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research paper

Hitchhiking bryozoans (Gymnolaemata) on sea turtles (Cheloniidae) from southeastern United States to Honduras

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ABSTRACT.—To understand the symbiosis between epizoic bryozoans and sea turtles, we examined 52 sea turtles whose range spanned from Georgia, United States to Honduras, from three host species: *Caretta caretta* (loggerhead), *Chelonia mydas* (green), and *Eretmochelys imbricata* (hawksbill). Of these, 13% were adults and 87% were juveniles. We found 18 bryozoan colonies belonging to seven different gymnolaemate bryozoan species. Five were cheilostomes (*Biflustra arborescens*, *Biflustra* cf. *conjunctiva*, *Bugula neritina*, *Schizoporella errata*, and *Aetea* sp.) and two were ctenostomes (*Alcyonidium hauffi* and *Anguinella palmata*). *Biflustra* cf. *conjunctiva* and *Aetea* sp. are reported here for the first time on sea turtles. *Biflustra* cf. *conjunctiva* is an invasive species from the South China Sea and reported here for the first time in the southeastern United States. Of the 52 sea turtles examined, 15% were fouled by bryozoans: 88% of the loggerheads, 3% of the greens, and none of the hawksbills. Combining all host species, 86% of adult sea turtles were fouled by bryozoans compared to 4% of juveniles. Fouled hosts were significantly larger than unfouled hosts. We attribute this to the target area hypothesis, as the juvenile sea turtles were significantly smaller targets for bryozoan larval settlement than the adult hosts. The bryozoans were all found on the hosts' dorsal carapace, and the number of bryozoan colonies increased significantly in a posterior direction across the carapace. Of the 18 bryozoan colonies, 89% were encrusting and 11% were erect, yet flexible. We describe this nonobligate/facultative commensal symbiotic relationship as phoretic (i.e., hitchhiking).

Epibiosis refers to the ecological association between an organism growing attached to a living surface, such as barnacles on whales. Most epibiosis is facultative commensalism (Wahl and Mark 1999), where the epibiont benefits without harming the basibiont, in the terminology of Wahl (1989). The sessile epibiont attached to the basibiont's outer surface does not trophically depend on it. All of the organisms together in an epibiotic association comprise a single holobiont communal entity, which forms an ecological unit (Pinou et al. 2019). Of all interspecific associations, epibiosis is one of the most intimate, as the basibiont and epibiont species live in close spatial association often for the entire lifespan of at least one of the organisms (Wahl 1996).

Fouling (short for biofouling) refers to the more general colonization process by epibionts of a solid biotic or abiotic surface (Wahl 1989). Here, epibiosis and fouling are used interchangeably. Understanding epibiosis is important because fouling epibionts degrade the functionality of ship hulls, heat exchangers, and water intake pipes (Flemming et al. 2009, Hellio and Yebra 2009). On living hosts, epibionts may obscure eyes, inhibit wound healing, and/or decrease hydrodynamic efficiency resulting in increased host energetic output (Key et al. 2010, 2023).

Bryozoans grow on a variety of sessile abiotic (e.g., marine hardgrounds; Taylor 2016) and motile biotic substrata, such as gastropods (Taylor and Schindler 2004), cephalopods (Landman et al. 1987), echinoids (Schneider 2003), pycnogonids (Key et al. 2013), horseshoe crabs (Key et al. 1996a,b, 2000), isopods (Key and Barnes 1999), brachyuran crabs (Key et al. 1999, Winston and Key 1999), lobsters (Key and Hendrickx 2022, Key et al. 2023, Key and Decker 2023, Key and Schorr 2023), sea snakes (Key et al. 1995, 1996b), and sea turtles (Frazier et al. 1992).

Bryozoans are the most diverse clade of macroepibionts (Wahl 2009, table 4.2). On marine debris, they are also one of the most ubiquitous (Barnes 2002, Thiel and Gutow 2005, Carlton et al. 2017) and the most diverse (Haram et al. 2023, fig. 1) groups of fouling animals. Invasive bryozoans hitchhike on anthropogenic floating substrata, such as plastic (Winston 1982a, Stevens et al. 1996, Winston et al. 1997, Barnes and Sanderson 2000, Barnes and Fraser 2003, Barnes and Milner 2005) and ship hulls (Ryland 1965, Kubanin 1979, Watts et al. 1998, Láruson et al. 2012, McCann et al. 2015), as well as in ship ballast water (Carlton 1985, Carlton and Geller 1993). Bryozoans effectively exploit naturally occurring floating marine debris by fouling pieces of pumice (Bryan et al. 2012, Rust 2015, Hirose and Kaneko 2023), tar balls (Shaw and Mapes 1979), wood debris (Donlan and Nelson 2003), sea grasses (Keough and Chernoff, 1987, Worcester 1994), and algae (Bushing 1994, Kuhlenkamp and Kind 2013, López et al. 2018, Avila et al. 2020). Bryozoans also have a long evolutionary history of hitchhiking on motile living host substrata with hard exoskeletons (Key et al. 2010, 2017, Wyse Jackson and Key 2014, Wyse Jackson et al. 2014, Key and Schweitzer 2020).

Sea turtles eat various organisms that are fouled by bryozoans and thus may be regularly exposed to bryozoan larvae living in the same environment. Sea turtles eat a variety of prey items, including soft corals and sponges (Carr and Stancyk 1975, Meylan 1988, Russell et al. 2011, Berube et al. 2012, Baumbach et al. 2019) which are known to have bryozoans encrusting them (Marcus 1939, Winston 1982b, Ruppert and Fox 1988, Vieira et al. 2014), sea grasses (Houghton et al. 2000, Arthur et al. 2008, Carrión-Cortez et al. 2010) which characteristically host bryozoans growing on them (Voigt 1981, Hageman et al. 2000, Moissette 2013), and a variety of macroalgae (Ross

1985, Plotkin et al. 1993, Burke et al. 1994, Witherington 1998) which may also host bryozoan epibionts (Ryland 1974, Withers et al. 1975, Winston and Eiseman 1980).

As large, hard-surface, motile structures, cheloniids provide a potentially viable substratum for invertebrate larvae present in the water column and are often fouled by a variety of commensal epibiotic organisms, especially stalked and encrusting barnacles, hydroids, bryozoans, and tunicates (Caine 1986, Dodd 1988, Covert et al. 2020, Robinson and Pfaller 2022). Epibiotic communities on sea turtles are not restricted to macroinvertebrates, but also include algae (Abel Sentíes et al. 1999, Báez et al. 2001, Sazima et al. 2010) and diverse meiofauna (Ingels et al. 2020). Individual epibiont species exhibit a variety of either accidental or specific, targeted associations (Badillo et al. 2003, Frick and Pfaller 2013).

To date, 30 published studies reported 17 different bryozoan species fouling sea turtles (Online Table S1). The fouling rate in these studies averaged 21%. This rate is likely inflated since 39% of those studies included dead turtles or sea turtles of unknown status. Including dead sea turtles likely inflates the fouling rate, as the host has more time to be fouled while drifting in the ocean with no chance for grooming. Dead sea turtles provide little insight into bryozoan-sea turtle epibiosis, as bryozoan larval settlement may have occurred *post-mortem*. For example, Frazier et al. (1992) pioneered work on bryozoan-sea turtle epibiosis, but 75% of their sea turtle hosts were dead. The low incidence of bryozoan fouling of sea turtles also extends into the fossil record, with only a single study by Zangerl (1948) documenting bryozoans fouling host sea turtles (Online Table S1). However, Dixon (1960) and Hutchison and Frye (2001) attributed pitting of the shell of Cenozoic turtles to infestations of the freshwater bryozoan *Plumatella*.

The latest fossil records of sea turtles from Denmark (Lindgren et al. 2017), Spain (Castillo-Visa et al. 2022), Panama (Cadena et al. 2023), and Germany (Augustin et al. 2023) provide no evidence of bryozoans and do not mention any in previous studies. Additionally, fossil sea turtles, so well preserved as to still retain their soft tissue and original DNA, lack evidence of epizoic bryozoans (Lindgren et al. 2017, Cadena et al. 2023). In summary, bryozoans appear to be relatively uncommon epibionts on sea turtles (Pfaller and Robinson 2022, Robinson and Pfaller 2022).

The purpose of this study was to quantitatively describe the frequency of epibiotic bryozoans fouling host sea turtles from the subtropical and tropical Atlantic basin spanning southeastern United States to Honduras. Furthermore, we considered and reported the variables that affect these bryozoan-sea turtle relationships by assessing basic conditions of turtle carapaces that favor or discourage bryozoan larval settlement.

