



***Biflustra irregularata* (Cheilostomata: Membraniporidae): A tsunami debris rafted Indo-Pacific bryozoan found in the eastern Pacific Ocean**

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Abstract

Previous studies documented colonies of the cheilostome bryozoan *Biflustra irregularata* rafting across the Pacific Ocean on debris from the 2011 Great East Japan megathrust earthquake and resulting tsunami. They arrived in the eastern Pacific on floating non-biodegradable tsunami debris from 2014 to 2016. Based on a newly discovered occurrence of this species off the west coast of Mexico, we report that this species has successfully expanded its range from the Indo-Pacific to the northeast Pacific following this dispersal event. Colonies were found encrusting barnacles on spiny lobsters from the southeastern Gulf of California.

Key words: bryozoans, range expansion, rafting, tsunami debris

Introduction

The 2011 Great East Japan megathrust earthquake and resulting tsunami generated the most diverse and best documented transoceanic species dispersal event in recorded history (Carlton *et al.* 2017). In the years following, an unprecedented number of poriferan, cnidarian, arthropod, molluscan, bryozoan, and other species were found rafting on debris transported by this tsunami to the Pacific coast of the U.S.A. (Calder *et al.* 2014; Elvin *et al.* 2018; McCuller & Carlton 2018; Miller *et al.* 2018a; Tanaka *et al.* 2018). Dispersal events like this have important implications for marine biogeography and long-term evolutionary consequences due to expanded gene flow (Briggs 1974; Thiel & Haye 2006).

Bryozoans, in particular, are one of the most ubiquitous faunal groups on marine debris (Barnes 2002; Thiel & Gutow 2005). They effectively exploit naturally occurring floating marine debris by fouling pieces of pumice (Bryan *et al.* 2012; Rust 2015), tar balls (Shaw & Mapes 1979), woody debris (Donlan & Nelson 2003), sea grasses (Keough & Chernoff 1987; Worcester 1994), and algae (Bushing 1994; Kuhlenkamp & Kind 2013; López *et al.* 2018; Avila *et al.* 2020). Bryozoans also have a long evolutionary history of hitchhiking on motile living host substrates with hard exoskeletons (Key *et al.* 2010, 2017; Wyse Jackson & Key 2014; Wyse Jackson *et al.* 2014; Key & Schweitzer 2019). Invasive bryozoans also hitchhike on anthropogenic floating substrates such as plastic (Winston 1982; Stevens *et al.* 1996; Winston *et al.* 1997; Barnes & Sanderson 2000; Barnes & Fraser 2003; Barnes & Milner 2005), ship bottoms (Ryland 1965; Kubanin 1979; Watts *et al.* 1998; Láruson *et al.* 2012; McCann *et al.* 2015), and in ship ballast water (Carlton 1985; Carlton & Geller 1993).

Following the 2011 tsunami, 289 living Japanese cyanobacteria, algae, invertebrate and fish species were found in the eastern Pacific on non-biodegradable Japanese Tsunami Marine Debris (JTMD) (Carlton *et al.* 2017; Hansen *et al.* 2018). Of those, 49 were bryozoans (McCuller & Carlton 2018). After the mussel *Mytilus galloprovincialis* Lamarck, 1819, cheilostomes were the second [*Scruparia ambigua* (d'Orbigny, 1841)], third [*Aetea anguina* (Linnaeus, 1758)/*Callaetea* sp.], and sixth (*Bugula tsunamiensis* McCuller *et al.*, 2018) most abundant living Japanese species on JTMD (Carlton *et al.* 2017; McCuller & Carlton 2018).

Of interest to this study is the Indo-Pacific species *Biflustra irregulata* (Liu, 1991) which has been found on JTMD (Carlton *et al.* 2017; McCuller & Carlton 2018). Until this study, it had not been detected in the eastern Pacific since those initial post-tsunami studies (Table 1). Our hypothesis is that this species survived the rafting trip across the Pacific Ocean and is now successfully reproducing in the eastern Pacific. We test this by documenting the pre- and post-tsunami geographic distribution of *B. irregulata* including a newly discovered occurrence off the west coast of Mexico.

