Stability and Change in the Indian River Area Bryozoan Fauna over a Twenty-Four Year Period

Judith E. Winston

ABSTRACT. Two surveys describe changes and stability in bryozoan assemblages at sites in the temperate to tropical transition zone of the Florida Atlantic coast over a 24-year interval in which seawater temperatures increased. Results of a monthly survey of the Indian River Area bryozoan fauna carried out in 1974–1975 as part of a postdoctoral fellowship at the Smithsonian Marine Station were published in 1982. The existence of this baseline work made it possible to resurvey some of the same areas during 1998–1999 to determine whether the bryozoan communities at three of the sites in the original study had changed or remained stable. Results showed that most of the species that had been abundant at a site still occurred at that site 24 years later, indicating a high degree of stability. However, there were some important changes. Temperate species such as *Hippoporina verrilli*, *Cryptosula pallasiana*, and *Bugula stolonifera*, which had been abundant in 1974, were rare or absent in 1998. Those species were replaced by Caribbean species, such as *Exechonella antillea* and *Caulibugula armata*. Although local seawater temperatures during the time period were not available, the Fort Pierce air temperature records indicated that despite the year-to-year variability in both minimum and maximum temperatures over the seasons, mean winter air temperatures maintained a slow increase from 1974 to 1999.

INTRODUCTION

Most ecological research projects are carried out over a very short time period, the length of a research grant or dissertation project, a few years at most, and once the researcher moves on to new studies these research efforts are seldom repeated. Long-term studies are essential to document effects of climate change in communities over time, but the number of such publications for marine communities is extremely low compared with the number documenting the effects of climate change in terrestrial systems (e.g., Richardson and Poloczanska, 2008). This paper describes a repeated survey of coastal and lagoon sites conducted 24 years after the original survey was completed.

In 1974 and 1975, as part of my research as a postdoctoral fellow at the Smithsonian Marine Station, I carried out monthly surveys of the bryozoan fauna at five intertidal sites in the Indian River Lagoon region, both in the lagoon itself and on the coasts of North and South Hutchinson Islands. Descriptions of the species found at these sites, together with descriptions of species taken in one-time

Virginia Museum of Natural History, 21 Starling Avenue, Martinsville, Virginia 24112, USA (judith.winston@vmnh.virginia.gov). *Manuscript received 13 May 2008; accepted 20 April 2009.*

collections at 18 additional localities in the region and notes on their distribution and ecology, were published in a taxonomic paper, "Marine Bryozoans (Ectoprocta) of the Indian River Area (Florida)" (Winston, 1982). Over the years I returned to the area many times to study various aspects of the biology and ecology of the bryozoans of the region. The apparent persistence of species at particular sites year after year led me to believe that bryozoan communities in the area might be very stable. Yet, the patchiness and limited extent of the hard substrata available for settlement, combined with the fact that certain species were found consistently at only a single site, made me wonder about the potential effect of a man-made or natural disturbance. If a site were to be destroyed, would that mean the regional extinction of the bryozoan species uniquely found there, or did they, in fact, have additional refuges at other sites in the area? To begin to answer these questions, 24 years after the first study, I resurveyed three of the original sites over a one year period in 1998–1999 to learn how stable was the species composition and to look for additions or losses of species at each site.

STUDY AREA

The Indian River Lagoon system, including Mosquito Lagoon, extends along about a third of the Atlantic coast of Florida, from Ponce de Leon Inlet to Jupiter Inlet, a distance of 295 km. Its western boundary is the Florida mainland, while a barrier island complex broached by several inlets forms its eastern boundary. The Indian River Lagoon proper is a shallow microtidal lagoon 195 km in length. It is believed to have the highest biodiversity of any estuarine system in North America, perhaps in part because of its location at the transition between two biogeographic provinces, the warm temperate Carolinean and the tropical Caribbean (Swain et al., 1995).

METHODS

The samples taken in the original survey had been gathered at first only to acquire living colonies of as many species as possible for behavioral and morphological studies (Winston, 1978). As I became interested in the life histories of the species involved, I began collecting at the most convenient and interesting sites in the south central part of the Indian River Lagoon area on an approximately monthly schedule from the fall of 1974 through the summer of 1975. The sites studied were the inner breakwater at Sebastian Inlet, the Johnson House seagrass bed at Harbor Branch Oceanographic Institution at Link Port, the North Beach breakwater at Fort Pierce Inlet, Walton Rocks, South Hutchinson Island, and Seminole Shores, South Hutchinson Island. Collections from those sites were taken in all seasons, an important consideration in the seasonal environment of the Indian River Lagoon region. For bryozoans, as for many organisms inhabiting the area, the highest diversity is achieved and the greatest amount of reproduction, recruitment, and growth of colonies of most species take place during the cooler months (Winston, 1982, 1995). However, tropical species are more apt to be present or active in summer. It was not possible to return to Florida monthly in 1998–1999, but for the best comparison to 1974–1975, the sampling dates were selected to span the seasons and thus reflect the known seasonality of the bryozoan fauna.

