.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_JTMD_McCuller_Carlton_SupplementaryTables.xlsx

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