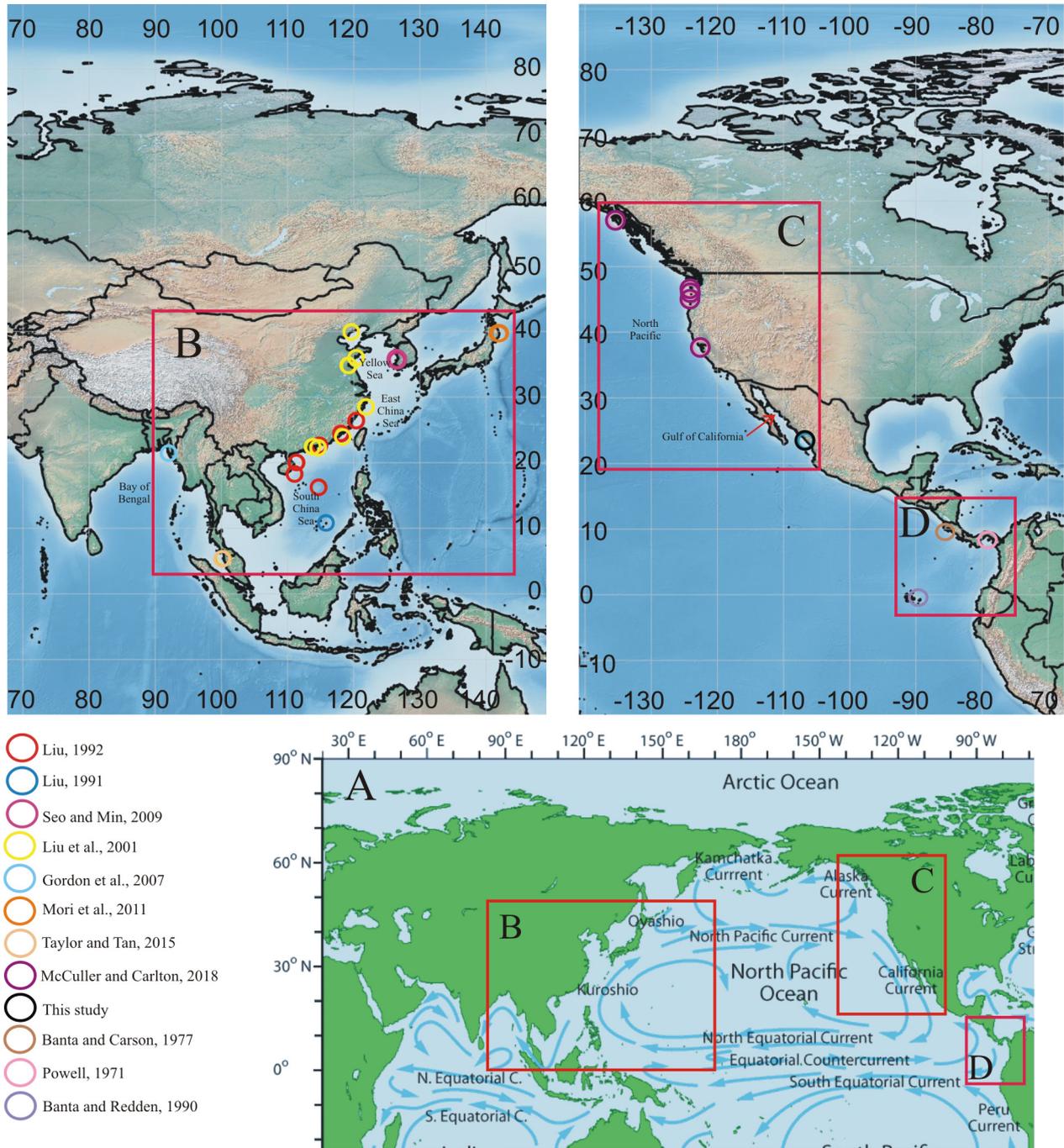


FIGURE 1. Map showing the North Pacific Ocean currents (A) relative to the reported occurrences of *Biflustra irregulata* before (B) and after (C) the 2011 tsunami (Mori *et al.* 2011). See Table 1 for details. Three pre-tsunami reports of *B. arborescens* in the eastern Pacific are shown for comparison (D).

Material and methods

The colonies for this study came from two lobsters caught by local fishermen with a gillnet at a depth of about 13 m, in the southeastern Gulf of California, off Mármol (north of Mazatlán; approximately 23°26'N, 106°40'W) on 29 March 2017 (Fig. 1). One acorn barnacle (*Balanus trigonus* Darwin, 1854) fouled by bryozoans was found on each lobster. The barnacles were 8–9 mm in diameter and located in the gastric region of the ventral cephalothorax of one specimen of an immature female of the green spiny lobster *Panulirus gracilis* Streets, 1871 (carapace length: 91 mm) (Fig. 2A) and one mature female of the blue spiny lobster *Panulirus inflatus* (Bouvier, 1895) (carapace length: 70 mm) (Fig. 2B). The lobsters and barnacles were photographed and the bryozoan colonies imaged with a scanning electron microscope (Fig. 3). The specimens were archived in the holdings of the Regional Collection of Marine Invertebrates at the Universidad Nacional Autónoma de México in Mazatlán, Mexico (ICML-EMU-13151).

To resolve the taxonomic assignment of the bryozoans, we culled the literature for data on autozoid length and width for any related species as done by Taylor & Tan (2015). Where such morphometric data were absent, and including the colonies from this study, we measured these characters from SEM images to the nearest 0.01 mm. Key's (2020) power function growth curve model was used to estimate colony age in encrusting cheilostomes based on the number of autozooids in the colony. For this, we counted the minimum number of autozooids in each colony to estimate minimum colony age.

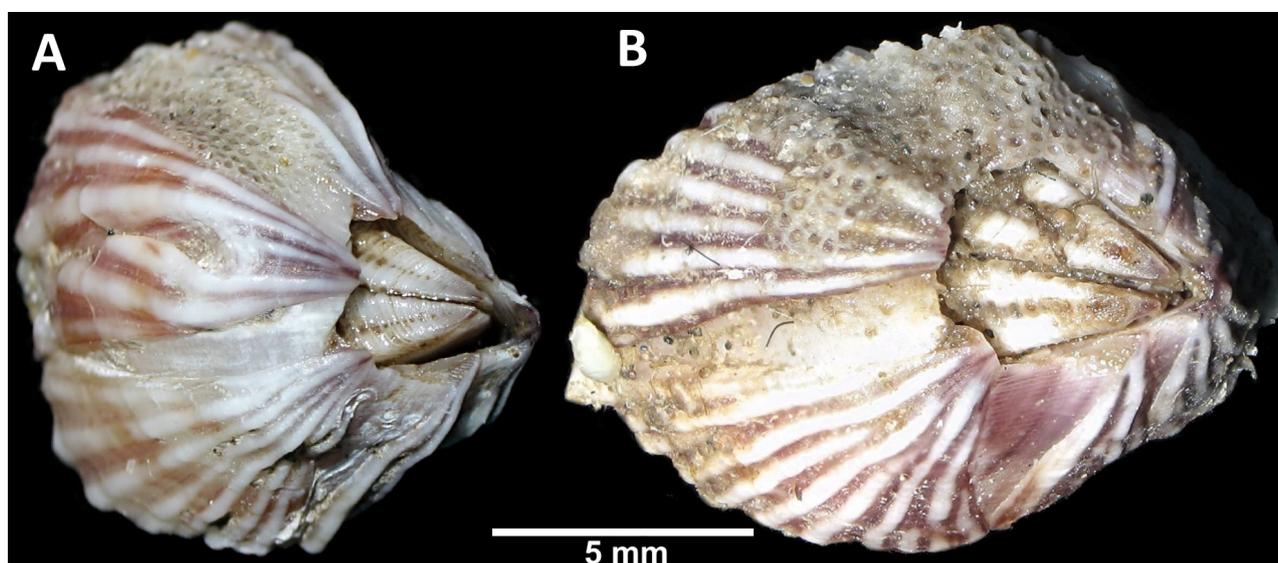


FIGURE 2. *Biflustra irregulata* bryozoan colonies encrusting *Balanus trigonus* barnacles on host spiny lobsters *Panulirus gracilis* (A) and *P. inflatus* (B) from the Gulf of California, Mexico.

