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NON-NATIVE BRYOZOANS IN COASTAL EMBAYMENTS OF THE SOUTHERN UNITED STATES: NEW RECORDS FOR THE WESTERN ATLANTIC

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ABSTRACT

Bryozoans are among the most common fouling organisms in coastal marine environments around the world, yet their distribution in many coastal areas is not well known. We surveyed the bryozoans in shallow coastal estuaries in the southern United States, focusing on Texas and Florida. We deployed settlement plates across six different estuaries at 61 sites. Thirty-five species of bryozoans were identified, including four non-native species described here for the first time from the United States: *Hippoporina indica* (Pillai, 1978), *Electra bengalensis* (Stoliczka, 1869), *Sinoflustra annae* (Osburn, 1953), and *Celleporaria pilaefera* (Canu and Bassler, 1929). At all six estuaries, non-native species were among the most common bryozoans. *Hippoporina indica* was the most abundant bryozoan, occurring in all estuaries sampled. In Jacksonville, Florida, *E. bengalensis* and *S. annae* dominated both the numbers and biomass of bryozoans. All four species have probable Indo-West Pacific origins. A literature-based analysis identified 39 additional non-native species of marine invertebrates and algae already established in the region, and over half are considered to have an Indo-West Pacific origin. Ships from Asia are regular visitors to Florida and the Gulf of Mexico, providing a possible mechanism of introduction for the non-native bryozoans.

The number of documented invasions in marine systems continues to increase in the United States and around the world (Carlton, 2001). There are approximately 350 non-native invertebrate and algal species established in coastal marine waters of the continental U.S. (Steves et al., 2006). This number is certainly an underestimate, as recent analyses are lacking for many regions and taxonomic groups (see also Carlton, 1996; Ruiz et al., 2000). Most marine invasions have been documented in bays and estuaries, and commercial shipping (either from ballast water or hull fouling) is the dominant transfer mechanism or vector for these invasions in coastal waters of the U.S. (Ruiz et al., 2000).

To measure the extent and pattern of marine invasions, we began a large scale survey of fouling communities in coastal estuaries across North America. Surveys were initiated in 2000, using standardized methods. Bays with high salinities (> 20) and at least one major port were selected for study. For some areas, this was the first comprehensive look at non-native species in these habitats. Our analyses focused primarily on the large, sessile invertebrates and identified new invasions to the United States by tunicates, hydroids, and bryozoans. Here, we report our findings on the bryozoans of Florida and Texas. Syntheses across broader spatial scales and other taxonomic groups will be the focus of future publications.

Bryozoans are an important component of the fouling community. With encrusting as well as arborescent forms (sometimes both in the same colony), bryozoans often dominate hard substrates. Encrusting colonies do quite well in fouling environments with crowded substrata as they can spread quickly or overgrow competitors

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(Hayward and Ryland, 1998). Bryozoans exhibit both sexual and asexual reproduction, and many species produce senescing or resting stages that may allow them to survive during adverse conditions. They readily colonize living organisms, including algae susceptible to breaking and drifting with the currents, and man-made materials (docks, pilings, boats). All of these characteristics make them relatively adaptable to large scale disturbances of their environment and well suited for human-mediated invasion.

Although many areas of the Gulf of Mexico and the western Atlantic have been surveyed for non-native species (United States Environmental Protection Agency, 2000; Benson et al., 2001; Gulf States Marine Commission, 2003; Gossett and Lester, 2004), little has been reported about bryozoans. Large scale studies in the gulf, like those conducted during oil drilling surveys (Galaway et al., 2003), identified many deep water bryozoans, most of which do not occur in shallow water communities. The few published studies on bryozoans from nearshore areas of the Gulf of Mexico are at least 50 yrs old (Canu and Bassler, 1928; Lagaaij, 1963; Maturo and Schopf, 1966). These studies, along with some fossil evidence (Cheetham and Sandberg, 1964), suggest that few invasions had occurred in this region by that time.

We report here the bryozoan species documented in our surveys of six estuaries, from the Atlantic coast of Florida to Texas, indicating the known geographic range and origin (native vs non-native status) of each species. We detected four non-native species, previously undescribed for the U.S., suggesting that non-native bryozoans are more prevalent in the Gulf of Mexico than previously thought (and see Gordon et al., 2006). For each of these new records, we provide a brief species description, SEM illustrations, and information on ecology and world distributions. Finally, we examine the geographic origin of other known marine invasions and commercial shipping, as a possible transfer mechanism, to the Gulf of Mexico and Florida.

Methods

Surveys.—Four embayments were sampled in the Gulf of Mexico in the summer of 2002 (Tampa and Pensacola Bays in Florida, and Galveston and Corpus Christi Bays in Texas), and two bays were sampled on the east coast of Florida in the summers of 2001 (Saint Johns River, Jacksonville, Florida) and 2005 (Indian River Lagoon, Florida) (Fig.1). Embayments were chosen to focus on high salinity communities in relatively large estuaries, in close proximity to major population centers and port systems. For each bay, we used a stratified sampling design, selecting approximately ten sites (marinas, ports, bridges, piers, and buoys) with salinity > 20. Bays were divided into sites of roughly equal size, 1–25 km apart. Twenty Poly Vinyl Chloride (PVC) settlement plates (14 × 14 cm) were suspended 1 m below mean low water at random locations at least 1 m apart within each site (for a total of 180–200 plates per bay). Settling plates were deployed in late spring or early summer and retrieved after 3 mo. Once retrieved, sessile invertebrates were collected live, sorted, and preserved for identification from 10 randomly selected plates per site (90–110 per bay). All major fouling taxa, including bryozoans, were identified to species level where possible.

A subset of samples of each species from each site was sent out for confirmation by taxonomic experts. A comprehensive review of the literature was conducted to evaluate the distribution and origins (or native region) of all species identified. Areas of origin were divided into five regions—Unknown, East Atlantic, West Atlantic, East Pacific, and Indo-West Pacific. Species were categorized as native, non-native, cryptogenic, or unknown based on this information (see Chapman and Carlton, 1991; Carlton, 1996). Briefly, non-native species as defined here, meet multiple criteria, among them: they appear suddenly in localities where there are

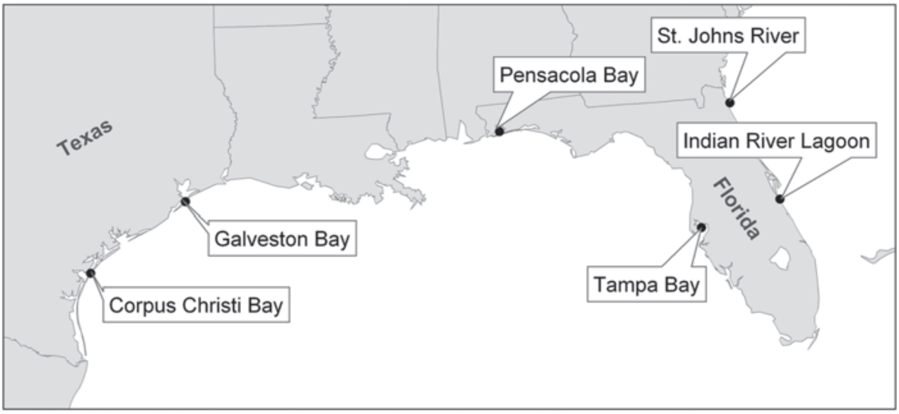

Figure 1. Map of the Southern United States with sample sites indicated.

no previous records, and they exhibit strong associations with artificial substrates, or an association with human mechanisms of dispersal. Cryptogenic species are those that occur widely throughout the world and have unclear origins. Taxa designated as unknown were those not identified to species level, due to poor condition, small size, or taxonomic issues. All material was deposited in the collections of the Smithsonian Environmental Research Center. A more detailed description of the sites, methods, and results for the larger study is given in Ruiz et al., 2004.