Materials and Methods

Sea turtles were sampled for bryozoans from five localities (Online Table S2) from north to south: (1) Wassaw National Wildlife Refuge, Wassaw Island, Georgia, US, (2) Jekyll Island, Georgia, US, (3) Atlantic coast, northeastern Florida, US, (4) Trident Submarine Basin, Patrick Space Force Base, Port Canaveral, Florida, US, and (5) Sandy Bay West End Marine Reserve, Roatán Island, Honduras. Turtle sighting locations were recorded by GPS. This study had a western north Atlantic focus with the five study sites ranging from 16°N to 32°N (mean = 28°N, standard deviation = 6°N; Online Table S2). All sampling was conducted under ongoing research permits

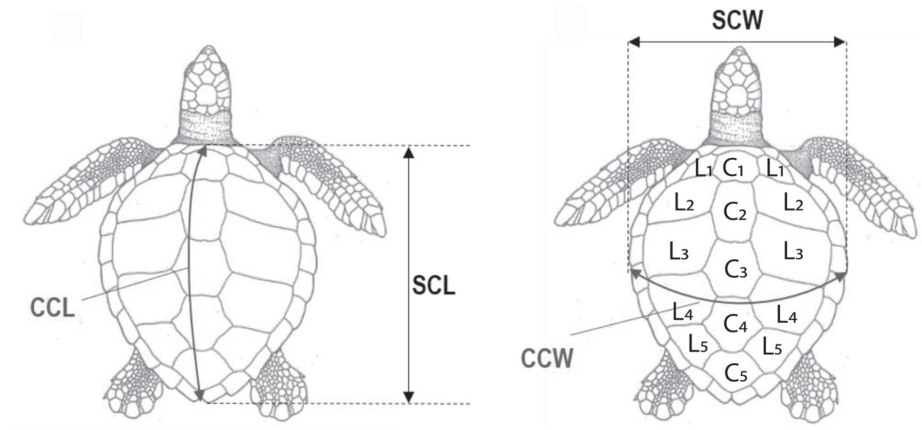

Figure 1. Morphometric characters measured on host sea turtles. CCL = Curved Carapace Length, SCL = Straight Carapace Length, CCW = Curved Carapace Width, SCW = Straight Carapace Width, $C_{1–5}$ = Central/vertebral/neural scutes, $L_{1–5}$ = Lateral/costal/pleural scutes. Modified from EAZA (2021, fig. 1) and Márquez-M (1990, fig. 1).

at each study site except for Jekyll Island, where we obtained additional bryozoan-specific scientific collecting permits from the Georgia Department of Natural Resources (permit #123049729) and the Jekyll Island-State Park Authority (permit # 072922).

At Wassaw and Jekyll islands, Georgia, US, we only had access to nesting sea turtles. Thus, all our samples were collected from the dorsal carapaces of adult nesting females, introducing sampling biases within our data. There were also sampling biases with our data from St. Augustine, Florida, US, as all the sea turtles came from a rehabilitation hospital (University of Florida's Sea Turtle Hospital). There were no adult or healthy sea turtles brought to the hospital during our study. Despite these biases, we chose these types of sampling as they were efficient ways to access neritic sea turtles.

Due to minimal sexual dimorphism in immature sea turtles (Wyneken 2001) other than egg-laying adult females, we were unable to determine the sex of the host sea turtles. We categorically aged the turtles as hatchlings, juveniles, or adults. When possible, sub-adult turtles were weighed to the nearest 0.1 kg with a spring scale. Nesting adult females could not be weighed. Turtles were then photographed and epibiont locations mapped on a sea turtle template (Fig. 1). The inability to access the plastron of larger turtles biased the data toward more dorsal occurrences. Bryozoan colonies were removed with a scalpel and preserved in 95% ethanol (EtOH: C_2H_5OH). No samples were taken from dead host sea turtles, as the fouling may have occurred *post-mortem* and would not be indicative of actual symbiosis. We did not measure the sizes of scutes as their edges were often obscured by algae, and our sampling permits did not permit us to remove the algae to see the edges of the scutes.

Following the sea turtle morphometric recommendations of Bolten (1999), Straight Carapace Length (SCL) was measured with calipers as the minimum SCL (a.k.a., notch-notch length) from the nuchal notch to the point at the midline notch between the supracaudal marginal scutes, and the maximum SCL (a.k.a., notch-tip length) from the anterior nuchal notch to the posterior tip of the supra-caudal marginal scutes (Fig. 1). Curved Carapace Length (CCL) was measured similarly with a fiberglass cloth tape. Carapace width was measured perpendicular to carapace length as the distance running across the carapace at the widest point (Fig. 1). Straight Carapace Width (SCW) and Curved Carapace Width (CCW) measurements were taken in the same manner as carapace length. CCL and CCW were not measured when epibionts, satellite transmitting tags, or morphologic abnormalities precluded it. All measurements were taken to the nearest 0.1 cm with the turtle laying on its plastron.

Once in the lab, we examined epibiont samples with a binocular dissecting microscope. We assessed bryozoan colonies for evidence of life when collected (i.e., opercula present and/or organic cuticle still covering skeleton in cheilostomes and presence of well-preserved polypides and/or partially extruded introverts in the ctenostomes). The largest bryozoan colony of each species from each sample was selected for species identification. Each colony was air dried, bleached to remove the organic cuticle to expose the mineralized skeleton, air dried again, and mounted with double sided carbon tape on Al stubs for scanning electron microscope (SEM) imaging. We then coated specimens with a gold-palladium alloy using Anatech USA's Hummer 6.2 sputter coater under a 65 millitorr vacuum with 10 milliamps voltage for 120 seconds. We collected images with a Hitachi S-4800 SEM at an accelerating voltage of 5.0 kV and an 8.0 mm working distance. In addition to using SEM images to identify bryozoan species, we also looked for evidence of sexual reproduction (e.g., ovicells).

RESULTS

EPIBIOSIS RESULTS.—We were able to examine 52 sea turtles from Georgia, US to Honduras, belonging to three host species: *Caretta caretta* (loggerhead), *Chelonia mydas* (green), and *Eretmochelys imbricata* (hawksbill; Fig. 2, Online Table S2). Of these, 13% were adults and 87% were juveniles.

We found 18 bryozoan colonies belonging to seven different bryozoan species (Fig. 3, Online Table S2). All were gymnolaemate bryozoans. Five were cheilostomes

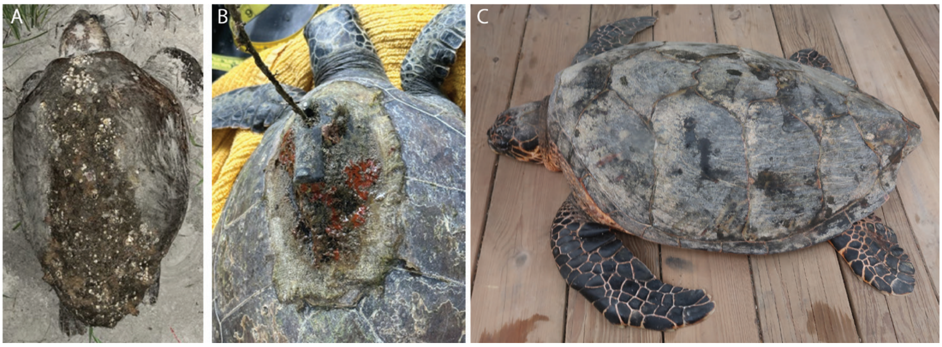

Figure 2. Examples of the three sea turtle species examined for bryozoans in this study: (A) *Caretta caretta* (loggerhead) from Jekyll Island, Gorgia, United States with CCL of 100 cm, (B) *Chelonia mydas* (green) from Port Canavaral, Florida, United States with a SCL of 26 cm, and (C) *Eretmochelys imbricata* (hawksbill) from Roatán Island, Honduras with a CCL of 63 cm. Note scratch marks on sides of carapace devoid of epibionts in A and C. Note pink colony of *Schizoporella errata* near base of antenna in B.

[*Biflustra arborescens* (Canu and Bassler 1928), *Biflustra* cf. *conjunctiva* (Zhang and Liu 1995), *Bugula neritina* (Linnaeus 1758), *Schizoporella errata* (Waters 1878), and *Aetea* sp.], and two were ctenostomes (*Alcyonidium hauffi* Marcus, 1939 and *Anguinella palmata* Van Beneden, 1845; Fig. 3).

All bryozoan colonies were found on host dorsal carapaces. Except for the green turtle from Port Canaveral, Florida, bryozoan colonies were found exclusively at the posterior end of host carapaces. The bryozoan on the green turtle from Port Canaveral, Florida, was found growing on the epoxy resin used to attach a Wildlife Computers Spot 387a satellite transmitting tag (ID 236374) near the anterior end of the carapace (scute C_2; Fig. 2B). The number of bryozoan colonies increased significantly in a posterior direction from C_1 to C_5 and L_1 to L_5 (Fig. 4).