Results

Taxonomy

The encrusting bryozoan species was identified as *Biflustra irregulata*, a species originally defined by Liu (1991) and reiterated (Liu 1992) as *Membranipora irregulata*. Tilbrook (2006) tentatively moved it into the genus *Biflustra*. Gordon *et al.* (2007) confirmed this, and Liu & Liu (2008) followed suit. Taylor & Tan (2015) tentatively moved it to *Acanthodesia* (i.e., *A. cf. irregulata*). Vieira *et al.* (2016) and Almeida *et al.* (2018) disagreed with Taylor & Tan (2015) and placed it back in *Biflustra*. Gordon (2016) also placed it in *Biflustra*.

Biflustra irregulata (Liu, 1991)

(Fig. 3)

Membranipora irregulata Liu 1991: 57, 78, fig. 1A–E.

Membranipora irregulata: Liu 1992: 124, figs 14–18; Liu *et al.* 2001: 416, pl. 10, figs 3–6; Seo & Min 2009: 20, fig. 2.
Biflustra irregulata: Tilbrook 2006: 354; Gordon *et al.* 2007: 46, fig. 1D; Liu & Liu 2008: 816; Gordon 2016: 606; McCuller & Carlton 2018: 147, 148, fig. S9A, B.
Acanthodesia cf. irregulata: Taylor & Tan 2015: 9, fig. 3G–L.
 Not *Biflustra irregulata*: Almeida *et al.* 2018: 1470, fig. 4.
 Not? *Biflustra irregulata*: Carlton *et al.* 2019: table S1.

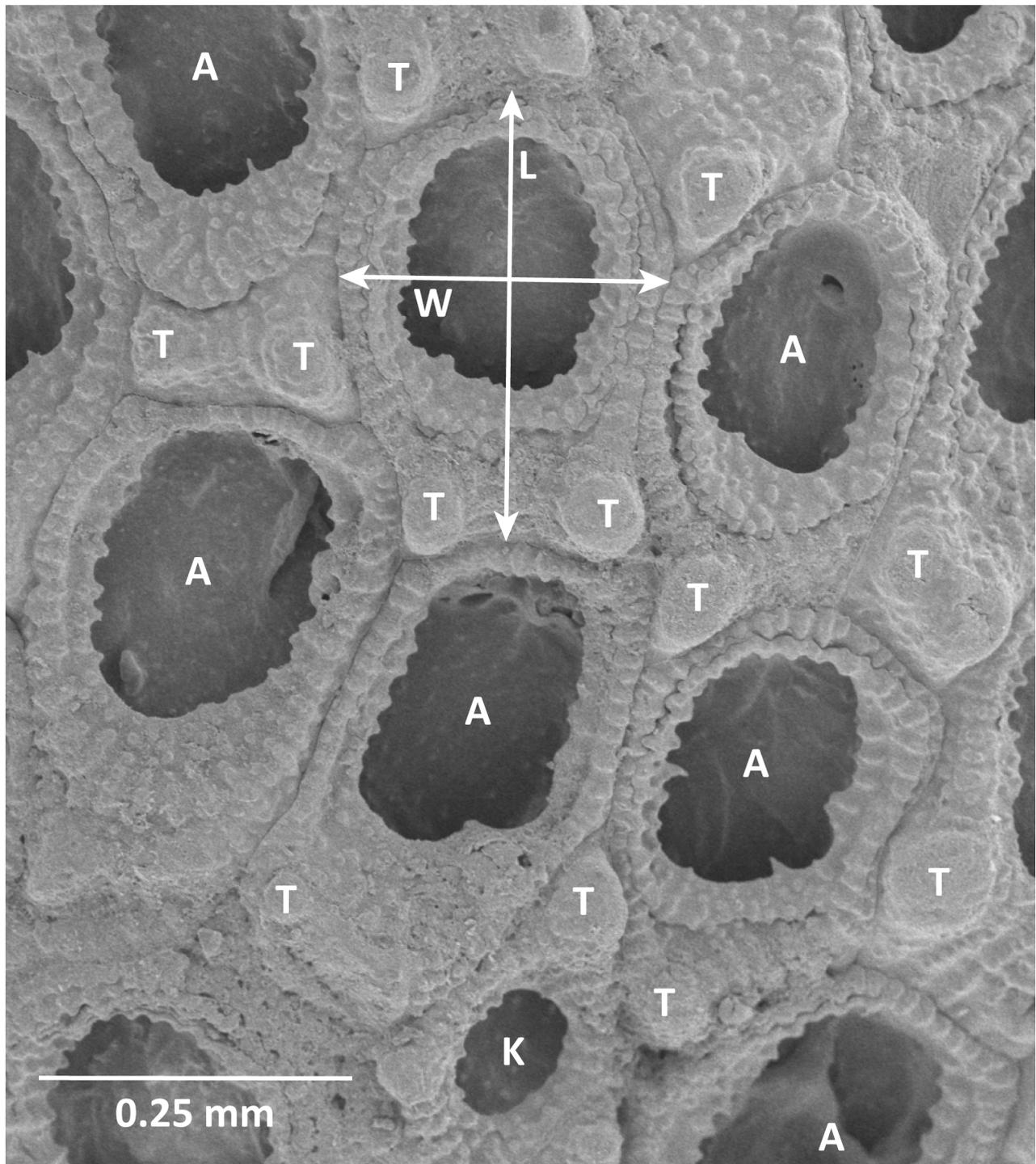


FIGURE 3. SEM photomicrograph of *Biflustra irregulata* bryozoan colony shown in Fig. 2A. A: autozooid, K: kenozooid, T: tubercle, L: autozooid length, W: autozooid width. Note mural pores in the upper right zooid marked A.

