

Marine Record

Cite this article: Trott TJ (2024). The Temperate North Pacific Bryozoan *Smittoidea prolifica* (Cheilostomatida: Smittinidae) in the Northwest Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **104**, e74, 1–18. <https://doi.org/10.1017/S0025315424000742>

Received: 26 May 2024

Revised: 31 July 2024

Accepted: 31 July 2024

Keywords:

Biogeography; Bryozoans; Non-native Invasive Species; Northwest Atlantic; Species Introductions

Corresponding author:

Thomas J. Trott

Email: ttrott@suffolk.edu

The Temperate North Pacific Bryozoan *Smittoidea prolifica* (Cheilostomatida: Smittinidae) in the Northwest Atlantic

Thomas J. Trott 

Department of Biology, Suffolk University, Boston, MA 02108, USA

Abstract

The Pacific bryozoan, *Smittoidea prolifica* Osburn, 1952, is reported for the first time from the Northwest Atlantic coast. Colonies were discovered during routine benthic sampling of Casco Bay, Maine, encrusting mussel shells and barnacles. Aiming to compare specimens from native and introduced locations, uncertainties about the Pacific range of *S. prolifica* were resolved by re-examining specimens from Japan, southern Korea, the United States west coast, and Mexico. The occurrence of this species in Japan was confirmed but southern Korea specimens were found to be *Smittoidea spinigera* (Liu, 1990). Comparisons of biometrics among specimens from widely dispersed locations where *S. prolifica* is native and introduced showed significant trends in variation with most characters largest for California and smallest for Germany. Zooid width was largest for Maine specimens. Comparisons between oceans showed that Pacific and Atlantic specimens differed significantly in all measures except zooid length and orifice width. Low substrate specificity and broad range of temperatures and salinities in occupied habitats suggests the potential for successful introduction is high. *Smittoidea prolifica* was most likely introduced through commercial shipping from the North Sea where it is an established non-native species. This was the third non-indigenous species found in Casco Bay discovered within the same timeframe and which shared the same likely region of origin. This spike matched a rise in commercial shipping from the Northeast Atlantic to Portland, Maine, suggesting this seaport is shifting towards becoming a bioinvasion hotspot.

Introduction

During routine identification of marine zoobenthos collected from Casco Bay, Portland, Maine, a bryozoan new to the Northwest Atlantic was found encrusting shells and barnacles. Zooids presented large areolar pores on their peripheries, lacked pseudopores centrally on their frontal walls, and had a medial avicularium placed just below the primary orifice. These features are among the characteristics of the genus *Smittoidea*. Worldwide there are 57 species in this genus, 13 of them known from the North Atlantic with only four occurring in the western Atlantic according to the World Register of Marine Species (Ahyong *et al.*, 2024). Of these four, three are warm water species, one reported from the Gulf of Mexico (Winston and Maturro, 2009) and two from the Caribbean (Winston and Woollacott, 2009; Winston and Jackson, 2021). The fourth species, *Smittoidea propinqua* (Smitt, 1868), ranges into the Gulf of Maine from its circumarctic-boreal distribution. The Casco Bay species resembled *S. propinqua*, but that species does not have a lyrula, the central tooth of a primary orifice which was prominent in the Casco Bay specimens. Using this feature and a suite of other diagnostic characteristics (Osburn, 1952; Soule, 1961; Soule and Soule, 1964; Banta, 1980), the bryozoan was identified as *Smittoidea prolifica* Osburn, 1952.

Smittoidea prolifica is considered a species of the temperate North Pacific realm (Nelson *et al.*, 2016) with a fossil record from northern Japan dating from the Neogene (Hayami, 1975). On the western North American coast, this species ranges from Baja California, Mexico to Washington, United States (Figure 1). Osburn (1952) described *S. prolifica* from specimens collected from southern California where it was a common shore species that also encrusted floats and pilings. He considered the *Smittia reticulata* of Robertson (1908) reported from southern California and the *Smittina reticulata* of Okada and Mawatari (1936) found in Japan to be *S. prolifica*. These synonymies established a present-day amphi-North Pacific distribution for this bryozoan which was supported by subsequent records from Japan (Long and Rucker, 1969) and southern Korea (Rho and Seo, 1986; Seo and Min, 2009). However, the synonymy of Osburn (1952) with specimens from Japan and some inconsistencies among species descriptions of specimens collected from southern Korea (Rho and Seo, 1986) have received critical attention (De Blauwe and Faasse, 2004). In that respect, specimens from the Northwest Pacific require re-examination to confirm their identification so to better understand the North Pacific distribution and morphological variation of *S. prolifica*.

Smittoidea prolifica has a history of introductions in European waters around the North Sea. It was first discovered in 1995 on the southwestern coast of the Netherlands (Van Moorsel, 1996) and at several additional locations there from 1998 to 2001 (De Blauwe and Faasse, 2004). New records of this species continued to appear along the coastline with



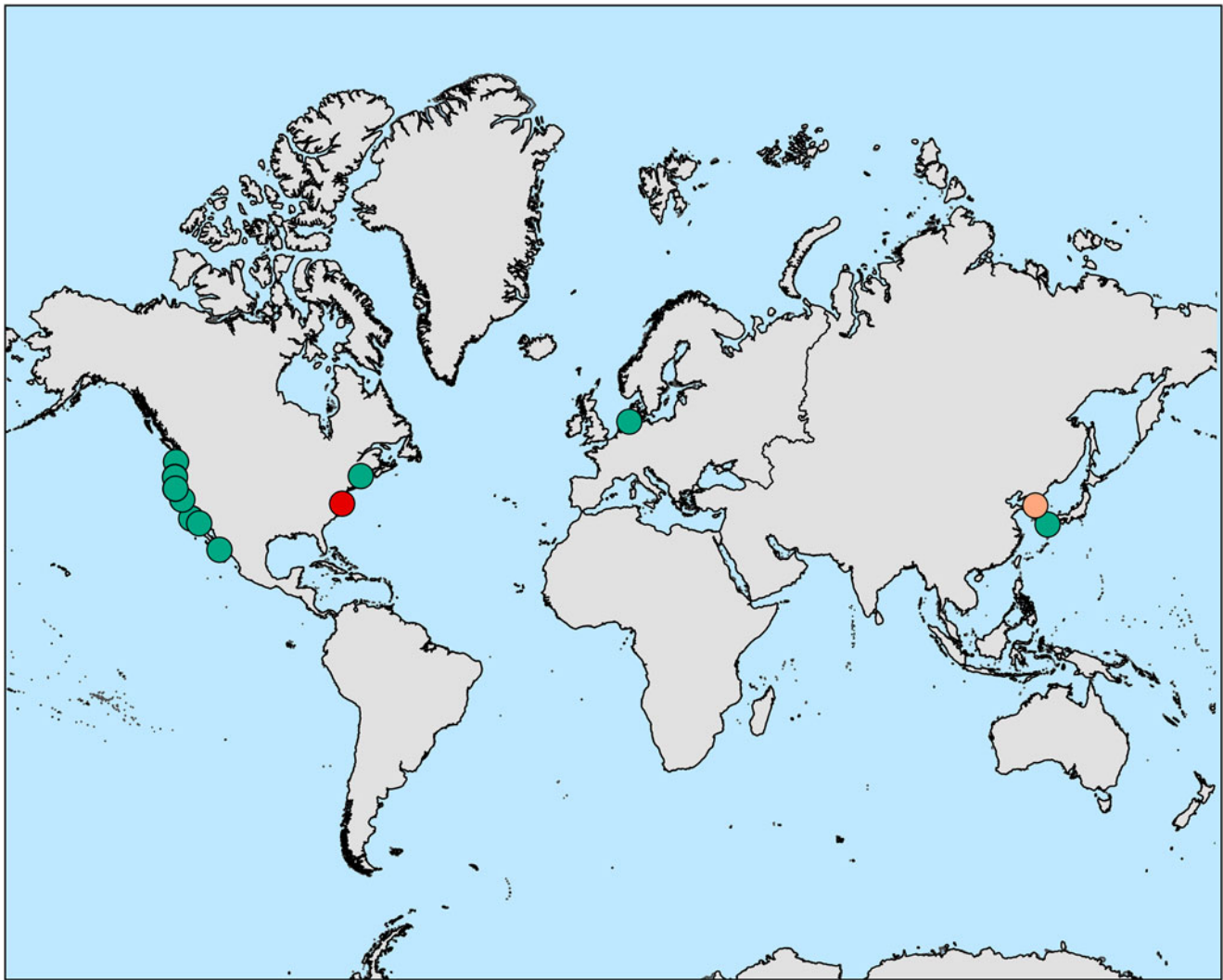


Figure 1. The global distribution *Smittoidea prolifica* based on collection locations (closed circles) of specimens used in analyses. Also shown are collection locations for *S. spinigera* and *Parasmittina nitida*. Symbology: *S. prolifica*, green; *Smittoidea spinigera*, orange; *P. nitida*, red.

discoveries progressing northeastwards (Dekker and Drent, 2013; Gittenberger *et al.*, 2015), eventually reaching the Central Wadden Sea coastline of Germany by the German Bight of the North Sea (Markert *et al.*, 2015). A few records were reported for offshore locations (Vanagt *et al.*, 2013; Kind and Kuhlenkamp, 2016). The most northerly published record of this species was from Tiefe Rinne near Helgoland (Kind and Kuhlenkamp, 2016). Aquaculture and its associated infrastructure were implicated as vectors for introductions (De Blauwe and Faasse, 2004; Markert *et al.*, 2015) as was encrusted floating debris and algae (Markert *et al.*, 2015; Kind and Kuhlenkamp, 2016).

In this paper, *S. prolifica* is redescribed from specimens discovered in Casco Bay, Maine. Morphology is compared, biometrics analysed, and the range of *S. prolifica* clarified by means of a review of collections from the coasts of the Northeast and Northwest Pacific, the Northwest Atlantic, and locations of introduction in European waters. Finally, preliminary ecological observations are discussed along with possible routes of introduction into the Gulf of Maine.

Materials and methods

Field survey and sample processing

The seabed was sampled near the mouth of the Presumpscot River, Casco Bay, located off Portland (43.6591°N, –70.2568°W) in

Cumberland County on the southern coast of Maine (Figure 2). Quantitative samples, three per station at depths of 4.18 to 7.71 m were taken at four stations approximately 1 h after low tide using a 0.05 m² Ponar grab sampler. Two stations were sampled on 18 August and the other two on 24 August 2020. Water column environmental parameters were measured with an EXO-1 YSI sonde attached to the grab sampler platform. The platform remained stationary on the bottom for at least 10 min for the sonde to equilibrate before retrieval. Retrieved samples were accessed for general sediment composition and then sifted on deck through a 1 mm mesh sieve. Sorted macrofauna, cobbles, and shells with epibionts were placed in Ziploc® bags containing seawater and stored on ice packs for transport. In the laboratory, all animals were initially sorted to phylum and preserved in 95% ethanol within 24 h of collection. Cobbles and shells were examined by stereomicroscope and preserved whole with attached fauna. Specimens were later identified to the lowest taxon possible, usually species. Voucher specimens of *S. prolifica* were deposited in the Yale Peabody Museum (YPM), Yale University, New Haven, Connecticut, USA.

Imaging

Digital images from light microscopy were taken as tiff files at a resolution of 300 dpi with an Olympus SZ61 stereoscopic microscope system and ImagePro®. Slide scan and SEM images were

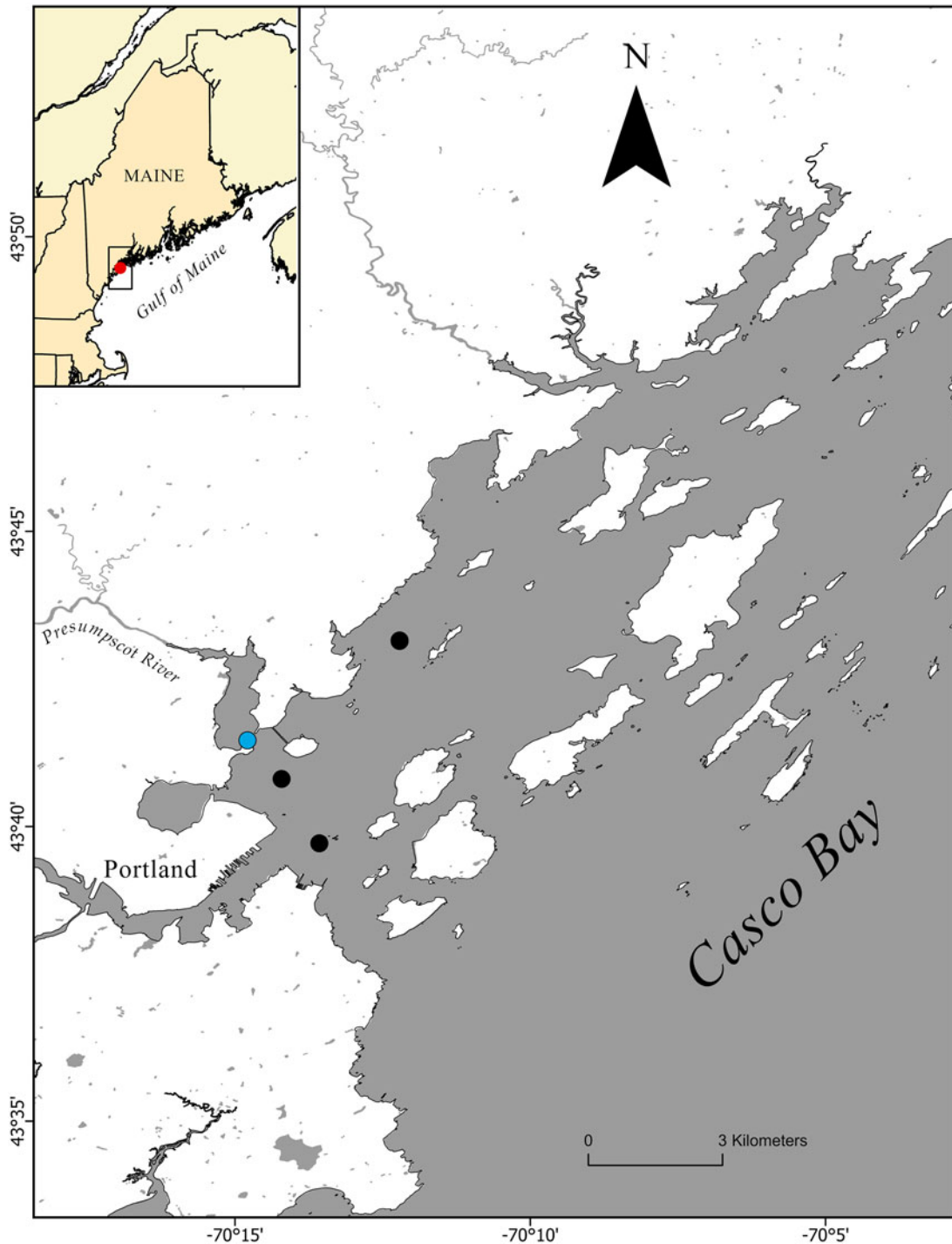


Figure 2. Casco Bay, Maine, USA showing location (blue) where *Smittoidea prolifica* was collected on 18 August 2020 in the Presumpscot River drainage. Other sampling stations (black) yielded no species of bryozoans. Upper inset shows Casco Bay region (frame) and Portland (red) in relation to the Gulf of Maine, New England states, and Canadian provinces.

