



Recruitment Dynamics of Serpulid Worms in Baffin Bay, Texas: Implications for Habitat Restoration in a Hypersaline Estuary

Natasha Breaux¹ · Auria Avalos¹ · Jennifer Gilmore¹ · Terence A. Palmer¹ · Jennifer Beseres Pollack¹

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Abstract

Low inflows cause predominantly hypersaline conditions in Baffin Bay, TX (USA), which are inhospitable for oysters, the dominant reef-builder in other northern Gulf of Mexico estuaries. Instead, extensive biogenic reefs contain dense aggregations of the ubiquitous tube-building serpulid worm, *Hydroides dianthus*. The distribution and size of these reefs have declined over the last several decades. Although serpulid reef habitats have increased in conservation importance, there is a need for ecological knowledge to inform resource management and habitat restoration planning. This study examined spatial and temporal recruitment patterns of serpulid worms and other encrusting species over an 18-month-long period, using recruitment tiles, and live serpulid reef as a reference. Recruitment of *H. dianthus* occurs year-round; however, the greatest recruitment occurs between September and December. No consistent differences in serpulid recruitment were detected among locations within Baffin Bay, which could be because salinity and temperature were similar among locations, and/or because sampling replication was low. *H. dianthus* cover was greater on the lower surface of horizontally oriented recruitment tiles (28% cover), whereas *Amphibalanus eburneus* (barnacle) cover dominated the upper surface of tiles (34% cover). Furthermore, there is no evidence that predation by megafauna (> 1 cm) is hindering serpulid recruitment. There is sufficient larval supply of *H. dianthus* to suggest that the restoration of serpulid reefs can be successful by providing additional substrate with appropriate microhabitat complexity. Study findings can be used to support planning and successful implementation of serpulid reef restoration.

Keywords Infauna · *Hydroides dianthus* · Restoration · Low-inflow estuary · Serpulid reef

Introduction

Low-inflow estuaries are globally distributed, but our understanding of ecological dynamics in these systems lags that of “classical,” inflow-dominated estuaries (Largier et al. 1996; Morgan et al. 2016). Although biogenic reefs are known to provide a broad range of ecosystem services to estuarine and coastal environments (Coen et al. 2007; Barbier et al. 2011; Kent et al. 2017), high salinities within low-inflow estuaries can inhibit the presence of many reef-building species (Gunter 1955; Andrews 1964; Castagna and Chanley 1973).

Within Baffin Bay, a low-inflow secondary bay of the Upper Laguna Madre, TX, USA, often-hypersaline conditions are inhospitable for Eastern oyster, *Crassostrea virginica*, the dominant reef-builder in northern Gulf of Mexico estuaries. Instead, biogenic reefs in Baffin Bay predominantly comprise dense aggregations of the ubiquitous tube-building serpulid worm, *Hydroides dianthus* (Polychaeta, Serpulidae), and relic calcareous tubes of the same and/or other serpulid species. Although serpulid worms commonly settle as individuals on hard substrates in marine and estuarine habitats, they can aggregate by the millions to form serpulid reefs in rare circumstances (ten Hove and van den Hurk 1993; Bastida-Zavala et al. 2017).

The biofouling ability of *H. dianthus* and other serpulids can be considered a nuisance when unintentionally occurring on man-made structures, or when occurring as an invasive species (Bastida-Zavala et al. 2017; Sun et al. 2017), but can have many positive ecological effects, especially when the biofouling occurs to form a serpulid reef

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✉ Terence A. Palmer
terry.palmer@tamucc.edu

¹ Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412, USA

(Montefalcone et al. 2022). Serpulid reefs' complex three-dimensional structures support high levels of biodiversity (Haines and Maurer 1980; Obenat et al. 2001; Chapman et al. 2011), and their suspension feeding activities improve water quality (Leung and Cheung 2017, and references therein). In Baffin Bay, serpulid reefs have proved to be valuable in enhancing benthic macrofauna communities ($191\times$ abundance and $97\times$ biomass than the surrounding soft-sediment bottoms; Palmer et al. 2022), which is thought to be linked to the productive commercial and recreational fisheries in Baffin Bay (especially *Pogonias cromis* and *Cynoscion nebulosus*; McKee 2008; Bohannon et al. 2015). However, the reefs in Baffin Bay have declined in distribution and size because of direct damage from boats, dredging, wade fishermen, and waves (McKee 2008; Hardegree 1997; Tunnell et al. 2001). Potential indirect causes of reef decline include changes in water quality, especially salinity, which physiologically affects *H. dianthus* (ten Hove and van den Hurk 1993), and pH, which can affect serpulid tube structure (Chan et al. 2012; Smith et al. 2013; Díaz-Castañeda et al. 2019). Bioerosion in the form of predation by finfishes and other fauna could also play a major role in decreasing serpulid reef size (Reed 1941; Dalrymple 1964). Given the importance of *H. dianthus* reefs for ecosystem service provision, and their sensitivity to anthropogenic disturbance and environmental change, there is a need for ecological knowledge that can inform future habitat conservation and restoration approaches.