Description. Colonies encrusting. Autozooids arranged quincuncially, rectangular to subhexagonal and vary with substrate relief, distal end rounded, proximal margin angular, both usually concave proximally, sometimes narrow proximally, with relatively high lateral beaded mural rims separated from adjacent zooids by chitinous interzooidal

grooves. No gymnocyst. Opesia elongate-oval and occupying nearly all of frontal surface, almost completely bordered by a narrower cryptocystal rim disto-laterally and a wider cryptocystal shelf proximally. Proximal cryptocyst well-developed, coarsely serrated/spinose in its inner border, densely granular on its surface. One or two globose tubercles at the proximolateral corners of the cryptocyst of some zooids. Kenozooids smaller and intercalated among larger autozooids, variable in size and shape, often developed at growth irregularities.

Remarks. We did not observe the following characteristics of the species that others have reported either because they are truly absent in our specimens, our images simply did not capture them, or our bleached skeletal SEM images do not show soft-parts: ancestrula twinned, different size and shape, reddish-brown chitinous line in interzooidal grooves, frontal membrane occupying the whole of the frontal area, chitinous spinules on the surface of the membrane and the operculum, and operculum small, semicircular, wider than long, and with a straight proximal border and a sclerite along its semicircular margin.

Either Liu's original (1991) definition of the species is incorrect, and Almeida *et al.*'s (2018) description of Brazilian colonies is correct, or the Brazilian *B. irregulata* with its gymnocystal tubercles belongs in *Jellyella* as the presence of cryptocystal tubercles require assignment to *Biflustra*. We think the tubercles are cryptocystal and our species is *B. irregulata* and Almeida *et al.*'s (2018) *B. irregulata* belongs in *Jellyella*. We agree with Almeida *et al.* (2018) and McCuller & Carlton (2018) that *B. irregulata* and *B. arborescens* (Canu & Bassler, 1928) are distinct species and the latter has an Atlantic distribution. Therefore, what we are calling *B. irregulata* had an Indo-Pacific distribution until it was rafted to the eastern Pacific following the 2011 East Japan earthquake and tsunami (Carlton *et al.* 2017; McCuller & Carlton 2018).

McCuller & Carlton (2018) stated that one characteristic of *B. irregulata* not observed in their material was the chitinous spines on the frontal membrane. The frontal spines were also absent in Taylor & Tan's (2015) material, and the material in this study. We feel this is simply a function of the lack of preserved soft-parts in the bleached skeletal SEM images of these three studies.

Morphometrics

The *B. irregulata* colonies ranged in size from 77 to 108 autozooids. Autozoid length averaged 0.39 mm (number: 10, range: 0.36–0.43 mm, standard deviation: 0.02 mm), and autozoid width averaged 0.23 mm (number: 9, range: 0.20–0.26 mm, standard deviation: 0.02 mm) (Fig. 4).

Discussion

Epibiosis

The presence of barnacles on decapod crustaceans has been commonly reported in previous studies (e.g., Key *et al.* 1997). Several species of the pedunculate barnacle *Octolasmis* are known to attach to these crustaceans (Machado *et al.* 2013), including lobsters (Jeffries *et al.* 1984). The pedunculate barnacle *Dianajonesia amygdalum* (Aurivillius, 1894) is associated with two species of spiny lobsters, *Panulirus japonicus* (von Siebold, 1824) and *P. penicillatus* (Olivier, 1791) (Bowers 1968). The barnacle *Austrominius modestus* (Darwin, 1854) is known to foul the spiny rock lobster *Jasus edwardsii* (Hutton, 1875) in New Zealand (Key *et al.* 2021). *Balanus trigonus*, the barnacle in this study, grows on a variety of motile hosts with hard exoskeletons including snails, scallops, lobsters, crabs, and sea urchins (Werner 1967). It was previously reported on both of the lobster species in this study (Hendrickx & Ramírez-Félix 2019). *Balanus trigonus* can also be a substrate for other fouling animals including bryozoans which often cover 20–100% of its plates (Werner 1967).

This is the first reported occurrence of *B. irregulata* fouling barnacles attached to lobsters. It is known to encrust a variety of organic and inorganic substrates. It has been found growing on organic substrates such as corals, molluscs, and other bryozoans (Liu 1992; Gordon *et al.* 2007; Seo & Min 2009; Taylor & Tan 2015). Inorganic substrates include rocks, plastic flotsam, fishing floats, buoys, cables, and ship hulls (Liu 1992; Liu *et al.* 2001; Gordon *et al.* 2007; Taylor & Tan 2015; McCuller & Carlton 2018).

There are many benefits of living on a motile host such as increased substrate space and geographic range if the encrusting animal is sessile, like bryozoans. An additional benefit accrues if the host is the encrusting animal's

predator such as the bryozoans that foul predatory pycnogonids (Key *et al.* 2013). Other species of *Panulirus* off the coast of Baja California Sur, Mexico do eat bryozoans (Castaneda-Fernandez-de-Lara *et al.* 2005), but the diets of *P. gracilis* and *P. inflatus* only include crustaceans, molluscs, polychaetes, sipunculids, and echinoderms (Aramoni-Serrano 1982; Lozano-Álvarez & Aramoni-Serrano 1996). Therefore, it is not likely this benefit accrues to the bryozoans in this study.

