

Relationship of diversity and habitat area in North Pacific plastic-associated rafting communities

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Abstract Plastic and other anthropogenic debris (e.g., rubber, tar) augment natural floating substrates (e.g., algal rafts, pumice) in the open ocean, allowing “islands” of substrate-associated organisms to persist in an otherwise unsuitable habitat. We examined a total of 242 debris objects collected in the eastern Pacific in 2009 and 2011 (32–39°N, 130–142°W) and the western Pacific in 2012 (19–41°N, 143–156°E). Here, we ask: (a) What taxa are associated with plastic rafts in the North Pacific? and (b) Does the number of taxa associated with plastic debris vary with the size of the debris “island?” We documented 95 rafting taxa from 11 phyla. We identified several potentially invasive plastic-associated rafting taxa,

including the coral pathogen *Halofolliculina* spp. In concordance with classic species–area curves, the number of rafting taxa was positively correlated with the size of the raft. Our findings suggest that diversity patterns on plastic debris are compatible with the concept of island biogeography.

Introduction

Naturally occurring floating objects in the pelagic environment have long played host to a suite of specialized species (Thiel and Gutow 2005a). These substrates, such as floating algae, pumice, and wood, provide transport and habitat for benthic organisms (Donlan and Nelson 2003; Thiel and Gutow 2005b; Bryan et al. 2012). In recent decades, natural rafts have been augmented by anthropogenic debris comprised primarily of non-biodegradable plastic polymers such as hard thermoplastic, foam, synthetic rubber, and fiberglass (Derraik 2002; Barnes et al. 2009).

Plastic debris was first detected in the open ocean in the early 1970s (Carpenter and Smith 1972; Venrick et al. 1973; Wong et al. 1974) and has now been observed all over the world (Thiel and Gutow 2005a). Plastic enters the marine environment through improper disposal (e.g., litter) or accidental loss (e.g., fishing gear; U.S. Environmental Protection Agency 2011). Debris from land-based sources is most common near highly populated areas, while debris from marine sources is most common on remote shores (Hammer et al. 2012). However, as debris is exposed to UV light and physical weathering, it fragments into small pieces, termed microplastics, that are frequently less than 5 mm in diameter (Andrady 2011; Hidalgo-Ruz et al. 2012). Microplastics now comprise the vast numerical majority of debris in the ocean (Goldstein et al. 2013) though larger objects that can

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support a more extensive rafting community are far from uncommon (Titmus and Hyrenbach 2011, Ryan 2013).

The composition of the rafting assemblage depends on the type of object, its stability, and the supply of propagules (Thiel and Gutow 2005b). In general, artificial substrates do not host the same communities as natural substrates (Tyrrell and Byers 2007; Pister 2009; but see Bravo et al. 2011). In the case of floating objects, biotic rafts (e.g., wood, detached kelp) do not float for as long as abiotic rafts (e.g., plastic, tar, pumice), but do provide a food source for rafting organisms, and therefore may be more successful at transporting a variety of species (Donlan and Nelson 2003; Thiel and Gutow 2005b). Items with a complex surface (e.g., pumice, macroalgae holdfasts) may provide better habitat than items with a smooth surface (e.g., plastic bottles; Thiel and Gutow 2005b). The rotational stability of the rafting object may also affect the diversity of the attached assemblage—pieces with fewer changes in orientation have greater species richness and cover than less stable pieces (Bravo et al. 2011; Bryan et al. 2012). Fouling also increases the specific density of the raft, which may cause sinking in the water column and potentially a subsequent rise to the surface if fouling organisms die or are removed by predators (Ye and Andrady 1991; Moret-Ferguson et al. 2010), though fouling can also help maintain the positive buoyancy of porous rafts (e.g., pumice, foam) by reducing gas permeability (Bryan et al. 2012). Lastly, the physical environment around the raft, such as distance from shore or water temperature, may be more significant to rafting species composition than characteristics of the raft itself (Clarkin et al. 2012). For example, rafts that were colonized in coastal waters may have different species composition than rafts colonized at sea (Astudillo et al. 2009), and the diversity of the rafting community may be enhanced by encounters with larval sources such as islands, reefs, and other shallow-water habitats (Bryan et al. 2012).

Diversity patterns in open-ocean rafting assemblages, particularly plastic-associated assemblages, are largely unexplored. In many ecosystems, diversity is predicted by the species–area curve, in which the number of species increases as a function of available surface area, though the shape of this curve has been a matter of some debate (He and Legendre 1996). Species–area curves can be explained by the concept of island biogeography, which predicts that species diversity is a balance between arrival of species through migration and the loss through extinction, both processes that vary with available habitat area (MacArthur and Wilson 1963). While species–area relationships are one of the most widely observed patterns in ecology, there are exceptions, such as the “small-island effect,” in which the areas of the ecosystems observed

are all too small for a diversity pattern to be detected (Lomolino 2000). It is unknown whether plastic-associated rafting assemblages follow the species–area pattern, particularly since organisms with certain life history traits, such as suspension feeding, are more likely to be successful rafters, especially on abiotic substrata such as plastic (Thiel and Haye 2006).

The light weight and durability of plastic make it a vector for the transport of non-indigenous species. For example, a piece of flotsam with traces of tropical biota, including self-fertilizing corals, was recently discovered in the Netherlands (Hoeksema et al. 2012), and Southern Ocean bryozoans in reproductive condition were found on a beached packing band in Antarctica (Barnes and Fraser 2003). Benthic organisms such as bryozoans, barnacles, and hydroids are commonly found on plastic debris (Aliani and Molcard 2003; Barnes and Milner 2005; Farrapeira 2011). The particular vulnerability of island ecosystems to invasions and the ubiquity of plastic debris on the mid-Pacific islands makes lateral transport of fouling species a matter of particular concern in the North Pacific (McDermid and McMullen 2004). Recently, a non-native hydroid and two ascidians were recorded from debris collected in the Northwest Hawaiian Islands (Godwin et al. 2008). However, most studies have examined beached material, not in situ debris (Winston et al. 1997; Barnes 2002; Barnes and Fraser 2003; Barnes and Milner 2005; Hoeksema et al. 2012; but see Astudillo et al. 2009).