Environmental Data.—Environmental parameters measured at deployment and retrieval at each site included: depth, temperature, salinity, and turbidity (secchi depth). Temperature was also recorded continuously during the 3 mo deployment. Study sites were generally shallow, ranging from 1.2–5 m, with the exception of Tampa Bay, where sites were as deep as 10 m. Temperature and salinity were fairly stable throughout the water column within each site and did not exhibit stratification. Temperature for all sites ranged from 25–32 °C over the 3 mo period of deployment. Salinity varied only slightly among sites within a bay and between bays (26.7–36.1), with the exception of Saint Johns River in Jacksonville (salinity declined progressively up river; 33.7–2.7) and Galveston Bay (salinity varied between 12.4 and 26.0 at different sites).

Literature-based Analysis of Regional Invasions.—We compiled a cumulative list of non-native marine invertebrates and algae reported from our study region, from the Atlantic coast of Florida to southern Texas. For each species, we identified the geographic origin. For this analysis, data were compiled from our surveys, published literature, unpublished reports, and personal communications (G. Lambert, University of California, Fullerton, and J. Carlton, Williams College, Connecticut). References for invertebrates other than bryozoans (discussed elsewhere) include: Van Name, 1921; Deevey, 1950; Hartman, 1951; Menzies, 1957; Wallour, 1960; Miller, 1968; Moore and McPherson, 1974; Marcus, 1977; McPherson et al., 1980; Monniot, 1983; Bertsch, 1988; Carlton, 1992; Zullo, 1992; Hicks and Tunnell, 1995; LeMaitre, 1995; Kensley and Schott, 1999; Benson, 2001, 2006; Ingrao, 2001; Bastida-Zavala and Ten Hove, 2002; Department of Systematic Biology: Invertebrate Zoology Collections Database, 2002; Roy and Sponer, 2002; Schrope, 2003; Baker et al., 2004; Bieler et al., 2004; Fenner and Banks, 2004; Foster et al., 2004; Walters, 2006. Our data are conservative in that non-native species recorded from the area more than 10 yrs ago with no additional records were not included.

Commercial Shipping Patterns.—We examined the source of commercial shipping traffic to the study region as a possible source of introduction for non-native fouling organisms. Commercial shipping traffic data to United States ports were obtained for July 1999 through December 2004 from the United States Department of Transportation's Maritime

Administration (MARAD) and the Panama Canal Authority Transit Statistics. Vessel arrivals from foreign and domestic ports were examined for all coastal ports in Florida and the Gulf of Mexico.

Results

Surveys.—Thirty-five species of bryozoans were collected and identified on 586 plates across the six bays (Table 1). Bryozoans were one of the three most abundant taxa on our plates at all sites, with the exception of Tampa Bay. Twelve of these species are considered native to Florida and Texas, four are considered non-native, and the rest were classified as cryptogenic or of unknown identity (and origin). The four non-native species include: *Hippoporina indica*, *Electra bengalensis*, *Sinoflustra annae*, and *Celleporaria pilaefera*. The Indo-West Pacific is considered the area of origin for all four of the non-native bryozoans. To our knowledge, these are the first records of these species reported in the United States.

The total number of bryozoans identified per bay ranged from 8–19 species, with the highest species richness occurring at the two sites on the Atlantic coast of Florida (Table 1, Fig. 2). A large portion of this difference resulted from a larger number (and percent) of non-native and cryptogenic species at the Atlantic bays compared to those in the Gulf of Mexico. All four non-native species were found in Saint Johns River, two in the Indian River Lagoon, and one at the four Gulf of Mexico sites (Fig. 2). A similar pattern was observed for the cryptogenic species diversity across bays.

In all embayments, the non-native *H. indica* was one of the most abundant species, occurring at seven to nine sites within each bay (42 of 61 total sites, Table 1), with the exception of Tampa Bay, where it was found at only four sites. The frequency of occurrence for all bryozoans in Tampa Bay was lower than at all other bays sampled. In Saint Johns River, *E. bengalensis* and *S. annae*, both non-native species, as well as *H. indica* dominated both the number and biomass of bryozoans on the fouling plates, occurring respectively at 9, 7, and 8 of the 10 sites sampled (Table 1). In Indian River, *E. bengalensis* (non-native), *H. indica* (non-native), *Hippopodina feegeensis* (Busk, 1884) (cryptogenic), and *Bugula neritina* (Linnaeus, 1758) (cryptogenic) dominated the bryozoan fauna. At the other sites, abundant bryozoans included *B. neritina* (Tampa and Pensacola Bays), *Biflustra denticulata* (Smitt, 1873) (Galveston and Pensacola Bays), *Victorella pavida* (Saville-Kent, 1870), and *Bowerbankia* sp. (Pensacola, Corpus Christi and Galveston Bays). Of these eight species, only *B. denticulata* (and probably the *Bowerbankia* species) is native to the tropical Western Atlantic.

Environmental Data.—Salinity and temperature were plotted for each site and compared to the distribution of bryozoans. No patterns were found in the distribution of any bryozoan species with respect to temperature. A few patterns were discernable with respect to salinity, especially in Jacksonville where salinity declined inland, moving up the St. Johns River. *Hippoporina indica* was not present at the lowest salinity sites (mean of deployment and retrieval) in Saint Johns River (< 11) or in Galveston (< 13). *Celleporaria pilaefera* was found only at one location in Saint Johns River, outside the mouth of the river where salinity was > 30. *Sinoflustra annae* was found at all but the two lowest salinity sites, and *E. bengalensis* was found at all but the lowest salinity site in Saint Johns River. The lowest salinity site (mean salinity of 10, retrieval salinity 2.7), River City Brewing Company, Saint Johns River, Jacksonville, Florida, had none of the non-native bryozoans.

Table 1. List of bryozoan species collected from settlement plates. Shown is the species status, number of blocks in which the species occurred per bay, and geographic distribution for each species. Species status: N = native, C = cryptogenic, I = invasive (non-native), and U = unknown (see text for details). Location: PB = Pensacola Bay, FL, TB = Tampa Bay, FL, CC = Corpus Christi, TX, GB = Galveston Bay, TX, IR = Indian River, FL, JX = Saint Johns River, Jacksonville, FL, and GOM = Gulf of Mexico. Distribution: Atl = Atlantic, Med = Mediterranean, and GOM = Gulf of Maine. Geographic distributions were compiled from the literature and included in our references.