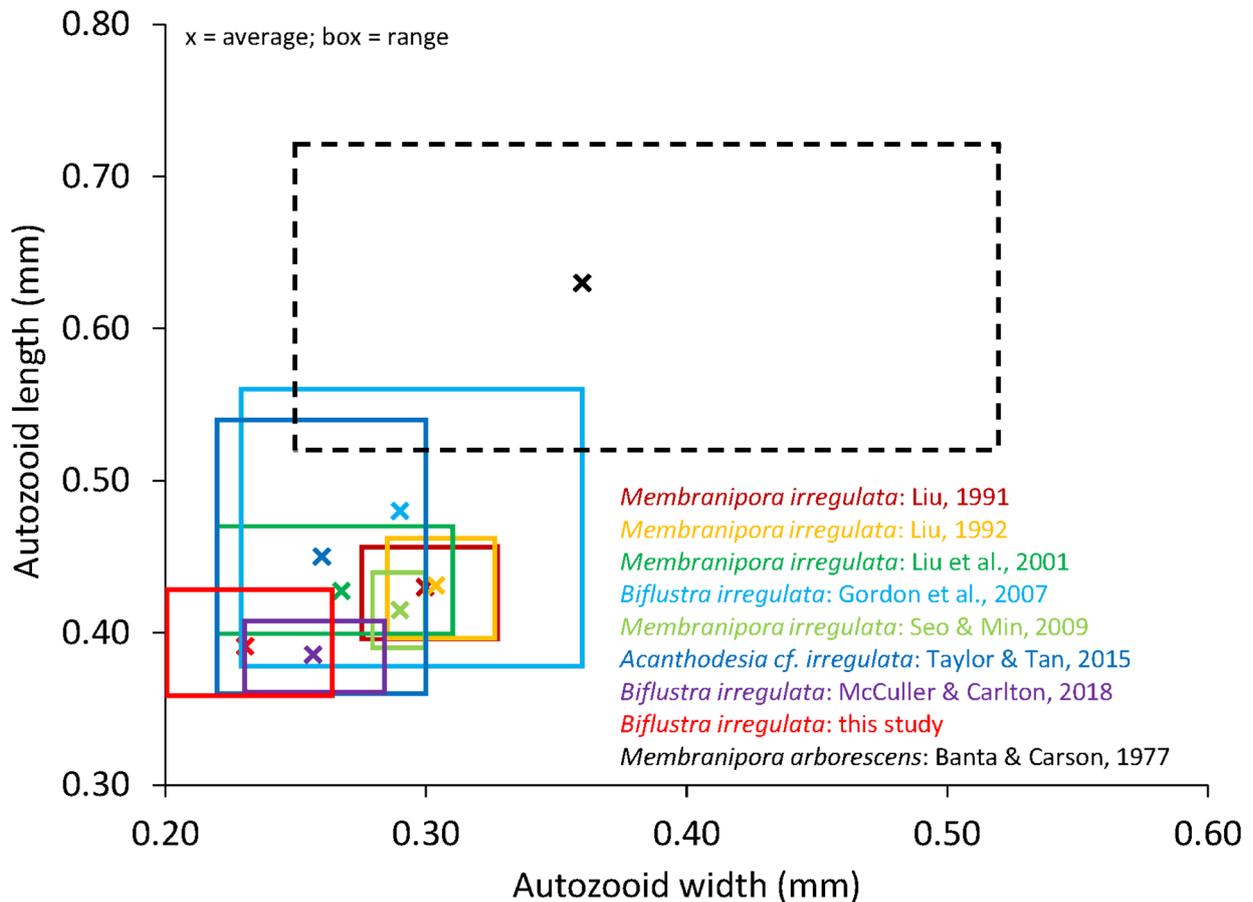


FIGURE 4. Plot of autozooid width versus length of the *Biflustra irregulata* colonies in this study compared to previously published studies including *Membranipora arborescens* from the eastern Pacific. Species names are as published.

Morphometrics

Based on the number of autozooids in a colony (Key 2020), we estimated the colonies were at least two weeks old (i.e., 14–16 days). This is similar to colony ages of other encrusting cheilostomes on lobsters (Key *et al.* 2021) which is strongly controlled by molting frequency (Key *et al.* 1996a, b, 1999, 2000; Key & Barnes 1999). Based on the diameter of the barnacles (8–9 mm), they were ~6 weeks old (Werner 1967, fig. 5). This age estimates are in keeping with the intermolt periods in mature females of *P. gracilis* of 22.6 weeks and *P. inflatus* of 20.6 weeks (Briones-Fourzán & Lozano-Álvarez 2003).

As expected, the smaller colony was found on the immature *P. gracilis* lobster, whereas the larger colony was on the mature *P. inflatus* lobster. As in other groups of decapod crustaceans, immature lobsters molt more frequently (Phillips *et al.* 1980; Gili *et al.* 1993) creating a younger substrate with less time for the bryozoans to asexually replicate to produce more autozooids like we found on the mature lobster. In addition, *P. gracilis* grows faster (i.e., molts more frequently) than *P. inflatus* (Briones-Fourzán & Lozano-Álvarez 2003; Briones-Fourzán 2014).

The autozooid lengths and widths of our colonies of *B. irregulata* fall within the range of this species in four of the seven (57%) previously published studies (Fig. 4). Our data are at the smaller end of the spectrum (Fig. 4). This may simply be due to the reduced surface area constraints of the barnacle substrates (i.e., 1 cm²) or more intriguingly, the temperature-size rule. The temperature-size rule in bryozoans results in smaller zooids in warmer waters (O’Dea & Okamura 2010; Okamura *et al.* 2011). We tested this using latitude as a rough proxy for temperature and

mean autozooid length \times autozooid width from Fig. 4 as a proxy for zooid size. The lower latitude occurrence of *B. irregulata* do have significantly (t-Test, $P = 0.04$) larger zooids (mean = 0.13 mm²) than the higher latitude specimens (mean = 0.11 mm²).

Our eastern Pacific values are most similar to those reported by McCuller & Carlton (2018) on JTMD in the eastern Pacific. We measured mean autozooid length at 0.39 mm, identical to that of McCuller & Carlton (2018). Our mean autozooid width (0.23 mm) is similar to theirs (0.26 mm). This makes sense as the colonies on JTMD would have been the parent colonies of our colonies.