Collections were made quarterly (in November 1998, and February, April, and July 1999) at four sites: two within the lagoon and two on the open coast.

Sites Sampled

It was not possible to resurvey all the sites sampled in the original study, for reasons of time and because changes such as the development of some sites into official county or state parks had increased restrictions on scientific collecting. The coastal sites sampled in the restudy were the North Beach breakwater, Fort Pierce Inlet State Park (by special permit), and the Walton Rocks area, South Hutchinson Island, plus one site in the Indian River Lagoon, the Johnson House seagrass bed. One additional site was chosen for the 1998–1999 survey: the intertidal bridge pilings on the east side of the Route A1A causeway to the North Beach in Fort Pierce. This site was added because it was within the Lagoon, yet was close enough to the Fort Pierce Inlet, local marinas, and the commercial port in Fort Pierce to be a likely settlement spot for any newly arrived bryozoan species.

Collecting Methods

Some bryozoan species have colonies several centimeters or more in size and are recognizable in the field, but in many other species the colonies are microscopic and cryptic. Therefore collections were made by scraping hard surfaces and by gathering encrusted substrata: algae, hydroid stems, rocks, shells, or trash. As in the original study, sampling was not quantitative but was thorough. At each locality all microhabitats available—crevices of break-

waters, surfaces of rocks, shells, wood, algae, hydroids, octocorals, sabellariid worm tubes, etc.—were examined carefully for bryozoans. In addition, encrusted examples of each kind of substratum available were taken back to the laboratory and examined alive in seawater; attached bryozoans were identified under a dissecting microscope at 12–100×. Careful microscopic examination made it possible to identify the many tiny and/or uncalcified specimens that could not be identified or even detected in the field. The condition of the colonies and the presence of reproductive structures and/or embryos were also noted, as was the relative abundance of each species at a site. Voucher samples for the project are deposited at the Virginia Museum of Natural History.

Temperature and Salinity Data

Seawater temperatures and salinities were recorded at each census in this study. Temperature ranges are given in the results for each site. Salinity varied little. All readings were in the normal ocean range of the area (35–37‰). The salinity range in the Indian River Lagoon can be more variable than that recorded at any of the sites during the resurvey, but low salinities are connected with periods of heavy rainfall, and 1998–1999 was a drought year. No temperature or salinity data were collected in the original study, and no seawater temperature data were available for the area that covered the entire time period. Air temperatures for Fort Pierce were available (Figure 1) and are summarized in the Discussion section.

RESULTS

North Beach Breakwater, North Hutchinson Island, Fort Pierce Inlet

This site was located at the southern tip of North Hutchinson Island. Specimens were collected from the intertidal rocks on the north side of the north breakwater that protects Fort Pierce Inlet. Habitats sampled included the rocks of the breakwater; sabellariid tubes, hydroids, octocorals, and algae attached to the rocks; and driftwood and other debris wedged among the rocks. The bryozoan diversity at the breakwater is largely dependent on the presence of the hydroid *Thyroscyphus ramosus* Allman, 1877 and the soft coral *Carijoa riisei* (Duchassaing and Michelloti, 1860), whose colonies provide habitat for most of the epifaunal invertebrates at the site. The large