In soft-bottom environments and on degraded reefs, limited availability of hard substrates can constrain larval recruitment and survival (Moore et al. 1998; Frandsen and Dolmer 2002; Schulte et al. 2009). Provision of substrate has been used as an effective method to facilitate larval attachment and reef growth for a variety of biogenic reef building species, including corals, mussels, and oysters (Seaman 2007; Graham et al. 2016; Omori 2019). However, less is known about the efficacy of substrate provision to facilitate serpulid recruitment and reef development. Although there is evidence that invertebrate communities inhabiting serpulid reefs in Baffin Bay are relatively stable compared to surrounding soft-sediment invertebrate communities, recent studies have been short in duration (<1 year) and have encompassed periods with limited changes in water quality (Hardegree 1997; Palmer et al. 2022). Aside from extensive understanding of long-term reef community dynamics, critical knowledge needed to support restoration planning incorporates the timing of recruitment for reef-building species (McAfee and Connell 2020; Cook et al. 2021); the response of new recruits and natural reefs to environmental change, including changes in water quality; and the effects of direct predation on serpulid recruitment. The aims of this study are to determine recruitment dynamics of serpulid worms and other encrusting species using recruitment tiles, to

compare recruitment patterns to temporal changes in existing serpulid populations on natural reefs, and to determine if predation is inhibiting serpulid recruitment. We hypothesize that (1) recruitment of serpulid worms onto tiles will vary in response to changes in salinity and season, (2) spatiotemporal differences in serpulid densities on natural reefs are not dominated by differences in short-term (quarterly) recruitment, and (3) predation of serpulids by finfish and macroinvertebrates will decrease serpulid establishment on recruitment tiles.

Methods

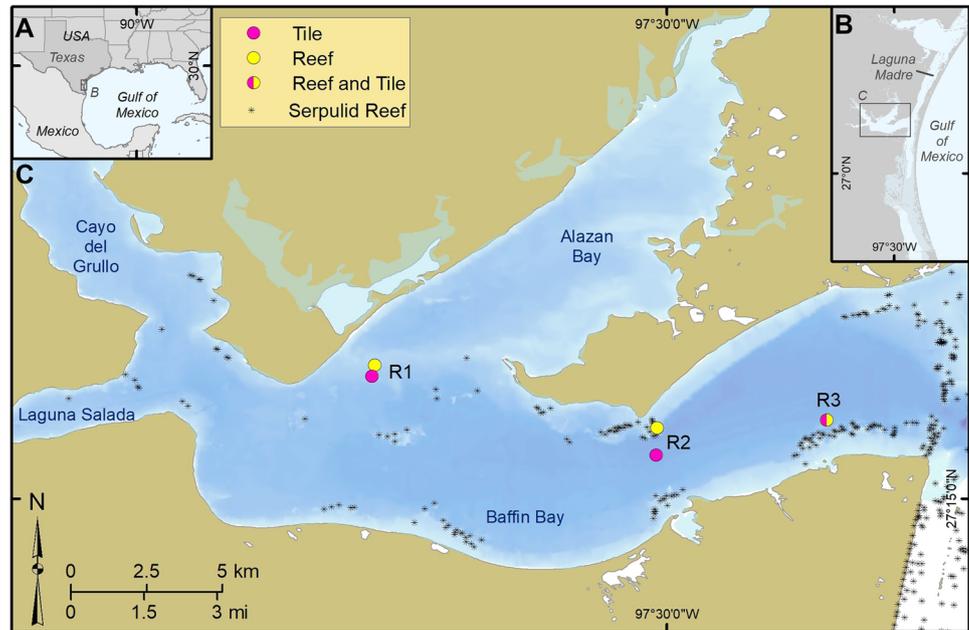
Study Area

Baffin Bay, TX is a shallow bay (mean depth = 2 m) with a semi-arid climate, which means that evaporation often exceeds freshwater input from the small ephemeral streams that flow into it (Fig. 1; Orlando et al. 1993). The serpulid reefs in Baffin Bay are estimated to have formed around 1000 BC, when salinities were mixoeuhaline (~ 30 ; ten Hove and van den Hurk 1993). Although the reefs were deemed to be living between 1875 and 1910 (Hedgpeth 1953), no living worms were documented after this into the early 1960s, during a period where salinities were much higher (up to 102; Breuer 1957; Brown et al. 1977) than recent conditions. Deepening of navigational channels, including dredging the Gulf Intracoastal Waterway in the Laguna Madre in 1946, has increased circulation and consequently moderated salinities in Baffin Bay. Baffin Bay now has relatively lower salinities (mean \pm SD from 1976 to 2007 of 35.9 ± 7.0) but annual salinity is increasing (0.3 yr^{-1} from 1968 to 2015; Wetz et al. 2017) and the system is often hypersaline (Montagna and Palmer 2012). Approximately 16 km^2 of serpulid reef was estimated to exist in Baffin Bay in the late 1970s, although the current area is likely much smaller (Breuer 1957; Brown et al. 1977; Hardegree 1997). The remainder of the bay bottom ($\sim 232 \text{ km}^2$) is primarily soft mud habitat.