Even when debris does not carry organisms to distant shorelines, debris can provide abundant habitat to fouling organisms. In coastal areas, abundance of floating macroalgae varies between 1 and 1,000 items km^{-2} , occasionally even exceeding values of 10,000 items km^{-2} (Thiel and Gutow 2005a). High densities of abiotic substrates can also occur in the open ocean—one eruption in Tonga was estimated to release over 2.5×10^{12} individual pumice clasts, more than 50 % of which were inhabited by rafting organisms (Bryan et al. 2012). Floating microplastic debris in the subtropical gyres can also reach high densities, such as a median of 425,000 items km^{-3} in the North Pacific subtropical gyre (Goldstein et al. 2012) and a mean of 20,328 items km^{-2} in the North Atlantic subtropical gyre (Law et al. 2010). This increase in habitat has the potential to expand populations of open-ocean rafting species, such as gooseneck barnacles (Whitehead et al. 2011) and oceanic insects (Goldstein et al. 2012; Majer et al. 2012).

In this study, we asked: (a) What taxa are associated with drifting plastic in the North Pacific? (b) Does the number of taxa associated with plastic debris vary with the size of the debris “island?”

Methods

Samples were collected on three cruises, the 2009 Scripps Environmental Accumulation of Plastics Expedition (SEAPLEX), the 2011 Algalita Eastern North Pacific Gyre Expedition, and 2012 Western North Pacific Gyre Expedition (Fig. 1).

For the 2009 samples, floating debris items were opportunistically collected by dip net (39 cm length \times 33.5 cm width, mesh 1 mm). If possible, the entire piece of debris with attached fauna was preserved in either 5 % formalin buffered with sodium borate or 95 % ethanol. An attempt was made to preserve portions of most samples in both preservatives to allow for both morphological and molecular studies. When the item was too large to be preserved, the item was either subsampled (e.g., portions of a tarp were cut and preserved) or the fauna were removed and preserved separately (e.g., in the case of a large fishing buoy). A subset of plastics collected using a standard manta net (0.86 \times 0.2 m) with 333- μ m mesh (Brown and Cheng 1981), towed for 15 min at 0.7–1 m s⁻¹, were also included in this study. For smaller Manta-net-collected debris particles, 50 % aliquots of the net-collected samples were analyzed. Since splitting samples cause the less abundant larger debris items to be undersampled, all Manta-net-collected objects with a diameter of greater than 2 cm were included in this study. For this reason, we found it practical to use the 2-cm cutoff to divide “fragments” from larger objects.

On the 2011 and 2012 expeditions, debris items were collected by dipnet during timed debris observation periods or

opportunistically during other daylight sightings. Debris items were inspected for attached organisms immediately and then taken to shipboard laboratory for microscope inspection, photography, and preservation. If possible, the entire piece of debris with attached fauna was preserved in 5 % formalin as on the 2009 cruise. Where not possible, organisms were removed and preserved separately. Three floating masses of nets, rope, and entangled debris were sampled differently. In 2011, the net mass was examined by divers in the water, who noted associated fishes, collected fouling organisms opportunistically, and subsampled the materials for inspection on board. In 2012, both net masses were inspected in the water first and then hauled on board and dissected on deck for a more thorough collection of fouling organisms.

In the laboratory, objects from the 2009 expedition were examined for rafting fauna under a Wild M-5 dissecting microscope. The preservative was also filtered through 150- μ m Nitex mesh to retain non-attached biota. During the 2011 and 2012 expeditions, organisms and small debris were inspected and photographed on board using a Dino-Lite Premiere digital microscope. All objects were photographed with in situ size references. Two-dimensional surface area was digitally measured using the NIH ImageJ software (Rasband 2012) and calibrated against manual measurements. Because of the flattened shape of most debris objects, we approximated total surface area by multiplying two-dimensional surface area by a factor of two. It should be noted that this approach substantially underestimates the total surface area of complex structures such as rope clumps and net balls.

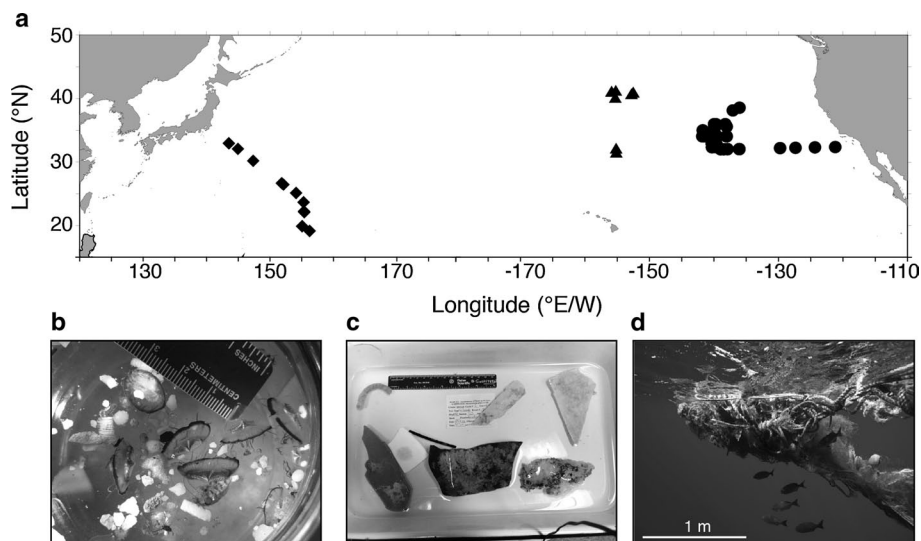


Fig. 1 Map of sampling locations and photographs of representative plastic debris. **a** Locations of debris collection in 2009 (circles), 2011 (triangles), and 2012 (diamonds). **b** Small plastic fragments intermixed with the chondrophore *Velella velella*; collected August 10, 2009, 03:57 GMT, 32° 37.91'N, 140° 18.61'W. **c** Medium plastic

fragments with 15-cm ruler; collected August 11, 2009, 07:30 GMT, 32° 54.99'N, 140° 19.81'W. **d** A large tangle of intermixed fishing-related nets, ropes, and buoys along with other hard plastic debris (“rope clump”); collected May 12, 2012, 03:00 GMT, 22° 13.35'N, 155° 21.17'E