Biogeography

Before the 2011 tsunami, *B. irregulata* had an Indo-Pacific biogeographic distribution (Table 1). It was best known from the western Pacific, especially in the South and East China seas (Fig. 1B). Its range extended from the Bay of Bengal, Bangladesh to the Malacca Strait, Malaysia and the Yellow Sea, China and Korea (Table 1, Fig. 1B). *Biflustra irregulata* is not known from Japan.

Biflustra irregulata was recorded six times from Alaska south to California from May 2014 to March 2016 (Table 2, Fig. 1C). Most of the material collected of this species on JTMD was dead with little remaining tissue (McCuller & Carlton 2018). This suggests the colonies had not died very long ago. Those with only skeletal remains probably died in transit due to inhospitable conditions during the 3.2–5.0 yr trip (Table 2). Those with remaining tissue probably died when washed ashore in North America due to subaerial exposure. Often, they were overgrown by other species as well. Since not all the colonies were dead, the survivors may have been able to establish viable populations in the eastern Pacific. Other species of JTMD bryozoans were found to be actively reproductive with ovicells upon arrival in North America, but not *B. irregulata* (McCuller & Carlton 2018). It is not impossible that *B. irregulata* was reproductively viable upon arrival; it just might not have been observed. *Biflustra irregulata* is likely to have survived the trip for two reasons. First, due to bryozoans' ability to survive adverse conditions, they often are the most abundant and diverse group in rafting communities (Winston 1982; Watts *et al.* 1998; Barnes & Fraser 2003; Thiel & Gutow 2005; Kiessling *et al.* 2015; McCuller & Carlton 2018; Miller *et al.* 2018b; Póvoa *et al.* 2021). Second, undoubtedly more living colonies of *B. irregulata* made it to the eastern Pacific as only a tiny fraction of the total JTMD was discovered and analyzed by Carlton *et al.* (2017).

McCuller & Carlton (2018) suggested that this bryozoan may have been acquired by JTMD as it was carried south by the Kuroshio Countercurrent (Uda & Hasunum 1969) before getting caught up in the north-bound Kuroshio Current. They suggested this as they thought it was a warm water species not found in Japan, but its range is 5–40°N (Table 1, Fig. 1A). Also possible is that this species may have recently moved poleward in response to global warming and had been living undocumented in Japan at the time of the tsunami. This poleward migration has been recognized for bryozoans in other oceans (Porter *et al.* 2015), including the Pacific (Jurgens *et al.* 2018). This is likely as the Kuroshio Current moves north toward Japan along the eastern edge of the South and East China Seas (Liu 2008, figs 1–3) (Fig. 1A), and could have entrained the bryozoan's larvae.

The 2011 East Japan megathrust earthquake and resulting tsunami impacted the Japanese Pacific coastline from 34°N to 44°N with the peak tsunami height occurring at 40°N (Mori *et al.* 2011) (Fig. 1B). JTMD would have been generated within this same latitudinal range. This range is within the pre-tsunami known Indo-Pacific latitudinal range (10–40°N) of *B. irregulata* (Table 1). There were four pre-tsunami occurrences of *B. irregulata* in the Yellow Sea, 35–40°N, west of the tsunami impacted area (Fig. 1B). The water temperatures in the Yellow Sea span the water temperatures found in the tsunami impacted area of Japan (Liu 2013, fig. 2). Thus, it is possible that *B. irregulata* was already living off the Japanese coast generating larvae that could have fouled JTMD as it washed offshore or had already colonized before the tsunami (e.g., boat hulls and docks).

The first major JTMD item (a dock from Misawa, Aomori, Japan) landed in the eastern Pacific on Agate Beach, Oregon, U.S.A. on 5 June 2012 (Carlton *et al.* 2017, table S1). That is a transit time of 1.2 years. Our bryozoan species' mean transit time was three times longer, 3.8 yr (number: 6, range: 3.2–5.0 yr, standard deviation: 0.7 yr) (Table 2). Which is almost identical to the 3.9 yr for all other species (number: 297, range: 1.2–5.9 yr, standard deviation: 1.0 yr) (McCuller & Carlton 2018, table S1). These multiyear transit times suggests the first dock may have been aided by a tail wind due to its greater windage/freeboard than most JTMD substrates. Additionally, some JTMD may have been caught up in eddies along the western boundary currents of the North Pacific Gyre (Ohshima *et al.* 2005, fig. 8).

TABLE 1. *Biflustra irregulata* published species names, sources, locations, latitudes, longitudes, and collection dates relative to 2011 tsunami (shaded in grey). Arranged by collection date.