captured at the Yale Peabody Museum facilities. Slide scan images were acquired using an Olympus BH-51 compound microscope featuring lenses that allow both transmitted (with Differential Interference Contrast filters) and reflected light, outfitted with a Teledyne Lumenera Infinity 3 digital camera. Positioning of the slide, and focus and image acquisition were controlled by software (Objective Imaging Surveyor version 9.4.0.5) along the x, y, and z axes. Individual position images were stitched together on a single plane, and multiple planes rendered into an extended focus image using Helicon Focus Pro version 8.2.0. For SEM, selected specimens were immersed in a sodium hypochlorite solution to remove soft tissue, rinsed in water, air dried, and mounted with

double-sided adhesive tape on aluminium SEM stubs. In some cases, specimens were then coated with 6–10 nm gold using a Cressington 208HR high resolution sputter coater. Specimens were observed with a Hitachi SU7000 scanning electron microscope at 15 kV accelerating voltage. All images were stored electronically as tiff files at a resolution of 200 pixels/cm².

Biometric measurements and analysis

Measurements of mature zooids and zooidal structures were made from tiff files using Adobe Photoshop®. Biometrics were defined according to dimensions illustrated by Pouyet and Herrera

(1986). Measurements were divided among five colonies, each encrusting a separate substrate. Three to eight zooids were measured per colony. Each suite of measurements (zooid length and width, orifice length and width, etc.) was taken from the same zooid. In some cases, structures were obscured or not parallel to the focal plane and could not be reliably measured on a zooid. Because of that, the number of measurements (N) among structures differed. Measurements of specimens from Glen Cove, Vallejo, Solano County, California and Sasebo, Nagasaki Prefecture, Japan were made for comparison with Casco Bay specimens using the same methods with the exception that only one colony was available from these locations. Quadrangle shaped zooids were infrequent, present only in the Glen Cove colony, and not measured.

Differences in morphological characters among locations were assessed graphically and statistically. Biometric comparisons of individual characters among locations were performed using one-way Analysis of Variance (SigmaPlot 15) when the data met the assumptions of normality and equal variance according to the Shapiro-Wilks and Brown-Forsythe methods, respectively. When differences among mean values were greater than would be expected by chance, *post-hoc* multiple comparisons were done using the Holm-Sidak method to find which measures differed statistically from one another. The Kruskal-Wallis test was chosen for analysis when the data did not meet test assumptions. When differences among median values were greater than would be expected by chance, *post-hoc* multiple comparisons were made using the Dunn's method. Biometric differences in characters between Atlantic and Pacific specimens were assessed by pooling measurements from each ocean and comparing them using a pooled two sample t test when the data met the test assumptions for normality and equal variance, each evaluated the same way as previously described. When test assumptions were not met, the pooled data were compared using the Mann-Whitney test. Finally, specimens were compared to test the hypothesis that zooids had similar average biometrics regardless of the localities they were collected from. Similarity was evaluated using PRIMER 7 nonparametric methods as described by Plymouth Routines in Multivariate Ecological Research (Clarke and Warwick, 2001). Initially, the means of each variable (lengths and widths of zooid, orifice, and ovicell) were square root transformed and tabulated for each location. A resemblance matrix was generated from the table using Euclidean distance of the square root transformed means. Finally, dissimilarity among locations was assessed using hierarchical cluster analysis on the resemblance matrix with group average as the cluster mode. Significant differences ($P < 0.05$) in similarity among locations were evaluated with the similarity profile test (SIMPROF).

Results

Habitat and environmental conditions

The shallow depths (4.18–7.71 m) that specimens of *S. prolifica* were retrieved from varied little in temperatures (18.98–19.32 °C) and the low salinities (28.86–29.72 psu) were indicative of the Presumpscot River drainage environment (Table 1). Specimens

were found in all three grab samples and for each the seabed consisted of unconsolidated sediments with shell. No bryozoans of any species occurred at stations sampled beyond the river where the seabed consisted of primarily soft sediments mixed with sand and gravel.

Colonies encrusted living and dead barnacles (*Balanus crenatus* Bruguière, 1789) and *Mytilus* shells with co-occurring *Amathia gracilis* (Leidy, 1855) and *Barentsia laxa* Kirkpatrick, 1890. No colonies of *S. prolifica* were overgrown or overgrew any associated epifauna, and none were found on cobbles. The bryozoan assemblage found on accompanying cobble included dense mats of *A. gracilis*, along with *Cryptosula pallasiana* (Moll, 1803) and *Pentapora americana* (Verrill, 1875).

Systematic account

Order CHEILOSTOMATIDA

Suborder FLUSTRINA

Superfamily SMITTINOIDEA Levensen, 1909

Family SMITTINIDAE Levensen, 1909

Genus *Smittoidea* Osburn, 1952

Smittoidea prolifica Osburn, 1952

(Figures 3–7)

Smittia reticulata Robertson, 1908, p. 306, Plate 23, Figures 75, 76

Smittoidea prolifica Osburn, 1952, pp. 408, 409, Plate 48, Figures 7, 8; Soule, 1961, pp. 33, 34; Soule and Soule, 1964, p. 24; Long and Rucker, 1969, p. 63; Banta, 1980, p. 388, Figure 24.81; De Blauwe and Faasse, 2004, p. 33, Figures 1, 2; Markert *et al.*, 2015, p. 717, Figure 2a–e; Kind and Kuhlenskamp, 2016, p. 1237, Figure 1

Material examined

NORTHWEST ATLANTIC– United States • Maine • Casco Bay, about 100 m north of Martin's Point, Presumpscot River, Cumberland County, Portland: YPM IZ 106905, 43.6910° N, –70.2465° W, depth 6.42 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *B. crenatus*; YPM IZ 106906, 43.6909° N, –70.2968° W, depth 4.18 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *Mytilus* shell; YPM IZ 106907, 43.6909° N, –70.2968° W, depth 4.18 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *Mytilus* shell; YPM IZ 106908, 43.6909° N, –70.2461° W, depth 7.71 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *Mytilus* shell; YPM IZ 106909, 43.6909° N, –70.2968° W, depth 4.18 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *Mytilus* shell; YPM IZ 106910, 43.6909° N, –70.2968° W, depth 4.18 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *B. crenatus*; YPM IZ 106813, 43.6909° N, –70.2461° W, depth 7.71 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *Balanus* plate; YPM IZ 106814, 43.6910° N, –70.2465° W, depth 6.42 m, Ponar grab, coll. T.J. Trott, 18 Aug 2020, 1 colony on *Mytilus* shell. United States • Virginia • Gates Channel, Accomack County, Wachapreague: USNM 1446003 (SERCINVERT1537), 37° 35.55' N, –75° 39.51' W, Trawl-Beam, 1 m, depth 2 m, coll. R. Aguilar, 27 Jun 2017, 1 colony on gravel.

Table 1. Geolocation, mean sea bottom environmental attributes, and substrate composition at collection locations of *Smittoidea prolifica* in Casco Bay, Maine

Station	Latitude	Longitude	Depth (m)	ODO (mg/L)	Sal (psu)	pH	Temp (°C)	Substrate Type
PR28-1	43.6909°	–70.2968°	4.18	6.80	28.86	7.68	19.32	shell, cobble, gravel
PR28-2	43.6910°	–70.2465°	6.42	7.13	29.72	7.82	19.02	muddy shell hash
PR28-3	43.6909°	–70.2461°	7.71	7.10	29.72	7.84	18.98	<i>Mytilus</i> shells



Figure 3. *Smittoidea prolifica* from Casco Bay, Maine. Mature colony on *Balanus crenatus* Bruguière, 1789 with co-occurring *Amathia gracilis* (Leidy, 1855) and *Barentsia laxa* Kirkpatrick, 1890. Insets: A, Immature colony on *Mytilus* shell; B, Close-up of mature colony. Scale: 500 μ m. Catalogue numbers: YPM IZ 106813: mature colony; YPM IZ 106814: inset A; YPM IZ 106813: inset B.

EAST PACIFIC – United States • Washington • Willapa Bay • Boat Basin, Pacific County, Nahcotta: SBNMH 641394, 46° 29.88' N, –124° 1.98' W, on old tires, intertidal, coll. K. McCain, 1973, 3 colonies (dry). Oregon • Coos Bay • Empire Boat Ramp, Coos County, Coos Bay: Smithsonian Environmental Research Center (SERC) 30222, 43° 23.5002' N, –124° 16.8' W, PVC settlement plate, depth 1 m, coll. E. Collinetti, 2000, 1 colony. Oregon • Coos Bay • Empire Boat Ramp, Coos County, Coos Bay: Smithsonian Environmental Research Center (SERC) 127986, 43° 23.6202' N, –124° 16.8492' W, PVC settlement plate, depth 1 m, coll. K. Larson, 2004, 2 colonies. Oregon • South Slough • Crown Point, Coos County, Coos Bay: Smithsonian Environmental Research Center (SERC) 128818, 43° 19.0338' N, –124° 19.2978' W, PVC settlement plate, depth 1 m, coll. K. Larson, 2004, 5 colonies. California • Channel Islands • off Santa Cruz Island, Ventura County, Albatross 2945: SBNMH 644249 (voucher), 34° 34' N, –119° 29.502' W, depth 55 m, coll. unknown, det. R.C. Osburn, 1889, 1 colony (slide). California • Channel Islands • 1 mi SE of Smugglers Cove on Santa Cruz Island, Santa Barbara County, Velero 1295-41: SBNMH 644250 (voucher), 33° 55.75' N, –119° 31.5' W, depth 27–38 m, coll. unknown, det. R.C. Osburn, 1941, 1 colony (slide). California • Channel Islands • 1.75 mi SE of Santa Cruz Island, Santa Barbara County, Velero 1662-48: SBNMH 644248 (voucher), 33° 55.75' N, –119° 31.0833' W, depth 42 m, coll. unknown, det. R.C. Osburn, 1948, 2 colonies (slide). California • Mission Bay • Dana Marina, San Diego County, San Diego: Smithsonian Environmental Research Center (SERC) 111834, 32° 45.9888' N, –117° 14.1396' W, PVC settlement plate, depth 1 m, coll. A.M. Leyman, 2003, 3 colonies. California •

San Francisco Bay • Glen Cove Marina, Solano County, Vallejo: Smithsonian Environmental Research Center (SERC) 308827, 38° 24.576' N, –122° 7.482' W, PVC settlement plate, depth 1 m, coll. G. Ashton, 2015, 1 colony. California • Humboldt Bay • Eureka Public Marina, Humboldt County, Eureka: Smithsonian Environmental Research Center (SERC) 305986, 40° 48.132' N, –124° 10.752' W, PVC settlement plate, depth 1 m, coll. S. Havard, 2015, 1 colony. California • Humboldt Bay • Kuiper Oyster Raft, Humboldt County, North Slough: Smithsonian Environmental Research Center (SERC) 103347, 40° 51.2418' N, –124° 8.736' W, PVC settlement plate, depth 1 m, coll. A.M. Leyman, 2015, 3 colonies. Mexico • Baja California • Gulf of California • off Coronado Island, Puritan 145: AMNH 480, 26° 7.142' N, –111° 16.4455' W, depth 73–82 m, coll. unknown, det. J.D. Soule, 1957, 1 colony (slide).

NORTHWEST PACIFIC– Japan • Sasebo, Nagasaki Prefecture: USNM 651039, 33° 9.8' N, 129° 42.7' E, asbestos/pine wood fouling panel, depth 10 m, coll. Long and Rucker, 1966, 1 colony (dry). Southern Korea • Maldo Island • J.E. Seo private collection, 37° 41.1306' N, 126° 7.9764' E, depth 18–23 m, SCUBA, coll. J.E. Seo, 1986.