Later identification of preserved specimens in the laboratory was made using dissection or compound microscopes. All fauna were identified to the lowest possible taxonomic level. When objects with different taxonomic resolutions were compared, taxa were collated to comparable levels. For example, *Lepas pacifica*, *L. anatifera*, and *Lepas* spp. were counted as one taxon. To determine whether taxa had previously been documented as rafting, we first consulted the comprehensive lists of rafting taxa given in Thiel and Gutow (2005b). If a given taxa were not listed in Thiel and Gutow (2005b), we conducted a literature search to determine whether we could find other documentation of rafting in the taxa. If we could not find such documentation, the taxa were listed as “not previously documented as rafting.” A complete list of debris locations and associated taxa is given in Supplemental Table 1. We determined the feeding type of each taxon from our own biological knowledge and from reference to the literature as necessary. When the feeding ecology of a specific taxon was unknown, we assigned it to the most probable feeding type. For example, an unidentified hydroid was classified as a “suspension feeder.”

Statistics and figures were generated with the R statistical environment, version R-2.13.1 (R Development Core Team 2012). Debris object areas were log-transformed for ease of display. We used the chi-square test to test whether rafting assemblage traits (e.g., phyla composition, feeding type) varied between cruises and years. We used Kendall's tau rank correlation coefficient to measure the strength of dependence between debris size and number of taxa. For one analysis, both taxa and debris area were linearized using log transformations so that the relationship could be more easily visualized, and analyzed using linear regression (Lomolino 2000) (Fig. 2).

Results

We examined a total of 242 debris objects and identified 95 associated rafting taxa (Table 1). The debris comprised 66 % rigid plastic fragments less than 2 cm in diameter, 21 % rigid plastic fragments or objects ranging from 2 to 100 cm in diameter, 7 % rope clumps, 3 % flexible substrates (e.g., tarps), and 3 % expanded foam (e.g., “Styrofoam”). Debris substrate area ranged from 2.54×10^{-7} to 15 m^2 , with a median of $1.18 \times 10^{-4} \text{ m}^2$.

Representatives of 11 phyla were found, with the most abundant phylum being the Arthropoda, followed by Mollusca and Cnidaria (Fig. 3a). The majority of these taxa were suspension feeders, though omnivores, grazers, and predators were also well represented (Fig. 3b). Slightly more taxa were mobile than were sessile (Fig. 3c). Of all 95 identified taxa, 25 (26 %) had not been previously found

to occur in rafting assemblages (Fig. 3d, Table 1). No differences in the composition of phyla, feeding type, and mobile/sessile taxa were found between cruise years/locations (chi-square test, $P > 0.5$ for all tests).

We found a significant positive correlation between the size of the debris object and the number of taxa found on that object (Fig. 4a, Kendall's tau, $\tau = 0.555$, $N = 242$, $P < 0.001$). This correlation remained significant when the data were linearized through log transformation (Fig. 4b, linear regression, $r^2 = 0.169$, $F_{1,66} = 48.69$, $P < 0.001$), as well as when the four largest items were removed (linear regression, $r^2 = 0.086$, $F_{1,66} = 22.45$, $P < 0.001$). When cruises were examined separately (Fig. S1), there was a significant positive correlation between debris size and taxon richness in 2009 (Kendall's tau, $\tau = 0.561$, $N = 208$, $P < 0.001$) and 2011 (Kendall's tau, $\tau = 0.650$, $N = 13$, $P = 0.003$), but not in 2012 (Kendall's tau, $\tau = 0.062$, $N = 21$, $P = 0.710$). We did not find a relationship between distance offshore and number of taxa.

The eight most taxon-rich phyla also exhibited significant positive relationships between object size and number of taxa (Fig S2, Kendall's tau $P < 0.01$ for all phyla). However, for the phyla that have few taxa (e.g., 1–3 taxa), these relationships are sensitive toward incidentally occurring individuals.

We noted a shallow parabolic shape, in both our overall taxa–area semi-log curve and for some of the phylum-specific curves, such as Arthropoda and Bryozoa. Higher numbers of taxa were found on medium-sized objects (approximately $1 \times 10^{-2} \text{ m}^2$) as compared to slightly larger objects (approximately 1 m^2), though the largest objects (approximately 10 m^2) retained the overall highest numbers of taxa.

Discussion

Composition of rafting assemblage

We found a diverse and widespread rafting assemblage inhabiting North Pacific plastic debris. The majority of taxa were known members of the rafting assemblage such as *Lepas* spp. barnacles and membraniporid bryozoans, but we documented 25 taxa that had not been previously found in rafting assemblages. Many of the previously undocumented taxa were from groups that are known to be prolific and successful rafters, such as the bryozoans, sponges, and peracarid crustaceans (Barnes 2002; Thiel and Gutow 2005b). We were surprised to find a small number of boring organisms rafting on pelagic plastic debris composed of foamed polystyrene. These included the bivalve *Zirfaea*, the shipworm *Teredo*, and a sphaeromatid isopod. While boring organisms are known to colonize rafts of biotic origin, such as wood and algae,