All bryozoan colonies were interpreted as alive when collected based on the presence of opercula and/or the organic cuticle still covering the skeleton in cheilostomes and well-preserved polypides (Fig. 3F) and/or partially extruded introverts (Fig. 3G) in the ctenostomes. No colonies showed evidence of sexual reproduction. Some colonies were too small to reach sexual maturity (e.g., *B. neritina* and *S. errata*). Other colonies do not produce visible morphological evidence of sexual reproduction because they are spawners (e.g., both *Biflustra* species), or produce transient ovisacs (e.g., *Aetea* sp.), or brood internally (both ctenostome species).

Of the 52 sea turtles examined, eight (15%) were fouled by bryozoans. Of the eight loggerheads, seven (88%) were fouled by bryozoans. Of the 37 greens, one (3%) was fouled, and of the seven hawksbills, none were fouled. Combining all host species, six of the seven adult sea turtles (86%) were fouled by bryozoans compared to 4% of the 45 juveniles. Combining all sea turtle species, fouled hosts were significantly larger (n = 7, CCL mean = 97 cm, range = 71–105 cm, standard deviation = 11 cm) than unfouled hosts (n = 44, CCL mean = 41 cm, range = 28–103 cm, standard deviation = 14 cm; t-test assuming unequal variance, t = 11.15, df = 9, $P < 0.0001$; Fig. 5).

Of the 18 bryozoan colonies we found, 89% were encrusting and belonged to the species *B. arborescens* (Fig. 3A), *B.* cf. *conjunctiva* (Fig. 3B), *S. errata* (Fig. 3D), *Aetea* sp. (Fig. 3E), and *A. hauffi* (Fig. 3F). The 11% of colonies that were erect belonged to *A. palmata* (Fig. 3G) and *B. neritina* (Fig. 3C). Some of the encrusting colonies of *A. hauffi* secondarily grew erect when encrusting flexible *Obelia* sp. hydroid stems (Fig. 3F). The erect colonies were flexible, rather than rigid.

Taxonomic Results

Order Cheilostomata

Biflustra arborescens (Canu and Bassler, 1928)

(Fig. 3A)

Description.—Colony encrusting substratum in one or more layers. Zooids rectangular proximally and laterally, slightly curved distally. Opesia rectangular to oval. Mural rims narrow, raised and beaded to serrated, zooid margins with distinct grooves between zooids, sometimes brown in color. The cryptocyst beneath the frontal membrane is narrow distally and laterally, but may form a more extensive shelf proximally, and occasional narrow curved spicules may project inward.

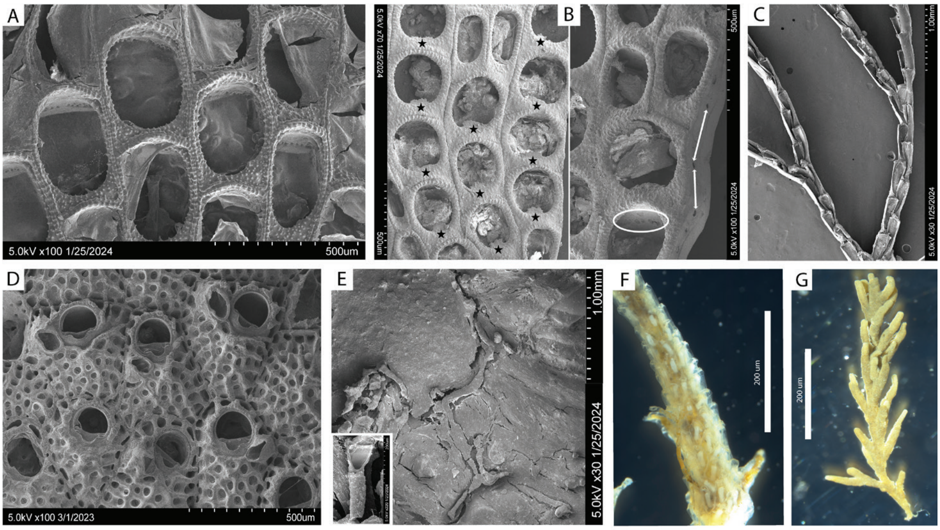

Figure 3. Examples of the seven bryozoan species found on sea turtles in this study. The cheilostomes: (A) *Biflustra arborescens*; (B) *Biflustra* cf. *conjunctiva*, stars on left indicate proximal-median processes immediately above, arrows and ellipse on right indicate lateral and transverse pore chambers, respectively; (C) *Bugula neritina*; (D) *Schizoporella errata*; and (E) *Aetea* sp., insert shows stalk and expanded distal portion of zooid; and the ctenostomes (F) *Alcyonidium hauffi* encrusting hydroid stem; and (G) *Anguinella palmata*.

*Geographic Range.—*Western Atlantic: Long Island, New York to Brazil, Caribbean, Gulf of Mexico; eastern Atlantic: Spain, Portugal and Africa; Mediterranean: Alboran Sea, West Africa (Cook 1968, Almeida et al. 2018)

Biflustra cf. *conjunctiva* (Zhang and Liu, 1995)

(Fig. 3B)

*Description.—*Colony encrusting substratum in a single layer. Zooids rectangular with curved distal margins. Colony expanding toward circular shape with growth, a line of broad zooids followed by two almost paired narrower zooids from which two rows of broader zooids proceed distally. Mural rims broad, raised and granular on uppermost surface, serrated next to the opesia, covering the junction between zooids, leaving only a narrow groove between zooid walls. Opesia oval to round, frontal membrane covering up to 2/3 of frontal surface. In many zooids a narrow to broad proximal-median process protrudes into the opesia from the center of the proximal mural wall (Fig. 3B left).

Our material consisted of a skeletal colony. Zooecia tended to separate in longitudinal rows, thus only some lateral pore chambers could be observed (Fig. 3B right). Transverse (frontal) pore chambers are shown in Figure 3B (right). Zhang and Liu (1995, p. 136) described the pore structure as, “Mural porechambers on the transverse wall uniporous, four to five of them being large and arranged in a transverse line near the basal side of the wall, six to eight being middle and arranged in a transverse 1 (sic) line near the side of the frontal membrane, and many being small and s[c]attered densely between the two lines. Mural porechambers on the lateral wall multiporous, consisting of two longitudinal rows, one of them being made up of four large pores arranged in a row near the side of the frontal membrane, the other being composed of six to eight small pores arranged in a row near the basal side of the wall."

Because we could not make an exact match to Zhang and Liu's description of pore chambers, we have left the species identity uncertain. However, it meets the description of *B. conjunctiva* in overall morphology, especially the paired zooids, zooid shape, proximal-median process, bulging mural walls rather than paired rims with distinct grooves as in *B. arborescens*, and in all but one of the morphometric characters measured.

To quantitatively compare our colonies of *B.* cf. *conjunctiva* to those of *B. arborescens*, we measured zooid length and width, as well as opesium length and width on six zooids from one colony of *B.* cf. *conjunctiva* and six zooids from each of two colonies of *B. arborescens* (Table 1). Zooid width, opesium length, opesium width, zooid area (i.e., zooid length × zooid width), and opesium area (i.e., opesium length × opesium width) were all significantly larger in *B. arborescens* than in *B.* cf. *conjunctiva* (t-tests assuming unequal variance: $P < 0.05$). Zooids were on average longer in *B.* cf. *conjunctiva*, although not significantly so (t-test assuming unequal variance, $t = -1.53$, df = 9, $P = 0.161$).

Geographic Range.—South China Sea (Zhang and Liu 1995, Liu et al. 2001).

Bugula neritina (Linnaeus, 1758)

(Fig. 3C)

Description.—Colony forming erect and somewhat flexible red-brown tufts on various substrata. Narrow lightly calcified, elongate, proximally tapering zooids with extensive frontal membrane occur biserially along the branches. No avicularia, unlike most *Bugula* species. Brood chambers are large globular structures, attached obliquely to branch axes at the distal corners of zooids.

Geographic Range.—Reported worldwide in tropical and subtropical regions. Western Atlantic: Massachusetts to Brazil, Gulf of Mexico, Caribbean (GISD 2024a).

Schizoporella errata (Waters, 1878)

(Fig. 3D)

Description.—Purple to orange colonies ranging from encrusting in one or several layers, to erect foliaceous or branched. Zooids rectangular to polygonal, regularly spaced in primary layer, jumbled orientation in frontally budding layers. Frontal wall rough textured with small sunken round pores. Orifice rounded distally with a U-shaped sinus. Triangular avicularia on mounds beside the orifice. Ovicells (not observed here) globular, also with small pores (Hayward and Ryland 1979).

Geographic Range.—Reported worldwide in tropical and subtropical regions. Western Atlantic: Cape Hatteras to Brazil, Gulf of Mexico, Caribbean Sea; West

Table 1. Morphometric data from the colonies of (A) *Biflustra arborescens* and (B) *Biflustra* cf. *conjunctiva* in the study. SD = standard deviation.