		Location						
Species	Status	JX	IR	TB	PB	CC	GB	Distribution
Aeverrilla armata (Verrill, 1873)	N				1	1		Maine to Brazil, Gulf of Mexico
Biflustra denticulata (Busk, 1856)	N	3		1	6	2	5	W. Atl: Beaufort to Brazil, GOM, Caribbean
Bowerbankia gracilis Leidy, 1855	N				3			W. Atl: Greenland to Brazil, invader in other areas
Bowerbankia maxima Winston, 1982	N			2				Florida to Brazil, Caribbean, Gulf of Mexico
Caulibugula armata Verrill, 1900	N		2					Bermuda, Florida
Conopeum chesapeakensis (Banta et al., 1995)	N	6		1			1	Virginia to Florida, Gulf of Mexico
Conopeum tenuissimum (Canu, 1908)	N	1	1				1	Atlantic, Gulf of Mexico, Introduced to E. Pacific
Membranipora tenuis Desor, 1858	N						2	W. Atl.: Massachusetts to Brazil
Schizoporella "unicornis" of Winston, 1982, not Johnston, 1874	N	1						Cape Hatteras to Brazil, Gulf of Mexico
Schizoporella floridana Osburn, 1914	N	1						Florida, Caribbean
Schizoporella pungens (Canu and Bassler, 1928)	N	1	2	3		4		Florida, Caribbean, Gulf of Mexico, introduced to E. Pacific (Hawaii)
Thalamoporella floridana Osburn, 1940	N		1					Florida
Aetea sica (Couch, 1844)	C		2					Cosmopolitan except polar seas
Alcyonidium cf mammillatum Alder, 1857	C						2	----
Amathia vidovici (Heller, 1867)	C	2	2					Circumtropical
Anguinella palmata Van Beneden, 1845	C		3					Cosmopolitan
Bugula neritina (Linnaeus, 1758)	C	3	9	4	5			Worldwide
Bugula stolonifera Ryland, 1960	C	1		1				E. and W. Atl. and Med., W. Atl: MA to FL, Gulf of Mexico, Brazil
Nolella stipata Gosse, 1855	C		1		3			W. Atl: Cape Hatteras to Brazil, Caribbean
Savignyella lafontii (Audouin, 1826)	C		5					Circumtropical
Scrupocellaria bertholletii (Van Beneden, 1848)	C	2	2					Circumtropical-Subtropical
Sundanella sibogae (Harmer, 1915)	C				1			Circumtropical

Table 1. Continued.

Species	Status	Location						Distribution
		JX	IR	TB	PB	CC	GB	
Victorella pavida Saville-Kent, 1870	C					6	5	Cosmopolitan in brackish water; previously in Indian River (Winston, 1982)
Watersipora subtorquata (d'Orbigny, 1842)	C	1	2					Worldwide in warm seas
Zoobotryon verticillatum (Delle Chiaje, 1928)	C	1	4					Circumtropical
Celleporaria pilaefera (Canu and Bassler, 1929)	I	1						Philippines, India, Malta, Saint Johns River, Jacksonville, Florida
Electra bengalensis (Stoliczka, 1869)	I	9	7					Tropical India, China, Australia, Panama (Pacific coast), Saint Johns River, Jacksonville and Indian River Lagoon, Florida
Hippoporina indica Pillai, 1978	I	8	7	4	7	7	9	Asia, Indian and Pacific Ocean, Florida, Gulf of Mexico
Sinoflustra annae (Osburn, 1953)	I	7						E. and W. Pacific, China, India, Panama, Saint Johns River, Jacksonville, Florida
Alcyonidium sp.	U		3			2		----
Bowerbankia sp.	U	3	6		6	9	6	----
Bugula sp.	U	1						----
Conopeum sp.	U			1				----
Schizoporella sp.	U		3	1		2		----
Total number of species:	35	18	19	9	8	9	8	
Total number of sites	61	10	11	10	10	10	10	

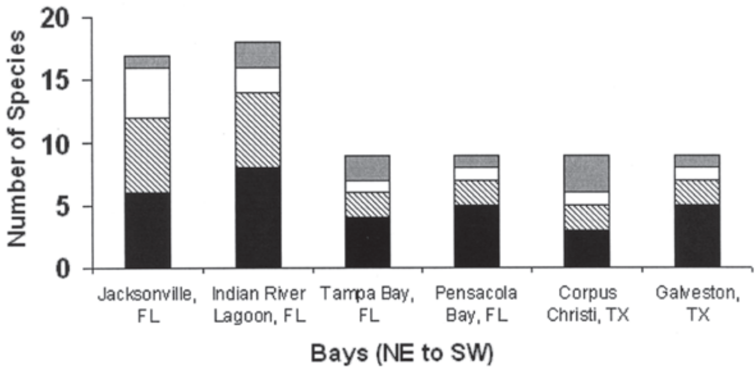

Figure 2. Total number of bryozoan species detected per bay by species status. The number of native (black), cryptogenic (cross-hatched), non-native (white), and unknown (grey) bryozoan species (based on Table 1) are plotted as a function of sample location from northeast to southwest.

Literature-based Analysis of Regional Invasions.—In addition to the non-native bryozoans identified in our survey for the first time, our literature analysis identified 39 non-native species of marine invertebrates and algae that are considered established in the same region, from the Atlantic coast of Florida to southern Texas. More than half of these species are thought to originate from the Indo-West Pacific (Fig. 3).

Commercial Shipping Patterns.—United States Maritime Administration (2004) data indicate that there were at least 34,654 vessel arrivals to the six sampled bays during the 4.5 yr period we examined. Of these vessels, 60% or more were classified as arrivals from foreign waters in any given year or port. Jacksonville (Saint Johns River), Florida, was the largest recipient of ships from foreign waters (Fig. 4),

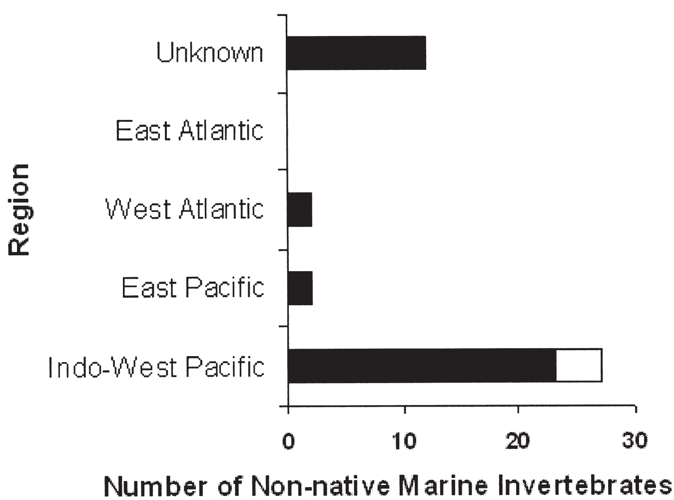

Figure 3. Total number of marine non-native invertebrates and algae (N = 43; does not include insects or diatoms) in Florida and the Gulf of Mexico and their region of origin (plotted in black). Bryozoans are plotted separately in white.

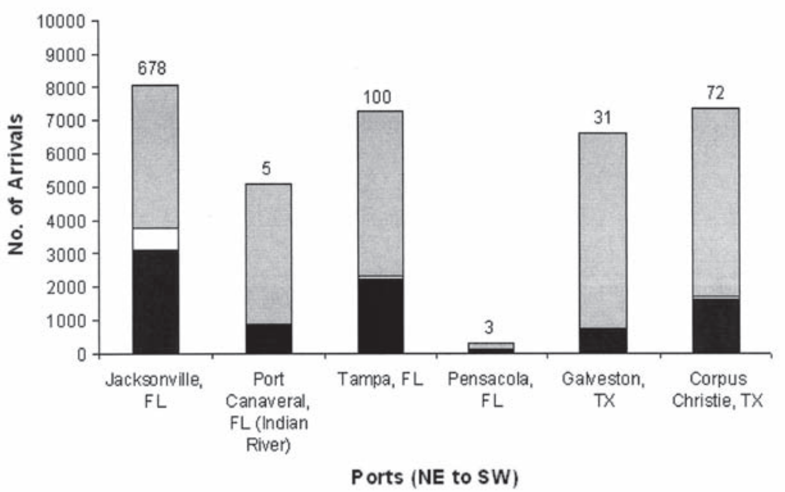

Figure 4. Number of ship arrivals to each port from domestic (solid black), Asian (white), and all other foreign ports (grey) (July, 1999–December, 2004). Numbers above each bar are arrivals from Asian ports.

receiving an average of four vessels per day. Pensacola received the least amount of foreign shipping traffic with an average of four arrivals per month. Vessels from Asia (including India, China, Japan, Philippines, Korea, Thailand, Singapore, Northern Mariana Islands, and Indonesia) made up 13.5% of all foreign traffic to Jacksonville, Florida while < 1.6% of foreign traffic to the other five ports originated in Asia. Three other Gulf ports had significant shipping traffic from Asia—Mobile, Alabama; New Orleans, Louisiana; and Houston, Texas. We did not sample these ports during the course of this study, due to their predominant low salinities.