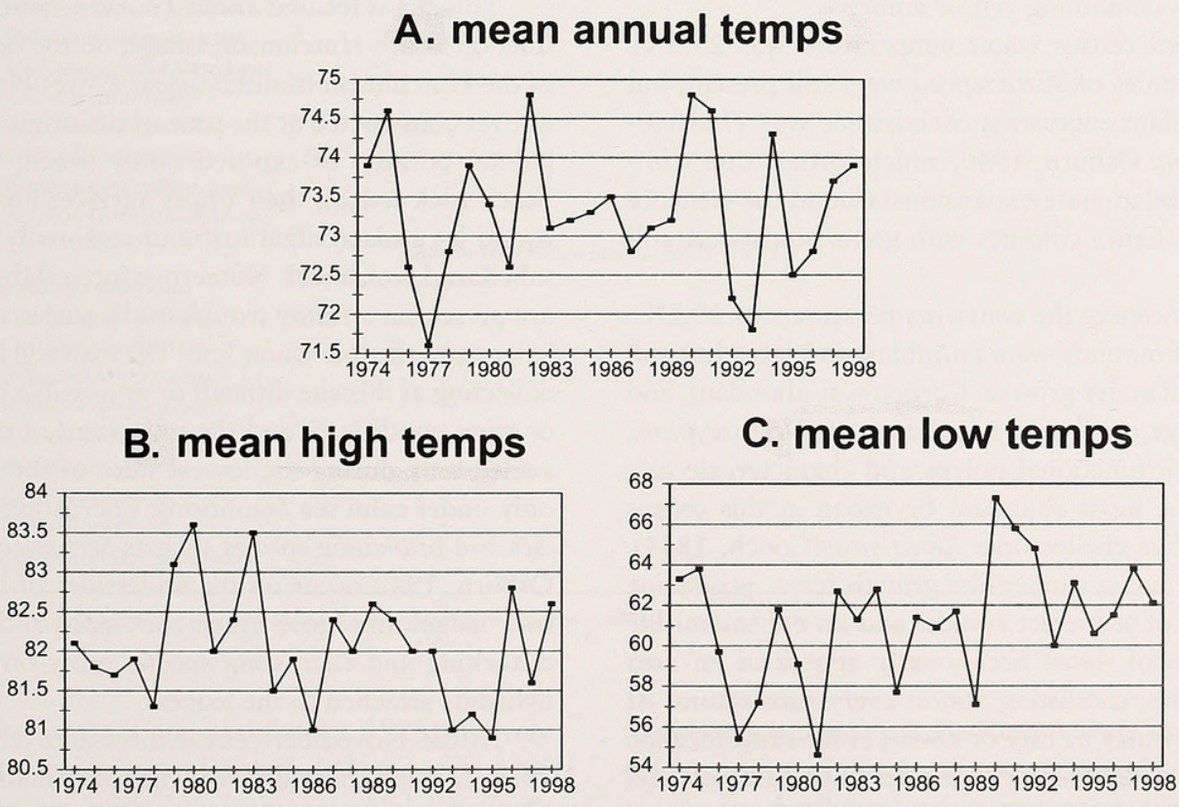

FIGURE 1. Mean annual (A), high (B), and low (C) air temperatures (in degrees Fahrenheit) for Fort Pierce, Florida, from 1974 to 1998. Note: lowest, 54°F = 12.2°C; highest, 83.6°F = 28.7°C.

mounds produced by the sabellariid worm *Phragmatopoma lapidosa* Kinberg, 1867 stay clean and unfouled when the worms are growing actively but break down as they age, the mounds dissolving or becoming riddled with holes and channels in which other organisms settle.

At the November census, water temperature was 23.3°C. New sabellariid tubes were covering the old eroded sabellariid mounds on many of the rocks. The hydroids *Thyroscyphus ramosus* and *Eudendrium carneum* Clarke, 1882 were in an active phase of growth. The cyclostome *Crisia elongata* Milne-Edwards, 1838 was the most common bryozoan found; masses of short young *Crisia* colonies were attached to hydroid roots and branches. Colonies of the encrusting cheilostome *Watersipora subtorquata* d'Orbigny, 1852 were also common, attached directly to the rocks near the low water mark.

At the February census the water temperature was 23.1°C. Hydroids had proliferated. *Thyroscyphus* and *Eudendrium* colonies were thriving, and *Tubularia* sp. and *Halocordyle disticha* (Goldfuss, 1820) were also present along with colonies of the octocoral *Carijoa riisei*. The worm reef was extensive and in healthy condition. *Watersipora* was abundant, with some small, recently recruited colonies present along with large mature colonies. *Crisia* was still a dominant, with large mature colonies producing gonozooids containing yellow embryos.

At the April census water temperature was 25.3°C. Old fouled colonies of *Watersipora* were still present, but the most abundant encrusting cheilostome was *Thalamoporella floridana* Osburn, 1940, which formed thin whitish crusts and bilaminate expansions around the stems of *Thyroscyphus*. *Crisia* colonies with gonozooids were still abundant.

At the July census the water temperature was 29.2°C. The worm reef mounds were crumbling in places but still showed areas of active growth. *Carijoa* was abundant, and there were large, well-grown colonies of *Thyroscyphus*, still active, with functional polyps and characteristic garlicky smell. The most abundant bryozoan at this census was the primitive cheilostome *Aetea sica* (Couch, 1844). This bryozoan has a runner-like growth form, producing uniserial rows of semierect zooids, and an ephemeral life history. Species of *Aetea* occasionally appear in an area in large numbers, encrusting almost every substratum. At other times they may be rare or absent at the same locality. At this census *Aetea* colonies were attached to sabellariid worm tubes, sponges, and *Codium* species of algae, as well as to hydroid stems. *Crisia* was still abundant, but colonies were short and there were very few gonozooids. The other species common at this census was the branching cteno-stome *Amathia distans* Busk, 1886, whose colonies form limp yellow-speckled clumps. They were attached to various substrata, including the senescent worm reef mounds.

Overall, the North Beach Breakwater site was remarkably stable in its bryozoan fauna over the 24-year interval. Thirty species were recorded at the site during this study, including 20 of the 31 species originally found there (Table 1). The species that were dominant in the original survey—*Amathia vidovici* (Heller, 1867), *Beania hirtissima* (Heller, 1967), *Beania klugei* Cook, 1968, *Celleporina hassalli* (Johnston, 1848), *Crisia elongata*, *Pasythea tulipifera* (Ellis and Solander, 1786), *Savignyella lafontii* (Audouin, 1826), *Synnotum aegyptiacum* (Audouin, 1826), *Thalamoporella floridana*, and *Watersipora subtorquata*—were still abundant and were present during at least three of the four censuses. In addition, two new species were common at this site. *Amathia alternata* Lamouroux, 1816 was present at other Indian River sites in the past and still occurs at those sites, but it had not previously been recorded at the North Beach Breakwater. *Caulibugula armata* Verrill, 1900 is new to the region since the original study was carried out.