(A) *Biflustra arborescens*

Sample ID	Zooid length (mm)	Zooid width (mm)	Opesium length (mm)	Opesium width (mm)	Zooid area (mm^2)	Opesium area (mm^2)
R404	0.40	0.23	0.32	0.18	0.09	0.06
R404	0.41	0.23	0.34	0.18	0.10	0.06
R404	0.43	0.23	0.36	0.18	0.10	0.06
R404	0.45	0.25	0.36	0.20	0.11	0.07
R404	0.45	0.25	0.36	0.22	0.11	0.08
R404	0.49	0.27	0.41	0.25	0.13	0.10
MK26	0.36	0.23	0.20	0.16	0.08	0.03
MK26	0.38	0.25	0.20	0.16	0.10	0.03
MK26	0.40	0.27	0.22	0.18	0.11	0.04
MK26	0.41	0.27	0.29	0.20	0.11	0.06
MK26	0.41	0.27	0.29	0.22	0.11	0.06
MK26	0.50	0.29	0.29	0.23	0.15	0.07
Count	12	12	12	12	12	12
Minimum	0.36	0.23	0.20	0.16	0.08	0.03
Mean	0.42	0.25	0.30	0.19	0.11	0.06
Maximum	0.50	0.27	0.41	0.25	0.15	0.10
SD	0.04	0.02	0.07	0.03	0.02	0.04

(B) *Biflustra* cf. *conjunctiva*

Sample ID	Zooid length (mm)	Zooid width (mm)	Opesium length (mm)	Opesium width (mm)	Zooid area (mm^2)	Opesium area (mm^2)
MK40	0.40	0.27	0.29	0.22	0.11	0.06
MK40	0.41	0.36	0.31	0.22	0.15	0.07
MK40	0.45	0.38	0.36	0.27	0.17	0.10
MK40	0.49	0.40	0.38	0.29	0.19	0.11
MK40	0.50	0.43	0.38	0.31	0.22	0.12
MK40	0.50	0.45	0.41	0.32	0.23	0.13
Count	6	6	6	6	6	6
Minimum	0.40	0.27	0.29	0.22	0.11	0.06
Mean	0.46	0.38	0.35	0.27	0.18	0.10
Maximum	0.50	0.45	0.41	0.32	0.23	0.13
SD	0.04	0.06	0.04	0.04	0.04	0.04

Africa; Red Sea; Persian Gulf; Australia; New Zealand; Hawaiian Islands; American Samoa; west coast of North America (Cook 1968, 1985, Winston 1982b, Winston and Hayward 2012, GISD 2024b).

Order Ctenostomata

Alcyonidium hauffi Marcus, 1939

(Fig. 3F)

Description.—Colony a firm white to grayish mass, transparent to translucent, growing around hydroids (*Obelia* sp.) and gorgonians (*Leptogorgia virgulata*). Zooids polygonal, with smaller kenozooids interspersed. Retracted polypides can be seen inside zooids. They extend a crown of 15–17 tentacles to feed.

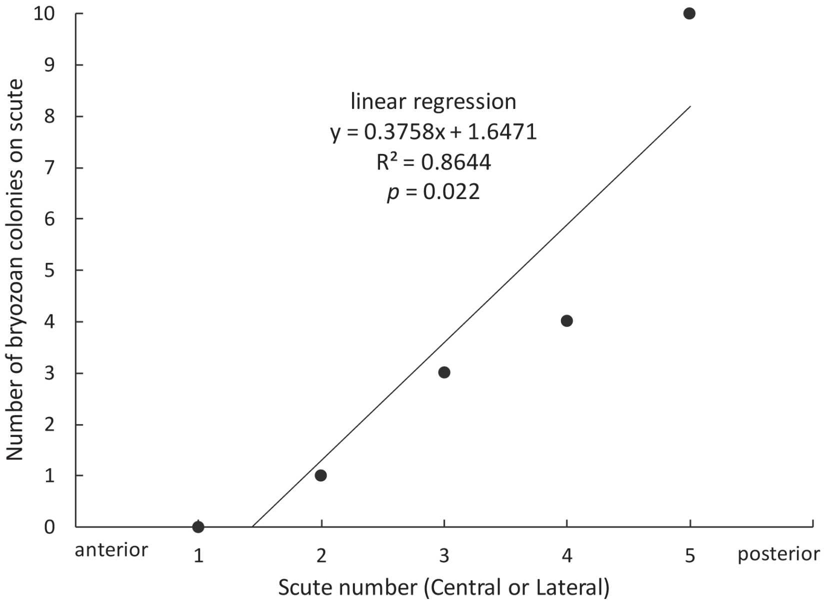

Figure 4. Plot showing the number of bryozoan colonies on scutes increasing significantly in a posterior direction across the dorsal carapaces of the host sea turtles.

*Geographic Range.—*Western Atlantic: Maine to Brazil; no records from eastern Atlantic or Pacific (Winston and Hayward 2012).

Anguinella palmata van Beneden, 1845

(Fig. 3G)

*Description.—*Colony consisting of closely branching brown tufts up to 20 cm long. As sediment coats and sticks to zooid surfaces, the colony at first glance resembles dirty seaweed. Zooids are long, straight to curved tubes, opening at their tips for 10 tentacles to be expanded for feeding. Found attached to various hard substrata, such as oyster shells, algae and other bryozoans.

*Geographic Range.—*Western Atlantic: Massachusetts to Brazil; eastern Atlantic: southern England to Senegal and Zaire (Cook 1985, Winston and Hayward 2012).

Discussion

This study has a focus on the northern hemisphere. Including this report, studies documenting bryozoan fouling of sea turtles range from 35°S to 40°N with a mean of 15°N (n = 41, standard deviation = 25°; Online Table S1). Distance from the equator ranges from 3° to 40°, with a mean of 28° (SD = 8°). These roughly parallel the biogeographic range of sea turtles today (Pike 2013, EAZA 2021).

Fouled host sea turtles were significantly larger than unfouled hosts (Fig. 5). Gramentz (1988) attributed some of the increase in epizoan fouling with increasing loggerhead carapace size as a function of increasing target area. We attribute this

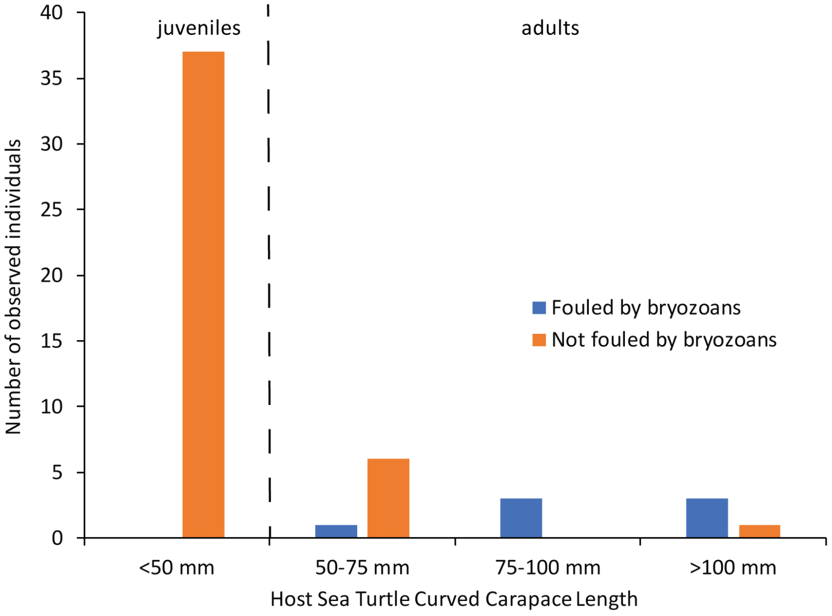

Figure 5. Frequency histogram of host sea turtle size showing those fouled by bryozoans are larger than those not fouled (*n* = 51).

to the Target Area Hypothesis (Lomolino 1990), in which larger sea turtles should be more heavily fouled by epibionts, including bryozoans. This hypothesis, derived from MacArthur and Wilson's (1967) Theory of Island Biogeography, argues that larger targets (e.g., islands or the carapaces of sea turtles) should have more epibionts simply because they are larger targets for "propagules" (Stracey and Pimm 2009). Thus, we expected a positive correlation between host size and fouling rate. This correlation is enhanced by larger turtles being older and thus having more time for larval settlement. In contrast, Dunbar et al. (2012) found small juvenile hawksbills in the shallow Gulf of Fonseca (GoF) on the Pacific coast of Honduras, had large numbers of fouling organisms, including heavy loads of barnacles and algae, although they did not investigate turtles for the presence of bryozoans at that time. These high fouling loads may be a function of the lack of cleaning fauna in the shallow, sediment-laden conditions of the GoF.