Description of Non-native Bryozoans.—The following descriptions, SEM illustrations, and information on ecology and world distributions are provided for bryozoan taxa identified from settlement plates to be new to the Gulf of Mexico and Florida.

Order Cheilostomatida

Suborder Malacostegina

Superfamily Membraniporoidea

Family Electridae

Electra bengalensis (Stoliczka, 1869)

(Fig. 5A,B)

Membranipora bengalensis, Stoliczka, 1869: 55, pl. 12, figs. 1–8; Thornely, 1907: 186, text-fig. 4; Annandale, 1907: 198.

Electra anomala, Osburn, 1953: 36, pl. 3, fig. 6; Androsova, 1963: 24, pl. 1, fig. 4.

Electra anormata, Huang et al., 1990: 741, fig. 3c.

Electra bengalensis, Cook, 1968a: 141; Menon and Nair, 1975: 561, text-figs. 2b–e; Pillai, 1981: 323, fig. 6.

Electra bengalensis, Liu et al., 2001: 435, fig. 14, 5–6.

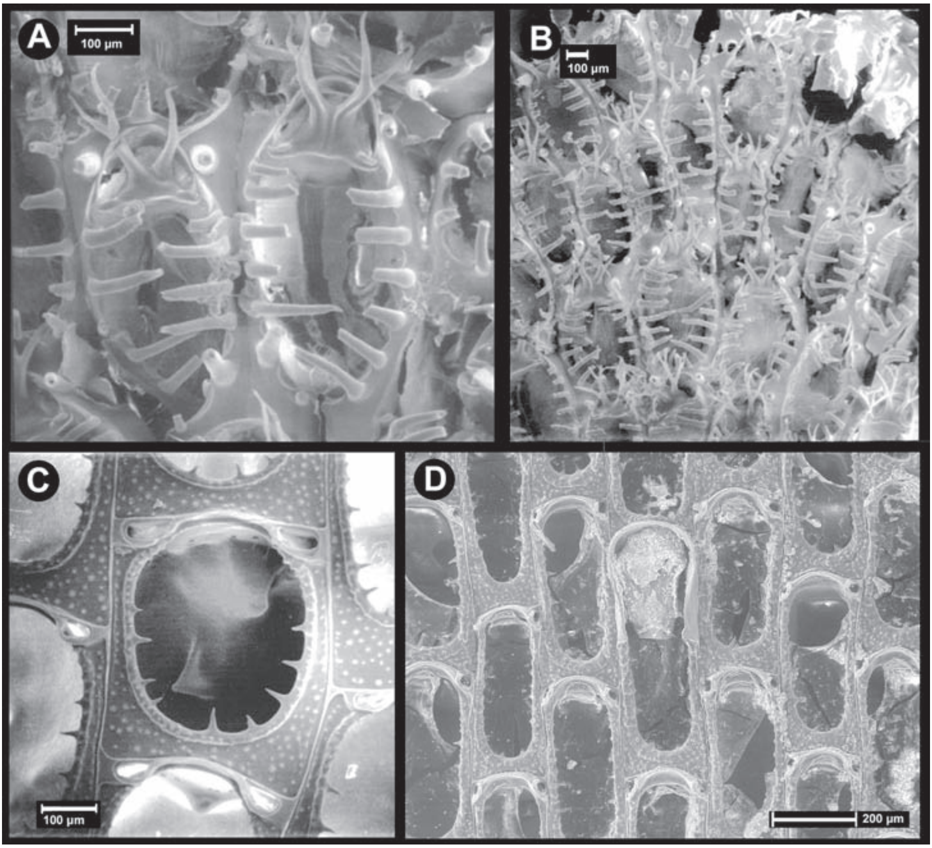

Figure 5. *Electra bengalensis* and *Sinoflustra annae*. (A) Two zooids of *Electra bengalensis*, showing antler-shaped chitinous spines on outer side of opercula, round, hollow, paired distal spines, and flattened lateral spines (scale = 100 µm). (B) *Electra bengalensis,* showing spiny appearance of colony surface. Smithsonian Environmental Research Center (SERC) specimens, Saint Johns River, Jacksonville, Florida, 2001 (scale = 100 µm). (C) *Sinoflustra annae*, close-up of young autozooid showing spiny projections of cryptocyst and paired lacunae at distal ends of zooid (scale = 100 µm). (D) *Sinoflustra annae*, section of partially cleaned colony showing autozooids and a large avicularium (arrow), mandible of avicularium intact. SERC specimens, Saint Johns River, Jacksonville, Florida, 2001 (scale = 200 µm).

Description.—Colony encrusting. Zooids moderately large, about 0.60 mm long by 0.25–0.30 mm wide, elongate-rectangular in shape, with an elongate ovoid membranous area that covers most of the frontal surface and is edged by smooth gymnocystal calcification. From the lateral and proximal margins of zooids, 11–14 slender, flattened spines arch over the frontal membrane (Fig. 5A,B). A distinct proximal spine, sometimes forked, may be present. A pair of distal spines occurs on either side of the operculum. They may bifurcate at the tips, and may overlap, but do not fuse. The most striking feature of the species is the pair of long, branching, chitinous spines which project outward from the outer surface of the D-shaped operculum (Fig. 5A). No avicularia, no ovicells.

Material Examined.—Seventy plates from Saint Johns River and Indian River, Florida.

Discussion.—Cook (1968a) synonymized Osburn's (1950) species, *E. anomala,* described from Balboa, at the Pacific entrance to the Panama Canal in 1953, with *E.*

bengalensis, described from Port Canning, West Bengal, India in the 19th century. The species' natural range appears to be Southeast Asia, but it has invaded other tropical ports and estuaries, e.g., Calliope River, central Queensland (Saenger et al., 1979), and Townsville Harbor, North Queensland, Australia (Hall, 1984).

Ecology.—A tropical brackish water fouling species, found in depths of 0–10 m, *E. bengalensis* is well studied in Indian and Chinese waters. It has a cyphonautes larva, is an early settler, grows rapidly, and reaches sexual maturity early (Satyanarayana-Rao and Ganapati, 1974; Udhayakumar and Karande, 1989). In Vishkhapatnam Harbor, its growth and breeding are continuous throughout the year with low settlement when temperature and salinity are the highest (Satyanarayana-Rao and Ganapati, 1974). It was the fastest growing of intertidal bryozoans in Cochin, India (Menon and Nair, 1972). In Bombay waters, *E. bengalensis* comprised almost 70% of total space occupied by bryozoans (Udhayakumar and Karande, 1989) and bred continuously year-round (Karande and Udhayakumar, 1992). In coastal waters off Xiamen (Amoy), China, settlement occurred from July to December, with peak settlement in October–November, and maximum numbers of colonies attached at 3 m depth (Liu et al., 2001). Plates exposed in Fort Pierce Inlet for 2 wks (September–October, 2005) had colonies reaching 4 cm in diameter.