Description of Casco Bay, Maine specimens

Colony

Unilaminar, glossy, pink, white, encrusting mollusc shells and plates of attached living and dead barnacles. Radiate growth from tafiform ancestrula, young colonies circular but losing shape with progressive development (Figure 3, Figure 4A, B). Largest observed approximately 1.5 cm across.

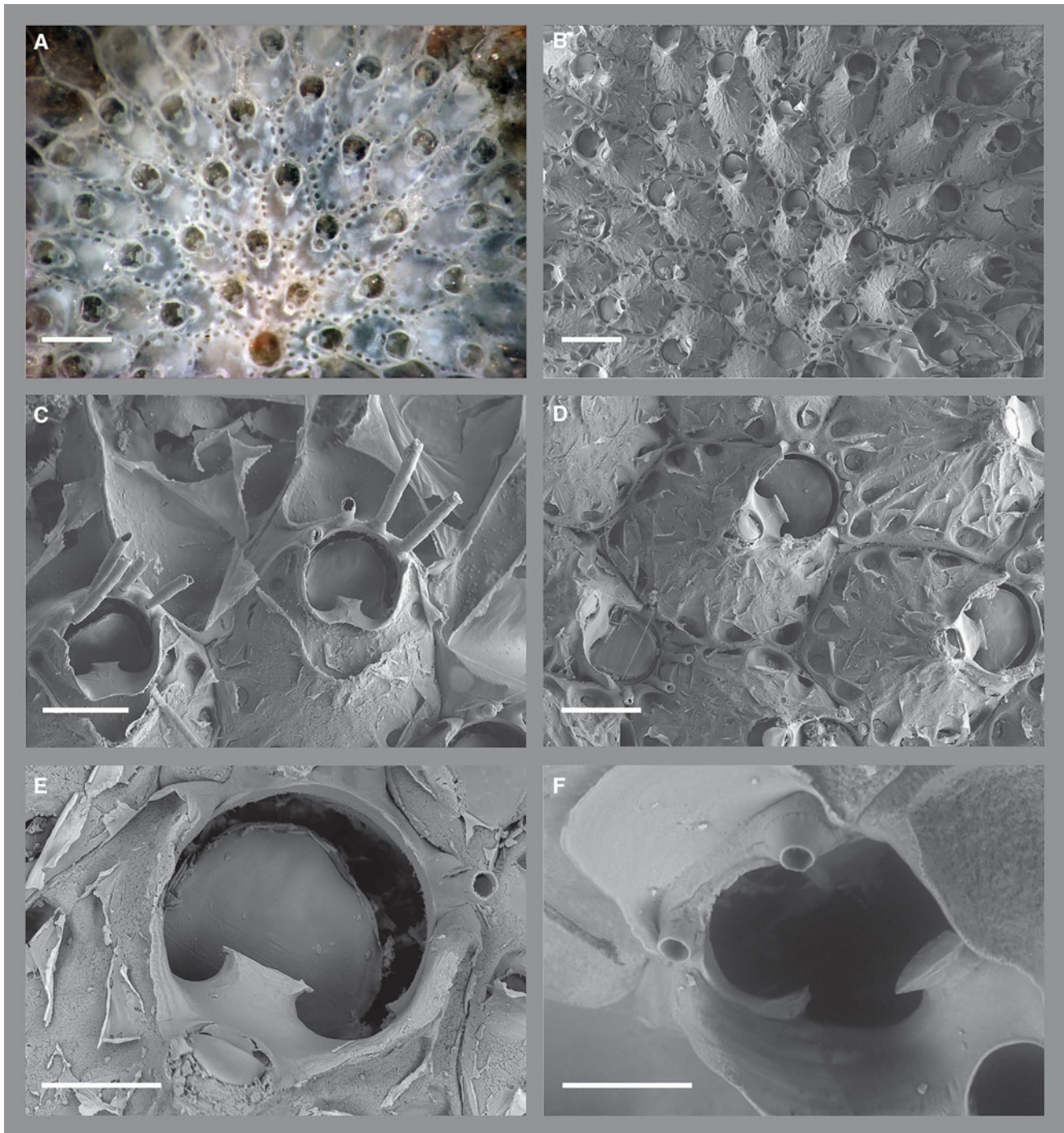


Figure 4. *Smittoidea prolifica* from Casco Bay, Maine. A, Immature colony. Note ancestrula, bottom, middle; B, Same as A in SEM; C, Immature zooid, primary orifice with spines; D, Immature zooids; E, Immature zooid, primary orifice with lyrula and small condyles; F, Mature zooid, primary orifice with spine remnants and prominent condyle. Catalogue numbers: YPM IZ 106814: A to E; YPM IZ 106905: F. Scale: A, B, = 300 μm ; C, D = 100 μm ; E, F = 50 μm . Scanning electron micrographs by L. Rojas.

Zooids

Zooecia distinct, ellipsoid to irregularly hexagonal, 437–382 μm long (\bar{x} = 414 μm , SD \pm 16, n = 22) by 225–382 μm wide (\bar{x} = 267 μm , SD \pm 41, n = 22), often separated at lateral and proximal margins by weak ridges formed by adjacent lateral walls.

Frontal wall

Convex, imperforate, smooth in young zooids (Figure 4C, D) becoming rough and more granular in larger zooids (Figure 5). Margin perforated with single row of 10–14 large irregularly sized areolar pores laterally and proximally, often overlapped by ovicells of neighbouring zooids. Ridges between marginal pores

weakly developed in young zooids; extend from margin centrally, in later ontogeny becoming so prominent and stout with age to occasionally obscure frontal shield (Figure 5).

Orifice

Primary orifice (Figure 4E, F) nearly circular, slightly wider than long, 94–120 μm long (\bar{x} = 109 μm , SD \pm 7, n = 22) by 103–132 μm wide (\bar{x} = 120 μm , SD \pm 6, n = 22), rounded distally but straighter proximally with prominent medial lyrula. Lyrula, 21–36 μm long (\bar{x} = 27 μm , SD \pm 5, n = 21) by 37–56 μm wide (\bar{x} = 47 μm , SD \pm 6, n = 21), anvil-shaped (Figure 6A), slightly basally directed with slight longitudinal ridge corresponding

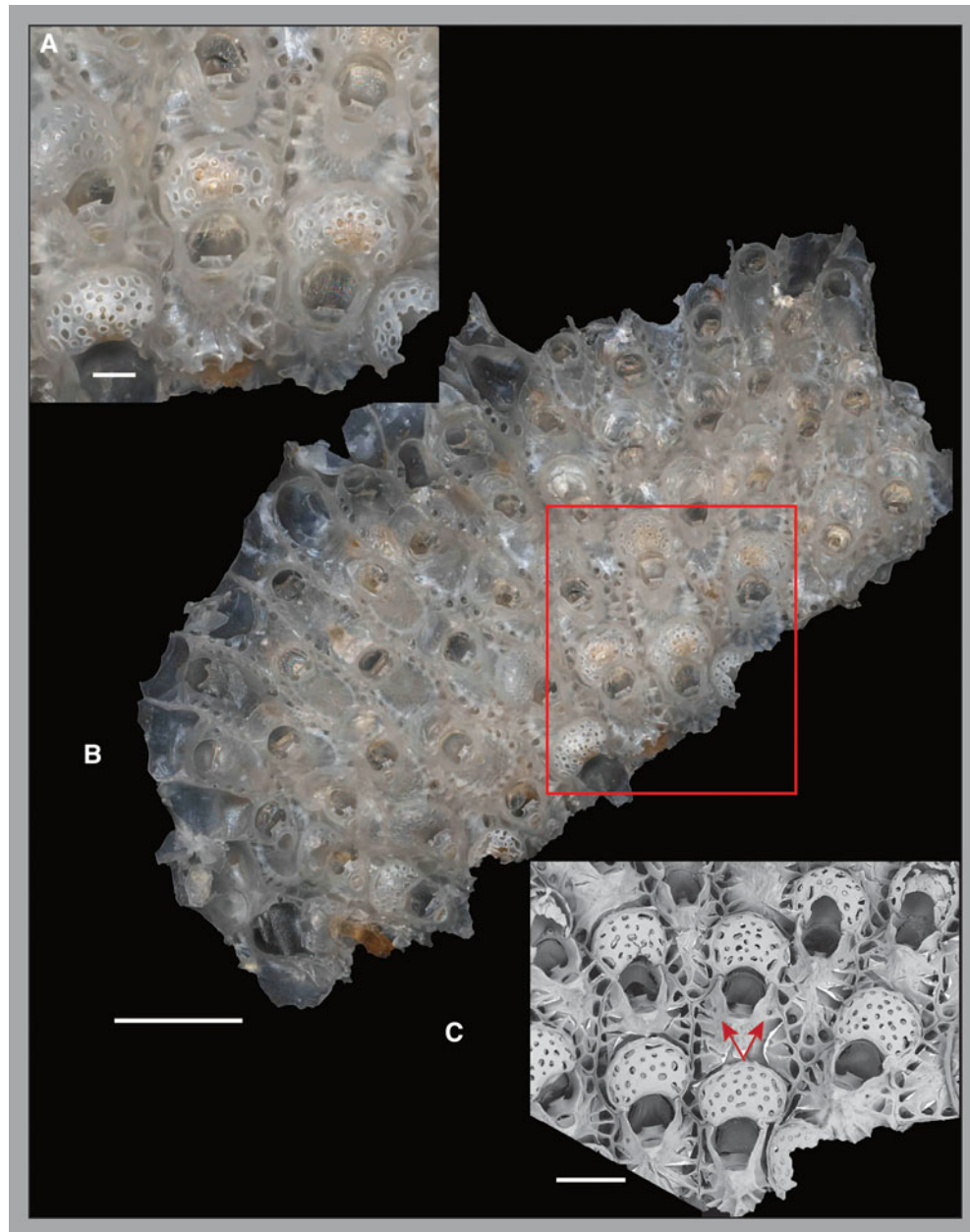


Figure 5. *Smittoidea prolifica* from Casco Bay, Maine. A, Close-up of colony shown in B. Note tubules in lyrulae; B, Slide scan of mature colony, region of close-ups A and C indicated by red rectangle; C, Scanning electron micrograph of same colony. Note small pores outside peristome flaps on the central zooid in C (arrows) and that the peristome does not extend across proximal rim of ovicell. Catalogue number: YPM IZ 106905. Scale: A, 100 μm ; B, 500 μm ; C, 200 μm . Slide scan by E. Lazo-Wasem. Scanning electron micrograph by L. Rojas.

with internal tubule (Figure 6B), translucent in light (Figure 5A, Figure 6A). Condyles distinct, subopercular, small in young zooids (Figure 4E) becoming more prominent with age (Figure 4F). Young zooids with four to occasionally five fragile ephemeral hollow spines near distal rim of orifice (Figure 4C), all lost early on except two (Figure 4F) eventually hidden by developing ovicell. Peristome slightly raised in young zooids (Figure 4D, E), later in ontogeny rises proximally appearing flap-shaped on either side of orifice, joining distal surface of umbo and proximal sides of ovicell at its juncture with orifice. Two small extra-aperture small pores, one on each side proximal to primary orifice (Figure 5C).

Avicularia

Single subapertural avicularium, 45–80 μm long (\bar{x} = 60, SD \pm 10, n = 18) by 95–112 μm wide (\bar{x} = 104 μm , SD \pm 6, n = 18), raised on prominent umbo medial and perpendicular to the frontal

wall (Figure 7A, E). Rostrum directed distally. Umbo rounded; spiky with flat distal face in early development (Figure 7B, C), avicularium developing within; avicularium chamber with unadorned pivotal bar; mandible blunt and semicircular (Figure 7D).

Ovicell

Prominent, slightly wider than long, 151–216 μm long (\bar{x} = 189 μm , SD \pm 18, n = 20) by 214–255 μm wide (\bar{x} = 234 μm , SD \pm 12, n = 20), flattened frontally, with scattered pores of varying shape and size, some appearing coalesced forming tube shapes (Figure 5C, Figure 7A). Peristome joins where ovicell corners meet at orifice but does not extend across distal rim (Figure 5C). Granular calcification appears with age as collar enclosing lateral and distal sides of ovicell (Figure 7E). Ovicell rests on distal zooid concealing partially.