When combining the results from this study with those from previously published studies (Online Tables S1 and S2), there was no correlation between host size and fouling rate when using data from all host species. When using only data from loggerheads for which we have the most of all the host species, and to eliminate interspecific variation, there was still no significant correlation. This suggests that the incidence of bryozoan fouling is not affected by host sea turtle size; nor is host sea turtle size affected by the presence of fouling bryozoans.

Of the eight previously reported sea turtle species fouled by bryozoans (Online Table S1), two were found to be fouled in the current study [*Caretta caretta* (loggerhead) and *Chelonia mydas* (green)], whereas *Eretmochelys imbricata* (hawksbill) was not found to host bryozoans. In contrast to our study, all three species have been reported before to house bryozoans (Online Table S1). Of the previous studies, 40%

of reported bryozoans were unidentified. Of those identified, there were 18 unique species, 82% of which were cheilostomes and 18% ctenostomes. Our study found seven bryozoan species, five of which have been reported before on sea turtles (Online Table S1). Two, *Biflustra* cf. *conjunctiva* and *Aetea* sp., are new records of epibiosis on sea turtles. Of the seven species found in our study, 71% were cheilostomes and 29% were ctenostomes. Of the 18 bryozoan colonies found in our study, 78% were cheilostomes and 22% were ctenostomes.

In previous studies, 36% of the hosts examined were adults, 26% juveniles, 22% mixed ontogenetic stages, and 16% unknown (Online Table S1). In contrast, in this study, 13% of the host sea turtles were adults and 87% were juveniles. The bias toward adults in most previous studies is a function of the research focus on females nesting on beaches which are often more accessible than offshore juveniles or adult males.

All bryozoans found in our study were on the hosts' carapaces. This is mainly a function of logistical inaccessibility to the plastron of egg laying females on the beach. Nevertheless, for juveniles in the current study where all parts of the host turtle were accessible, bryozoans were only found on the carapace. Previous studies have reported 76% of the bryozoans on the carapace, 9% on the plastron, and 36% unknown (Online Table S1). This propensity for bryozoans to occur on the carapace may also be a function of abrasion of colonies on the plastron, especially among adult females as they must crawl across beach habitats to lay eggs at the dune line.

Spatial Distribution of Bryozoans Across Carapace.—All bryozoan colonies were found on host dorsal carapaces, except for the green turtle from Port Canaveral, Florida, US. The number of bryozoan colonies increased significantly in a posterior direction across the host carapace (Fig. 4). We are as yet uncertain if this distribution is reflective of currents over the carapace, related to characteristics of the carapace that attract bryozoan larvae, a result of sampling bias of adult females, or a result of self-grooming. There is a logistical problem with sampling nesting females, as some of their scutes, except C_{4-5} and L_4, may be covered by sand during the emergence and nesting process (Caine 1986). This bias did not exist for our juvenile hosts, as both dorsal and ventral surfaces of turtles were free of any covering sand. Other studies of epibionts on clean sea turtles have found a similar posteriorly increasing distribution on hosts (Gramentz 1988, fig. 1, Schärer 2001, fig. 4, Casale et al. 2012, fig. 2, Majewska et al. 2015, fig. 2b, Ingels et al. 2020, table 1, Blasi et al. 2021, fig. 1b). This distribution may be due to different bacteria on the posterior versus anterior carapace scutes, at least on loggerheads (Blasi et al. 2021). Mohanty-Hejamdi et al. (1989) attributed the paucity of epibionts on the anterior portion of olive ridley (*Lepidochelys olivacea*) sea turtle carapaces to abrasion from the foreflippers during swimming, while Caine (1986) attributed the same pattern in loggerheads to the habit of placing the front flippers over the carapace while resting in the water. Caine (1986) noted that the spatial distribution of epibionts on loggerhead carapaces was similar in both male and female adults, and since males do not nest, the distribution of carapace epibionts was likely the result of folding the flippers over the carapace. The compiled current evidence suggests the increase in bryozoan colonies in the posterior direction of host carapaces (Fig. 4) is likely not due to spatial sampling bias.

Of the 18 bryozoan colonies discovered in this study, only five (28%) grew directly on the hosts' scutes. These colonies belonged to the two species of *Biflustra* described above. All others were growing on epoxy resin, barnacles (*Chelonibia testudinaria*), hydroids (*Obelia* sp.), polychaete worm tubes (*Sabellaria floridensis*), sediment, or other bryozoans. On the two loggerheads from Wassaw Island, Georgia, US, colonies were partially growing on test plates of the turtle barnacle *C. testudinaria*. Bryozoan larvae may preferentially settle on barnacle plates and then spread onto scutes of the turtle. This is what Key and Hendrickx (2022) observed with the bryozoan *B. irregulata* growing on the plates of the barnacle *Balanus trigonus* on host spiny lobsters (*Panulirus gracilis* and *Panulirus inflatus*) from the Gulf of California, Mexico. Similarly, Frick et al. (2004) reported the same *Schizoporella* species as in the current study, although it was not growing directly on the host scutes, but instead on the plates of a dead *C. testudinaria* barnacle attached to the scute. Finally, Overstreet (1979) reported the cheilostome *Conopeum tenuissimum* encrusting the barnacles *Chelonibia patula* and *Balanus venustus niveus* on the blue crab *Callinectes sapidus*, rather than directly on the host carapace.

As only 28% of the bryozoan colonies were growing directly on the host scutes, we here consider the host substrate suitability for other organisms, such as barnacles, hydroids, and polychaete worm tubes that may be attracted to a different bacterial flora of the carapace, yet also provide secondary substrata for the bryozoans. All loggerheads studied by Frick et al. (1998) in Georgia, USA were fouled by barnacles, hydroids, or polychaetes and thus were available secondary substrates themselves for settling bryozoan larvae. Over the course of the loggerhead nesting season in Georgia, USA, up to 75% of the host carapace surface areas were eventually covered by barnacles, hydroids, polychaetes, and bryozoans in that colonization order (Frick et al. 2002). Thus, barnacles, hydroids, and polychaetes are not only epibionts themselves, but they also function as substrata for other invertebrates such as amphipods (Lazo-Wasem et al. 2011) and the bryozoans documented in this study.

Fouling Rates.—Bryozoans are rarely reported on sea turtles (Robinson and Pfaller 2022, fig. 2a). This may be a result of the small size of bryozoan zooids, which are about 1 mm^3 (Fig. 3), and difficult to see with the unaided eye. Colonies, however, can be a few cm across. This suggests the lack of reported bryozoan colonies may be due to the relative ease by which they may be removed during mating or self-grooming, as compared to other epibionts.

Fouling rates may also vary by host species. Of the sea turtles examined in this study, 88% of the loggerheads were fouled, while only 3% of the greens, and no hawksbills had evidence of bryozoans. In previous studies, 56% of the reported cases of bryozoans fouling sea turtles were on loggerheads, 20% on hawksbills, and 12% on greens (Online Table S1). These relative frequencies do not follow the relative populations of these three sea turtle species. Globally, greens are three times more common than loggerheads and 18 times more common than hawkbills (Wallace et al. 2011, Wallace 2020). These interspecies differences may also be due to differences in the life histories of the sampled populations. For example, greens from northeastern Florida, US were juveniles from nearshore waters, whereas loggerheads from Georgia, US were nesting adult females.

It may be possible that the hawksbills were devoid of bryozoans because their carapace is less attractive to larval settlement. Most juvenile hawksbills from the same study site in Honduras hosted other epibionts (e.g., cirripedes 77% of the samples, polychaetes 70%, amphipods 37%, gastropods 7%, and bivalves 7%; Covert et al. 2020). Another explanation may be that there were fewer bryozoan larvae in this particular tropical marine habitat as compared with other sites. Despite SEM imaging multiple samples of epibionts, we found no bryozoans, although bryozoans were found encrusting local sea grasses.

While a heavy epibiont load may occur on healthy sea turtles (Stamper et al. 2005), heavy infestations of encrusting organisms are more commonly associated with chronically debilitated (older, starving, injured, or diseased turtles) sea turtles (Stacy et al. 2018) or ones living in estuarine or shallow inshore habitats (Dunbar et al. 2012, 2020). This is especially true of loggerheads (Stamper et al. 2005, Deem et al. 2009) which support the most diverse epibiont communities of any of the marine turtle species (Frick et al. 1998, Robinson and Pfaller 2022, fig. 2a).

Bryozoan larval settlement is strongly controlled by chemical cues from microbial biofilms (Mihm et al. 1981, Maki et al. 1989, Dahms et al. 2004, Wahl et al. 2012). Epibiotic bacterial communities on greens and hawksbills are different from each other (Loghmannia et al. 2023), and also differ from loggerheads, which have a more diverse microepibiotic community than either of the other two species (Robinson et al. 2016, table 2, Kanjer et al. 2022). Perhaps the biofilms on green and hawksbill turtle carapaces lack the chemical cues required for bryozoan settlement.