Distribution.—Balboa, Panama; Ganges Delta, India (Powell, 1971); China: Xiamen (Liu et al., 2001); Australia (Hall, 1984); West Africa (Cook, 1968a); Saint Johns River, and Indian River, Florida (this study).

Suborder Flustrina

Superfamily Flustroidea

Family Flustridae

Sinoflustra annae (Osburn, 1953)

(Fig. 5C,D)

Acanthodesia serrata, Hastings, 1930: 707, pl. 4, figs. 13–15. (Not *Membranipora membranacea* form *serrata* Hincks)

Membranipora hastingsae, Osburn, 1950: 29, pl. 2, fig. 1; not *Electra hastingsae,* Marcus, 1940.

Membranipora annae, Osburn, 1953: 774; Cook, 1968b: 128; Powell, 1971: 766, 768; Liu, 1992: 139–141.

Sinoflustra annae, Liu and Yang, 1995: 348; Liu et al., 2001: 451, pl. 17, figs. 3–5.

Description.—Colony encrusting. Zooids rectangular in outline, about 0.40–0.60 mm in length by 0.20–0.45 mm in width, with a round to oval membranous frontal opesia area (Fig. 5C). At the distal end of the zooid, the operculum is bordered on each side by a pair of small, subtriangular kenozooids resembling avicularia but lacking mandibles, instead being frontally walled by membrane. Laterally and proximally the membranous opesia is surrounded by a beaded cryptocyst, from the raised inner rim of which small sharp-pointed denticles extend under the membranous surface. No ovicells. Large vicarious avicularia with rounded mandibles may occur (Fig. 5D).

Material Examined.—Thirty five plates from Saint Johns River, Jacksonville, Florida.

Discussion.—The original description of the species was from Balboa (Pacific Ocean at the Panama Canal entrance). It was first noted by A. Hastings (1930), who described the large vicarious avicularia, but considered it merely a variant of *Membranipora membranacea* Linnaeus, 1767. Osburn (1953) recognized it as a new species and gave it the name *M. annae*. As currently recognized, members of the Membraniporidae do not have avicularia, therefore Liu and Yang (1995) transferred the species to a new genus, *Sinoflustra*.

Ecology.—Found in shallow water of reduced or variable salinity.

Distribution.—Balboa, Panama; Perlas Islands, Gulf of Panama (Powell, 1971); West Africa (Cook, 1964; Cook, 1968b); India (Satyanarayana-Rao and Balaji, 1988; Swami and Karande, 1994); China: Zhejuang, Fujian, Guangdong, Hainan, Daya Bay (Li, 1989); and Saint Johns River, Florida (this study).

Suborder Ascophora

Superfamily Lepralielloidea

Family Celleporariidae

Celleporaria pilaefera (Canu and Bassler, 1929)

(Fig. 6A–D)

Holoporella pilaefera, Canu and Bassler, 1929: 422, pl. LV, figs. 2–6, text-fig. 165, A–E.

Celleporaria pilaefera Harmer, 1957: 679, pl. XLII, fig. 25, text figs. 54, 57; Hayward, 1988: 343, pl. 16, figs. E, F; Tilbrook et al., 2001: 70, fig. 13A–C; Tilbrook, 2006: 135, pl. 24 A–B.

Description.—Colony encrusting (Fig. 6A). Zooids irregularly polygonal in outline, about 0.40 mm long by 0.35 mm wide. Polypide with 13–16 brown tipped tentacles. Frontal wall convex, with a raised imperforate region of roughly granular calcification centered around the orifice and suboral avicularium umbo, and large round pores scattered at or near zooid margins (Fig. 6B–C). Orifice large relative to zooid size, slightly more than semi-circular distally, with a smooth un-notched and shallowly concave proximal margin, with small condyles at hinge (Fig. 6D). A low peristome with granular calcification surrounds the orifice, rising proximally into a sharp pointed, occasionally tall umbo, on the side of which is a small suboral avicularium with a dentate rostrum and complete cross-bar. No lateral interzooecial avicularia. Vicarious avicularia present, but rare in our material, longer than autozooids, with rostrum narrowest at crossbar, cup-like distally with a smooth, untoothed edge. Ovicells (Fig. 6B) are cap-shaped, and open with imperforate granular calcification. In some cases, ovicells are asymmetric over the operculum.

Material Examined.—Two plates with one colony each at the Mayport Naval Station, Saint Johns River, Jacksonville, Florida.

Discussion.—Several species of *Celleporaria* are known from the Gulf of Mexico-Western Atlantic-Caribbean region. The orifice shape (lacking one or more suboral notches), the pointed suboral umbo and the shallow cap-like ovicell place this species in the *albirostris-pilaefera-columnaris* group of species. The only species of that group known from the region is *Celleporaria albirostris* (Smitt, 1873), a common Caribbean reef species. The species found on our plates differs from that species in the smaller suboral umbo spine, narrower shape, lack of lateral-oral avicularia, and more rugose calcification of the ovicell. Our material also closely resembles *Celleporaria*

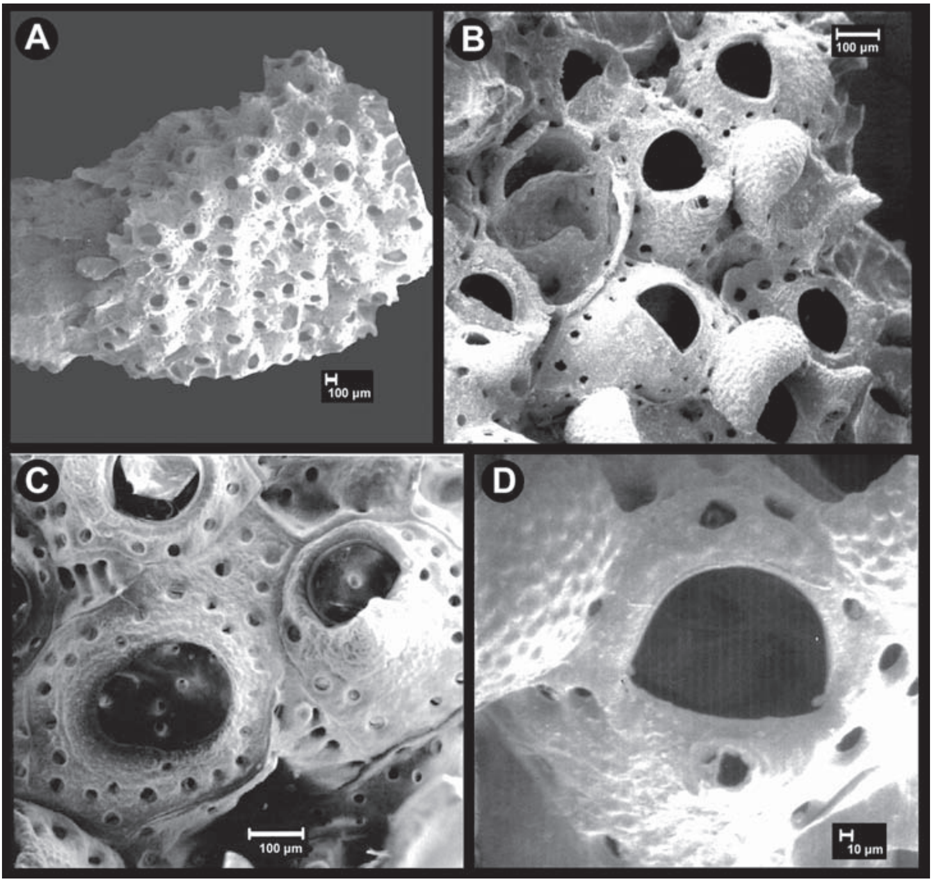

Figure 6. *Celleporaria pilaefera*. (A) Colony encrusting hydroid stem. SERC no. 31865, Saint Johns River, Jacksonville, Florida, 2001 (scale = 100 µm). (B) Group of frontally budded zooids, some with cap-like ovicells (scale = 100 µm). (C) Three recently budded zooids, right-hand one with fully formed rostral avicularium (scale = 100 µm). (D) Close-up of a zooid orifice. SERC no. 69989, Saint Johns River, Jacksonville, Florida, 2001 (scale = 10 µm).

melanodermorpha (Liu et al., 2001: 556, 794, pl. 39, figs. 1–6) in overall morphology and especially in the position of suboral avicularia on the umbos, but Liu's species appears to lack orifice condyles, and to possess lateral-oral avicularia.