Study Design

Encrusting faunal communities were sampled from three existing serpulid reefs (labeled R1, R2, R3) in Baffin Bay quarterly for 1 year (December 2020; March, June, and September 2021; Fig. 1). New recruitment was sampled using recruitment tiles that were replaced quarterly for 18 months, which includes the existing reef faunal community-sampling dates (December 2020 to June 2022). A multiparameter instrument (YSI ProDSS) was used to synoptically measure temperature, dissolved oxygen, pH, and salinity 0.1 m from the bottom of the water column during sampling/deployment and retrieval events, and

Fig. 1 Map of Baffin Bay showing estimated locations of serpulid reef and monitoring sites (R1, R2, R3). Estimated serpulid reef locations are derived from National Oceanic and Atmospheric Administration Electronic Navigational Chart US5TX24M (NOAA 2019)



opportunistically on four other dates (September 2020 and May, August, and September 2021).

Recruitment Tiles

Recruitment tile arrays were constructed and placed on the bay bottom at three locations adjacent to existing serpulid reef (within 600 m). Arrays were placed next to existing pilings to avoid loss of equipment. For each array, two 10-cm² PVC tiles (3-mm thickness) were sanded and affixed with horizontal orientation to a sampling tray (0.45 × 0.30 m, 0.1-m height) using cable ties (= zip ties). On each tray, one tile was caged using a stainless-steel basket lined with 1-cm mesh, and one tile was left exposed. The purpose of the cages was to determine any effects of predation. Recruitment tile arrays were deployed in September of 2020 and retrieved and replaced quarterly for 18 months (December 2020 to June 2022). On each retrieval date, one set of caged and open tiles was collected and replaced with clean tiles (Fig. 2). Retrieved tiles were preserved in 10% buffered formalin for future assessment of both top and bottom surfaces. The total number of tile replicates analyzed was 84: 2 caged treatments (caged and uncaged) × 2 vertical surfaces (top and bottom) × 3 locations (R1, R2, R3) × 7 dates.

Existing Reef

Small pieces of serpulid reef (~9 cm³) were collected by hand in the field at each of three serpulid reef stations in coordination with tile array retrievals (quarterly December 2020–September 2021). Reef pieces were immediately transferred to a 500-μm mesh bag to prevent loss of invertebrates

in the water column. Two replicate pieces were collected at each reef station on each sampling date and preserved in 10% buffered formalin.

Laboratory Procedures

The coverage of encrusting organisms on recruitment tiles was assessed by visual estimate using a mesh grid laid over each tile. Encrusted material was scraped off the top and underside of each tile separately. Material that fell off the tile into the storage container before scraping was assumed to be motile and was not sorted or counted. For reef pieces, volume (mL of water displaced) and wet weight measurements were obtained; then, mollusks and other hard-shelled organisms were counted and identified.

Reef and tile samples collected from December 2020 to September 2021 were individually placed in 12 N HCL for 24 h to dissolve calcareous substrate. The undissolved organisms were rinsed in freshwater, washed onto a 500-μm sieve, and then identified under a dissecting microscope to the lowest possible taxon (usually species). Biomass measurements were obtained after combining individual macrofauna into species or family groups, drying at 55 °C for 24 h, and weighing. Reef samples were subsampled using a Folsom plankton splitter when abundances were too high (> ~1000 individuals) to reasonably count.

Statistical Analysis

The efficacy of using percent cover as an approximation of serpulid (*H. dianthus*) and barnacle (*Amphibalanus eburneus*, the other dominant encrusting organism in the study)



Fig. 2 Examples of deployed tiles. Top: Station 1, uncaged, top surface deployed from September to December 2020. Bottom: Station 2, caged, bottom surface deployed from September to December 2020

abundance and biomass was evaluated using Spearman rank correlations (ρ_s). The effects of physico-chemical variables (salinity, temperature, dissolved oxygen concentration, pH on the date of tile retrieval) and seasonality (date deployed, date retrieved, Julian day) on serpulid cover were also evaluated using Spearman rank correlations. Differences in percent cover of serpulids and barnacles among the vertical surface (top and bottom), caged treatments (caged and uncaged), and dates were determined using a three-way ANOVA on

\log_e -transformed percent cover data. The normality of residuals was assessed using a Shapiro–Wilk test (Shapiro and Wilk 1965), and the homogeneity of variances was assessed using the Brown-Forsythe test (Brown and Forsythe 1974). Serpulid and barnacle abundances on reef were correlated with abundances on tiles to determine if recent (~3 month) recruitment on the tiles was similar to abundance on the reefs. All data management and data analyses were conducted using SAS 9.4 software (SAS Institute Inc. 2019).