Walton Rocks

This site is located about 13.7 km south of Fort Pierce Inlet on South Hutchinson Island, on the beach just south of the Hutchinson Island Nuclear Power Plant (which was not yet constructed at the time of the original survey). The habitat consists of exposed sandy beach, with intertidal beach rock ledges; their upper surfaces are covered year-round by a macroalgal turf and seasonally by mounds of sabellariid worm reef. Numerous loose slabs of beach rock are present in a sandy trough in the surf zone between the ledges and the low water line. The exposed location makes collecting at this site difficult or impossible under high surf or wind conditions, and the full extent of the ledges is revealed only during the lowest tides of the year, and then only under calm sea conditions. Encrusting bryozoan species and branching species such as *Scrupocellaria regularis* Osburn, 1940 occur on the undersides of both the beach rock ledges and loose beach rock slabs and stones. Other branching and encrusting species grow on the algae and hydroids attached to the ledges.

At the November census the water temperature was 23.3°C. Most common were the spiny mats of the cheilostome *Beania hirtissima*, which were found on the underside of almost every piece of beach rock. Also common were the beach rock-encrusting species *Exechonella antillea* (Osburn, 1927), *Schizoporella "unicornis,"* and

TABLE 1. Bryozoans found (+) in 1998–1999 four-season resurvey in comparison with those found in original survey at the North Beach Breakwater, North Hutchinson Island, Fort Pierce, Florida. Dominant species are shown in **bold** type; a dash (–) indicates species not found during the resurvey.

Species	November 1998	February 1999	April 1999	July 1999
Species found in 1974–1975 survey				
Aetea sica	–	–	–	+
Aeverrillia armata	+	+	–	–
Amathia distans	–	–	–	–
Amathia vidovici	+	+	+	–
Anguinella palmata	–	–	–	–
Antropora leucocypha	–	–	+	–
Beania hirtissima	+	+	+	–
Beania klugei	–	+	+	+
Beania mirabilis	–	–	–	–
Bowerbankia imbricata	+	–	–	+
Bowerbankia maxima	+	+	–	–
Bugula minima	–	–	–	–
Bugula turrita	–	–	–	–
Celleporina hassalli	+	+	+	+
Crisia elongata	+	+	+	+
Cryptosula pallasiana	–	–	–	–
Exechonella antillea	–	–	–	–
Hippoporina verrilli	–	–	–	–
Jellyella tuberculata [a]	+	–	–	–
Nolella stipata	+	–	–	–
Pasythea tulipifera	+	+	+	+
Pourtalesella incrassata [a]	–	–	–	–
Savignyella lafontii	+	+	–	+
Scrupocellaria regularis	–	–	–	+
Synnotum aegyptiacum	+	+	+	+
Thalamoporella floridana	+	+	+	+
Valkeria atlantica	–	–	–	–
Vittaticella contei	+	+	–	–
Vittacella uberrima	–	–	–	+
Watersipora subtorquata [a]	+	+	+	+
Zoobotryon verticillatum	–	–	–	–
Additional species found, 1998–1999				
Amathia alternata	+	+	+	–
Caulibugula armata	+	+	+	+
Caulibugula pearsei	–	–	+	–
Biflustra arborescens [a]	–	–	–	+
Biflustra denticulata [a]	–	+	+	–
Bugula neritina	–	+	–	–
Bugula stolonifera	–	+	+	–
Parasmittina sp. 3	–	–	–	+
Rhynchozoon sp.	–	–	–	+
Schizoporella "unicornis"	–	+	–	–

[a] Species for which nomenclature has been revised since Winston (1982).

Pourtalesella incrassata (Canu and Bassler, 1928), actively growing peach or pink colonies with red embryos present in ovicells, along with the ctenostome *Nolella stipata* Gosse, 1855. *Nolella* zooids are straight mud-covered tubes resembling miniature polychaete tubes. They are connected by a thin stolon, but at this site zooids were so thickly aggregated that the stolons were invisible and the colony appeared as a fuzzy mat of tubes.

At the February census the water temperature was 23.0°C. The wind was strong because of a cold front, and the surf was high, making collection difficult. The macroalgal turf was thriving and mostly unfouled except

by epiphytic hydroids. There were few branching bryozoans. Loose rock in the trough was almost all buried under sand. The colonies of beach rock-encrusting bryozoans collected were abraded and bleached in color.