Ecology.—Members of the genus *Celleporaria* are diverse and successful in warm water regions of the world (Powell, 1971; Ristedt and Hillmer, 1985). Many species inhabit shallow coral reef habitats (Winston, 1986; Hayward and Ryland, 1992; Tilbrook et al., 2001). Others are characteristic of warm water ports and harbors where their rapid growth and superior competitive ability make them important fouling organisms (Woods Hole Oceanographic Institute, 1952; Li, 1989; Udhayakumar and Karande, 1989; Nandakumar and Tanaka, 1994; Liu et al., 2001).

Distribution.—Malta (Agius et al., 1977); Philippines, Hawaii (Canu and Bassler, 1929); India (Swami and Karande, 1988); Indian Ocean and Red Sea (Harmer, 1957); Mauritius (Hayward, 1988); Vanuatu (Tilbrook, 2001); and Saint Johns River, Jacksonville, Florida (this study).

Superfamily Smittinoidea
Family Betectiporidae
Hippoporina indica Pillai, 1978
(Fig. 7A–D)

Hippoporina indica, Pillai, 1978: 62, figs. 1–4.
Cosciniopsis hongkongensis, Liu and Li, 1987: 55, 60, pl. 1, figs. 4–5; Li, 1989: 107; 1992:63; Huang et al., 1990: 748, figs. 6E–6F.
Hippothyris hongkongensis, Liu et al., 2001: 577, pl. 45, figs. 1–2, 4.

Description.—Colony encrusting. Zooids, short, rectangular, variable in size (mean zooid length = 0.37 mm, mean zooid width = 0.27 mm, n = 65). Zooid frontal surfaces with large marginal and equally large frontal pores except for a granular imperforate central portion of frontal wall adjacent to the orifice (Fig. 7A–B). Up to three spines occur above the orifice; they are usually lost early in colony development, but the spine bases sometimes remain visible (Fig. 7D). Orifice large relative to zooid size, hoof shaped, with a sub-circular anterior region and a shallowly convex proximal region (Fig. 7B and 7D), the two separated by triangular, proximally slanting, hinging denticles. The granular calcification below the orifice is raised into a low peristome with a central peak (Fig. 7C). Orifice sometimes with two lateral processes on rim. On one or both sides of the orifice are large umbones supporting avicularia (some zooids may have up to three avicularia, many zooids have none). These are rounded proximally, with narrow crossbars and short, pointed, triangular mandibles, and oriented laterally or distolaterally toward the orifice (Fig. 7C). Similar triangular avicularia may also occur on lateral margins or frontal surfaces of zooids. Ovicell hyperstomial, with granular calcification and irregular pores (in size, shape, and spacing) covering most of its frontal surface (Fig. 7A and 7C).

Material Examined.—We examined specimens from 373 plates from the Indian River, Saint Johns River, Tampa and Pensacola, Florida, Corpus Christi and Galveston Bay, Texas, Chesapeake Bay, Virginia (in the latter, one specimen at each of three sites was found). We also examined western Atlantic species from the National Museum of Natural History, including *Hippoporina americana* Verrill USNM #648039 from the Gulf of Mexico, that may or may not be the same species, but is probably not *H. americana*. There appear to be several species that are confused in the Atlantic and Caribbean.

Discussion.—*Hippoporina indica* was originally described from Bombay Harbor, where it was an abundant member of the fauna from 1968–1977 (Pillai, 1978). Li (1992) noted the presence of an identical morphotype in the South China Sea sometime between 1979 and 1989, present possibly as early as the 1960s. It was described by Liu and Li in 1987, under the name *C. hongkongensis,* from fouling panels collected in Datan Bay in southern Hong Kong in 1983. Based on their extensive descriptions and electron micrographs, it appears to be the same species, although we have not been able to secure specimens from China or India to confirm this. When compared to measurements in Liu et al. (2001), our specimens were, on average, smaller but matched in all other characters. *Hippoporina indica* has also been reported as a dominant fouling bryozoan in many areas of Hong Kong, found on fouling panels, ships, buoys, and in aquaculture facilities (Li, 1989). This aggressive, adaptable spe-

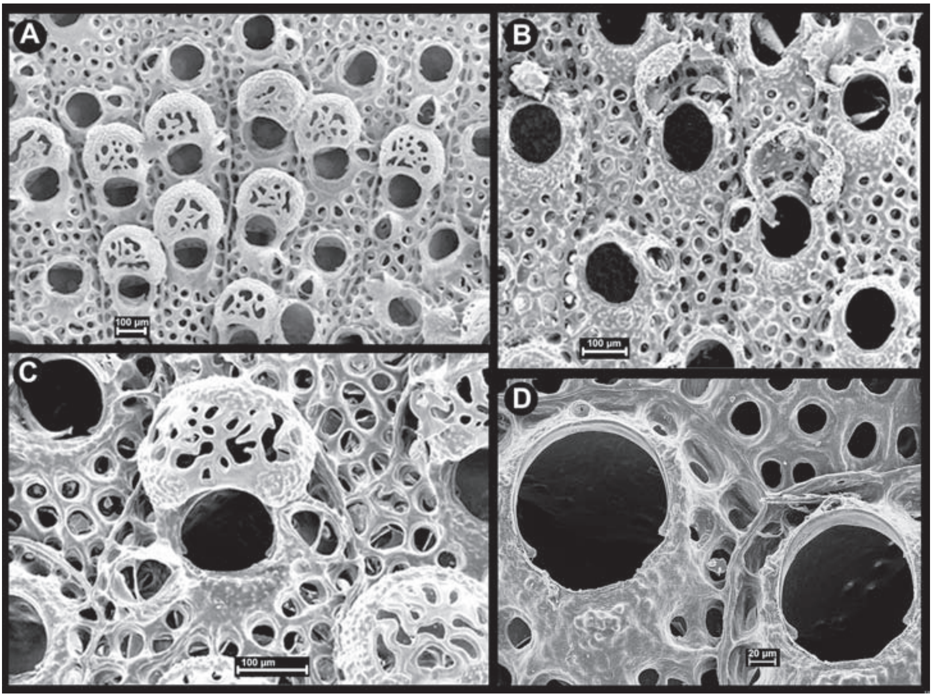

Figure 7. *Hippoporina indica*. (A) Group of zooids, many with ovicells, SERC no. 76115, Tampa Bay, Florida, 2002 (scale = 100 µm). (B) Another group of zooids, showing hoof-shaped orifice and developing ovicells, SERC no. 38760, Saint Johns River, Jacksonville, Florida, 2001 (scale = 100 µm). (C) Close-up of an ovicelled zooid, showing placement of frontal avicularia, SERC no. 89509, Galveston Bay, Texas, 2002 (scale = 100 µm). (D) Close-up of zooid orifices, note oral spine base visible on left-hand zooid. SERC no. 89509, Galveston Bay, Texas, 2002 (scale = 20 µm).

cies has not been reported in earlier fouling studies in the Atlantic, but appears to have established itself in warm water ports far from the site of its origin.