| Species name as published | Source | Location | Latitude | Longitude | Year(s) collected |
|------------------------------------|---------------------------|---|---------------|----------------|-------------------|
| <i>Membranipora irregulata</i> | Liu 1992 | South China Sea | 20°00'N | 111°15'E | 1959 |
| <i>Membranipora irregulata</i> | Liu 1992 | South China Sea | 18°15'N | 111°00'E | 1960 |
| <i>Membranipora irregulata</i> | Liu 1992 | Niushan Island, China, East China Sea | 26°25'N | 120°20'E | 1984 |
| <i>Membranipora irregulata</i> | Liu 1992 | Xiamen (Amoy), China, South China Sea | 24°29'N | 118°4'E | 1984 |
| <i>Membranipora irregulata</i> | Liu 1992 | Macclesfield Bank, South China Sea | 16°12'N | 114°39'E | 1985 |
| <i>Membranipora irregulata</i> | Liu 1992 | Daya Bay, China, South China Sea | 22°37'N | 114°40'E | 1985 |
| <i>Membranipora irregulata</i> | Liu 1991 | Spratly (a.k.a., Nansha) Islands, South China Sea | 10°45'57"N | 115°49'14"E | 1987 |
| <i>Membranipora irregulata</i> | Seo & Min 2009 | Byeonsan Beach, Korea, Yellow Sea | 35°40'48.41"N | 126°31'50.44"E | 1993 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Qinhuangdao, Bohai Bay, China, Yellow Sea | 39°54'31.84"N | 119°37'12.89"E | ≤2001 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Qingdao, China, Yellow Sea | 36°2'27.13"N | 120°24'0.70"E | ≤2001 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Lianyungang, China, Yellow Sea | 34°46'23.72"N | 119°19'13.37"E | ≤2001 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Dachen Island, China, East China Sea | 28°29'8.35"N | 121°54'2.95"E | ≤2001 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Xiamen, China, Yellow, South China Sea | 24°24'21.89"N | 118°10'10.65"E | ≤2001 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Daya Bay, China, South China Sea | 22°35'20.71"N | 114°41'16.48"E | ≤2001 |
| <i>Membranipora irregulata</i> | Liu <i>et al.</i> 2001 | Xinyin, China, South China Sea | 22°24'52.92"N | 113°52'57.09"E | ≤2001 |
| <i>Biflustra irregulata</i> | Gordon <i>et al.</i> 2007 | Cox's Bazar beach, Bangladesh, Bay of Bengal, Indian Ocean | 21°25'25.64"N | 91°58'14.26"E | ≤2007 |
| Tsunami peak height | Mori <i>et al.</i> 2011 | Miyako, Iwate Prefecture, Japan | 39°38'13.2"N | 141°58'26.4"E | 2011 |
| <i>Acanthodesia cf. irregulata</i> | Taylor & Tan 2015 | Pulau Betong, Penang Island, Malaysia, Malacca Strait | 5°18'N | 100°11'E | 2013 |
| <i>Acanthodesia cf. irregulata</i> | Taylor & Tan 2015 | Balik Pulau, Penang Island, Malaysia, Malacca Strait | 5°22'N | 100°12'E | 2013 |
| <i>Acanthodesia cf. irregulata</i> | Taylor & Tan 2015 | Batu Maung, Penang Island, Malaysia, Malacca Strait | 5°27'N | 100°17'E | 2013 |
| <i>Biflustra irregulata</i> | McCuller & Carlton 2018 | Dunes City, Oregon, U.S.A., northeastern Pacific Ocean | 43°48'10.97"N | 124°10'13.41"W | 2014 |
| <i>Biflustra irregulata</i> | McCuller & Carlton 2018 | Sitka, Alaska, U.S.A., northeastern Pacific Ocean | 57°3'48.089"N | 135°21'34.43"W | 2014 |
| <i>Biflustra irregulata</i> | McCuller & Carlton 2018 | Daly City, California, U.S.A., northeastern Pacific Ocean | 37°40'7.118"N | 122°29'46.23"W | 2014 |
| <i>Biflustra irregulata</i> | McCuller & Carlton 2018 | Oysterville, Washington, U.S.A., northeastern Pacific Ocean | 46°33'3.730"N | 124°3'42.81"W | 2014 |
| <i>Biflustra irregulata</i> | McCuller & Carlton 2018 | Long Beach, Washington, U.S.A., northeastern Pacific Ocean | 46°28'31.84"N | 124°4'19.088"W | 2015 |
| <i>Biflustra irregulata</i> | McCuller & Carlton 2018 | Lincoln City, Oregon, U.S.A., northeastern Pacific Ocean | 45°0'29.070"N | 124°0'34.780"W | 2016 |
| <i>Biflustra irregulata</i> | This study | Mármol, Gulf of California, Mexico, eastern Pacific Ocean | 23°26'N | 106°40'W | 2017 |

TABLE 2. Locations and landing dates of *Biflustra irregulata*-bearing Japanese Tsunami Marine Debris (JTMD) found along the western US Pacific coast and resulting calculated transit times. Locations and landing dates from McCuller and Carlton (2018, table S1) and arranged by landing date.

| JTMD-BF number from McCuller & Carlton (2018, table S1) | Location | Landing date | Transit time since 11 March 2011 tsunami (years) |
|---|-------------------------|------------------|--|
| JTMD-BF-215 | South of Dunes City, OR | 19 May 2014 | 3.2 |
| JTMD-BF-237 | Sitka, AK | 24 May 2014 | 3.2 |
| JTMD-BF-240 | Daly City, CA | 9 August 2014 | 3.4 |
| JTMD-BF-264 | Oysterville, WA | 22 December 2014 | 3.8 |
| JTMD-BF-378 | Long Beach, WA | 30 April 2015 | 4.1 |
| JTMD-BF-533 | Lincoln City, OR | 27 March 2016 | 5.0 |
| | Count: | 6 | 6 |
| | Minimum: | 19 May 2014 | 3.2 |
| | Mean: | | 3.8 |
| | Maximum: | 27 March 2016 | 5.0 |
| | Standard deviation: | | 0.7 |

If *B. irregulata* fouled JTMD while floating south as suggested by McCuller & Carlton (2018), then its transit time to the eastern Pacific should be longer than the rest of the species' transit times. This was not the case. The mean transit time from the date of the tsunami to when *B. irregulata* was found in the eastern Pacific was almost identical for all other species. These means of 3.8 yr and 3.9 yr, respectively, were not significantly different (t-test, $P = 0.85$). This suggests *B. irregulata*'s range may have already expanded to Japan at the time of the tsunami as a longer transit time to the south was not evident or it suggests most JTMD took a similar southerly detour. This second hypothesis is supported by the fact that all species' mean transit time of 3.9 yr is twice as long as the normal duration of 2 yr (McCuller & Carlton 2018). In addition, multiple warm water species were found encrusting on top of colder water species from the tsunami epicenter (McCuller & Carlton 2018).