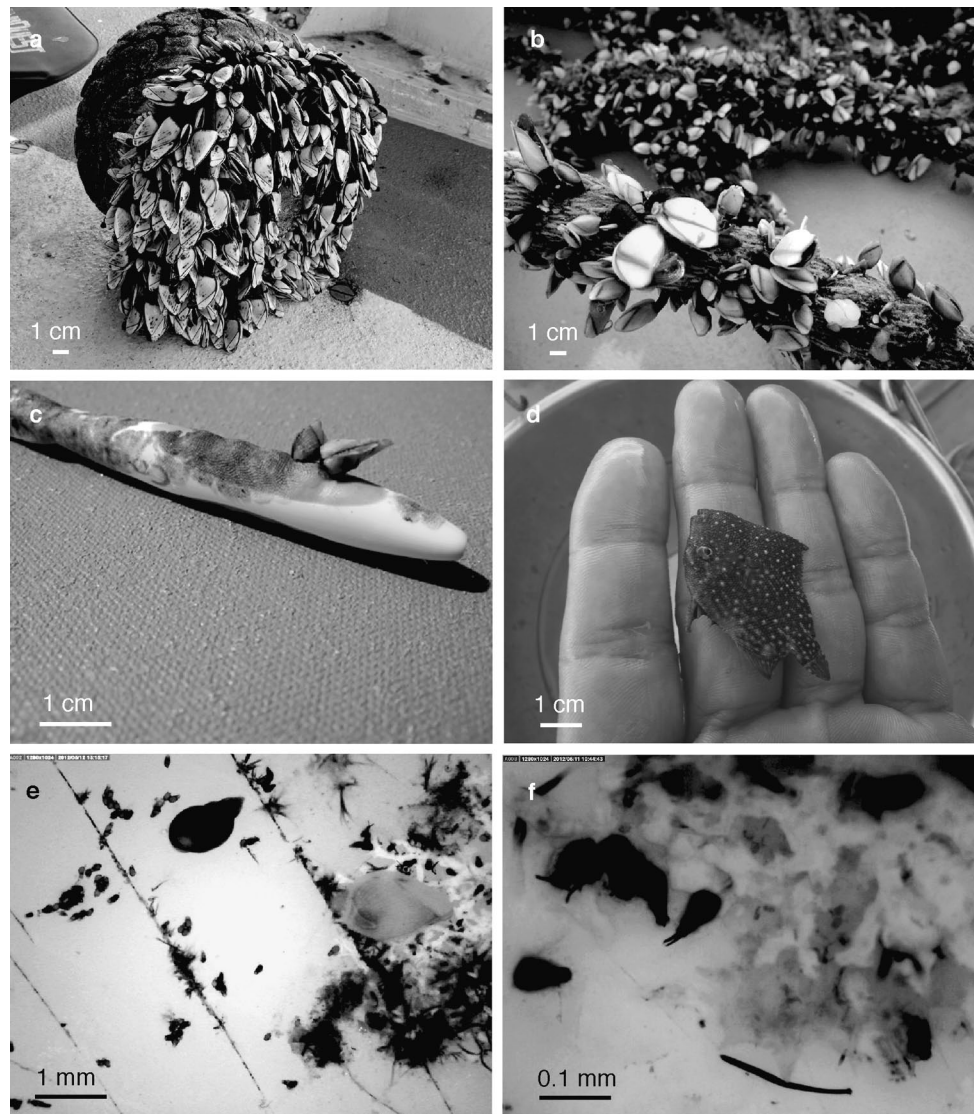


Fig. 2 Photographs of assorted debris. **a** *Lepas* barnacles growing on buoy; collected June 22, 2012, 02:00 GMT, 29°11.9'N, 170°35.2'E. **b** *Lepas* barnacles growing on a rope; collected May 14, 2012, 20:00 GMT, 26°26.56'N, 152°07.44'E. **c** Two *Lepas* barnacles and membraniporid bryozoans growing on a toothbrush handle, collected June 17, 2012, 02:00 GMT, 15°26.3'N, 150°30.0'E. **d** A juvenile triggerfish *C. maculata* found associated with a bleach bottle, collected May

12, 2012, 21:00 GMT at 22°11.06'N, 155°22.07'E. **e** Close view of fragment showing folliculinid ciliates and other organisms; collected May 10, 2012, 22:15 GMT, 19°53.05'N, 155°04.22'E. **f** Close view of folliculinid ciliates showing the two pericytostomial wings extending from the lorica, collected May 10, 2012, 22:15 GMT, 19°53.05'N, 155°04.22'E

they are relatively rare on plastic debris (Thiel and Gutow 2005b; Thiel and Haye 2006), although sphaeromatid isopods are known to burrow in polystyrene floats in coastal ecosystems (Davidson 2012).

Another organism of particular interest was the folliculinid ciliate (*Halofolliculina* spp.), found in abundance on some western Pacific plastic debris. These ciliates are pathogens that cause skeletal eroding band (SEB) disease in corals (Rodriguez et al. 2009). Though originally thought to be limited to the Indian Ocean and South Pacific, SEB disease was discovered in Caribbean corals in 2004 (Croquer

et al. 2006) and in Hawaiian corals in 2010 (Palmer and Gates 2010). The mechanism behind the spread of SEB is not known (Croquer et al. 2006), but since the Hawaiian Islands are highly impacted by plastic debris collected by the North Pacific subtropical convergence zone (Dameron et al. 2007), it is possible that debris facilitated the dispersal of *Halofolliculina* to this area. Like many rafting substrates, plastic debris has the potential to disperse non-ciliate pathogens, such as viruses, but the role of debris as a disease fomite has been little studied (Maso et al. 2003; Pham et al. 2012).