Ecology.—Depth range 0–15 m. In addition to fouling panels, *H. indica* has been recorded from fishing rafts, fish cages, buoys, oysters, and barnacle shells. Liu et al. (2001) summarized recruitment of the species in Chinese waters. Maximum recruitment occurred at the shallowest depth studied (2 m). Off Xiamen, China, settlement occurred from April to December with peak settlement during October–November. In India, it occurred year round with the same peak settlement time (Pillai, 1978). *Hippoporina indica* was relatively slow growing and had delayed maturity when compared to other bryozoan foulers in Bombay, India (Udhayakumar and Karande, 1989). However, its superior overgrowth ability and zooids with longer life spans allowed it to persist and dominate fouling communities (Karande and Udhayakumar, 1992).

Distribution.—Hong Kong (Li, 1989; Huang et al., 1990); China: Xiamen, East China Sea, Fujian, Guangdong, Hainan Island and South China Sea (Liu and Li, 1987); India (Pillai, 1978); Saint Johns River, Indian River, Tampa Bay and Pensacola, Florida, Galveston Bay and Corpus Christi, Texas, (this study); Norfolk (Chesapeake Bay), Virginia, and Charleston, South Carolina (additional Smithsonian surveys).

Discussion

Bryozoans are well suited for human-mediated invasion. Many species have wide salinity tolerances, are fast growing, have a high reproductive potential and settle on a wide variety of substrates. It is interesting that the four non-native bryozoan species described here exhibit a diverse range of life history characteristics (e.g., reproduction, longevity, larval type), suggesting many different attributes affect invasion outcome. *Hippoporina indica* was the most dominant and wide spread bryozoan found among the six sites in this study. Despite its slower growth rate, delayed sexual maturity, and lower fecundity due to brooding of embryos in ovicells rather than broadcasting large number of eggs (Karande and Udhayakumar, 1992), its zooids have superior overgrowth ability and a longer lifespan than other species. It can therefore compete well and persist to become dominant in the fouling community (Li, 1989). Well studied in Indian fouling communities, *E. bengalensis* is fast-growing, matures early, and produces a large number of eggs (Udhayakumar and Karande, 1989), allowing it to colonize new surfaces quickly. This species is also highly tolerant of salinity changes and pollutants but often cannot compete in cleaner waters where species with longer lifespans persist (Swami and Karande, 1994). *Sinoflustra annae* is fast growing, produces many eggs, and overgrows spatial competitors well, but displays later sexual maturity and shorter lifespan (Karande and Udhayakumar, 1992). However, it has a wide tolerance for salinity changes (Cook, 1968b), which makes it a good competitor in many harbors. Interestingly, *C. pilaefera* also appears in Indian harbors along with *E. bengalensis* and *H. indica*; although *C. pilaefera* exhibits superior overgrowth ability like the latter species (Swami and Karande, 1988; Udhayakumar and Karande, 1989), its distribution was much more patchy.

All four of the non-native bryozoans in our surveys are considered native to the Indo-West Pacific, where they have been reported to co-occur (as above). Our collections are first records for these species in the western Atlantic and Gulf of Mexico, and we have also recently recorded *H. indica* in both Chesapeake Bay (Virginia) and Charleston Harbor (South Carolina) using similar surveys. In other warm-water ports, *S. annae* and *E. bengalensis* are often found with *H. indica* and have been shown to dominate fouling communities in China and India (Huang et al., 1990; Karande and Udhayakumar, 1992; Liu et al., 2001). The former two species were also documented by Powell (1971) in the Bay of Panama and Balboa Harbor, on the Pacific side of the Panama Canal. Whether these species were brought to Texas and Florida from Panama or from elsewhere is unknown.

More broadly, available data from the literature and our surveys in Florida and Texas indicate that non-native invertebrate and algal species in this region are frequently of Asian and Indo-West Pacific origin (Ruiz et al., 2000; Steves et al., 2006). Given the diversity of taxonomic groups represented, it appears that life-history may not greatly constrain invasion opportunity. Although the impacts of most non-native species remain undescribed, some Asian species new to the Gulf that could have substantial impacts on local ecosystems, include the green mussel, *Perna viridis* (Linnaeus, 1758), the green alga, *Caulerpa brachypus* (Harvey, 1860), and the Asian swimming crab, *Charybdis hellerii* (Milne-Edwards, 1867) (Gossett and Lester, 2004; Steves et al., 2006).

Ships from Asia are regular visitors to Florida and the Gulf of Mexico, creating the opportunity for transfer of organisms on the hulls or in ballast water (see Ruiz et al., 2000 for discussion). Approximately 13,000 commercial ships transit the Panama Canal per year in recent time, of which half of the traffic moves from the Pacific to Atlantic (Ruiz et al., 2006). Panama traffic that arrives to ports of the U.S. Gulf coast and eastern Florida is predominantly Asian in origin (58% and 82%, respectively; Panama Canal Authority Transit Statistics, 2005). Of these ports, Jacksonville, Florida has the highest percentage of its vessel traffic arriving from Asia, mostly originating in China or Japan (United States Maritime Administration, 2004). Freeport, Grand Bahamas, also receives a high volume of Asian container traffic (Panama Canal Authority Transit Statistics, 2005), 90% of it bound for the Atlantic coast of Florida. Thus, commercial shipping is a likely mechanism of introduction for the four newly detected bryozoan species, and in combination with recreational boat traffic, may also have facilitated the spread of these non-native bryozoans.

While shipping provides the opportunity for invasion, the environment of each bay affects its susceptibility to these invaders. Among other factors considered important in invasion establishment is disturbance (Williamson, 1996; Ruiz et al., 2000; Fausch et al., 2001). The east coast of Florida was hit hard by two large hurricanes in 2004, which may have facilitated transport of some of these invaders from one estuary to another and created conditions which allowed their establishment. Since the early 1970s the bryozoan fauna in the Fort Pierce area (southern end of the Indian River Lagoon) has been extensively monitored by Winston and 2005 is the first year that *H. indica*, *E. bengalensis*, and *H. feegeensis* have been detected there. During 2005, parts of the southern end of the lagoon suffered severe environmental degradation when heavy rains caused water levels in Lake Okeechobee to rise to the point where water managers flushed water from the lake causing it to rush into the Caloosahatchee (draining into the Gulf of Mexico) and Saint Lucie (draining into the Indian River Lagoon) Rivers. Decades of input of phosphorus and pesticides that had settled in the sediments of Lake Okeechobee were stirred up by the previous fall's hurricanes and became part of this outflow. By July 2005, the Saint Lucie River was choked with toxic blue-green algae (cyanobacteria), salinities declined to freshwater levels, marine invertebrates died, and diseased fish were found (Harris, 2005; Hiaasen, 2005; Morgan, 2005; Musgrave, 2005). This type of disturbance combined with opportunistic species already settled in surrounding areas (such as Saint Johns River to the north) may have contributed to the changes in fauna we documented.