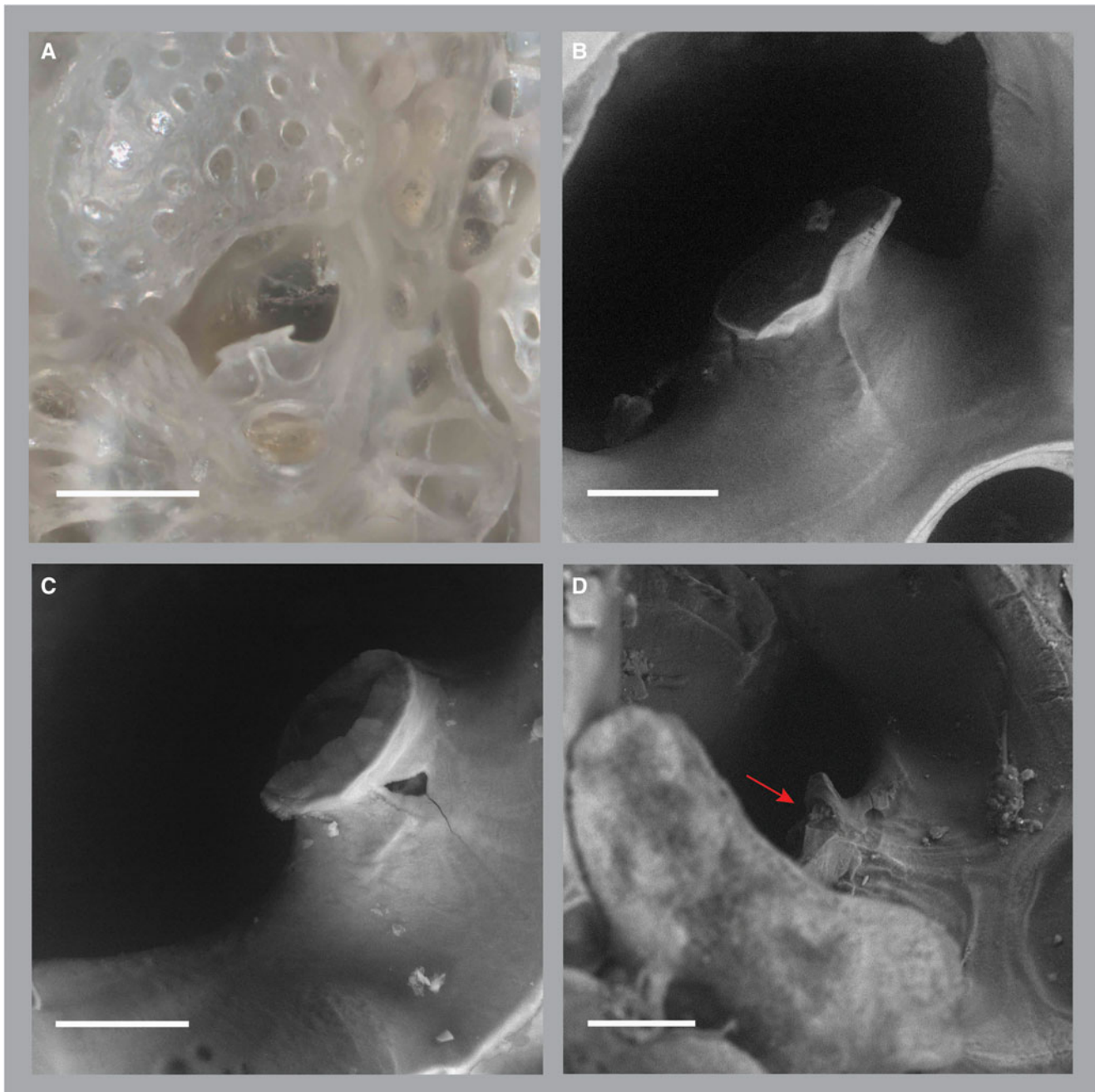


Figure 6. Lyrula of *Smittoidea prolifica* from Casco Bay, Maine. A, Light microscope image of a zooid showing internal tube of lyrula; B, Close-up of lyrula with longitudinal ridge corresponding to placement of internal tube; C, Damaged lyrula with distal portion broken off revealing internal tube; D, Sagittally damaged lyrula showing internal tube (arrow). Catalogue numbers: YPM IZ 106905: A to C; YPM IZ 90444: D. Scale: A = 100 μ m; B, D = 30 μ m; C = 20 μ m. Light micrograph by E. Lazo-Wasem. Scanning electron micrographs by L. Rojas.

Embryo

Orange in life, appearing yellow, white in 90% ethanol.

Polypide

With 12 tentacles.

Remarks

Smittoidea prolifica formed small colonies on mussel shells and attached live and dead barnacles. These specimens bore a close resemblance to those collected from Glen Cove, California and are similar in their general morphology to descriptions from the Northeast Atlantic (De Blauwe and Faasse, 2004; Markert *et al.*, 2015) and East Pacific (Osburn, 1952; Soule, 1961; Soule and Soule, 1964; Banta, 1980). There were subtle differences:

occasionally 5 instead of 4 maximum number of ephemeral spines as reported from California (Osburn, 1952; Soule, 1961; Soule and Soule, 1964; Banta, 1980) and the Netherlands (De Blauwe and Faasse, 2004), no quadrate-shaped zooids as seen in material from California (SERC 305986) and the Netherlands (De Blauwe and Faasse, 2004), and no twinned ovicells as observed in material from California (SBNMH 644250, SERC 305986) and the Northeast Atlantic (Markert *et al.*, 2015; Kind and Kuhlenskamp, 2016). The two small pores proximal to primary orifice have not been described previously but can be seen in Figure 2e of Markert *et al.* (2015). Zooids were wider than all published measures and the outcomes of an analysis of specimen biometrics follows in the Results. In summary, while these variations are of importance, the general morphology of Casco Bay, Maine specimens did not differ remarkably from previous descriptions.

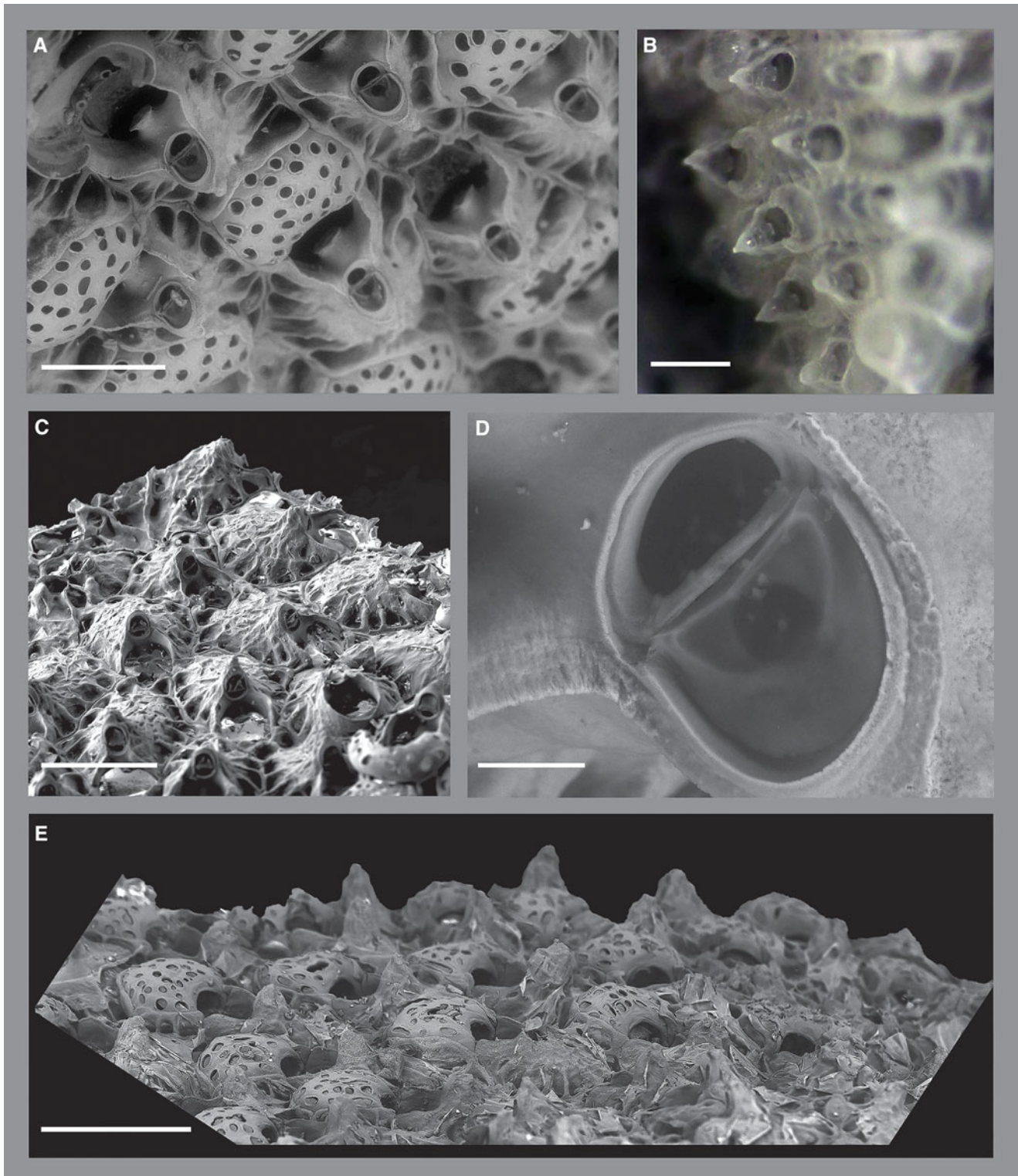


Figure 7. *Smittoidea prolifica* from Casco Bay, Maine. A, Oblique distal view of mature zooids showing avicularia; B, Spiky umbos on developing avicularia of young zooids; C, Spiky umbos on developing avicularia of young zooids, SEM; D, Avicularium of mature zooid with simple unadorned cross bar; E, Lateral view of mature colony showing avicularia projecting upward, perpendicular to the frontal wall. Catalogue number: YPM IZ 106905: A, C, D, E; YPM IZ 106813: B; Scale: A, 150 μm ; B, 250 μm ; C, 200 μm ; D, 20 μm ; E, 300 μm . Scanning electron micrographs by L. Rojas.

Regional comparisons of Smittinidae

The only records of Smittinidae in the current study region of the Northwest Atlantic were for *S. propinqua* (Smitt, 1868), *Parasmittina jeffreysi* (Norman, 1876), and *Parasmittina nitida* (Verrill, 1875) (OBIS, 2023). Specimens of *S. propinqua* from the northern Gulf of Maine were examined for comparison (Atlantic Reference Centre: ARC 0057156; ARC 0057157).

Smittoidea propinqua resembled *S. prolifica* primarily by the flap-like shape of the peristome bordering the primary orifice and the presence of a rounded subapertural avicularium. However, *S. propinqua* was easily distinguished from *S. prolifica* by the absence of a lyrula.

The similarity of the genus *Parasmittina* with *Smittoidea* is superficial since the marginal pores surrounding the frontal wall

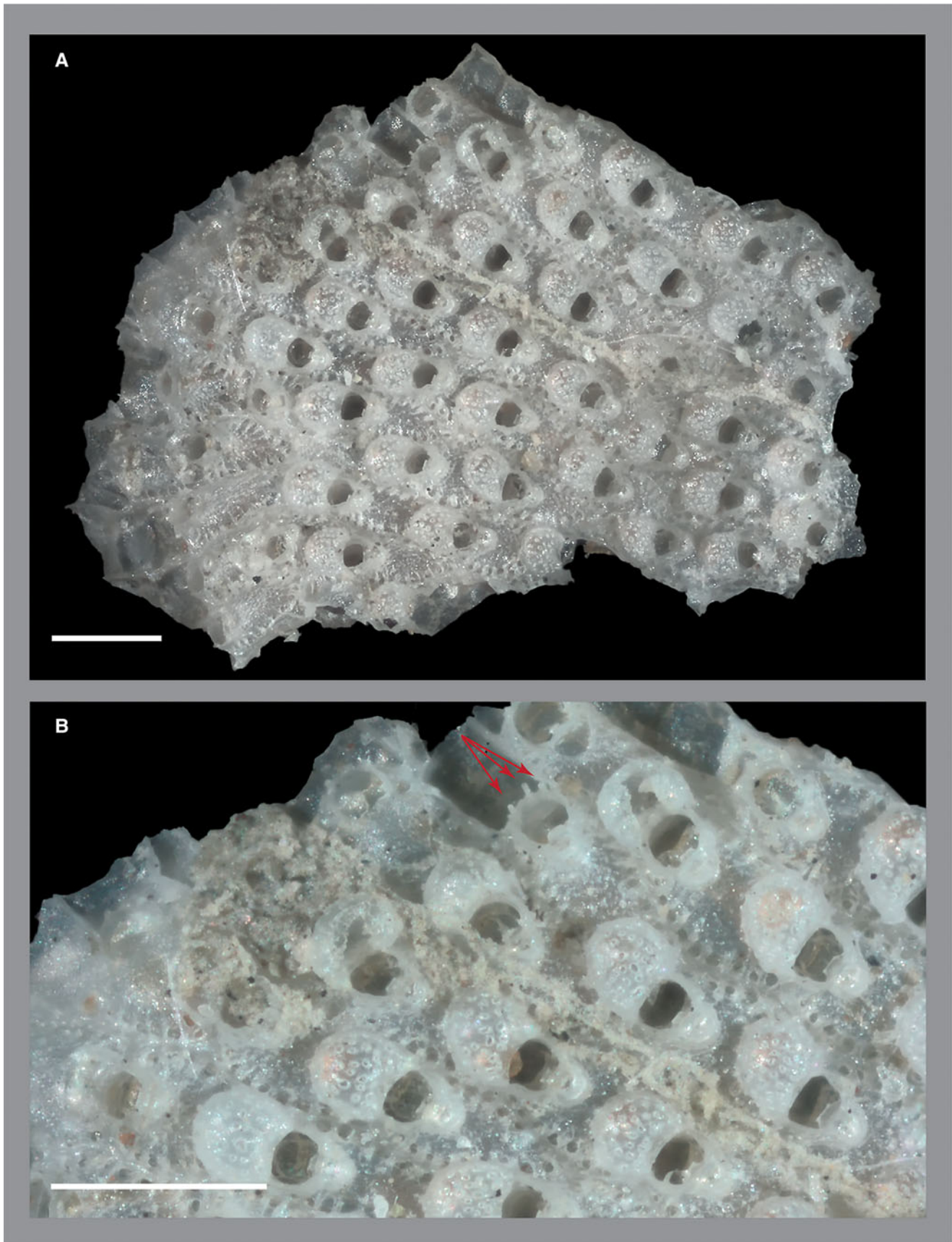


Figure 8. *Smittoideaprolifica* from Sasebo, Japan. A, Whole specimen; B, Colony edge top right, zoid primary orifice distal edge with three remnant spines (arrows). Catalogue number: USNM 651039; Scales: 500 μ m. Micrographs by E. Lazo-Wasem.