At the April census the water temperature was 23.7°C. The algal turf was growing luxuriantly. Many more beach rock stones, some freshly broken off the ledges, were uncovered. The undersides of most rocks were completely covered by a cryptic community that included zooanthids, didemnid ascidians, sponges, anemones, and branching and encrusting bryozoans. *Beania hirtissima* was again dominant, but other colonies of encrusting bryozoans, including *Schizoporella "unicornis," Exechonella antillea*, *Watersipora subtorquata*, and *Cryptosula pallasiana* (Moll, 1803), were brightly colored and healthy. *Nolella stipata* zooids were clean and translucent, less mud-coated than in February. Colonies were sexually reproductive, as well; many zooids brooded two or three yellow-ochre eggs near their distal ends.

At the July census water temperature was 30.9°C. Surf was moderate, sand had filled in around ledges again, and a considerable amount of detached beach rock ledge algae was washed up on the beach. The undersides of large beach rock slabs still had a healthy cryptic fauna consisting of zooanthids, ascidians, sponges, and bryozoans on their undersides, despite being buried in sand. Dominant bryozoans were *Exechonella antillea*, *Biflustra denticulata* (Busk, 1856), and *Beania hirtissima*, as well as *Nolella stipata* (which was still reproducing), plus two erect branching species, the ctenostome *Amathia vidovici* and the cyclostome *Crisia elongata*, both present as large, old, fouled colonies.

This site, Walton Rocks, had been the most diverse intertidal site in the original study, with 36 species recorded at that time. Twenty-five of the same species were found in 1998–1999 (Table 2). Of the dominant species in the original survey, all were still present in at least two of the four censuses, and all but one, *Parasmittina betamorphaea* Winston, 2005, was present at three of the four.

The biggest change at this site was a decline in abundance of *Cryptosula pallasiana* and its apparent replacement in beach rock undersurface habitats by *Exechonella antillea*, which in 1974 had been found only once, at the North Beach Breakwater, and which had not been collected at Walton Rocks.

Johnson House Seagrass Bed, Indian River Lagoon

This seagrass bed is located about 9.7 km north of Fort Pierce Inlet. It lies in a shallow cove just north of the Harbor Branch Canal, behind the Johnson residence on the campus of Harbor Branch Oceanographic Institution. The grass bed has been the site of several studies of seagrass and soft substratum communities (e.g., Mook, 1976; Kulczycki et al., 1981; Virnstein and Carbonara, 1985; Virnstein and Howard, 1987) and was one of the bryozoan sites studied monthly in 1974–1975. The turtle grass, *Thalassia testudinum* Banks and Soland. ex Koenig, is the most abundant seagrass at this site, but manatee grass, *Syringodium filiforme* Kuetz., is also common. Drift algae float among the grass blades.

At the November census water temperature was 24.4°C. Collections were made of all substrata: *Thalassia*, *Syringodium*, and drift algae. Most drift algae were fouled by a colonial ascidian, *Lissoclinum fragile* (Van Name, 1902). The stoloniferous ctenostome *Bowerbankia maxima* Winston, 1982, and the encrusting cheilostome *Conopeum tenuissimum* (Canu, 1908) were the dominant bryozoans.

At the February census, the water temperature was 15.2°C, with a strong north wind. Masses of drift algae had been cast up on shore. *Bowerbankia maxima*, *Conopeum tenuissimum*, and the branching cheilostome *Bugula neritina* (Linnaeus, 1758) were the dominant bryozoans on seagrass and drift algae, respectively.

At the April census the water temperature was 23.5°C. Drift red algae appeared bleached in color compared with their February condition; other algal species appeared to be thriving. There had been a new settlement of spirorbid polychaetes onto the seagrass since February, and *Conopeum* had decreased in abundance on *Thalassia*. However, there were larger numbers and larger sexually reproductive colonies of *Bugula neritina* on the *Syringodium*, along with small recent recruits.

At the July census the water temperature was 29.7°C. *Thalassia* and *Syringodium* blades were heavily fouled by filamentous algae and hydroids. Large colonies of *Bowerbankia maxima*, clean and healthy in appearance, with long free-trailing masses of stolons and zooids, occurred on the drift algae. *Conopeum tenuissimum* and *Schizoporella floridana* Osburn, 1914, with recently settled recruits and with embryos in mature colonies, were found on the *Thalassia*.

In the original study nine species of bryozoans were recorded from this site. Six of these were collected at least once in the re-study (Table 3). The dominant species, *Conopeum tenuissimum*, *Schizoporella floridana*, and *Bowerbankia maxima*, remained unchanged. Four additional species, *Aetea sica*, *Aeverrillia armata* (Verrill, 1873), *Hippoporina verrilli* Maturo and Schopf, 1968, and *Scrupocellaria "bertholletii,"* not recorded here in

TABLE 2. Bryozoans found (+) in 1998–1999 four-season resurvey in comparison with those found in original survey at Walton Rocks, South Hutchinson Island, St. Lucie County, Florida. Dominant species are shown in **bold** type; a dash (–) indicates species not found at this location during the resurvey.