Table 1 Rafting taxa

Phylum	Class	Order	Finest taxon identified	Year observed	Previously documented as rafting
Annelida	Polychaeta	Aciculata	<i>Eunice</i> spp.	c	1
Annelida	Polychaeta	Amphinomida	<i>Amphinome rostrata</i>	c	1
Annelida	Polychaeta	Amphinomida	<i>Hipponoe gaudichaudi</i>	a, b	1
Annelida	Polychaeta	Phyllodocida	<i>Halosydna</i> spp.	b	N
Annelida	Polychaeta	Phyllodocida	Nereididae	c	1
Annelida	Polychaeta	Phyllodocida	<i>Nereis</i> spp.	c	1
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	c	1
Annelida	Polychaeta	Sabellida	<i>Salmacina</i> spp.	c	N
Annelida	Polychaeta	Sabellida	Subfamily Serpulinae	c	1
Annelida	Polychaeta	Sabellida	Subfamily Spirorbinae	a, c	1
Arthropoda	Malacostraca	Amphipoda	<i>Caprella</i> spp.	a, c	1
Arthropoda	Malacostraca	Amphipoda	<i>Elasmopus</i> spp.	a	1
Arthropoda	Malacostraca	Amphipoda	Hyalidae	a	1
Arthropoda	Malacostraca	Amphipoda	Isaeidae	b	N
Arthropoda	Malacostraca	Amphipoda	Pleustidae	c	N
Arthropoda	Malacostraca	Amphipoda	Stenothoidae	a	1
Arthropoda	Malacostraca	Amphipoda	Suborder Gammaridea	c	1
Arthropoda	Malacostraca	Decapoda	<i>Chorilia</i> spp.	c	N
Arthropoda	Malacostraca	Decapoda	Superfamily Majoidea	c	1
Arthropoda	Malacostraca	Decapoda	Megalopae	b	1
Arthropoda	Malacostraca	Decapoda	<i>Palaemon affinis</i>	c	1
Arthropoda	Malacostraca	Decapoda	<i>Pilumnus</i> spp.	c	N
Arthropoda	Malacostraca	Decapoda	<i>Plagusia</i> spp.	c	1
Arthropoda	Malacostraca	Decapoda	<i>Plagusia squamosa</i>	a	1
Arthropoda	Malacostraca	Decapoda	<i>Planes cyaneus</i>	a, c	1
Arthropoda	Malacostraca	Decapoda	<i>Planes minutus</i>	a	1
Arthropoda	Malacostraca	Decapoda	<i>Planes</i> spp.	b, c	1
Arthropoda	Malacostraca	Isopoda	Cirolanidae	a	1
Arthropoda	Malacostraca	Isopoda	<i>Idotea</i> spp.	a, b, c	1
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	a	1
Arthropoda	Maxillopoda	Harpacticoida	Harpacticoida	a	1
Arthropoda	Maxillopoda	Kentrogonida	<i>Heterosaccus</i> spp.	c	N
Arthropoda	Maxillopoda	Lepadiformes	Barnacle cyprids	a	1
Arthropoda	Maxillopoda	Lepadiformes	<i>Lepas anitifera</i>	a, c	1
Arthropoda	Maxillopoda	Lepadiformes	<i>Lepas pacifica</i>	a	1
Arthropoda	Maxillopoda	Lepadiformes	<i>Lepas</i> spp.	a, b, c	1
Arthropoda	Maxillopoda	Sessilia	(<i>Amphi</i>) <i>balanus amphitrite</i>	b	1
Arthropoda	Maxillopoda	Sessilia	<i>Chthamalus</i> spp.	c	N
Arthropoda	Maxillopoda	Sessilia	<i>Megabalanus rosa</i>	c	N
Arthropoda	Pycnogonida	Pantopoda	<i>Phoxichilidium quadridentatum</i>	a	N, may encyst in hydroids ²
Arthropoda	Pycnogonida	Unknown	Unknown	c	1
Bryozoa	Gymnolaemata	Cheilostomatida	<i>Bugula</i> spp.	a, b, c	1
Bryozoa	Gymnolaemata	Cheilostomatida	<i>Jellyella eburnea</i>	a	1
Bryozoa	Gymnolaemata	Cheilostomatida	<i>Jellyella tuberculata</i>	a	1
Bryozoa	Gymnolaemata	Cheilostomatida	<i>Jellyella/Membranipora</i>	b,c	1
Bryozoa	Gymnolaemata	Cheilostomatida	<i>Membranipora tenella</i>	a	1
Bryozoa	Gymnolaemata	Ctenostomatida	<i>Bowerbankia</i> spp.	a	1