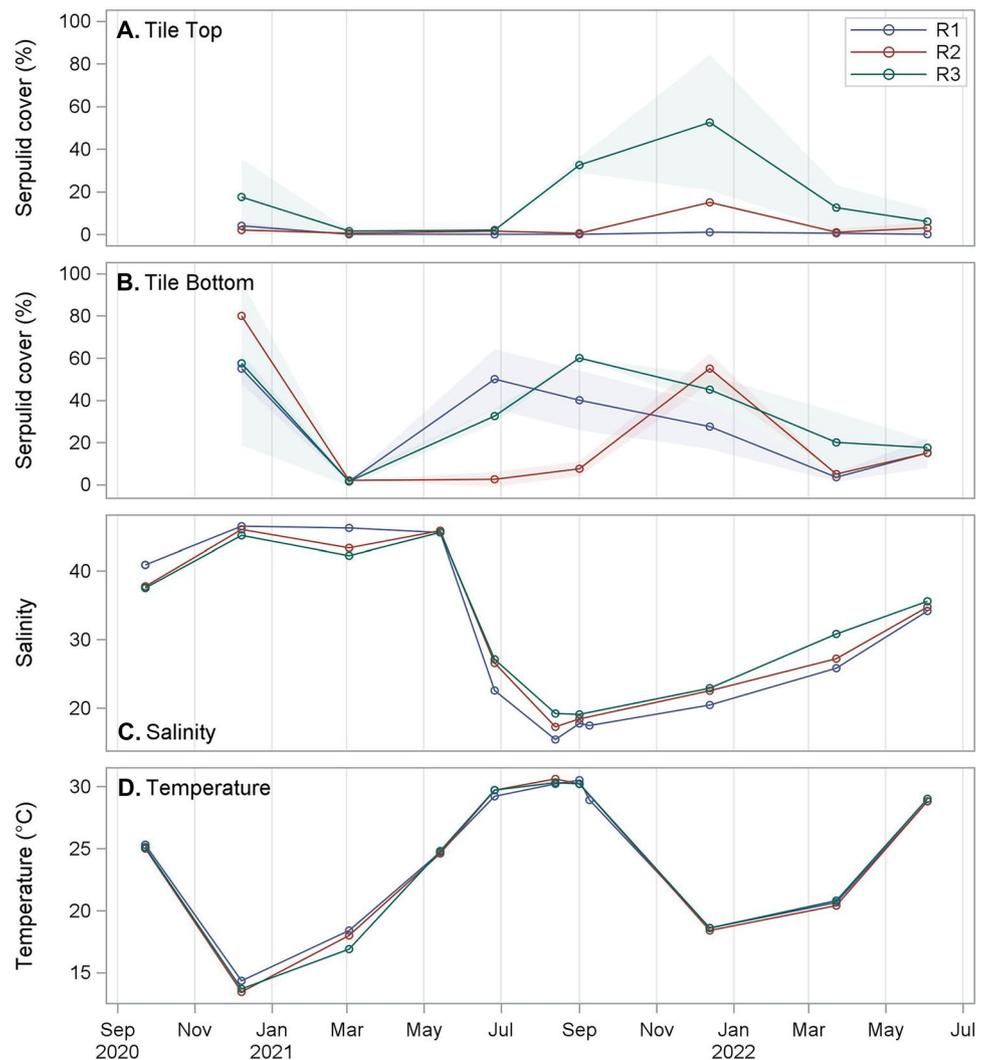
Results

Conditions were hypersaline (36 to 46) at all three sites in the first 8 months of the study (Fig. 3; 11 September 2020 to 14 May 2021). A mesoscale convective system (large thunderstorm complex) from 18 to 20 May 2021 generated up to 364 mm of rain in the Baffin Bay watershed (including 278 mm on 19 May 2021; NWS 2022), which is 46% of the mean annual precipitation (786 mm/yr for 1991–2020). This weather event lowered salinities at the serpulid reefs in Baffin Bay between 17 and 19 by August 2021. Salinities steadily increased from September 2021 to between 34 and 36 in September 2022. Salinity was 0 to 6 higher near the mouth of Baffin Bay (BBS3) than the upstream sites before the inflow event, but 1 to 5 lower after the inflow event.

Water temperature followed a predictable seasonal pattern at all three sites, with minima ranging from 13.5 to 14.4 °C in December 2020 and maxima ranging from 30.2 to 30.6 in August and September 2021 (Fig. 3). Dissolved oxygen (DO) concentrations varied seasonally (Fig. S1), with maxima occurring in December (7.9 to 8.5 mg L⁻¹) and minima occurring in June (4.0 to 5.7 mg L⁻¹) and September (4.6 to 6.0 mg L⁻¹). The large variability in DO concentrations among stations (mean difference among sites = 1.0 mg L⁻¹) might be partially attributable to the difference in time during the day that each site was sampled (mean difference = 2.0 h). pH followed a roughly seasonal pattern with maxima in the winter and minima in the summer, aside from uncharacteristically large decreases in pH occurring in May and June 2021 (from 8.3 to 8.4 in March 2021 to 7.5 to 7.7 in June 2021).