in *Parasmittina* are smaller, indistinct, and without ridges between them (Hayward and Ryland, 1999). More obvious differences include lateral avicularia with occasional adventitious

avicularia instead of a single medial avicularium, ovicells with only a few large perforations instead of scattered pores, and a round rather than oval orifice with either no peristome,

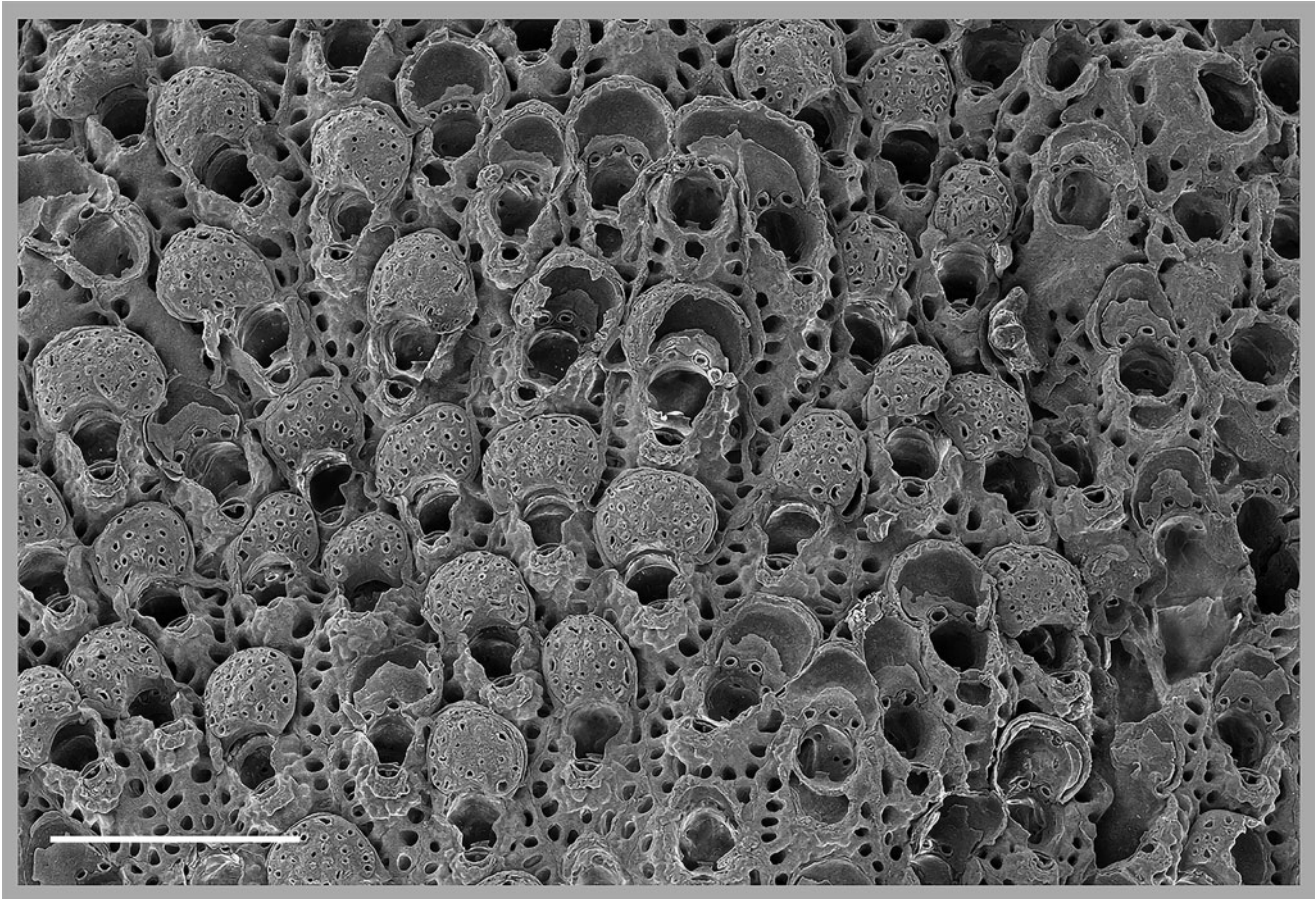


Figure 9. *Smittoidea spinigera* (Liu, 1990) from Maldo Island, southern Korea. Note the obliquely upward directed orientation of the suboral avicularia and ligulas on pivotal bars. Relatively large marginal pores occupy most of the frontal plate on some zooids. Scale: 500 μm . Scanning electron micrograph by Ji Eun Seo. (Courtesy of Ji Eun Seo).

e.g., *P. jeffreysi*, or low and less developed flaps, e.g., *P. nitida*. Specimens previously identified as *S. prolifica* from Virginia and deposited at the Smithsonian Institution (USNM 1446003) were examined and determined to be *P. nitida*.

Towards Establishing the Northwest Pacific Range of *Smittoidea prolifica*

Remarks

The specimen of *S. prolifica* collected from a fouling panel from Sasebo, Japan was examined to validate the identification by Long and Rucker (1969). This single dried specimen, a portion of one of the large colonies found, was similar in general morphology to descriptions from the East Pacific (Osburn, 1952; Soule, 1961; Soule and Soule, 1964; Banta, 1980) and Northeast Atlantic (De Blauwe and Faasse, 2004; Markert *et al.*, 2015) (Figure 8). In particular, each zooid had a single subapertural avicularium oriented perpendicular to the frontal wall, rounded with a pivotal bar without a ligula. Marginal pores separated by ridges surrounded the frontal wall which was not perforated.

The specimen collected at Maldo Island, southern Korea (Seo and Min, 2009) was re-examined from an unpublished SEM sent to the author by J.E. Seo (Figure 9). Using Liu *et al.* (2001) as a guide, the specimen was determined to be *Smittoidea spinigera* (Liu, 1990). The specimen was re-examined by J.E. Seo and agreement was met with the revised identification. Diagnostic characters were the orientation of the suboral avicularium that was directed obliquely upward and the presence of a

ligula on the pivotal bar. In *S. prolifica*, the suboral avicularium was oriented perpendicular to the frontal plate (Figure 7E) and the ligula was lacking (Figure 7D). Also noteworthy were the relatively large marginal pores that sometimes occupied most of the frontal plate, a situation resembling species of the genus *Smittina* (Figure 2A-D in Liu, 1990).

Reconsideration of the Northwest Pacific range

De Blauwe and Faasse (2004) raised questions concerning potential differences in the morphology of the specimens collected from the Northwest Pacific and called for re-examination. The current study confirmed the identification of Long and Rucker (1969) of *S. prolifica* in Japan. On the other hand, specimens of Seo and Min (2009) from southern Korea were *S. spinigera*. Another Northwest Pacific record questioned by De Blauwe and Faasse (2004) concerned the specimen collected in southern Korea and described as *S. prolifica* by Rho and Seo (1986). Specifically, potential differences involved the size and distribution of pores on ovicells, number and shape of spines, and protracted orifice. These features were re-examined by J.E. Seo and the present author. The raised margins on the ovicell pores seen in the light micrograph Plate 11, Figure 1 of Rho and Seo (1986) aligned this specimen with *S. spinigera*, not *S. prolifica*, as did the obliquely upward orientation of the suboral avicularium and a ligula on the pivotal bar, though this was infrequent. The number of ephemeral spines was three, but re-examination showed that number was based on the spines that remain during ovicell development as shown in the current paper for *S. prolifica* (Figure 4F).

Table 2. Measurements of *Smittioidea prolifica* collected from the Northwest Atlantic (Maine), East Pacific (California), Northwest Pacific (Japan), and the Northeast Atlantic (Germany)

Location	Zooid length	Zooid width	Orifice length	Orifice width	Ovicell length	Ovicell width	Lyrula length	Lyrula width	Avicularia length	Avicularia width
Casco Bay, Maine										
Mean (μm)	414	267	109	120	189	234	27	47	60	104
SD (μm)	16	41	7	6	18	12	5	6	10	6
Min (μm)	382	225	94	103	151	214	21	37	45	95
Max (μm)	437	382	120	132	216	255	36	56	80	112
Median (μm)	418	263	111	121	193	230	27	47	61	104
N	22	22	22	22	20	20	21	21	18	18
Glen Cove, California										
Mean (μm)	452	239	124	131	220	239	25	33	76	85
SD (μm)	18	14	3	3	15	9	2	4	2	3
Min (μm)	412	207	118	122	203	225	23	28	72	81
Max (μm)	477	255	128	134	248	252	29	39	80	93
Median (μm)	452	244	124	132	218	242	25	33	76	85
N	15	15	15	15	15	15	15	15	15	15
Sasebo, Japan										
Mean (μm)	411	231	106	124	185	206	23	40	66	91
SD (μm)	20	21	3	2	12	6	2	3	3	4
Min (μm)	376	201	101	121	155	197	19	33	61	85
Max (μm)	457	268	110	129	204	216	27	43	69	97
Median (μm)	412	232	107	124	184	204	23	40	67	91
N	15	15	15	15	15	15	15	15	15	15
Jade Weser Port & Wilhelmshaven, Germany										
Mean (μm)	448	236	91	99	160	188	–	–	–	–
SD (μm)	35	29	11	8	12	10	–	–	–	–
Min (μm)	388	177	73	79	124	168	–	–	–	–
Max (μm)	527	290	120	116	179	205	–	–	–	–
Median (μm)	446	241	94	100	162	186	–	–	–	–
N	20	20	20	20	20	20	–	–	–	–

Examination of zooids of *S. spinigera* from Maldo Island in zones of astogenic growth found they had 4-7 spines, and the ancestrula had 9 spines. In summary, all records of *S. prolifica* in southern Korea were mistaken identifications of *S. spinigera* and the localities of occurrences there were therefore unsupported.

The occurrence of *S. prolifica* in Japan reported by Rho and Seo (1986) was based on the opinion of Osburn (1952) who equated the *S. reticulata* of Okada and Mawatari (1936) from Japan with *S. prolifica*. The grounds for Osburn's judgement were found to be vague and unpersuasive by De Blauwe and Faasse (2004) because mandible shape and orientation were not considered, only the placement and shape of the avicularium. In particular, the mandible of *S. prolifica* was rounded, not acute as described by Okada and Mawatari (1936) who also stated it 'pointed downward,' which could mean directed proximally or perpendicular to the frontal plane as in *S. prolifica*. This ambiguity in meaning was clarified in the present study by reviewing the specimen from Sasebo, Japan as well as other species descriptions in Okada and Mawatari (1936) that were accompanied by text figures. When 'pointed downward(s)' was used, mandibles were directed proximally. Examples of this were given in the descriptions of *Pleurocodonellina signata* (Waters, 1889), i.e., *Smittina*

elongata Okada and Mawatari, 1936 and *Parasmittina rouvillei* (Calvet, 1902). Also included in this group was their new species *Smittina projecta*, an obvious *Parasmittina*, and is revised here to *Parasmittina projecta* (Okada and Mawatari, 1936). Clearly, given this clarification, the *S. reticulata* of Okada and Mawatari (1936) was not *S. prolifica* and consequently locations for *S. prolifica* in Japan stemming from Osburn (1952) are unsound. In summary, the only valid records of extant *S. prolifica* in the Northwest Pacific are those of Long and Rucker (1969) from Sasebo, Japan.

Biometric comparisons among geographically widely separated locations

Measurements of zooid characters from Maine colonies varied in comparison to sizes from other locations with statistical significance, but only one character, zooid width, proved largest among all recorded for that biometric (Table 2, Figures 10 and 11). Otherwise, when biometric differences occurred among locations, none were unique to Maine. For example, Maine and Japan zooid lengths were significantly different and smaller than measures from California and Germany specimens (Figure 11). Primary orifice length was significantly different