Table 1 continued

Phylum	Class	Order	Finest taxon identified	Year observed	Previously documented as rafting
Bryozoa	Gymnolaemata	Ctenostomatida	<i>Victorella</i> spp.	a	N, may disperse through fragmentation of substrate ³
Bryozoa	Stenolaemata	Cyclostomatida	<i>Filicrisia</i> spp.	a	N
Bryozoa	Stenolaemata	Cyclostomatida	<i>Stomatopora</i> spp.	a	N
Bryozoa	Stenolaemata	Cyclostomatida	<i>Tubulipora</i> spp.	a	1
Chordata	Perciformes	Actinopterygii	<i>Abudefduf</i> spp.(<i>vaigiensis</i> ?)	b, c	N/A
Chordata	Perciformes	Actinopterygii	<i>Canthidermis maculata</i>	c	N/A
Chordata	Perciformes	Actinopterygii	<i>Chirolphis</i> spp.	c	N/A
Chordata	Perciformes	Actinopterygii	<i>Coryphaena hippurus</i>	b	N/A
Chordata	Perciformes	Actinopterygii	<i>Elagatis bipinnulata</i>	b	N/A
Chordata	Perciformes	Actinopterygii	<i>Histrio histrio</i>	c	N/A
Chordata	Perciformes	Actinopterygii	<i>Kyphosus</i> spp. (<i>vaigiensis</i> ?)	b, c	N/A
Chordata	Perciformes	Actinopterygii	<i>Meiacanthus</i> spp.	c	N/A
Chordata	Perciformes	Actinopterygii	<i>Seriola rivoliana</i>	c	N/A
Chordata	Unknown	Unknown	Beige fish eggs	c	1
Chordata	Unknown	Unknown	Blue fish eggs	c	1
Chordata	Unknown	Unknown	Fish eggs	a,b	1
Ciliophora	Heterotrichea	Heterotrichida	<i>Halofolliculina</i> spp.	c	N on plastic, documented on wood ⁴
Cnidaria	Anthozoa	Actinaria	Actiniidae	b	1
Cnidaria	Anthozoa	Actinaria	<i>Anthopleura</i> spp.	a,b	N, may disperse through detachment ⁵
Cnidaria	Anthozoa	Actinaria	<i>Calliactus</i> sp.	c	7
Cnidaria	Anthozoa	Actinaria	<i>Metridium</i> spp.	a	N, may disperse through detachment ⁵
Cnidaria	Anthozoa	Actinaria	Hormathiidae	c	1
Cnidaria	Anthozoa	Scleractinia	stony coral	b	1
Cnidaria	Hydrozoa	Leptothecata	<i>Clytia gregaria</i>	a	N, though 9 other <i>Clytia</i> species documented as rafting ¹
Cnidaria	Hydrozoa	Leptothecata	<i>Obelia</i> spp.	a	1
Cnidaria	Hydrozoa	Leptothecata	<i>Plumularia setacea</i>	a	1
Cnidaria	Hydrozoa	Unknown	Hydroid	b, c	1
Echinodermata	Ophiuroidea		<i>Ophiuroidea</i> spp. 1	c	
Echinodermata	Ophiuroidea		<i>Ophiuroidea</i> spp. 2	c	
Echinodermata	Ophiuroidea		<i>Ophiuroidea</i> spp. 3	c	
Foraminifera	Polythalamea	Rotallida	<i>Planulina ornata</i>	a	N
Mollusca	Bivalvia	Arcoidea	Arcidae	c	N
Mollusca	Bivalvia	Myoida	<i>Teredo</i> spp.	c	1
Mollusca	Bivalvia	Myoida	<i>Zirfaea</i> spp. (<i>pilsbryi</i> ?)	b	N
Mollusca	Bivalvia	Mytiloidea	<i>Mytilus galloprovincialis</i>	a, c	1
Mollusca	Bivalvia	Ostreoida	<i>Crassostrea gigas</i>	b, c	1
Mollusca	Bivalvia	Pectinoidea	<i>Chlamys</i> spp.	c	1
Mollusca	Bivalvia	Pteroida	<i>Pinctada</i> spp.	c	1
Mollusca	Bivalvia	Unknown	Lower valve of oyster	c	1
Mollusca	Gastropoda	Caenogastropoda	<i>Litiopa melanostoma</i>	c	1

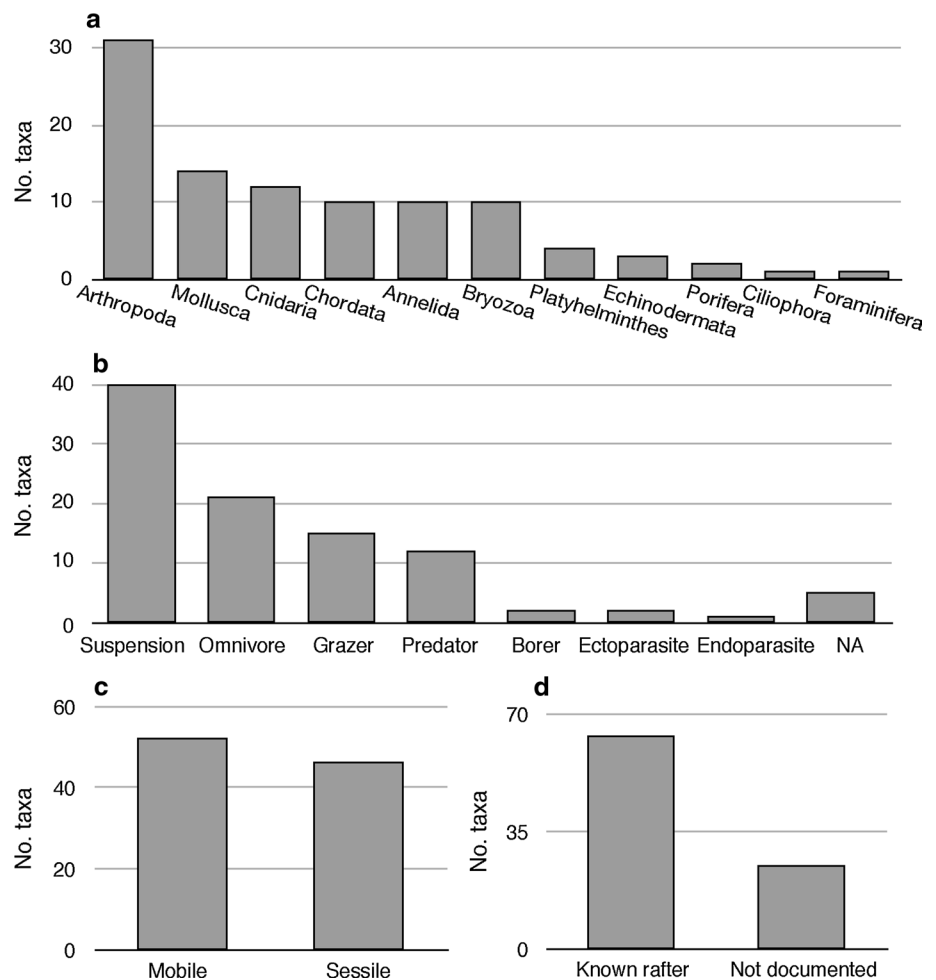
Table 1 continued

Phylum	Class	Order	Finest taxon identified	Year observed	Previously documented as rafting
Mollusca	Gastropoda	Littorinimorpha	<i>Erronea</i> spp.	c	N, may have widespread larval transport ⁶
Mollusca	Gastropoda	Nudibranchia	<i>Fiona pinnata</i>	a, b, c	1
Mollusca	Gastropoda	Nudibranchia	<i>Fiona pinnata</i> eggs	a	1
Mollusca	Gastropoda	Pleurobranchomorpha	<i>Berthella</i> spp.	c	N
Mollusca	Gastropoda	Superfamily Pyramidelloidea	<i>Odostomia (Evalea)</i> <i>tenuisculpta</i>	a	N
Platyhelminthes	Rhabditophora	Polycladida	Rhabditophora	c	1
Platyhelminthes	Rhabditophora	Rhabdozoa	Rhabdozoa	c	1
Platyhelminthes	Turbellaria	Unknown	Flatworm	a, b	1
Platyhelminthes	Turbellaria	Unknown	Flatworm	b	1
Porifera	Calcarea	Leucosolenida	<i>Sycon</i> spp.	b, c	N
Porifera	Demospongiae	Halichondrida	<i>Halichondria panacea</i>	a	N