The serpulid, *H. dianthus* and the Thoracican, *Amphibalanus eburneus* were the dominant encrusting fauna that attached to horizontally oriented recruitment tiles (Table S4; Fig. 2). All other encrusting fauna, including Actinaria, *Obelia bidentata* (Hydroidolina), and *Brachidontes exustus* (Mytilidae), made up less than 0.4% of fauna abundance and biomass, and 2.1% of cover combined. Other biological matter that covered the tiles included filamentous green algae and amphipod tubes built by the amphipod *Apocorophium louisianum*. Mean serpulid densities on the bottom side of the tiles ranged from 2 n tile⁻¹ in March 2021 to 192 n tile⁻¹

Fig. 3 Mean spatial coverage by *H. dianthus* (\pm standard deviation) on the **A** top and **B** bottom side of tiles, with corresponding **C** salinities and **D** temperatures. Each point represents the end of an approximately 3-month deployment



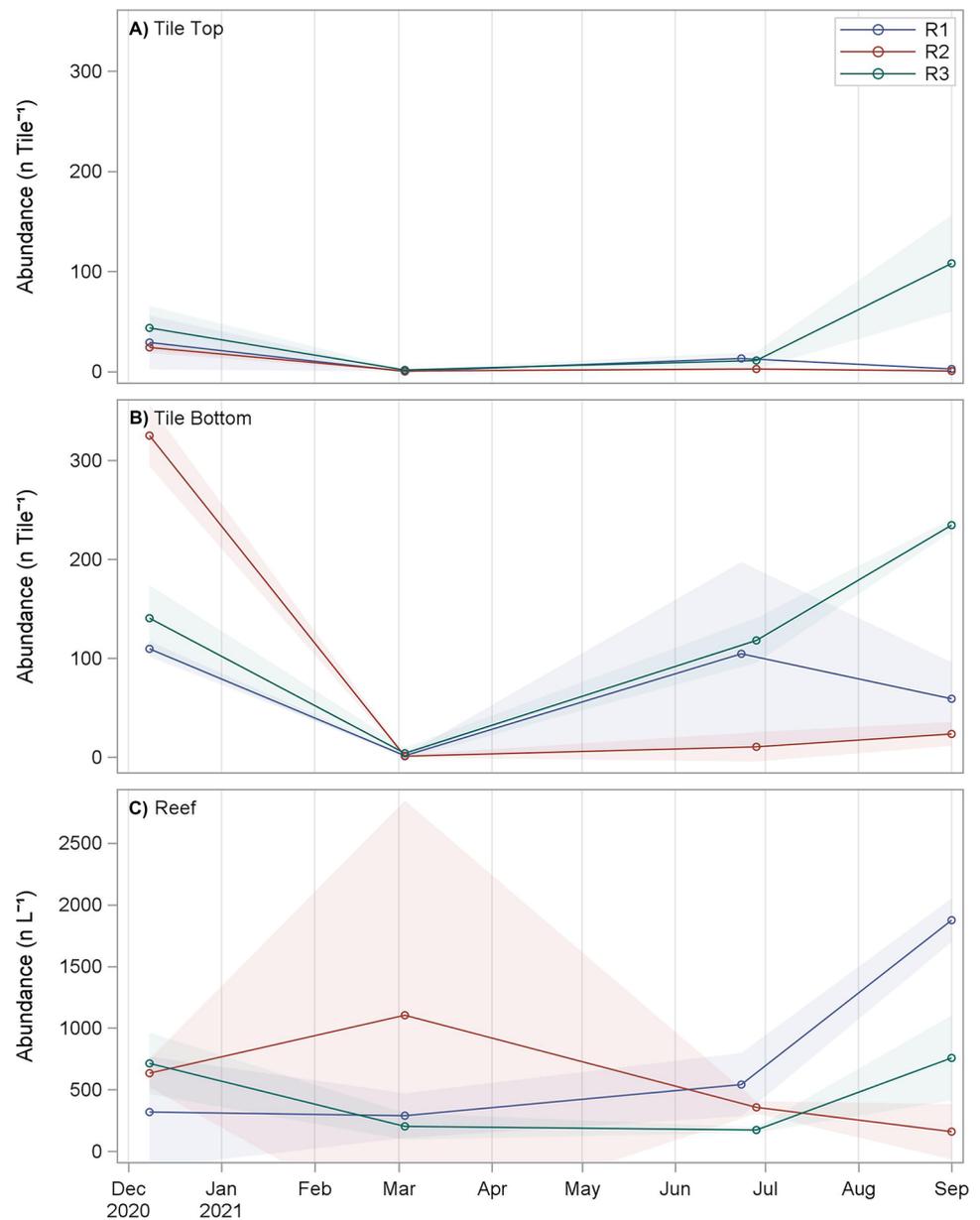
in December 2020 (217 to $19,167$ $n\ m^{-2}$) with an overall mean of 94 $n\ tile^{-1}$ (9429 $n\ m^{-2}$; Fig. 4). Mean serpulid densities on the top side of the tiles ranged from 1 $n\ tile^{-1}$ in March 2021 to 37 $n\ tile^{-1}$ in September 2021 (67 to 3700 $n\ m^{-2}$) with an overall mean of 20 $n\ tile^{-1}$ (1967 $n\ m^{-2}$). Tile coverage by *H. dianthus* tubes was positively correlated with *H. dianthus* abundance ($\rho_s = 0.90$) and biomass ($\rho_s = 0.88$; both $p < 0.0001$, $n = 48$) in the four sampling periods when abundance and biomass were determined (December 2020 to September 2021; Fig. 5). Similarly, tile coverage by *A. eburneus* was positively correlated with *A. eburneus* abundance ($\rho_s = 0.90$) and biomass ($\rho_s = 0.94$; both $p < 0.0001$, $n = 48$) in the same four sampling periods. Tile coverage was therefore used as a proxy for abundance and biomass for further analyses of the full 18-month sampling period (seven sampling events, December 2020 to June 2022).