Although the precise timing of invasions by these four newly reported bryozoan species is unclear, we suspect that these are recent arrivals to the region, especially given the background monitoring in both the Indian River and Chesapeake Bay. It is clear that new invasions are continuing to occur in coastal waters of the U.S. and elsewhere around the world (Ruiz et al., 2000; Hewitt et al., 2004), changing the structure and function of coastal habitats. Combined with climate change, invasions have the potential to dramatically alter the face of the planet as we know it (Engle and Summers, 1999; Stachowicz et al., 2002). The available data demonstrate a dramatic increase in the rate of discovery for new invasions for many different coastal systems. Management strategies are being implemented to reduce the transfer of non-native organisms, focusing especially on ships' ballast water, but the effects on invasion risk are still being quantified (Minton et al., 2005). Importantly, there are also differences in invasion risk associated with different species (Kolar and Lodge, 2002; Miller et al., 2007) and for different environmental conditions, including disturbance regimes (Hobbs, 1998), but robust predictions about these interactions are not yet available.

Understanding these relationships and developing predictive ability is a high priority for invasion biology and management.

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Appendix A. List of marine invertebrate species introduced to the study area (GOM = Gulf of Mexico widespread). Where the taxon was found in the broad surveys used in this study, the date of these records is listed second. Records older than one decade were only included if more recent verification of the species presence exists.

Introduced to	Species	Common Name	Group	First record	Origin	Reference(s)
FL	*Caulerpa brachypus*	Green alga	Algae	2001	Indo-West Pacfic	Schrope, 2003
FL	*Celleporaria pilaefera*	Bryozoan	Bryozoa	2001	Indo-West Pacfic	This study
FL	*Electra bengalensis*	Bryozoan	Bryozoa	2002	Indo-West Pacfic	This study
FL, GOM	*Hippoporina indica*	Bryozoan	Bryozoa	2001	Indo-West Pacfic	This study
FL	*Sinoflustra annae*	Bryozoan	Bryozoa	2001	Indo-West Pacfic	This study
TX, FL	*Diadumene lineata*	Striped sea anemone	Anthozoa	1948	Indo-West Pacfic	Baker et al., 2004
FL, LA, TX	*Garveia franciscana*	Rope hydroid	Hydrozoa	1999	Unknown-Marine	Deevey, 1950; Baker et al., 2004
FL	*Tubastraea coccinea*	Orange cup coral	Hydrozoa	2002	Indo-West Pacfic	Fenner and Banks, 2004
FL, AL, MS, TX	*Phyllorhiza punctata*	Brown-spotted jellyfish	Scyphozoa	2000	Indo-West Pacfic	Benson et al., 2001
FL	*Caprella scaura*	Caprellid	Amphipoda	1998	Unknown-Marine	Foster et al., 2004
FL, LA, TX	*Balanus amphitrite*	Striped barnacle	Cirripedia	1931, 2002	Indo-West Pacfic	McPherson et al., 1989; Baker et al., 2004; this study
FL, TX	*Balanus reticulatus*	Reticulated barnacle	Cirripedia	1969, 2001	Indo-West Pacfic	McPherson et al., 1980; Baker et al., 2004; this study
FL	*Balanus trigonus*	Barnacle	Cirripedia	1954, 2001	Indo-West Pacfic	Moore and McPherson, 1984; Zullo, 1992; this study
FL, LA, TX	*Megabalanus coccopuma*	Pink barnacle	Cirripedia	2006	East Pacific	This study
FL	*Charybdis helleri*	Asian swimming crab	Decapoda	1986	Indo-West Pacfic	LeMaitre, 1995
FL	*Platychirograpsus spectabilis*	Saber crab	Decapoda	1936	West Atlantic	Baker et al., 2004
FL, LA, TX	*Iais floridana*	Isopod	Isopoda	1993	Indo-West Pacfic	Kensley and Schotte, 1999
FL, GOM	*Ligia exotica*	Sea roach	Isopoda	1883	Indo-West Pacfic	Baker et al., 2004
FL	*Limnoria pfefferi*	Gribble	Isopoda	1950	Indo-West Pacfic	Menzies, 1957
FL, LA, TX	*Sphaeroma terebrans*	Mangrove isopod	Isopoda	1897	Indo-West Pacfic	Baker et al., 2004
FL	*Sphaeroma walkeri*	Isopod	Isopoda	1965	Indo-West Pacfic	Miller, 1968; Benson et al., 2001
FL	*Pullosquilla litoralis*	Mantis shrimp	Stomatopoda	1999	Indo-West Pacific	Benson et al., 2001

Appendix A. Continued.

Introduced to	Species	Common name	Group	First record	Origin	Reference(s)
FL	*Ophiactis savignyi* lineage B	Savigny's brittle star	Echindoderm	2002	Indo-West Pacfic	Roy and Sponer, 2002
FL	*Perna viridis*	green mussel	Bivalve	1999	Indo-West Pacfic	Bensen et al., 2001; Ingrao, 2001
FL	*Pinctada margaritifera*	black-lipped oyster	Bivalve	1992	Indo-West Pacfic	Benson et al., 2001
TX	*Perna perna*	brown mussel	Bivalve	1993	Indo-West Pacfic	Hicks and Tunnell, 1995
TX, FL	*Teredo navalis*	naval shipworm	Bivalve	1889	Unknown-Marine	Wallour, 1960
FL	*Hyotissa hyotis*	giant Coxcomb oyster	Bivalve	2003	Indo-West Pacfic	Benson et al., 2001; Bieler et al., 2004
FL	*Mytella charruana*	Charru mussel	Bivalve	1986	West Atlantic	Carlton, 1992; Bensen, 2006
FL, GOM	*Cuthona perca*	Lake Merritt Aeolis	Gastropoda	1969, 2001	Unknown-Marine	Marcus, 1977; this study
FL	*Glossodoris sedna*	nudibranch	Nudibranch	1980	Indo-West Pacfic	Bertsch, 1988
FL, LA, TX	*Ficopomatus uschakovi*	serpulid tubeworm	Polychaeta	1996, 2001	Indo-West Pacfic	L. McCann, unpubl. data; this study
TX, FL	*Ficopomatus enigmaticus*	serpulid tubeworm	Polychaeta	1952, 2001	Unknown-Marine	Hartman, 1951; this study
TX, FL	*Hydroides elegans*	serpulid tubeworm	Polychaeta	1954, 2002	Unknown-Marine	Hartman, 1951; Bastida-Zavala and Ten Hove, 2002; this study
TX, FL	*Hydroides diramphus*	serpulid tubeworm	Polychaeta	2001	Unknown-Marine	Bastida-Zavala and Ten Hove, 2002; this study
FL, LA, TX	*Didemnum perlucidum*	colonial tunicate	Tunicata	1980, 2002	Indo-West Pacfic	Monniot, 1983; this study
FL, TX	*Didemnum psammathodes*	colonial tunicate	Tunicata	1982, 2005	Indo-West Pacfic	Monniot 1983; this study
FL, GOM	*Botryllus schlosseri*	golden star tunicate	Tunicata	1887, 2001	Unknown-Marine	Van Name, 1921; this study
FL	*Diplosoma spongiforme*	colonial tunicate	Tunicata	2003	Unknown-Marine	this study
TX, FL	*Diplosoma listerianum*	colonial tunicate	Tunicata	1885, 2002	Unknown-Marine	Van Name, 1921; this study
FL, GOM	*Styela canopus*	rough tunicate	Tunicata	1887, 2001	Unknown-Marine	Baker et al., 2004; this study
FL, GOM	*Styela plicata*	pleated tunicate	Tunicata	1877, 2001	Unknown-Marine	Baker et al., 2004; this study
FL	*Polyandrocarpa zorritensis*	tunicate	Tunicata	2005	East Pacific	this study