Years observed are a = Eastern Pacific 2009; b = Eastern Pacific 2011; c = Western Pacific 2012. Previously documented as rafting are N = Not listed as rafting in the scientific literature, N/A = fishes

¹ listed in Thiel and Gutow 2005b, ² Lovely 2005, ³ Carter et al. 2010, ⁴ Matthews 1963, ⁵ Riemann-Zürneck 1998, ⁶ Emerson and Chaney 1995, ⁷ Bryan et al. 2012

Fig. 3 Characteristics of rafting taxa. **a** Phyla found on or around floating plastic debris. **b** Feeding types of rafting taxa. NA denotes eggs. **c** Mobile taxa versus sessile taxa. Fishes are excluded. **d** Taxa that have previously been documented to occur in rafting communities versus taxa that have not been documented. There was no statistical difference between cruise years/locations (chi-square test, $P > 0.5$ for all tests) for these analyses, so data from all cruises were combined in this figure. $N = 95$ taxa



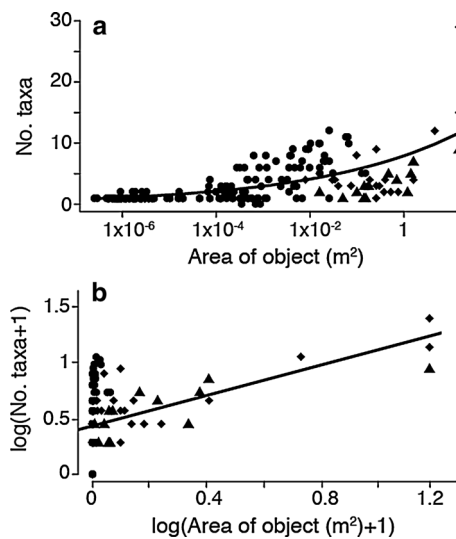


Fig. 4 Number of taxa versus surface area (m^2) of debris object. **a** Semilog plot. *Solid line* is an exponential nonlinear least squares regression. Kendall's tau, $\tau = 0.555$, $P < 0.001$. **b** Log–log plot. *Solid line* is a linear regression (linear regression, $r^2 = 0.169$, $F_{1,66} = 48.69$, $P < 0.001$). Symbols in both plots correspond to year and location of collection: eastern Pacific 2009 is shown in *circles*, eastern Pacific 2011 in *triangles*, and western Pacific 2012 in *diamonds*. Note that many of the symbols denoting small plastic objects overlap, making the sample size hard to discern visually. $N = 242$ debris objects

Origin of rafting organisms

Many of the rafting taxa found are known invaders, but could have come either from their native range or from an area in which they are already established as a non-native species. These include the acorn barnacle *Megabalanus rosa*, native to Japan but an invasive species in Australia, and the mussel *Mytilus galloprovincialis* and acorn barnacle *Amphibalanus amphitrite*, which are invasive to the eastern Pacific (Fofonoff et al. 2012). Other taxa may have settled onto debris in coastal areas and been transported offshore (Astudillo et al. 2009), such as the bryozoan *Victorella* spp., which primarily occurs in estuarine waters (Carter et al. 2010).

Because most of the fauna present were either known members of the North Pacific rafting assemblage or widely distributed taxa, the source of the debris objects could not be determined from the associated assemblage. We know of no other reliable way to age or source plastic debris (though see the general analysis of net type in Jacobsen et al. 2010). Even debris with some identifying markings or text in a particular language cannot always be attributed to a country of origin due to the extent of international trade and the variety of household items used on ships.

The transport of invasive species on debris originating during the March 11, 2011, Tohoku Earthquake and

subsequent tsunami event has received much attention recently, especially regarding objects such as docks that harbor entire communities of coastal organisms (Choong and Calder 2013; Gewin 2013). It is possible that some debris collected during the 2011 and 2012 expeditions originated from the Japan tsunami. However, we believe this is unlikely, since both expeditions occurred outside of the locations where high tsunami debris concentrations were predicted to occur at the time of the expedition (Lebreton and Borrero 2013).

Relationship between number of taxa and debris size

We found a greater number of taxa on larger debris items than on smaller items. A positive relationship between object size and taxa number has also been observed in algal rafts (Ingólfsson 1995; Hobday 2000; Clarkin et al. 2012), fish aggregation devices (Nelson 2003), and pumice (Bryan et al. 2012). The greater number of taxa on larger objects could be a stochastic effect. If individuals are randomly distributed over all floating objects available, then larger objects would receive more species. However, this relationship may also be driven by both physical and biological factors. Physically, larger objects are more likely to remain buoyant, even after developing a substantial rafting assemblage (Thiel and Gutow 2005a). Smaller objects with a substantial rafting assemblage may have become negatively buoyant and were therefore not sampled by this study or by other studies focusing on material at the sea surface. In addition, some objects were likely to have entered the water without attached biota (e.g., a toothbrush), while some objects were likely to have had some attached biota at the time they were lost (e.g., an eel trap). Larger items were primarily associated with fishing activities and may be more likely to have a higher number of taxa due to previous attachments.