The paucity of bryozoans on hawksbills and greens may be due to differential bryozoan larval preference for certain sea turtle carapaces. Bryozoan larval settlement can be affected by mechanical properties of the substratum, such as texture and hydrophobicity (Gray et al. 2002). Bryozoans may also show rugophilic (groove-seeking) and rheophilic (current-seeking) behavior. Frazier et al. (1992) reported epizoic bryozoans concentrated in tiny irregularities with accompanied microeddies in the more shingled surface of loggerheads, yet absent from the smooth carapaces of greens and olive ridleys.

The less frequent reporting of fouling bryozoans on hawksbill and green sea turtles would make sense if they swam faster than other species of sea turtles, making larval settlement more difficult. Bryozoan larval settlement decreases with increasing ambient water flow rate (Qian et al. 2000). Swim speeds of sea turtles vary with size, age, weight, and current direction, however, multiple studies suggest loggerheads are generally faster than greens (Hirth 1971, Wyneken 1997, Watanabe et al. 2011, Putman and Mansfield 2015, Kinoshita et al. 2021), which are faster than hawksbills (de Silva 1995, Wyneken 1997, Troëng et al. 2005, Walcott et al. 2012). Since bryozoan larvae likely have a more difficult time settling on faster, rather than slower moving hosts (Qian et al. 2000), we may expect more bryozoans on hawksbills and greens. Our results do not support this. However, concentrations of settling larvae may be highly conditional on several other environmental characteristics, including spawning season, water temperatures, population densities of reproducing individuals, and availability of appropriate settlement substrata.

A higher proportion of bryozoan larvae in the environments where loggerheads live, than where greens and hawksbills live, may also be a factor. Nevertheless, the discrepancy between bryozoan fouling of the loggerheads and greens is not likely to be due to different environmental exposure to bryozoan larvae, because the distributions of loggerheads and greens overlap in this study (i.e., northeast Florida coast). Sea turtles are potentially exposed to different species of larvae depending on where they are geographically in response to what life history stage they are in (Seminoff et al. 2012, fig. 1.2). Epibionts have been used to determine the geographic range of loggerheads in the Mediterranean (Báez et al. 2001). Caine (1986) reported

48 species of epibionts from six phyla from nesting loggerheads in Florida and South Carolina, US, including loggerheads nesting north of Daytona Beach, Florida, US which carried an epibiotic community distinct from that on loggerheads nesting south of Cape Canaveral, Florida, US. Caine's hypothesis that this distinction reflected discrete loggerhead populations in these two areas was later confirmed by mitochondrial DNA evidence (Bowen et al. 1993, Encalada et al. 1998, Shamblin et al. 2011).

All three of the host sea turtle species occur throughout the Georgia, USA to Honduras latitudinal range of this study (Márquez-M 1990, Wallace et al. 2011). Five of the seven bryozoan species found have ranges that cover locations from Georgia to Honduras or a larger area. *Biflustra arborescens* has a broad distribution in the East and West Atlantic. Two species, *B. neritina* and *S. errata,* are recognized as major warm water fouling species worldwide (GISD 2024a, b). No range can be given for the *Aetea* sp. without a species level identification, although various species of *Aetea* have been reported worldwide in temperate to tropical seas. *Biflustra conjunctiva* is so far only known from the South China Sea, but as pointed out by Almeida et al. (2018), who found Asian *Biflustra* species and other malacostegine taxa introduced into Bahia state, Brazil, species in this group are commonly found in ports and bays around the world, live on floating or ephemeral substrata, grow quickly and tolerate environmental changes. *Biflustra* species also have long lived planktotrophic larvae. These characteristics make them potentially good bioinvaders.

Global bryozoan biodiversity peaks in the northern and southern mid-latitudes dropping to lows at both poles (Kopperud et al. 2022, fig. 1). Such a bimodal biodiversity distribution pattern has been suggested for bryozoans in general and cheilostomes in particular, the dominant species in this study (Schopf 1970, Clarke and Lidgard 2000, Barnes and Griffiths 2008, Kopperud et al. 2022). This relationship has been broadly correlated with sea water temperatures (Denisenko and Grebmeier 2015) probably in response to the energetics of biomineralization (Figuerola et al. 2023).

To determine if there is a latitudinal or temperature-based influence on fouling of the sea turtles in this study, we grouped the USA turtles from Georgia and Florida (n = 45, latitude range = 28.42°N–31.87°N, mean = 30.10°N, standard deviation = 0.80°N) and compared them to the tropical ones from Honduras (n = 7, latitude range = 16.28°N–16.30°N, mean = 16.29°N, standard deviation = 0.01°N). The mean annual sea surface water temperature of the USA localities is 26.0 °C while in Honduras it is 27.5 °C (NOAA, 2002). The higher latitude localities had a higher fouling rate (mean = 71%) and hosted more bryozoan species (total of 7, 0.6 per turtle) than the lower latitude localities which had no bryozoans growing on sea turtles. This roughly parallels the bimodal global bryozoan biodiversity pattern described above.

Epibiont Loss From Mating.—Sea turtle mating is a very aggressive activity (Schofield et al. 2006, fig. 3j–l, Carr 2011), during which sea turtle epibionts may be removed (Caine 1986, Carr 2011, Frick and Pfaller 2013). Hernández-Vázquez and Valadez-González (1998) suggested epibionts are removed from the female central carapace during mating due to abrasion from the male plastron, leaving epibionts on the lateral areas of the female carapace less distributed. However, Caine (1986) interpreted the similar central versus lateral epibiont distribution on male and female loggerheads, as indicative of a minimal effect of mating on epibiont loss. We found no evidence of mating-induced bryozoan loss.

Epibiont Loss From Self-Grooming.—Self-grooming refers to sea turtles actively swiping their carapaces with their flippers or wedging themselves under or rubbing against submerged coral or other hard surfaces to scrape off epibionts (Schofield et al. 2006, fig. 3f, Frick and Mcfall 2007, fig. 1, Carr 2011). Loggerheads and greens are known to do this more than hawksbills (Parrish 1958, Caine 1986, Heithaus et al. 2002, Frick and McFall 2007, Frick and Pfaller 2013). Female loggerheads have been seen rubbing against a discarded boat anchor in Laganas Bay, Greece (Schofield et al. 2006, fig. 3f), whereas subadult loggerheads have been photographed using reef overhangs to scratch epibionts off their carapaces at Gray's Reef National Marine Sanctuary, Georgia, US (http://www.seaturtle.org/imagelib/data/128loggerheadgrooming-med.JPG). High epibiont loads may indicate an inability to dive to clean by rubbing on abrasive surfaces (Heithaus et al. 2002).

It is relatively difficult to observe self-grooming as it occurs, however, resulting scratch marks may be more easily seen. Anterior-posterior oriented scratch marks on the carapace occur in areas lacking sessile epibionts (Caine 1986, Frick and McFall 2007, fig. 1). We observed scratch marks on the sides of carapaces devoid of epibionts on our loggerheads (Fig. 2A) and hawksbills (Fig. 2C).

Epibiont Loss From Scute Shedding.—Turtles, like all reptiles, have scales (Zangerl 1969, Alibardi and Toni 2006). The number and pattern of the flat horny scales on their shell (i.e., scutes) are important diagnostic species-specific traits in sea turtles (Wyneken 2001). In all sea turtle species aside from the leatherback (*Dermochelys coriacea*), the shell is covered with firm, yet flexible scutes. Despite this, little is known of the periodicity of their shedding or sloughing (Boyd et al. 2021). Some aquatic terrestrial turtles shed their scutes annually (e.g., Sexton 1965, Alibardi 2005, 2006, 2013). The length of time between shedding scutes in sea turtles is currently unknown, but it may occur annually based on other turtle species (Sloan 2011). Chelonians often only lose individual scutes (Solomon et al. 1986, Elkan and Cooper 1980). Shedding of scutes in loggerheads varies from minor scaling, where thin layers of keratin peel away, to entire scutes being shed (Caine 1986). In addition to allowing ontogenetic growth, the function of shedding is mainly attributed to epibiont removal, especially in freshwater turtles (Gibbons 1968, Frazier et al. 1992, Schärer 2001, Szczygielski et al. 2018). Gramentz (1988) attributed some of the increase in epizoan fouling with increasing loggerhead carapace size as a function of decreased scute shedding with increased age. We found no evidence of scute shedding on any of the turtles in this study. However, if there are differences among host species in the frequency of renewal by scute shedding, this could affect the differences in fouling rates among sea turtle species.