H. dianthus had greater cover on the bottom surface of the tiles ($28 \pm 25\%$) than the top surface ($7 \pm 14\%$; $p < 0.0001$, $n = 84$; Fig. 3 and Table S1). In contrast, *A. eburneus* had

greater cover on the top surface of the tiles ($34 \pm 33\%$) than the bottom surface ($6 \pm 7\%$; $p < 0.0001$, $n = 84$). There were differences in percent cover of *H. dianthus* and *A. eburneus* among dates ($p < 0.0001$ and $p \leq 0.0001$), with the least cover occurring in March 2021 for both species. Cover by *H. dianthus* increased with increasing month regardless of year (March < June < September < December; Table S2). Cover by *A. eburneus* did not have the same consistent monthly pattern (Table S3). There were no differences in cover between caged and uncaged tiles for *H. dianthus* ($18 \pm 23\%$ and $18 \pm 23\%$, $p \leq 0.9066$; Fig. S2) and *A. eburneus* ($23 \pm 30\%$ and $17 \pm 25\%$, $p \leq 0.4579$).

H. dianthus cover (%) on the bottom surfaces of the tiles was most highly correlated with the Julian day of retrieval ($\rho_s = 0.79$, $p < 0.0001$), dissolved oxygen concentration at the time of tile deployment ($\rho_s = -0.66$, $p = 0.0012$), and temperature at the time of tile deployment ($\rho_s = 0.65$, $p = 0.0013$; all $n = 21$). *H. dianthus* cover on the top surfaces of the tiles was also most highly correlated

Fig. 4 Mean abundances of *H. dianthus* (\pm standard deviation) on **A** top and **B** bottom surfaces of tiles and **C** on the reefs. Each tile is 100 cm²



with the Julian day of retrieval ($\rho_s = 0.44$, $p = 0.0455$), dissolved oxygen concentration at the time of tile deployment ($\rho_s = -0.49$, $p = 0.0248$), and temperature at the time of tile deployment ($\rho_s = 0.41$, $p = 0.0683$; all $n = 21$); however, relationships were weaker than with the bottom surfaces. Bottom water temperatures were lowest in December months and highest in June and September in this study, while the opposite was true for dissolved oxygen concentrations.

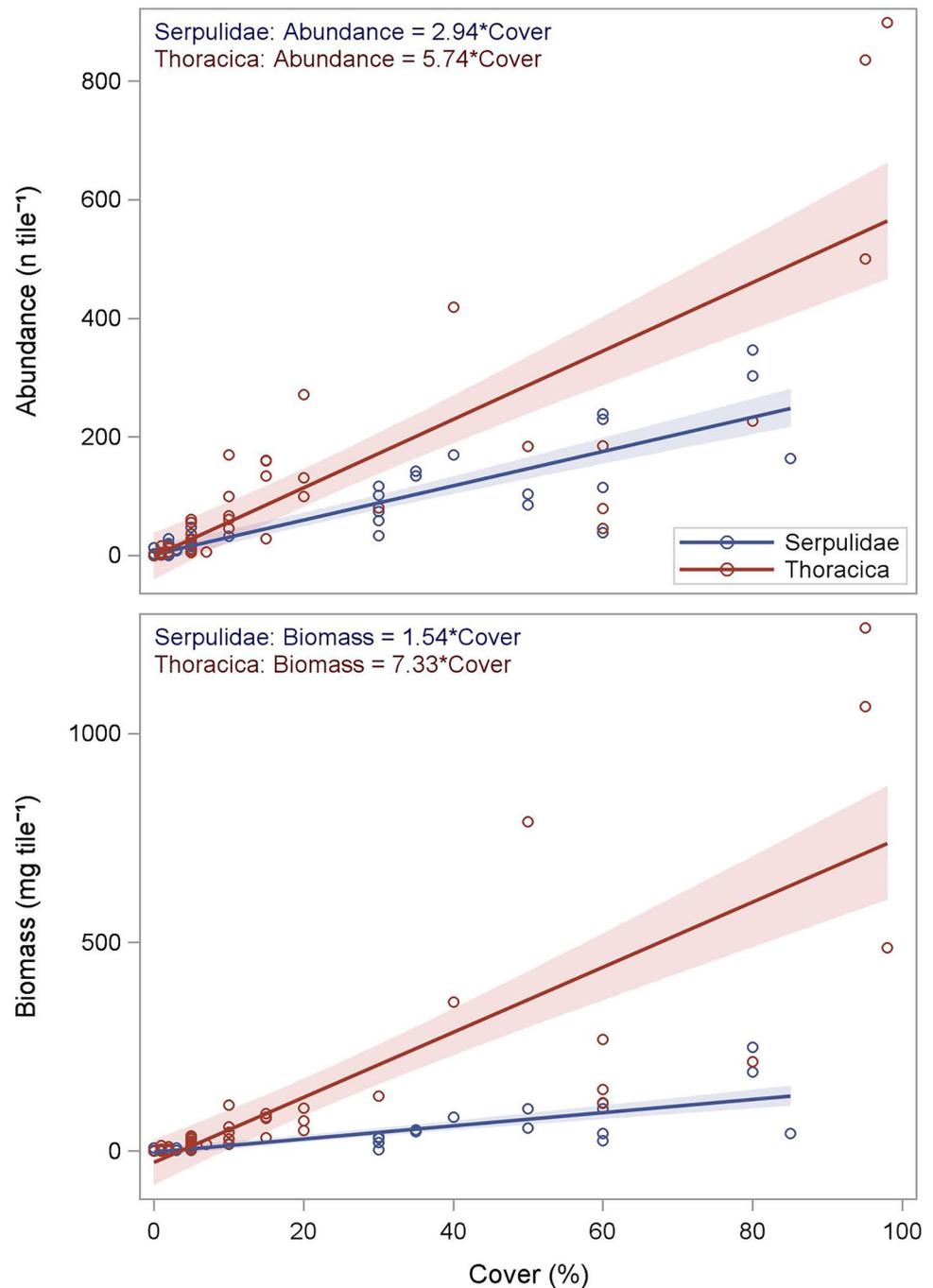
Serpulid abundance and biomass on the reef were not correlated with serpulid abundance and biomass on the top or bottom surfaces of tiles ($0 < |\rho_s| < 0.34$; $0.27 < p < 1.00$, $n = 12$). Motile species that occurred on the tiles included at