Species	November 1998	February 1999	April 1999	July 1999
Species found in 1974–1975 survey				
Aetea sica	–	–	–	+
Alcyonidium polypylum	+	+	+	–
Amathia alternata	–	–	+	+
Amathia distans	–	–	+	+
Anguinella palmata	–	–	–	–
Antropora leucocypha	–	+	–	–
Beania hirtissima	+	+	+	+
Beania klugei	–	+	+	+
Biflustra denticulata [a]	–	–	+	+
Bowerbankia gracilis	–	–	–	–
Bowerbankia imbricata	–	–	–	–
Bowerbankia maxima	–	+	–	–
Bugula neritina	–	+	–	–
Bugula stolonifera	+	+	+	–
Bugula turrita	–	–	–	–
Bugula uniserialis	–	–	–	–
Caulibugula pearsei	–	–	–	–
Celleporella carolinensis	–	–	–	+
Crisia elongata	+	+	+	+
Cryptosula pallasiana	+	+	+	
Electra bellula	–	–	–	–
Jellyella tuberculata [a]	+	+	–	+
Microporella umbracula	–	–	–	–
Nolella stipata	+	+	+	+
Parasmittina betamorphaea [a]	–	+	+	–
Pourtalesella incrassata [a]	+	+	+	
Savignyella lafontii	–	–	–	–
Schizoporella "unicornis"	+	+	+	+
Scrupocellaria regularis	+	–	+	+
Sundanella sibogae	+	–	–	–
Synnotum aegyptiacum	–	+	–	+
Thalamoporella floridana	–	–	–	+
Vittaticella contei	–	–	–	–
Vittacella uberrima	–	–	–	–
Watersipora subtorquata	–	+	+	+
Zoobotryon verticillatum	–	–	–	–
Additional species found, 1998–1999				
Aimulosia spp	+	–	+	+
Amathia vidovici	+	+	+	+
Celleporaria sp. 2	+	+	+	
Escharoides costifer	–	–	–	+
Exechonella antillea	–	+	+	+
Biflustra arborescens	–	+	–	+
Lichenopora sp.	–	–	–	+
Parasmittina sp. 2	–	–	–	+
Pasythea tulipifera	+	+	–	–
Scrupocellaria "bertholletii"	–	+	–	–

[a] Species for which nomenclature has been revised since Winston (1982).

TABLE 3. Bryozoans found (+) in 1998–1999 four-season resurvey in comparison with those found in original survey at the Johnson House Seagrass Bed, Harbor Branch Oceanographic Institution, Link Port, Fort Pierce, Florida. Dominant species are shown in **bold** type; a dash (–) indicates species not found at this location during the resurvey.

Species	November 1998	February 1999	April 1999	July 1999
	Species found in 1974–1975 survey			
Amathia distans	–	–	–	–
Beania klugei	–	–	+	–
Bugula neritina	–	+	+	–
Bowerbankia gracilis	–	–	–	–
Bowerbankia maxima	+	+	+	+
Conopeum tenuissimum	+	+	+	+
Electra bellula	–	–	–	–
Nolella stipata	–	+	+	–
Schizoporella floridana	+	+	+	+
	Additional species found in resurvey			
Aetea sica	–	–	+	+
Aeverrillia armata	+	–	–	–
Hippoporina verrilli	+	–	–	–
Scrupocellaria "bertholletii"	–	–	+	–

1974–1975, were also found at one or more censuses in 1998–1999. The three species not found during the restudy, *Amathia distans*, *Bowerbankia gracilis* Leidy, 1855, and *Electra bellula* (Hincks, 1881), were still present in the lagoon at other sites.

A1A Causeway

In addition to the three sites from the original study, one new site was also surveyed quarterly. The site is a shaded spot under the east end of the Route A1A causeway bridge to North Hutchinson Island. This site was chosen because of its position in the Indian River Lagoon, about 3 km north of the mouth of Fort Pierce Inlet, and close to Little Jim Island, where in 1989 a *Scrupocellaria* species previously unrecorded in the region had first been collected (Winston, 1995). Material was collected from bridge pilings, from drift algae, and from submerged wood.

At the November census water temperature was 23.3°C. The most abundant species were *Bugula neritina*, *Caulibugula armata*, *Bugula stolonifera* Ryland, 1960 (the latter two reproductive), and *Zoobotryon verticillatum* (Delle Chiaje, 1828). Medium-sized *Zoobotryon* colonies had some areas of new growth with actively feeding polypides.

At the February census the water temperature was 21.1°C with a cold north wind and turbid water conditions. *Bugula neritina* was again dominant, with large, bright wine red-colored, sexually reproductive colonies. Other abundant species were *Amathia vidovici* (colonies mostly mud coated, but with clean actively growing branch tips) and long stalks of *Caulibugula armata*. *Zoobotryon verticillatum* was present only as short, heavily fouled, and senescent clumps.