Epibiont Loss From Cleaner Fishes.—Epibionts are groomed by multiple cleaner fishes on a variety of sea turtle species (Sazima et al. 2010). High epibiont loads, especially algae, may indicate a turtle's inability to dive to access cleaner fishes (Losey et al. 1994), or a lack of cleaner fauna in the habitat. Female loggerheads in the Mediterranean are known to visit fish "cleaning stations" (Schofield et al. 2006, fig. 3g). This benefits the turtles by reducing the amount of drag (Sazima et al. 2010). There are far fewer fish species that clean loggerhead turtles compared to greens and hawksbills (Sazima et al. 2010, table 1). Sea turtle cleaner fishes have not been reported to eat bryozoans, although several species of fishes do feed on bryozoans based on stomach contents of the fishes. Multiple species of monacanthid filefishes feed on bryozoans in *Sargassum* rafts (El-Ganainy and Sabrah 2013, Mancera-Rodríguez and Castro-Hernández 2015), as do *Pomacanthus* angelfish and *Scarus* parrotfish on reefs (Brock 1979, Shraim et al. 2017). The omnivorous sheepshead fish (*Archosargus probatocephalus*) eats bryozoans and lives in the same environment as sea turtles in this study (Overstreet and Heard 1982, Sedberry 1987). Juvenile sheepsheads have a diet dominated by bryozoans both in frequency and volume, whereas the larger fish feed heavily on bryozoans as well as other invertebrates (Sedberry 1987). The stomach contents of these fishes demonstrate that they eat at least 24 different cheilostome and ctenostome species, including *S. errata* (Sedberry 1987), found in the current study.

Bryozoan Epibiont Community.—Each sea turtle may act as a motile island of life hosting a diverse community of symbionts, commensals, and parasites (Frick et al. 1998). Caine (1986) found 48 epibiont species on loggerheads along the South Carolina and Florida, US coasts. Frick et al. (1998) discovered 86 species fouling loggerheads from Georgia, US. Most recently, Frick et al. (2000) reported 93 species on loggerheads from Georgia, US. Much of the diversity reported in those studies are nonobligate epibiont species and represent a subset of the local benthic diversity (Lazo-Wasem et al. 2011).

Six of the seven bryozoan species we found fouling sea turtles in Florida and Georgia are not unique to their hosts. *Biflustra arborescens* commonly encrusts gastropod shells, other bryozoans, as well as hydroid and soft coral stems (Winston 1982b, Winston and Hayward 2012). It was previously reported on a loggerhead turtle from Canaveral National Seashore, Florida, US (Pfaller et al. 2008). *Bugula neritina* grows on most submerged substrata, including oyster shells, docks, fishing floats, sea grasses, sea grapes, and sea squirts (Maturo 1957, Winston 1982b, 1995, Ruppert and Fox 1988, Winston and Hayward 2012). It is the most ubiquitous fouling bryozoan globally (Winston 1982b, Winston and Hayward 2012) and is the most commonly reported bryozoan on sea turtles (Online Table S1). It occurs on loggerhead turtles from Pamlico and Core Sounds, North Carolina, the coastal barrier islands of Georgia, and an array of sites across Florida, including South Ponte Vedra Beach, Flagler Beach, Cape Canaveral National Seashore, Melbourne Beach, and Hutchinson Island, US (Caine 1986, Frazier et al. 1992, Frick et al. 1998, 2002, Stamper et al. 2005, Pfaller et al. 2006). *Schizoporella errata* (incorrectly reported as *Schizoporella unicornis* in the southeastern US (Winston and Hayward 2012)) encrusts hard substrata, such as rocks, shells, wood, algae, decapods, and horseshoe crabs (Maturo 1957, Winston 1982b, Winston and Hayward 2012). It was reported previously on loggerhead turtles from the barrier islands of Georgia and Canaveral National Seashore, Florida, US (Frick et al. 2004, Pfaller et al. 2008). Encrusting *Aetea* species are known from the western Atlantic, from the east coast of US and from northeast Brazil (Maturo 1957, Winston 1982b, Winston and Hayward 2012, Vieira et al. 2016).

Among ctenostomes, *A. hauffi* encrusts skeletons of gorgonian soft corals and hydroid stems (Marcus 1939, Maturo 1957, Ruppert and Fox 1988, Winston and Hayward 2012, Vieira et al. 2014). It was reported previously on a loggerhead turtle from Cumberland Island, Georgia, US (Frazier et al. 1992). *Anguinella palmata* grows on hard substrata, such as pilings, seawalls, rocks, and oyster reefs (Winston

1982b, Winston and Hayward 2012, Vieira et al. 2014). It was reported previously on loggerhead turtles from Wassaw and Little Cumberland Islands, Georgia, US (Frazier et al. 1991, 1992, Frick et al. 1998).

Biflustra cf. *conjunctiva* is a fouling species, originally found on pearl oysters from the South China Sea (Zhang and Liu 1995, Liu et al. 2001) and is here reported for the first time in the southeastern US. The type locality for *B. conjunctiva* is off Baon in Shenzhen, Guandong Province, China (Zhang and Liu 1995), in the East China Sea in the central Indo-Pacific (JTMD 2024). It has not been previously reported as an invasive species (Carlton et al. 2018, GISD 2024c).

Epibiont Community Succession.—Many factors undoubtedly contribute to the presence or absence of epibiont species on sea turtles, including predation, physical stress, disturbance, recruitment dynamics, and competition, all of which may alter the distribution and composition of species within the epibiotic community (Frick et al. 2000). However, it is not yet known at what point in the formation of the sea turtle epibiont community bryozoans typically arrive. Wahl (1989) described early epibiont community succession as beginning with biochemical conditioning of the substratum whereby surfaces absorb dissolved macromolecules, followed by bacterial colonization, unicellular eukaryote colonization (e.g., protists and diatoms). Macroepibiont colonization follows, which begins with hard, sessile forms, such as barnacles that colonize the relatively bare carapace (Frick et al. 2002). These pioneers facilitate the subsequent colonization by other epibiota by increasing the surface area for colonization and changing water flow patterns across the carapace (Pfaller et al. 2006). Secondary colonizers include other sessile forms (e.g., hydrozoans and bryozoans). Accumulation of sediment among primary and secondary sessile forms then facilitates the colonization by sessile tunicates and small motile epibionts (Frick and Pfaller 2013). Community succession can be disrupted when host turtles migrate to environments not conducive to the epibionts, when the hosts groom themselves, or when fishes clean them (Frick and Pfaller 2013). In this model of sea turtle epibiont community succession, bryozoans are mainly secondary colonizers, yet may at times be pioneers, as was observed in this study with colonies that settled directly on scutes and then overgrew barnacles.

Potential Costs to Bryozoans.—There are five potential costs to bryozoans living on sea turtles: (1) abrasion from mating and self-grooming, (2) scute shedding, (3) fish cleaning, (4) shared doom, and (5) exposure to deleterious environmental conditions. We have addressed the first three above. Shared doom refers to death of the bryozoan in response to death of the sea turtle due to predation of the host. Sea turtles are eaten by a variety of predators, including sharks, killer whales, and crocodiles (Heithaus et al. 2008).

Sea turtle behaviors may expose bryozoans to deleterious marine conditions, as sea turtles are able to dive to great depths (Wyneken 1997) and migrate vast distances (Luschi et al. 2003, Bowen and Karl 2007). These movements may take epibionts from oceanic to coastal environments with potentially different water pressures, pH, temperatures, and salinities, causing less tolerant epibionts to die off (Frick and Pfaller 2013). Additionally, sea turtles may emerge out of water (e.g., nesting females or basking turtles) where epibionts that are especially sensitive may succumb to desiccation (Caine 1986, Bjorndal 2003, Frick and Pfaller 2013).

We concluded that all the bryozoan colonies we encountered were likely alive when collected, based on the presence of well-preserved polypides and/or partially extruded introverts in the ctenostomes as well as opercula present and/or organic cuticle still covering skeletons in cheilostomes. While intertidal bryozoans are diverse (e.g., Dick et al. 2005), it is unclear if the species associated with sea turtles can survive subaerial exposures. Bryozoans may simply close their opercula and survive the brief subaerial exposure during host nesting or basking. Three of the fouling bryozoan species in our study are adapted to life out of water during low tide, with *B. neritina*, *A. hauffi*, and *A. palmata* all being intertidal species (Winston 1982b, 1995, Ruppert and Fox 1988, Vieira et al. 2014).

Based on the five loggerhead sea turtles we sampled on Jekyll Island, Georgia, US, nesting turtles spend on average 74 min out of the water (n = 5, range: 13–115 min, standard deviation = 33 min). Caine (1986) reported nesting loggerhead turtles in Florida were out of the water <45 min on narrower Florida beaches and 90 min on wider South Carolina beaches. Nesting hawksbills are known to spend 60–150 min out of water (reviewed by Witzell 1983). These numbers are much less than the duration of a typical 6 hour low tide cycle. Therefore, some of the bryozoans would likely survive the exposure interval that results from host nesting.