The bryozoans fouling JTMD that did not sink were carried 7000 km to North America via the Kuroshio and North Pacific Currents which form the northern boundary currents of the North Pacific Gyre (Carlton *et al.* 2017, fig. S1) (Fig. 1A). Establishment of rafted species depends on frequency of delivery of reproductively viable individuals and the presence of suitable environment in the eastern Pacific (Carlton *et al.* 2017). Once in the eastern Pacific, they and/or any larvae they released were carried south along the west coast of North America by the California Current (Carlton *et al.* 2017, fig. S1). The California Current is the eastern boundary current of the North Pacific Gyre, and it runs south from British Columbia, Canada to Baja California Sur, Mexico (Sydeman & Elliott 2008, fig. 1) (Fig. 1A). Most of the California Current heads west past the tip of Baja California peninsula and becomes the North Equatorial Current which is the southern boundary current of the North Pacific Gyre (Tabata 1975, fig. 3; Karl 1999, fig. 1) (Fig. 1A). Some of the California Current wraps around the tip of the Baja peninsula into the Gulf of California (Lavin *et al.* 2014, figs 1, 2). The colonies of *Biflustra irregulata* were found 336 km ENE of the tip of the Baja California peninsula (Fig. 1C). Thus, the colonies we found may have come from post 2014 colonies from JTMD whose larvae were carried southward by the California Current into the Gulf of California where now-established, but yet unknown, populations are living. Once *B. irregulata* made it to the eastern Pacific it would easily expand its range southward. This would have been aided by *B. irregulata*'s planktotrophic cyphonautes larvae (Nielsen & Worsaae 2010) which are easily dispersed by currents.

This study suggests *B. irregulata*'s distribution has expanded from the western Pacific to the Gulf of California in the eastern Pacific Ocean off the coast of Mexico. This expansion is here attributed to transoceanic rafting following the 2011 Great East Japan earthquake and tsunami as this species was found on JTMD (Carlton *et al.* 2017; McCuller & Carlton 2018). But could *B. irregulata* have already spread beyond the western Pacific and was in the eastern Pacific before the tsunami? Could *B. irregulata* have already been in the eastern Pacific and simply misidentified as *Biflustra arborescens* (Canu & Bassler, 1928) (McCuller & Carlton 2018)? Carlton *et al.* (2019, table S1) said Banta & Redden (1990) misidentified *Biflustra irregulata* as *M.* (now *Biflustra*) *arborescens* collected in 1980 from the Galápagos. If reports of *B. arborescens* actually corresponded to *B. irregulata*, then *B. irregulata* was in

the eastern Pacific before the tsunami as it was reported in Costa Rica in 1964 (Banta & Carson 1977), Panama in 1969 (Powell 1971), and in the Galápagos in 1980 (Banta & Redden 1990) (Fig. 1D). These tropical eastern Pacific bryozoan populations may have expanded their range northward into the Gulf of California before the tsunami. This is possible as invasive bryozoan species can expand their range quickly (Micael *et al.* 2016). This is, however, unlikely as their larvae would have to be transported against the southward flowing California Current.

Unfortunately, of these three reports of *M. arborescens* in the tropical eastern Pacific, only Banta & Carson (1977) described or illustrated *M. arborescens*. The Costa Rican specimens lack the distinctive globose tubercles at the proximolateral corners of the zooidal cryptocysts in *B. irregularata*, and its zooids are twice as large as those of *B. irregularata* (Fig. 4). Thus, these are separate species, and *B. irregularata* was not in the eastern Pacific before the tsunami. This is supported by the fact that Winston & Hayward (2012) considered *B. arborescens* a separate species from *B. irregularata* and assigned it to *Biflustra* as *B. arborescens* (basionym, *Acanthodesia arborescens* new combination, *M. arborescens*) (Canu & Bassler 1928; Cook 1968). Almeida *et al.* (2018) agreed and questionably cited Powell's (1971) eastern Pacific record of *M. arborescens* as *B. arborescens*. Except for Powell's (1971) report at the mouth of the Panama Canal, which was possibly from ship ballast water transport from the Caribbean (Carlton 1985), *B. arborescens* has an Atlantic distribution.

Biflustra irregularata has also been reported pre-tsunami in the Atlantic Ocean in Brazil between 1997 and 2002 (Almeida *et al.* 2018; Miranda *et al.* 2018). Taxonomic assignment of these bryozoans has been challenging. For example, due to the general morphology being relatively simple and variable, there are many cases where zooids on the same colony could be referred to different species, genera, or in some cases different families (Banta & Carson 1977). Vieira *et al.* (2016) agreed and stated that these morphologically simple and related species will eventually require molecular studies to sort out. Based on the morphology we have and as discussed above under taxonomy, *B. irregularata*'s tubercles are cryptocystal, so Almeida *et al.*'s (2018) *B. irregularata* belongs in *Jellyella*. Therefore, *B. irregularata*'s range includes the Indian Ocean and the northern Pacific Ocean.

Could *B. irregularata* have rafted to the eastern Pacific on earlier JTMD? The massive 1896 Meiji-Sanriku and 1933 Sanriku earthquakes and tsunamis are the most likely candidates (Carlton *et al.* 2017). They would have produced less non-biodegradable JTMD, and no reports of JTMD in North America from these tsunamis were ever found (Carlton *et al.* 2017). As *B. irregularata* was not recorded in the earlier bryozoan faunal studies of the Pacific coast of the US and Mexico, including the Gulf of California (Osburn 1950; Soule 1959), it was probably limited to the Indo-Pacific before 2011. But as McCuller & Carlton (2018) noted, *B. irregularata* was not described as a distinct species until 1991. Thus, it was not on the "menu of choices" for earlier faunal surveys, unless earlier workers had recognized it as an undescribed species.

Conclusion

The presence of *B. irregularata* in the eastern Pacific documented in this study shows that this species survived the three year post-tsunami rafting voyage across the Pacific and three years after that was successfully reproducing in the Gulf of California. Surveying the commercial lobster fishery in western Mexico is an ongoing, routine project sponsored by government fishery agencies. Carapace samples of commercial species fouled by bryozoans might therefore be made available on a regular basis over the upcoming years to confirm this species' survival.

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