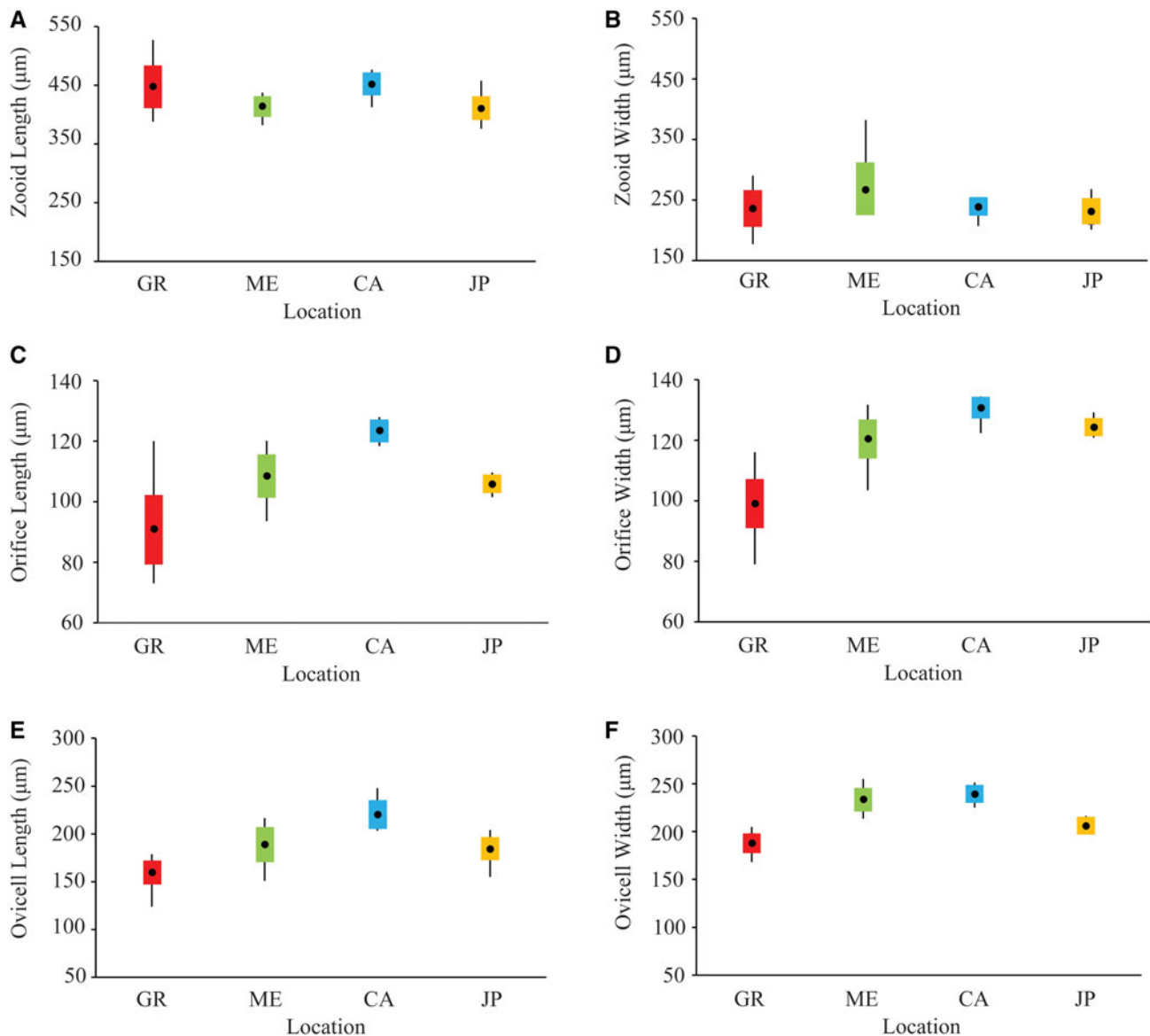


Figure 10. Measurements of *Smittoidea prolifica* from widely separated geographic locations arranged from NE Atlantic to NW Pacific. A, Zooid length; B, Zooid width; C, Orifice length; D, Orifice width; E, Ovicell length; F, Ovicell width. Abbreviations: CA, California; GR, Germany; JP, Japan; ME, Maine. Symbology: Mean, solid black circle; Standard deviation, box; Maximum and minimum values, whiskers (visible only when exceeding SD). Data used to construct plots are presented in Table 2.

and smaller for Maine and Japan compared to California, however it was smallest for Germany as was orifice width that was significantly different from all locations. Ovicell length was significantly different and smaller for Maine, Germany, and Japan compared to California, but among all locations it was significantly different and smallest for Germany. Ovicell width was significantly different and smallest for Germany followed by Japan, each significantly different and smaller than California and Maine. In summary, California zooids were larger in all dimensions except zooid width and Germany the smallest except for zooid length. No location was significantly dissimilar when averages of all biometrics per locality were compared ($P = 0.12$, SIMPROF test; Figure 12). However, specimens from Germany were most different with hierarchical cluster analysis placing them on a separate branch (Figure 12). Comparisons of biometrics between oceans showed that Pacific and Atlantic specimens differed significantly in all measures except zooid length and orifice width (Figure 13). Zooid width was the only character that was significantly different ($U = 453$, $P = 0.043$) and larger for Atlantic specimens compared to Pacific ones.

Discussion

The discovery of *S. prolifica* in Casco Bay, Maine, is the first for the Northwest Atlantic Ocean. There are no reports of Smittinidae in Casco Bay dating back to the earliest and exhaustive 1873 faunal surveys by Verrill (1874a, 1874b), so it is unlikely that *S. prolifica* was present there prior to this finding and misidentified. On a broader geographic scale, the only records of Smittinidae in the Gulf of Maine are for *P. jeffreysi*, *P. nitida*, and *S. propinqua*. The chance of confusing the identities of these species with *S. prolifica* is small. So, while misidentification of an introduced species as a local species does occur (Chapman, 1988), the obvious distinguishing features of these co-occurring species make that error improbable. The chance for misidentification is reduced further by other more detailed characteristics which differentiate these species.

Specimens of *S. prolifica* from Casco Bay, Maine were morphologically indistinguishable from ones collected at geographically widely dispersed locations in the temperate North Pacific and places of introduction in northern European waters. However,

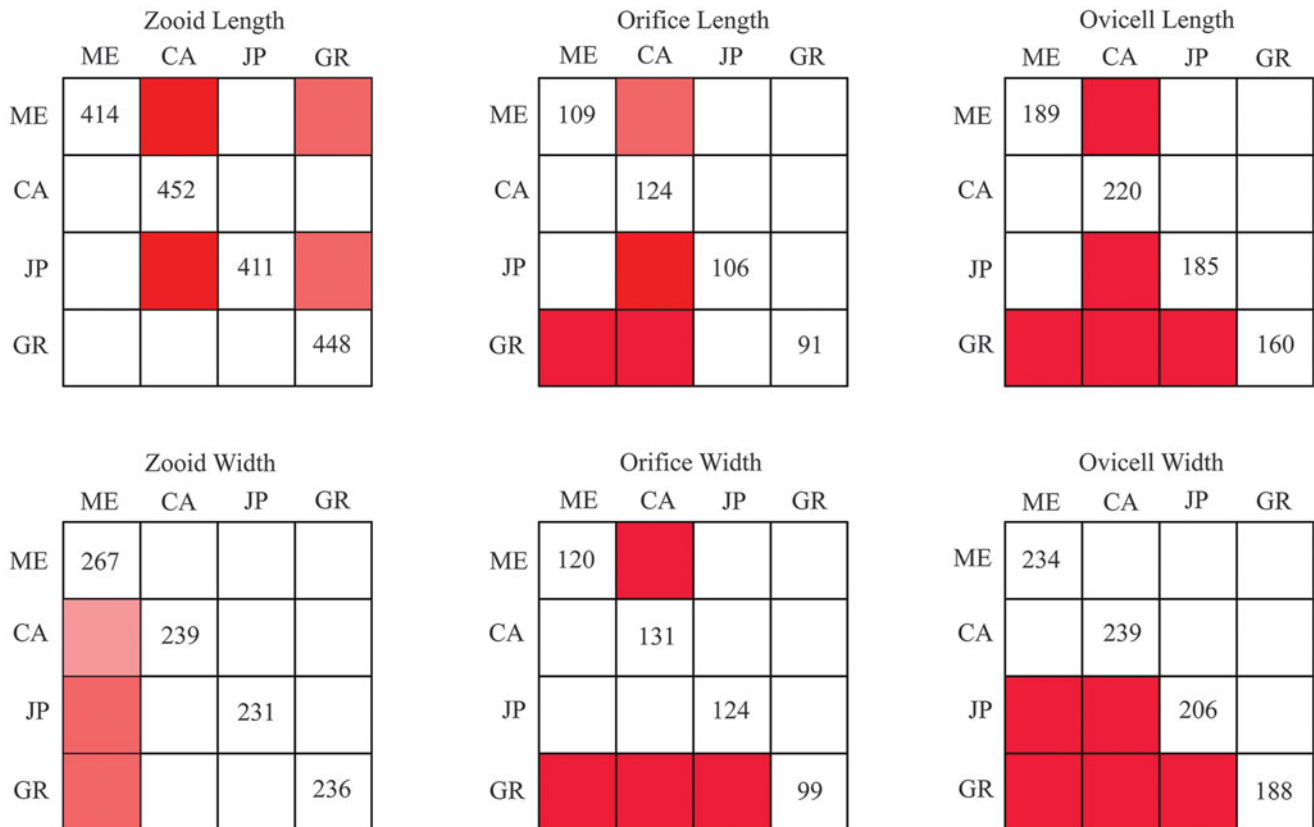


Figure 11. Contrasts of character measurements of *Smittoidea prolifica* from geographically widely separated locations. Matrices are interpreted by comparing column with row labels. Coloured squares indicate statistical significance: light pink, $P < 0.05$; pink, $P < 0.01$; red, $P < 0.001$. Numbers are mean measurements (μm). Abbreviations: CA, California; GR, Germany; JP, Japan; ME, Maine.

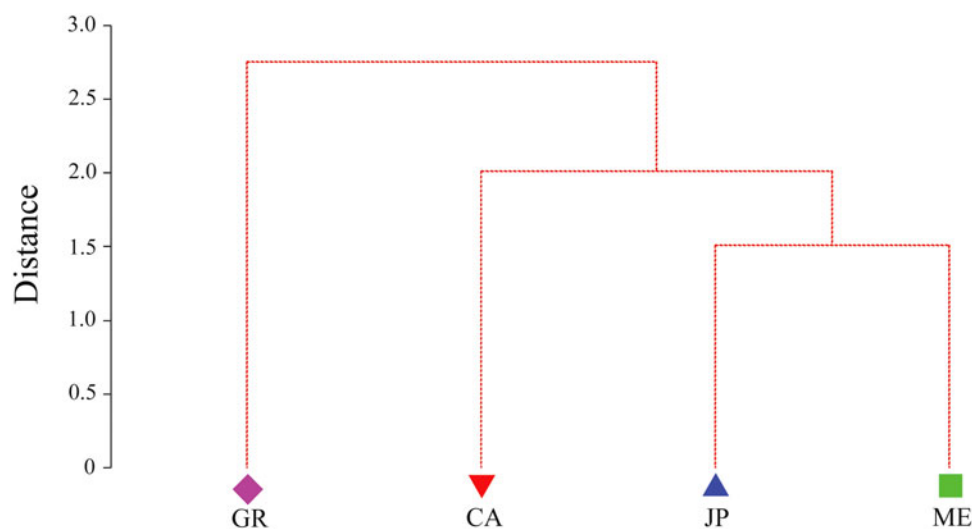


Figure 12. Dendrogram of zooid biometrics of colonies of *Smittoidea prolifica* collected from geographically widely separated locations, using group-average clustering from Euclidean similarities on square root transformed averages. No locations differed significantly as indicated by the red dotted lines ($P = 0.12$, SIMPROF test). Abbreviations: CA, California; GR, Germany; JP, Japan; ME, Maine.

comparisons among locations revealed that a few characteristics varied. The number of ephemeral spines was up to five in Maine specimens, 2 or 3 in Germany (Markert *et al.*, 2015), and 2 to 4 in southern California (Robertson, 1908; Osburn, 1952), Baja California (Soule and Soule, 1964), Gulf of California (Soule, 1961; Banta, 1980), and the Netherlands (De Blauwe and Faasse, 2004). The number of marginal pores, 10 to 14 for Maine specimens, agreed with a 'dozen or so' reported by Banta (1980) but was less than 18 to 22 and 16 to 18 described

by Soule (1961) and Soule and Soule (1964), respectively. Zoecia shape was most frequently described as ovate and ellipsoid to irregularly hexagonal like for Maine specimens but was also quadrate for the Netherlands (De Blauwe and Faasse, 2004) and some specimens from California (personal observation). There were no instances of zooids with twin ovicells seen in specimens from Germany (Markert *et al.*, 2015; Kind and Kuhlenkamp, 2016) and California (personal observation). In summary, some morphological characteristics of *S. prolifica* were variable and whether

	Atl	Pac		
Zooid Length			$P>0.05$	t test
Zooid Width			$P<0.05$	Mann–Whitney test
Ovicell Length			$P<0.001$	Mann–Whitney test
Ovicell Width			$P>0.05$	Mann–Whitney test
Ovicell Length			$P<0.001$	t test
Ovicell Width			$P=0.04$	Mann–Whitney test

Figure 13. Statistical comparisons of biometrics of zooid characters pooled among Atlantic (Germany and Maine) and Pacific (California and Japan) specimens of *Smittidea prolifica*. Red indicates which ocean had the larger measurement when test results were statistically significant ($P<0.05$).

this is of minor in consequence or carries some significance is subject to further study.

Some features of Maine specimens were not included in previous descriptions of *S. prolifica*. For zooids in zones of astogenic growth, the umbo was spiky with a flat distal face in early development and not rounded as it appeared later in development. There were two small extra-aperture pores, one on each side of primary orifice, proximally. Also, the lyrula had a longitudinal ridge that corresponded with a medial translucent tubule visible in light microphotographs that was drawn in Figure 8 by Osburn (1952) but not described. The tubule was internal to the lyrula and no connection to the avicularium chamber was seen.

Specimens of *S. prolifica* from different locations were remarkably similar in morphometry, none being statistically dissimilar in comparisons of their averaged zooid biometrics. If significant dissimilarity had been found, that could have raised questions about conspecificity. When individual character measurements were compared, however, there were significant variations. In general, biometrics of California specimens were the largest and Germany the smallest, a trend in difference that continued on a broader spatial scale when biometrics were compared by ocean. Maine specimens did not stand out as being particularly different biometrically and varied most by one character alone, zooid width, that was the largest among its measurements from all localities. For the remaining biometric comparisons, there was always one other location in common with Maine that had significantly different measures. A statistical evaluation unfortunately could not be done using all published character measurements. Only ranges in zooid length and width were published for specimens from the Netherlands and the number of measurements that determined the ranges were not (De Blauwe and Faasse, 2004). The raw data were not available to be assessed for normality and equal variances, and ranking. That said, the range in ovicell width (200–250 μm) was greatest among measurements for specimens from the Netherlands, as was zooid length (500–700 μm) (De Blauwe and Faasse, 2004). These biometrics blur conclusions about larger biometrics for *S. prolifica* in its native vs introduced range that might otherwise be made. As for differences in biometrics, some of the character variation among locations might be explained by differences in sea water temperature since its effects on bryozoan growth and zooid morphology are known (O’Dea and Okamura, 1999; Amui-Vedel *et al.*, 2007; Okamura *et al.*,

2011). Likewise, such differences could be the consequence of genotypic variation (Hageman *et al.*, 1999).