Biological interactions, as predicted by island biogeography, may also be an important driver of the positive species–area relationship on pelagic plastic debris. As on islands, the rate of migration to large pieces of plastic debris may exceed the rate of extinction (Simberloff 1976). Higher rates of migration to larger objects could be driven by larval settlement. For example, due to their greater surface area, larger objects may be more likely to give off the appropriate cues for larval settlement (Rodriguez et al. 1993). Larger objects may also be easier for fishes to detect through visual and auditory cues (Dempster and Kingsford 2003). Furthermore, they are more stable at the sea surface, which is an important driver of diversity (Bravo et al. 2011; Bryan et al. 2012). Large items without spatial stability may contain low diversity, such as a meter-long cylindrical polystyrene buoy that “rolled” along the sea surface (H.S.C. *pers. obs.*). Lastly, successional stage may

influence diversity. A study in the western Pacific found that diversity was highest during early stages of succession and then reduced by *Lepas* dominance (Tsikhon-Lukanina et al. 2001). The authors suggested that diversity may increase once more at later successional stages, which they define as being dominated by bivalves. However, floating debris in their study never reached this stage, perhaps due to lack of physical stability or limited larval supply. A study on algal rafts suggested that the separation and exchange of rafting materials may affect the successional progression, which may also apply to some marine debris (e.g., rope and net masses) but may not apply to solid plastic objects that are less likely to coalesce (Clarkin et al. 2012).

We have two potential explanations for the shallow parabolic shape of some of the taxa–area semi-log curves presented here: (1) it could be an artifact of different sampling methodologies for medium and large objects; (2) higher predator abundance on large objects suppresses prey diversity. We cannot rule out the parabola as a sampling artifact, because medium objects (e.g., plastic fragments) were preserved without subsampling, while large objects (e.g., buoys) had to be subsampled at sea. The difference in preservation strategy could have caused inconspicuous taxa on large objects to be undersampled. To address the sampling issue, future studies should consider subsampling larger items with non-selective methodology such as suction.

However, it is also possible that there is a threshold debris size beyond which fish and decapod predators suppress prey taxa diversity through direct predation and/or non-consumptive predator effects (Matassa and Trussell 2011). Some epipelagic fishes preferentially associate with fouled rafting objects as opposed to unfouled rafting objects, suggesting that some of these fishes may prey on rafting invertebrates (Nelson 2003, Thiel and Gutow 2005b), though other studies have not found significant predation on the fouling community (Ibrahim et al. 1996; Nelson 2003; Vassilopoulou et al. 2004). Most fishes observed in this study were associated with the three net and rope masses, with the exception of one juvenile triggerfish (*Canthidermis maculata*) on a bleach bottle and a school of sergeant majors (*Abudefduf* spp.) inside a plastic crate. The net-associated fishes exhibited all three types of behavior identified by Hirosaki (1960) for macroalgae-associated fishes: staying almost exclusively within the net mass, such as the sargassum frogfish (*Histrio histrio*); remaining underneath or around the mass in close association, such as the sergeants; and swimming around the mass without close association, such as the mahi mahi (*Coryphaena hippurus*). We also observed fish entangled in net masses that were still alive, recently dead, and partially decomposed. The conspicuously low abundance or absence of some species such as *Lepas* spp. and *Halobates* spp. eggs on net masses compared with isolated fragments may be partially

attributed to these net-mass-associated fishes. For example, the forward half of a small fishing boat floating upright in the western Pacific had more than 50 associated individual fish, but very little attached biota (M.E. pers. obs.).

Plastic-associated rafting organisms may also be impacting the pelagic ecosystem by reworking the organic particle size spectrum through ingestion and egestion (Mook 1981). Suspension-feeding rafting organisms prey on a variety of particle sizes, from 3 to 5 μm for *Mytilus* mussels (Lesser et al. 1992), 10–20 μm for bryozoans (Pratt 2008), 20–125 μm for caprellid amphipods (Caine 1977), and 0.5 to more than 1 mm for lepadid barnacles and hydroids (Evans 1958; Boero et al. 2007; Goldstein and Goodwin 2013). This size range encompasses much of the non-microbial organic particle size spectrum of the oligotrophic North Pacific (Sheldon et al. 1972). Since organic particle size determines whether energy flows into the microbial loop or into the metazoan food web, large-scale alterations in particle size could substantially influence the species composition of the North Pacific subtropical gyre (Karl et al. 2001). Future research should also consider phytoplankton and microbial interactions with pelagic plastic macrodebris (Maso et al. 2003; Zettler et al. 2013; Carson et al. 2013).

Though the majority of plastic debris items in the North Pacific are small fragments (Goldstein et al. 2013), we found in this study that such particles carry few taxa, most of which are known subtropical rafters such as *Jellyella* or *Membranipora* bryozoans. We found the majority of displaced taxa on large items such as net balls, though the coral pathogen *Halofolliculina* spp. was found on medium-sized plastic fragments (0.03–0.1 m^2). Species introductions from beached debris are most likely to occur on surfaces similar to the hard raft substrate (i.e., bedrock shorelines) and during large debris deposition events (i.e., storms). While debris removal operations are important to engaging the public on marine debris issues, they are unlikely to significantly reduce the chances of non-native species introductions from plastic debris. This is because coastal cleanups frequently occur on sandy beaches that are inherently inhospitable to rafting organisms and at predetermined dates unlikely to coincide with major debris deposition events. While some rapid-response operations to large debris beachings, such as ships and docks originating from the 2011 Japanese tsunami event, may have been effective in preventing species introductions in limited circumstances, large-scale debris cleanup on rocky, remote shores is impracticable. Efforts to prevent debris input from both coastal sources (e.g., urban areas) and ocean sources (e.g., fishing debris) are likely the most efficient means of controlling debris-mediated species introductions.

Durable plastic “islands” are hosts to a diversity of coastal organisms in the pelagic environment, but the ecological role of plastic-associated rafting assemblages on

the open ocean remains unclear. Whether or not the plastic rafts introduce new species to distant coastal regions, the consequences of these “misplaced” organisms to open-ocean ecosystems, especially in debris-accumulation zones, merits further study. However, any potential impacts of the debris-associated rafting community on coastal or pelagic ecosystems can be most effectively limited by an overall reduction in the quantity of plastic pollution introduced into the marine environment.

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