At the April census water temperature was 23.2°C, with almost no wind and extremely clear water. *Bugula neritina* was still dominant on bridge pilings, with more mature and senescent colonies than in February. *Zoobotryon verticillatum* was still present, as large colonies drifting among seagrasses and short clumps attached to pilings, all of them heavily fouled, but with some young actively growing branches. *Caulibugula armata* was still present, with large and unfouled colonies. *Amathia vidovici* was still abundant, but colonies were heavily fouled.

At the July census water temperature was 28.8°C, wind calm, with fairly clear water (visibility about 1 m). *Bugula neritina* and *Zoobotryon verticillatum* were absent. Dominant species were *Caulibugula armata* (old, fouled colonies, with many brown bodies in the lower parts of branches, but with zooids containing feeding polypides and ovicelled zooids containing creamy white embryos near branch tips), *Savignyella lafontii*, a delicate branching cheilostome, *Nolella stipata*, and *Amathia vidovici* (as small, heavily fouled colonies).

Twelve species were found at this site (Table 4), making it less diverse than the open coast sites but more diverse

TABLE 4. Bryozoans found (+) in the 1998–1999 four-season survey at the AIA Causeway Bridge, North Hutchinson Island, Fort Pierce, Florida. Dominant species are shown in **bold** type; a dash (–) indicates species not found at this location during the resurvey.

Species	November 1998	February 1999	April 1999	July 1999
Aetea sica	–	+	+	–
Amathia vidovici	+	+	+	+
Beania klugei	–	+	+	+
Bowerbankia gracilis	–	–	–	+
Bowerbankia maxima	+	+	+	–
Bugula neritina	+	+	+	–
Bugula stolonifera	+	–	–	–
Caulibugula armata	+	+	+	+
Nolella stipata	+	+	+	–
Savignyella lafontii	+	+	+	–
Scrupocellaria "bertholletii"	–	+	+	–
Zoobotryon verticillatum	+	–	–	–

than the Johnson House Seagrass Bed site (10 species) further up the lagoon from Fort Pierce Inlet. Species composition was stable; most species found there were collected in at least three of the four censuses. Overall dominants were *Amathia vidovici*, *Bugula neritina*, *Zoobotryon verticillatum*, and *Caulibugula armata*, a species that had not been collected in the area until about 1994.

DISCUSSION

In the 1974–1975 study, 55 species were recorded from all lagoon and shallow coastal sites. Forty-nine species were recorded at the three sites later resurveyed. During the 1998–1999 survey, 39 species were found at those three sites. Thus, 80% of the bryozoan species known originally from those sites were recollected after a 24-year interval, despite a smaller sampling effort (4 versus 12 collections). Seventy percent of the species found originally from all inshore sites combined were also found in the four-site resurvey, again with a much smaller sampling effort involved. There has been remarkable stability in species composition of the bryozoan fauna over the time period.

Sixteen species had additional localities (that is, they were present in the area originally, but occurred at a different site in the second study than that from which they had been recorded in the original survey), indicating that most species were not restricted to one site and could be expected at any or all sites provided the appropriate substratum and environmental conditions were present. Even though most of the species involved have nonfeeding, rapidly settling larvae, there is apparently enough dispersal and recruitment that disappearance from one site would not mean that a species would disappear from the region entirely. Only one species, *Schizoporella floridana*, was limited to one site, the Johnson Seagrass Bed, and to one substratum, *Thalassia testudinum*, and was not collected elsewhere in 1998–1999.

Species new for inshore intertidal sites, but known from offshore hard substrata or algae (Winston and Eisman, 1980; Winston and Håkansson, 1986), included *Aimulosia uvulifera* (Osburn, 1914), *Aimulosia pusilla* (Smitt, 1873), and *Escharoides costifer* (Osburn, 1914). Four species were newly recorded for the region during the study: two species of *Parasmittina*, a species of *Celleporaria*, and a *Lichenopora* species.

Although species composition remained very stable, species abundances changed considerably, not only from season to season but also between the two studies. The most notable changes involved the decline in abundance of the warm temperate species *Bugula stolonifera*, *Cryptosula pallasiana*, and *Hippoporina verrilli*, all of which have western Atlantic distributions extending northward to Long Island or Cape Cod. During the original study period abundant *Bugula stolonifera* colonies were found attached to the proximal portions of *Bugula neritina* colonies. In the re-study only a few colonies were found, and they were not in association with *Bugula neritina*. *Hippoporina verrilli* was a common species on Indian River Lagoon panels (Mook, 1976) and on panels and seagrasses in 1974–1975, and it was also found at two coastal sites

at that time. Reproduction and settlement were heaviest in the cooler months (October–January). In the re-study only a few small colonies were found at the Johnson Seagrass Bed. *Cryptosula pallasiana* is a cosmopolitan temperate fouling species. In 1974–1975 it occurred at four intertidal coastal sites. In the re-survey, however, it was found only at Walton Rocks where it was much less abundant under beach rock stones than originally. Instead, in the underrock habitat the dominant encrusting bryozoans in 1998–1999 included *Exechonella antillea*, a Caribbean species which, in the original study, had been collected only one time, at the North Beach Breakwater site. That original record itself may have indicated a range expansion for the species because a distributional survey by Maturo (1968) reported the species only from Miami south.