least eight polychaete species, caprellids, isopods, and the amphipod *A. louisianum* (Table S4).

Discussion

The first hypothesis of this study is that recruitment of serpulid worms onto tiles will vary in response to changes in salinity and season. Variations in response to salinity and season were able to be tested because a large-inflow event decreased the salinity of Baffin Bay substantially from hypersaline conditions (mid-40 s) to the high teens within 3 months during the study period. Despite *H. dianthus*

Fig. 5 Regression between *H. dianthus* (Serpulidae) and *A. eburneus* (Thoracica) abundance (top) and biomass (bottom) on tiles. Shaded areas represent the 95% confidence intervals for the expected abundance or biomass value for each cover value



having a euryhaline tolerance (salinity range of 1 to 52; Bastida-Zavala et al. 2017), it was previously speculated that serpulid reefs have maximum growth during moderate salinities, and cease during periods of hypersalinity in Baffin Bay (Dalrymple 1964). Research on other species demonstrates that lower salinities (≤ 20) inhibit the early development (settlement, survivorship, development duration) of *Hydroides elegans* in a laboratory setting (Qiu and Qian 1997), and settlement of *H. uncinata* occurred in salinities ≥ 20 but growth was poor in salinities of 30–33 in Lagos Harbour, Nigeria

(Hill 1967). Although recruitment was lowest during the highest salinities in this study (42 to 46, December 2020 to March 2021), the second lowest recruitment occurred in relatively low salinities (20 to 30, December 2021 to March 2022). Serpulid cover followed a seasonal pattern, with recruitment increasing throughout the calendar year despite this large change in salinity. Seasonal variation appears to have a greater influence on serpulid recruitment and potential reef growth than changes in salinity, at least within the range of salinities experienced during our study.

The minima in *H. dianthus* recruitment that occurred in March and maxima in December indicate that the lowest amount of recruitment occurs between December and March, while the greatest recruitment occurs from September to December. Positive correlations of *H. dianthus* cover (%) with day of the year (Julian day) of tile retrieval and temperature at the time of tile deployment and negative correlations with dissolved oxygen concentration at the time of tile deployment confirm this seasonal pattern. *H. dianthus* breeds from June to October/November in Woods Hole Massachusetts, with trochophore larval settlement occurring between 4 days (at 20 °C; Toonen and Pawlik 2001) and 11 days after fertilization (Grave 1933). Chapman et al. (2007) observed *Hydroïdes* spp. recruitment occurring from mid-July to mid-November but peaking in July and August in Loch Creran, Scotland, which overlaps with the months of peak recruitment in Baffin Bay. The serpulid, *Pomatoceros* spp., peaked in recruitment in summer months in May/June in Loch Creran, and July/August in Bantry Bay, Ireland (Cotter et al. 2003), while *Serpula vermicularis* peaked in August/September in Loch Creran (Chapman et al. 2007). All serpulids (*Hydroïdes* spp., *Pomatoceros*, *S. vermicularis*) had very little or no recruitment in the winter months in Loch Creran and Bantry Bay. Although the peak in *H. dianthus* recruitment occurred later in Baffin Bay than in Massachusetts and Scotland, it also occurred year-round. This year-round recruitment could be related to latitudinal differences, such as warmer temperatures, that occur in Baffin Bay.