In its native range and locations of introduction, *S. prolifica* occurred in subtidal and intertidal habitats, within a broad range of temperatures and salinities, and on a diversity of substrates. Water temperatures ranged from 8.6 °C (Long and Rucker, 1969) to tropical waters (Soule and Soule, 1964) with salinities spanning brackish (De Blauwe and Faasse, 2004) to full sea water. Features of the subtidal habitat where Maine specimens occurred were within the limits of these environmental conditions. Substantially more is known about the kinds of substrates *S. prolifica* attaches to where it was introduced than in its native range where only general information was published with species descriptions (Robertson, 1908; Osburn, 1952; Soule, 1961; Soule and Soule, 1964; Banta, 1980). Biogenic (empty shells or shells of living animals, wood, macroalgae), inorganic (rocks ranging in size from small stones to boulders), and artificial (floats and fouling panels made of asbestos/wood or PVC) substrates were colonized. In Maine, *S. prolifica* encrusted mussel shells and plates of attached living and dead barnacles as reported elsewhere (e.g., Markert *et al.*, 2015). The low specificity for attachment substrates was contrary to not finding *S. prolifica* on seawalls around Helgoland (Kind and Kuhlenkamp, 2016), an observation which might imply that wave exposure influenced successful colonization. In summary, *S. prolifica* is a eurythermal and euryhaline species with low substrate specificity. These features indicate a high potential for successful introduction into subtidal habitats and wave protected bays and harbours.

The source populations where Casco Bay *S. prolifica* originated were most likely in the Northeast Atlantic at locations of established introductions in the North Sea. Portland is the only container cargo port in Maine, a major New England seaport (Anonymous, 2001; United States Department of Transportation, 2018) that is currently experiencing record growth in imports (LaClaire, 2022). This port receives commerce with container ships originating in the North Sea (McGuire, 2019) and likely the biofouling communities which can establish on such vessels (Davidson *et al.*, 2009). Ship-borne species spread is unquestionable at global scales (Carlton, 1996; Seebens *et al.*, 2013; Cuthbert *et al.*, 2022) and is understood at finer scales among ports using eDNA metabarcoding (Andrés *et al.*, 2023). Knowing the haplotype network for native and introduced populations would be valuable for understanding the dispersal of *S. prolifica* into the Northwest Atlantic and elsewhere. More extensive taxonomic and morphological comparisons could reveal patterns in phenotypic character variation to complement and aid the interpretation of genetic analyses like was done by Dick *et al.* (2020) for the bryozoan *Juxtacribrilina mutabilis* (Ito, Onishi & Dick, 2015).

The issue of the timing for the arrival of *S. prolifica* into Casco Bay can be explored through a brief history of Portland’s commercial shipping industry as it relates to ship-borne species spread. In 1999, over 90% of ballast water discharge into Casco Bay did not undergo any at sea exchange (Ruiz *et al.*, 2001), a process voluntary at a time when Portland was the second largest oil port on the US East coast (Anonymous, 2001). Portland kept that shipping status until 2016. The origin of oil shipments was not overseas. Portland container cargo commerce with North Sea seaports began in earnest in 2013 (Bennett, 2016). In 2018, two introduced species, the bryozoan *Juxtacribrilina mutabilis* and the amphipod *Grandidierella japonica* Stephensen, 1938, were discovered in Casco Bay during benthic surveys. The North Sea was likely the ultimate source of these introductions into the Northwest Atlantic (Trott and Enterline, 2019; Dick *et al.*, 2020; Trott *et al.*, 2020). The following year an eelgrass (*Zostera marina* Linnaeus, 1753) faunal survey (Maine Coastal Program, 2019) tracked the occurrence of *J. mutabilis* and *G. japonica* during

summer-fall but did not sample the location where *S. prolifica* was found by the present study. This contemporary bay-wide benthic investigation was only the second one ever conducted, the first in 1980 that did not find these invasives (Larsen *et al.*, 1983). Considering the timing of discoveries, probable source populations, and the history of Portland container cargo commerce, *S. prolifica* was most likely introduced in 2013 or thereafter. None of the three introductions were found by ongoing regional invasive monitoring programmes that primarily monitor floating docks. These are the Rapid Assessment Survey (RAS) and Marine Invader Monitoring and Information Collaborative (MIMIC) established in 2000 (Pederson *et al.*, 2001) and 2006 (Massachusetts Office of Coastal Zone Management, 2024), respectively. The unquestionable success of these programmes has been proven through their discoveries of species introductions and tracking range shifters. Adding a benthic survey component to their protocols would diversify the types of habitats examined and consequently improve their power of detection.

Establishment of *S. prolifica* beyond the scope of Casco Bay seems likely if its history of invasion in northern Europe is an indication of its success. This species has low substrate specificity and broad tolerance of environmental conditions. In fact, the success of this species being introduced and established makes it difficult to rule out the possibility that it was introduced into Sasebo, Japan by ships originating in California. The impact of *S. prolifica* may be low as predicted in the Netherlands (De Blauwe and Faasse, 2004). However, while invasive species with negligible effects often provoke slight to no concern, that dismissive perspective belies the significance of their signal of species arriving outside of their native range. Indifference risks playing ecological roulette in a time of unprecedented unpredictability, and the detection of three invasives in the course of three years in Casco Bay, each of them new to the Northwest Atlantic, gives a strong signal of more introductions to come.

Data. The data that support the findings of this study are available from the corresponding author upon reasonable request.

Acknowledgements. I express my sincere appreciation and gratitude to the many who helped during the development of this project in various indispensable ways. The helpful and constructive readings with discussion by Hans De Blauwe, external collaborator at Royal Belgian Institute of Natural Sciences, Eric Lazo-Wasem, Division of Invertebrate Zoology, Peabody Museum, Yale University, Linda McCann, Smithsonian Environmental Research Center (SERC), and Ji Eun Seo, Department of Life Science, Woosuk University lead to a much-improved manuscript. Lily Berniker, Division of Invertebrate Zoology, American Museum of Natural History, Vanessa Delnavaz, Division of Invertebrate Zoology, Santa Barbara Museum of Natural History, William Moser, Department of Invertebrate Zoology, National Museum of Natural History, and Nicholas Drew and Jessica Nakano, Department of Paleobiology, National Museum of Natural History prepared and sent loans of specimens. Linda McCann and Natasha Hitchcock of the Smithsonian Environmental Research Center sent additional specimens. Ji Eun Seo of the Woosuk University Department of Life Science supplied SEM images of specimens from southern Korea and kindly joined in helpful and essential discussions on identifications. The efforts of all the SERC staff, interns, and fellows who tirelessly processed fouling panels and vouchered specimens are gratefully acknowledged. A special thank you to Claire Goodwin, Huntsman Marine Science Centre, New Brunswick, Canada for providing access to specimens from the Atlantic Reference Centre. Alexandra Markert and Kei Matsuyama generously shared their biometric data from specimens collected in Germany. Eric Lazo-Wasem and Lourdes Rojas of the Peabody Museum of Natural History, Yale University, provided expert technical support and light and SEM imagery. Fieldwork was supported by the Maine Department of Environmental Protection and the Maine Coastal Program. My heartfelt appreciation to the crew of the R/V Amy Gale for assistance in the field. I thank the anonymous reviewer and Paul D. Taylor, Natural History Museum, London for constructive comments which greatly improved the quality of the manuscript.

Financial support. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Competing interests. Not applicable.

Ethical standards. Not applicable.

References

- Ahyong S, Boyko CB, Bailly N, Bernot J, Bieler R, Brandão, SN, Daly M, De Grave S, de Voogd NJ, Gofas S, Hernandez F, Hughes L, Neubauer TA, Paulay G, van der Meij S, Boydens B, Decock W, Dekeyser S, Goharimanesh M, Vandepitte L, Vanhoorne B, Adlard R, Agatha S, Ahn KJ, Alonso MV, Alvarez B, Amler MRW, Amorim V, Anderberg A, Andrés-Sánchez S, Ang Y, Antić D, Antonietto LS, Arango C, Artois T, Atkinson S, Auffenberg K, Bailly N, Baldwin BG, Bank R, Barber A, Barrett RL, Bartsch I, Bellan-Santini D, Bergh N, Berta A, Bezerra TN, Bieler R, Blanco S, Blasco-Costa I, Blazewicz M, Błędzki LA, Bock P, Bonifacino M, Böttger-Schnack R, Bouchet P, Boury-Esnault N, Bouzan R, Boxshall G, Bray R, Brito Seixas AL, Broda FT, Bruce NL, Bruneau A, Budaeva N, Bueno-Villegas J, Calvo Casas J, Cárdenas P, Carstens E, Cartwright P, Cedhagen T, Chan BK, Chan TY, Choong H, Christenhusz M, Churchill M, Collins AG, Collins GE, Collins K, Consorti L, Copilaş-Ciocianu D, Corbari L, Cordeiro R, Costa VMdM, Costa Corgosinho PH, Coste M, Costello MJ, Crandall KA, Cremonte F, Cribb T, Cutmore S, Dahdouh-Guebas F, Daneliya M, Dauvin JC, Davie P, De Broyer C, de Lima Ferreira P, de Mazancourt V, de Moura Oliveira L, Decker P, Defaye D, Dekker H, Di Capua I, Dippenaar S, Dohrmann M, Dolan J, Domning D, Downey R, Dreyer N, Eisendle U, Eitel M, Eleaume M, Enghoff H, Epler J, Esquete Garrote P, Evenhuis NL, Ewers-Saucedo C, Faber M, Figueroa D, Fišer C, Fordyce E, Foster W, Fransen C, Freire S, Fujimoto S, Furuya H, Galbany-Casals M, Gale A, Galea H, Gao T, Garic R, Garnett S, Gaviria-Melo S, Gerken S, Gibson D, Gibson R, Gil J, Gittenberger A, Glasby C, Glenner H, Glover A, Gómez-Noguera SE, Gondim AI, Gonzalez BC, González-Solis D, Goodwin C, Gostel M, Grabowski M, Gravili C, Grossi M, Guerra-García JM, Guerrero JM, Guidetti R, Guiry MD, Gutierrez D, Hadfield KA, Hajdu E, Halaných K, Hallermann J, Hayward BW, Hegna TA, Heiden G, Hendrycks E, Hennen D, Herbert D, Herrera Bachiller A, Hodda M, Høeg J, Hoeksema B, Holovachov O, Hooge MD, Hooper JN, Horton T, Houart R, Huys R, Hyžný M, Iñiesta LFM, Iseto T, Iwataki M, Janssen R, Jaume D, Jazdzewski K, Jersabek CD, Jiménez-Mejías P, Józwiak P, Kabat A, Kakui K, Kantor Y, Karanovic I, Karapunar B, Karthick B, Kathirithamby J, Katinas L, Kilian N, Kim YH, King R, Kirk PM, Klautau M, Kocielek JP, Köhler F, Konowalik K, Kotov A, Kovács Z, Kremenetskaia A, Kristensen RM, Kroh A, Kulikovskiy M, Kullander S, Kupriyanova E, Lamaro A, Lambert G, Larridon I, Lazarus D, Le Coze F, Le Roux M, LeCroy S, Leduc D, Lefkowitz EJ, Lemaitre R, Lichter-Marck IH, Lim SC, Lindsay D, Liu Y, Loeuille B, Lörz AN, Ludwig T, Lundholm N, Macpherson E, Mah C, Mamos T, Manconi R, Mapstone G, Marek PE, Markello K, Márquez-Corro JJ, Marshall B, Marshall DJ, Martin P, Martínez Arbizu P, McFadden C, McInnes SJ, McKenzie R, Means J, Mees J, Mejía-Madrid HH, Meland K, Merrin KL, Miller J, Mills C, Moestrup Ø, Mokievsky V, Molodtsova T, Monniot F, Mooi R, Morandini AC, Moreira da Rocha R, Morrow C, Mortelmans J, Müller A, Muñoz Gallego AR, Muñoz Schüller P, Musco L, Nascimento JB, Nesom G, Neto Silva MdS, Neubert E, Neuhaus B, Ng P, Nguyen AD, Nielsen C, Nielsen S, Nishikawa T, Norenburg J, O'Hara T, Opreško D, Osawa M, Osigus HJ, Ota Y, Páll-Gergely B, Panero JL, Patterson D, Pedram M, Pelser P, Peña Santiago R, Pereira JdS, Pereira PHM, Pereira SGG, Perez-Losada M, Petrescu I, Pflingst T, Piasecki W, Pica D, Picton B, Pignatti J, Pilger JF, Pinheiro U, Pisera AB, Poatskievick Piezezan B, Polhemus D, Poore GC, Potapova M, Praxedes RA, Půža V, Read G, Reich M, Reimer JD, Reip H, Resende Bueno V, Reuscher M, Reynolds JW, Richling I, Rimet F, Ríos P, Rius M, Rodríguez E, Rogers DC, Roque N, Rosenberg G, Rützler K, Sá HAB, Saavedra M, Sabater LM, Sabbe K, Sabroux R, Saiz-Salinas J, Sala S, Samimi-Namin K, Santagata S, Santos S, Santos SG, Sanz Arnal M, Sar E, Saucède T, Schärer L, Schierwater B, Schilling E, Schmidt-Lebuhn A, Schneider S, Schönberg C, Schrével J, Schuchert P, Schweitzer C, Semples JC, Senna