The other new species in the study are similarly warm-water species. *Caulibugula armata* was described by Verrill from Bermuda, and it is known from the Tortugas, Puerto Rico, and Brazil, according to Osburn (1940). *Aimulosia pusilla* was described from the Tortugas by Smitt (1873) and *Aimulosia uvulifera* and *Escharoides costifer* from the same locality by Osburn (1914). The typical *Scrupocellaria bertholletii* is a circumtropical species, often associated with coral reefs (Winston, 1986), but Indian River and other western Atlantic specimens show some morphological differences to those from other localities, indicating that *Scrupocellaria bertholletii* is a species complex rather than a single widespread species. It was first recorded in the Indian River lagoon in 1989 and continues to occur at both coastal and lagoon sites. The genera *Celleporaria* and *Parasmittina* contain numerous species that are extremely successful in both tropical fouling and cryptic coral reef communities (Winston, 1986). The addition of species in this group is not surprising.

The increase in warm-water species has continued since the re-study was completed. *Nellia tenella* (Lamarck, 1816), another circumtropical fouling and reef-associated species, was first found in the Indian River area in 1999, in intertidal collections in Fort Pierce Inlet. It has been found every year since then, although its abundance has varied. *Hippopodina irregularis*, a species described form Guanica Harbor, Puerto Rico, by Osburn (1940), was first found on *Syringodium* seagrass in Fort Pierce inlet in the summer of 2001. *Schizoporella pungens* (Canu and Bassler, 1928), the massive dark purple, Caribbean–Gulf of Mexico *Schizoporella*, whose colonies are characteristically found on submerged mangrove roots and in harbor fouling communities, had been on noted on drift plastic items washed ashore in the area for several years, always with an associated fauna of small corals and *Millepora* species that suggested the debris had been colonized further south, perhaps in the Straits of Florida or the Florida Keys. *Schizoporella pungens* colonies first recruited to panels in Indian River Lagoon (Faber Cove), as well as to numerous benthic substrata in Fort Pierce Inlet between July 2002 and July 2003. *Celleporaria sherryae* Winston, 2005, another Caribbean fouling and shallow reef-associated species, has also appeared at some coastal sites (2001) and within the Fort Pierce Inlet (2003).

Reasons for the increase in warm-water species are harder to identify. One explanation might be global warming. As noted by many recent studies, the decade of the 1990s was the warmest on record (Levitus et al., 2000). The effects of warming seawater temperatures on marine organisms, including bryozoans (Kelmo et al., 2004), have been noted worldwide. In addition to direct effects on growth and survival of benthic organisms, changes in water temperature also affect food supply (Menge et al., 2008; Richardson, 2008), as well as producing indirect effects via changes in ocean chemistry and circulation (Harley et al., 2006).

For these collecting sites no records of seawater temperature exist for the entire time period of the two studies (1974–1999). However, as these sites are all intertidal, it seemed reasonable to make use of the published air temperature data that were available for Fort Pierce as a substitute. Although mean annual temperatures and mean annual high temperatures (based on monthly averages) showed no discernible statistically significant pattern (Figure 1A,B), there is a suggestion in the data that mean annual low temperatures (Figure 1C) have increased over the time period. If warm-water species are more susceptible to cold-water shock than high temperatures, as has been shown in studies of Florida fish kills after freezes in the region (Gilmore et al., 1978), warmer winter temperatures might be a factor permitting the invasion and survival of populations of the more tropical species, as has been shown to be the case for some introduced marine invertebrates in other studies (Stachowicz et al., 2002).

However, other factors are involved. The Indian River Lagoon is part of the Intracoastal Waterway, a passage for boat traffic moving up and down the Atlantic coast, as well as in and out of the Gulf of Mexico and the Caribbean. Fort Pierce has a small commercial port with shipping traffic from the Bahamas (especially Freeport, where containers from China and other distant sources are transferred for transshipment into the USA), the Gulf of Mexico, and the Caribbean, as well as U.S. ports along the east coast. Species could be introduced through ballast water exchange by larger ships, as well as by hull fouling of small and large vessels.

Although the stability of the bryozoan fauna over this time period gives a positive picture of the health and stability of the lagoon epifauna overall, there is no way to predict the long-term impact of these factors. The dependence of many bryozoans on living substrata such as seagrasses, hydroids, and octocorals also makes it clear that disturbances affecting substratum organisms would have a major impact on the bryozoans and would probably be more destructive to their local diversity than the environmental fluctuations noted so far.

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