Epibionts on sea turtle carapaces can also be exposed to subaerial exposure when their host basks in the sun to warm its body temperature. Pacific greens bask on land (Whittow and Balazs 1982, Van Houtan et al. 2015), and loggerheads bask on the ocean surface while floating (Sapsford and van der Riet 1979, Caine 1986). Duration of terrestrial basking by greens is on average 3 hours (Whittow and Balazs 1982, fig. 4), and mean ocean basking by loggerheads is 2 hours (Sapsford and van der Riet 1979, fig. 1). Both are less than the duration of a typical 6 hour low tide cycle. Therefore, if the sea turtles in the current study were to exhibit basking behavior, some of the bryozoans would likely survive.

POTENTIAL BENEFITS TO BRYOZOANS.—By living on a motile host, bryozoans potentially benefit in three ways: (1) increased gene dispersal and geographic range, (2) reduced substrate competition, and (3) reduced predation pressure. Epibiosis on sea turtles facilitates long dispersal distances for limited motility or sessile epibionts (Schärer and Epler 2007). Bryozoans are poor dispersers, as their benthic sessile colonies and their lecithotrophic larvae (i.e., with a short life span based on yolk supplied via the egg) are characteristics which potentially limit range expansion (Taylor 2020, Gruhl 2021). However, hosts, such as some sea turtles, may undertake transoceanic migrations which provide a mechanism for long-distance bryozoan dispersal (Luschi et al. 2003, Bowen and Karl 2007).

Sea turtle carapaces may act as motile hard substratum islands for bryozoan larval settlement in marine environments with soft bottoms. Bryozoan larvae need a hard substratum on which to settle and metamorphose (Taylor 2020, Gruhl 2021). In sessile marine communities, hard substratum space is often a limiting resource (Dayton 1971, Paine 1974, Jackson 1977). Thus, by settling and growing on sea turtle carapaces, bryozoan colonies may reduce substratum competition typical of conventional hard substrata.

Motile predators of bryozoans include Pycnogonida (sea spiders), Gastropoda (sea slugs), Echinoidea (sea urchins), Osteichthyes (fishes), and Chelonidae (sea turtles; Lidgard 2008). By living on host sea turtle carapaces, bryozoans may be removed from their typical predators when on conventional sessile hard substrata. Nevertheless, sea spiders, sea slugs, and sea urchins are all known to colonize the carapaces of several sea turtle species (Frick and Pfaller 2013, Pfaller and Robinson 2022).

Sea turtles eat bryozoans (Table 2), although it is unclear if this is intentional or incidental predation. While two studies have argued it is purposeful, one study suggested it is possibly accidental (Table 2). If the former, then living on the back of a predator would eliminate predation pressure, as documented for bryozoans living on the legs of their sea spider predators (Key et al. 2013). However, the potential for ecological or evolutionary benefit to the bryozoans requires the colonies grow large enough to reach the size necessary for sexual reproduction. None of the colonies we examined met these criteria, nor did they show any visible evidence of sexual reproduction.

Potential Costs to Sea Turtles.—Epibionts contribute to the epibiotic load of host sea turtles and may also facilitate infection or disease. Epibiotic load refers to cumulative weight and drag of epibionts on the host. An increase in the mass of epibionts may cause an increase in overall weight and difficulty of movement and swimming for the turtle (Bolten 2003, Loghmani-Devin and Sadeghi 2010, Dunbar et al. 2012). Energetic costs of swimming may be substantially increased by the increased drag caused by epibionts (Bjorndal 2003). Hydrodynamic effects vary with the size, number, and location of epibionts. Logan and Morreale (1994) reported that drag coefficients increased by 0%–5% for sea turtles with one barnacle on the rear carapace, 30% with one barnacle on the front carapace, and 1000% with a heavy epibiotic load over the entire shell. Per unit volume of epibiont, filamentous algae exert substantially more drag than barnacles (Wahl 1996). Bryozoans contribute to both the weight and drag of hosts, although not to the extent of barnacles and algae due to the bryozoans' rarity (Online Tables S1 and S2) and small size (Fig. 3).

Epizoans have been linked to the transmission of turtle diseases, such as the turtle herpes virus (Greenblatt et al. 2004, Lazo-Wasem et al. 2007). Epibionts, especially worms, can cause various diseases and infections and in some cases even the death of the host turtle (Frazier et al. 1985, George 1997, Stamper et al. 2005). Barnacles can penetrate into the host turtle's tissues resulting in deep tissue lesions (Hendrickson 1958, Green 1998, Frick and Zardus 2010, Hyatt et al. 2023), eye lesions, and infections (Zardus and Balazs 2007). To date, however, there is no evidence of bryozoans being involved in sea turtle diseases. In contrast, there may actually be benefits for turtle hosts that maintain light epibiotic loads.

Potential Benefits to Sea Turtles.—Epibionts can reinforce a turtle's carapace and provide some protection from predation via camouflage by breaking up the carapace outline shape and increasing its size (Frazier et al. 1991, Bjorndal 2003). However, the bryozoan colonies we found were both small (Fig. 3) and mostly encrusting, so that these benefits are unlikely to accrue for the host sea turtles we studied.

Table 2. Previously published studies reporting bryozoans in lavage, fecal, or stomach samples collected from sea turtles. Arranged by publication date. Bryozoan names as published.

Source	Sea turtle species	Bryozoan species	Bryozoan order	Comments
Carr et al. (1966)	*Eretmochelys imbricata* (hawksbill)	*Amathia*	Ctenostomata	- - -
Carr et al. (1966)	*Eretmochelys imbricata* (hawksbill)	*Steginoporella*	Cheilostomata	- - -
Carr and Stancyk (1975)	*Eretmochelys imbricata* (hawksbill)	*Hippoporina*	Cheilostomata	In 25% of turtles
Carr and Stancyk (1975)	*Eretmochelys imbricata* (hawksbill)	*Schizoporella*	Cheilostomata	- - -
Casas-Andreu and Gómez-Aguirre (1980)	*Chelonia mydas* (green)	Unidentified	Unidentified	- - -
Montenegro Silva et al. (1986)	*Lepidochelys olivacea* (olive ridley)	Unidentified	Unidentified	Not volumetrically important (0.2%) but frequently present (13%) and varies seasonally
Zangerl et al. (1988)	*Natator depressus* (flatback)	Unidentified	Unidentified	- - -
Márquez-M. (1990)	*Chelonia mydas* (Galápagos green)	Unidentified	Unidentified	Minor
Márquez-M. (1990)	*Lepidochelys olivacea* (olive ridley)	Unidentified	Unidentified	0.6% of turtles
Witherington (1998)	*Caretta caretta* (loggerhead)	*Membranipora* sp.	Cheilostomata	Not accidental
Seminoff et al. (2002)	*Chelonia mydas* (green)	*Hyppothoa* sp. (sic)	Cheilostomata	Juveniles intentionally eat bryozoans, 4.6% of fecal samples
Witzell and Schmid (2005)	*Lepidochelys kempi* (Kemp's ridley)	Unidentified	Unidentified	4.5% of turtles
Seney and Musick (2007)	*Caretta caretta* (loggerhead)	Unidentified	Unidentified	Up to 5% of turtles
Casale et al. (2008)	*Caretta caretta* (loggerhead)	Unidentified	Unidentified	Larger part of the diet of inshore-neritic-bottom feeding turtles than open water-pelagic-oceanic turtles
Russell et al. (2011)	*Chelonia mydas* (green)	Unidentified	Unidentified	Up to 0.4% of turtles
Nagaoka et al. (2012)	*Chelonia mydas* (green)	Unidentified	Unidentified	7.5% of turtles
Redfoot et al. (2016)	*Chelonia mydas* (green)	Unidentified	Unidentified	<0.9% by volume of juvenile turtles
Stokes et al. (2019)	*Chelonia mydas* (green)	Unidentified	Unidentified	Possibly accidentally ingested on plant matter, but 65% of gravid turtles as opposed to 4% of male and nonbreeding females

Conclusions

Sessile bryozoans potentially benefit from living on motile sea turtles by increasing bryozoan gene dispersal and geographic range, reducing substrate competition, and reducing predation pressure. For any of these potential benefits to accrue to the bryozoans in an ecological or evolutionary context, the bryozoans must grow large enough to reach sexual reproductive size. Since none of the bryozoans in this study demonstrated any evidence of sexual reproduction that we detected, this relationship is best described as facultative hitchhiking. An epibiotic community that contained numerous, large, erect, and/or rigid bryozoan colonies, may negatively impact their hosts by increasing the epibiont load and drag. In our study, this was not the case, suggesting the host sea turtles were relatively unaffected. Therefore, we refer to this type of nonobligate, commensal relationship between the bryozoans and the host sea turtles as phoretic.

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