- AR, Sennikov A, Serejo C, Shaik S, Shamsi S, Sharma J, Shear WA, Shenkar N, Short M, Sicinski J, Sidorov D, Sierwald P, Silva DKFd, Silva ESS, Silva MLCN, Simmons E, Sinniger F, Sinou C, Sivell D, Smit H, Smit N, Smol N, Sørensen MV, Souza-Filho JF, Spelda J, Sterrer W, Steyn HM, Stoev P, Stöhr S, Suárez-Morales E, Susanna A, Suttle C, Swalla BJ, Taiti S, Tanaka M, Tandberg AH, Tang D, Tasker M, Taylor J, Taylor J, Taylor K, Tchesunov A, Temereva E, ten Hove H, ter Poorten JJ, Thirouin K, Thomas JD, Thuessen EV, Thurston M, Thuy B, Timi JT, Todaro A, Todd J, Turon X, Uetz P, Urbatsch L, Uribe-Palomino J, Urtubey E, Utevsky S, Vacelet J, Vader W, Väinölä R, Valls Domedel G, Van de Vijver B, van Haaren T, van Soest RW, Vanreusel A, Velandia J, Venekey V, Verhoeff T, Vinarski M, Vonk R, Vos C, Vouilloud AA, Walker-Smith G, Walter TC, Watling L, Wayland M, Wesener T, Wetzel CE, Whipps C, White K, Wieneke U, Williams DM, Williams G, Wilson KL, Wilson R, Witkowski J, Wyatt N, Xavier J, Xu K, Zanol J, Zeidler W, Zhao Z and Zullini A (2024) World Register of Marine Species. Available at <https://www.marinespecies.org>. Accessed 04 February 2024.
- Amui-Vedel AM, Hayward PJ and Porter JS** (2007) Zooid size and growth rate of the bryozoan *Cryptosula pallasiana* Moll in relation to temperature, in culture and in its natural environment. *Journal of Experimental Marine Biology and Ecology* 353, 1–12.
- Andrés J, Czechowski P, Grey E, Saebi M, Andres K, Brown C, Chawla N, Corbett JJ, Brys R, Cassey P and Correa N** (2023) Environment and shipping drive environmental DNA beta-diversity among commercial ports. *Molecular Ecology* 2023, 6696–6709.
- Anonymous** (2001) Portland remains New England's largest tonnage port. *Maritime Reporter and Engineering News* 6, 81.
- Banta WC** (1980) Bryozoa (moss animals). In Brusca RC (ed.), *Common Intertidal Invertebrates of the Gulf of California*, 2nd Edn. Tucson: University of Arizona Press, pp. 356–396.
- Bennett M** (2016) Eimskip in Maine: a saga for the 21st-century Arctic. Cryopolitics. Available at <https://www.cryopolitics.com/2016/05/05/eimskip-in-maine-a-saga-for-the-21st-century-arctic>. Accessed 30 December 2023.
- Carlton J** (1996) Marine bioinvasions: the alteration of marine ecosystems by nonindigenous species. *Oceanography* 9, 36–43.
- Chapman JW** (1988) Invasions of the Northeast Pacific by Asian and Atlantic gammaridean amphipod crustaceans, including a new species of *Corophium*. *Journal of Crustacean Biology* 8, 364–382.
- Clarke KR and Warwick RM** (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd Edn. Plymouth: Plymouth Marine Laboratory.
- Cuthbert RN, Kotronaki SG, Carlton JT, Ruiz GM, Fofonoff P and Briski E** (2022) Aquatic invasion patterns across the North Atlantic. *Global Change Biology* 28, 1376–1387.
- Davidson IC, Brown CW, Systma MD and Ruiz GM** (2009) The role of containerships as transfer mechanisms of marine biofouling species. *Biofouling* 25, 645–655.
- De Blauwe H and Faasse M** (2004) *Smittoidea prolifica* Osburn, 1952 (Bryozoa, Cheilostomatida), a Pacific bryozoan introduced to the Netherlands (Northeast Atlantic). *Bulletin de l'Institut royal des sciences naturelles de Belgique, Biologie* 74, 33–39.
- Dekker R and Drent J** (2013) The macrozoobenthos in the sublittoral of the western Dutch Wadden Sea in 2008 and a comparison with 1981–1982. Royal Netherlands Institute for Sea Research, NOIZ-Report 2013-5, 102 pp.
- Dick MH, Waeschenbach A, Trott TJ, Onishi T, Beveridge C, Bishop JD, Ito M and Ostrovsky AN** (2020) Global distribution and variation of the invasive cheilostome bryozoan *Cribrilina mutabilis*. *Zoological Science* 37, 217–231.
- Gittenberger A, Rensing M, Dekker R, Niemantsverdriet P, Schrieken N and Stegenga H** (2015) Native and non-native species of the Dutch Wadden Sea in 2014. Office for Risk Assessment and Research, The Netherlands Food and Consumer Product Safety Authority, GiMaRIS 2015_08, 94 pp.
- Hageman SJ, Bayer MM and Todd CD** (1999) Partitioning phenotypic variation: genotypic, environmental and residual components from bryozoan skeletal morphology. *Journal of Natural History* 33, 1713–1735.
- Hayami T** (1975) Neogene Bryozoa from northern Japan. *The science reports of the Tohoku University, Second series, Geology* 45, 83–126.
- Hayward PJ and Ryland JS** (1999) Cheilostomatous Bryozoa. Part 2, Hippothooidea – Celleporoidea. Field Studies Council Shrewsbury. Dorset Press, Dorchester [Synopsis of the British Fauna (New Series) No. 14.].
- Kind B and Kuhlenkamp R** (2016) Discovery of the non-indigenous bryozoan *Smittoidea prolifica* Osburn, 1952 near Helgoland: first record in 2011 for the German North Sea. *Marine Biodiversity* 48, 1237–1240.
- LaClaire H** (2022) Cargo volume in Portland Harbor headed for another record year. *Portland Press Herald* 161(44), B3. <https://www.pressherald.com/2022/08/10/cargo-volume-in-portland-harbor-headed-for-another-record-year>. Accessed 27 December 2023.
- Larsen PF, Johnson AC and Doggett LF** (1983) Environmental benchmark studies in Casco Bay, Maine, April 1980. Northeast Monitoring Program (NOAA Technical Memorandums) NMFS-F/NEC-19, 190 pp.
- Liu X** (1990) Three new cheilostome bryozoans from the coasts of Shandong and Zhejiang Provinces. *Studia Marina Sinica* 31, 121–128.
- Liu X, Yin X and Ma J** (2001) *Biology of Marine-Fouling Bryozoans in the Coastal Waters of China*. Beijing: Science Press.
- Long ER and Rucker JB** (1969) A comparative study of cheilostome Bryozoa at Yokosuka, Maizuru, and Sasebo, Japan. *Pacific Science* 23, 56–69.
- Maine Coastal Program** (2019) Invasive Species in Casco Bay: discovery, distribution and biological assessment. Maine Outdoor Heritage Fund, Final Report 191-01-09, 10 pp. Available at <https://www.cascobayestuary.org/publication/invasive-species-in-casco-bay-discovery-distribution-and-biological-assessment>. Accessed 27 December 2023.
- Markert A, Matsuyama K, Rohde S, Schupp P and Wehrmann A** (2015) First record of the non-native Pacific bryozoan *Smittoidea prolifica* Osburn, 1952 at the German North Sea coast. *Marine Biodiversity* 46, 717–723.
- Massachusetts Office of Coastal Zone Management** (2024). Marine Invader Monitoring and Information Collaborative (MIMIC). Available at <https://www.mass.gov/info-details/marine-invader-monitoring-and-information-collaborative-mimic>. Accessed 6 January 2024.
- McGuire P** (2019) Eimskip brings in bigger ship as cargo through Portland skyrockets. *Portland Press Herald* 157(259), A8. <https://www.pressherald.com/2019/04/17/eimskip-adds-new-ship-as-cargo-through-portland-skyrockets>. Accessed 30 December 2023.
- Nelson JC, Murray CC, Otani M, Liggan L, Kawai H, Ruiz GM, Hansen and Carlton JT** (2016) PICES Japanese Tsunami Marine Debris (JTMD) database. Available at <https://invasions.si.edu/nemesis/jtmd>. Accessed 14 February 2024.
- OBIS** (2023) Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. Available at www.obis.org. Accessed 27 February 2024.
- O'Dea A and Okamura B** (1999) Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati*. *Marine Biology* 135, 581–588.
- Okada Y and Mawatari SH** (1936) Bryozoa fauna collected by the 'Missago' during the zoological survey around Izu Peninsula (II). *Science Reports of the Tokyo Bunrika Daigaku. Section. B. Zoology and Botany* 3, 53–73.
- Okamura B, O'Dea A and Knowles T** (2011) Bryozoan growth and environmental reconstruction by zooid size variation. *Marine Ecology Progress Series* 430, 133–146.
- Osburn RC** (1952) Bryozoa of the Pacific Coast of America. Part 2, Cheilostomata–Ascophora. *Allan Hancock Pacific Expeditions (Allan Hancock Foundation Publications)* 14, 271–611.
- Pederson J, Bullock R, Calder D, Carlton JT, Chapman JW, Cohen A, Dean H, Drynda P, Harris L, Lambert C, Lambert G, Mathieson A, Tyler S and Winston J** (2001) Rapid assessment survey of nonindigenous species in coastal Massachusetts. In Barrett-O'Leary, M. (compiler) *International Conference on Marine Bioinvasions (Abstracts)*, 9–11 April 2001, New Orleans, Louisiana: Louisiana Sea Grant College Program, pp. 122.
- Pouyet S and Herrera Y** (1986) Systematics and paleogeographical studies of some species of Bryozoa (Cheilostomata) from the Gulf of Mexico. *Revisita Mexicana de Ciencias Geológicas* 6, 204–221.
- Rho BJ and Seo JE** (1986) A systematic study of the marine bryozoans in Cheju-do. *The Korean Journal of Zoology* 29, 31–60.
- Robertson A** (1908) The incrusting cheilostomatous Bryozoa of the West Coast of North America. *University of California Publications in Zoology* 4, 253–344.
- Ruiz GM, Miller AW, Lion K, Steves B, Arnwine A, Collinetti E and Wells E** (2001) Status and trends of ballast water management in the United States. First Biennial Report of the National Ballast Information Clearinghouse. Appendix B. Smithsonian Environmental Research Center, Edgewater, Maryland, Appendix B, 45 pp.
- Seebens H, Gastner MT and Blasius B** (2013) The risk of marine bioinvasion caused by global shipping. *Ecological Letters* 16, 782–790.

- Seo JE and Min BS** (2009) A faunistic study on cheilostomatous bryozoans from the shoreline of South Korea, with two new species. *Korean Journal of Systematic Zoology* **25**, 19–40.
- Soule JD** (1961) Results of the Puritan-American Museum of Natural History expedition to western Mexico 13. Ascophoran Cheilostomata (Bryozoa) of the Gulf of California. *American Museum Novitates* **2053**, 1–66.
- Soule DF and Soule JD** (1964) The Ectoprocta (Bryozoa) of Scammon's Lagoon, Baja California, Mexico. *American Museum Novitates* **2199**, 1–56.
- Trott TJ and Enterline C** (2019) First record of the encrusting bryozoan *Cribrilina (Juxtacribrilina) mutabilis* (Ito, Onishi and Dick, 2015) in the Northwest Atlantic Ocean. *BioInvasions Records* **8**, 598–607.
- Trott TJ, Lazo-Wasem EA and Enterline C** (2020) *Grandidierella japonica* Stephensen, 1938 (Amphipoda: Aoridae) in the Northwest Atlantic Ocean. *Aquatic Invasions* **15**, 282–296.
- United States Department of Transportation** (2018) U.S. Waterborne Foreign Container Trade by U.S. Customs Ports 2000–2017. Available at <https://www.maritime.dot.gov/data-reports/data-statistics/us-waterborne-foreign-container-trade-us-customs-ports-2000-%E2%80%932017>. Accessed 30 December 2023.
- Vanagt T, Van de Moortel L and Faasse M** (2013) Development of hard substrate fauna in the Princess Amalia Wind Farm. Monitoring 3.5 years after construction. eCoast Marine Research, Oostende, Belgium, eCoast report 2011036, 75 pp.
- Van Moorsel GWNM** (1996) Biomonitoring van levensgemeenschappen op sublitorale harde substraten in Grevelingenmeer, Oosterschelde, Veerse Meer en Westerschelde, resultaten t/m 1995. Bureau Waardenburg bv / Rijksinstituut voor Kust en Zee, Culemborg, the Netherlands, Rapport. 96.14, 66 pp.
- Verrill AE** (1874a) Explorations of Casco Bay, by the United States Fisheries Commission in 1873. *Proceedings of the American Association for the Advancement of Science* **22**, 340–395.
- Verrill AE** (1874b) Brief contributions to zoology, from the museum of Yale College; No. XXVII, Results of recent dredging expeditions on the coast of New England, No. 5. *American Journal of Science* **3**, 131–138.
- Winston JE and Jackson JB** (2021) Coral reef-associated bryozoans of Jamaica. *Zootaxa* **4988**, 1–218.
- Winston JE and Maturo JF Jr** (2009) Bryozoans (Ectoprocta) of the Gulf of Mexico. In: Felder D.L. and Camp D.K. (eds) *Gulf of Mexico—Origins, Waters, and Biota. Biodiversity*. College Station: Texas A&M Press, pp. 1147–1164.
- Winston JE and Woollacott RM** (2009) Scientific results of the Hassler Expedition. Bryozoa. No. 1. Barbados. *Bulletin of the Museum of Comparative Zoology* **159**, 239–300.