The second hypothesis of this study is that spatiotemporal differences in serpulid densities on natural reefs are not dominated by differences in short-term (quarterly) spatiotemporal differences in potential recruitment. This was tested by comparing serpulid abundances on the natural reef with serpulid recruitment on the tiles. The seasonal abundances of serpulids on the recruitment tiles did not correlate with abundances on the surface of the reef, indicating that new recruitment does not dominate existing populations. This lack of correlation indicates that *H. dianthus* live for at least 3 months in Baffin Bay, and possibly several years, as estimated for individuals in the Lagoon of Orbetello, Italy (Bianchi and Morri 2001). It is not possible to determine recruitment on the reefs, and if reefs are accreting and eroding from this study. The density of *H. dianthus* recruits on tiles in Baffin Bay (mean of 9429 n m⁻², maximum seasonal mean of 19,167 n m⁻² on the bottom side of tiles) is much greater than recruits of *Hydroïdes* spp. (peak of 100 m⁻²) and greater than other serpulid species (*Pomatoceros* peak of 8900 m⁻², *S. vermicularis* peak of 1100 m⁻²) occurring in Loch Creran (Chapman et al. 2007), but much fewer than summertime peaks of 264,356 m⁻² and 141,911 n m⁻² in Bantry Bay (*Pomatoceros* spp.; Cotter et al. 2003). However, the tiles in the Loch Creran and Bantry Bay studies were

only deployed for 1 month and the tiles in the current study (Baffin Bay) were deployed for 3 months.

Aside from seasonal dynamics, important information pertinent to serpulid reef restoration in Baffin Bay includes microhabitat preference and spatial differences in serpulid recruitment. Serpulids strongly preferred the bottom rather than the top surfaces of horizontally oriented tiles in Baffin Bay, as occurred in Bantry Bay (*Pomatoceros* spp.; Cotter et al. 2003) and Loch Creran (Chapman et al. 2007). In Loch Creran, serpulids also preferred the sides of vertically oriented tiles. In Baffin Bay, the barnacle *A. eburneus* dominated upper surfaces, while *H. dianthus* dominated bottom surfaces. Statistical differences in recruitment among sampling sites could not be tested in this study because of lack of replication within sites; however, there did not appear to be major or consistent differences within Baffin Bay. The distances from reefs could be important for larval supply, although reefs in Loch Creran with limited reef development had 3.6 times more *S. vermicularis* recruitment than sites with well-established reefs (Cook et al. 2021). The presence of existing serpulid reef may play some role in recruitment dynamics because settlement of *H. dianthus* is greater in the presence of conspecifics in the laboratory (Toonen and Pawlik 2001), although this could be related to the presence of crevices and microstructures, rather than the serpulids themselves (Walters et al. 1997).

High abundances of serpulids on the reefs in Baffin Bay are likely indicative of a stable or accreting reef. Under seemingly optimal conditions in a water intake tunnel 60 km north of Baffin Bay, in Nueces Bay, TX, *H. norvegica* accumulations grew approximately 8 cm yr⁻¹, with ~3 cm occurring in the first month (Behrens 1968). This accumulation in Nueces Bay is an example of unexpectedly rapid accretion. It is equivocal whether serpulid reefs in Baffin Bay grew at similar rates under optimal conditions in historical times. Although we did not measure vertical growth (thickness of tubes above or below the tiles) by *H. dianthus*, we estimate that recent growth during this study period (2020–2022) was 0.5 to 2 cm in each 3-month deployment period on and around the tiles in Baffin Bay. This observed range of growth rates is comparable to 6.6 cm yr⁻¹ that was observed in Massachusetts (Grave 1933), although accurate comparisons cannot be made because growth rate decreases with serpulid age (Ten Hove and van den Hurk 1993). Future research is warranted to quantify both vertical growth by *H. dianthus* and short-term changes in reef size (e.g., height, volume) to determine whether Baffin Bay reefs are currently stable or accreting. Over the longer term, evidence indicates that serpulid reefs in Baffin Bay have decreased in size and distribution over the last 50 years or more (Hardegreer 1997; McKee 2008), likely due to a combination of direct impacts (e.g., trampling, hit by boats) and indirect causes (e.g., dissolution, bioerosion).

The third hypothesis tested in this study is that predation of serpulids by finfish and macroinvertebrates will decrease

serpulid establishment on recruitment tiles. Bioerosion is likely occurring to some extent from finfish feeding on invertebrates in the reef (Reed 1941), as has been observed by *Archosargus probatocephalus* (sheepshead) biting off small chunks of serpulid reef in Baffin Bay (Palmer, personal observations), and by hermit crabs and blennies (that do not normally occur on the reefs in Baffin Bay) in laboratory settings (Dalrymple 1964). Despite evidence of bioerosion from finfish on the serpulid reefs, there were no differences in serpulid densities between caged and uncaged tiles. This similarity between uncaged and caged treatments may indicate that reef consumption by fishes and large (> 1 cm) crabs on in Baffin Bay is minor relative to serpulid tube growth or that serpulid concentrations on the tiles were too small to attract predators. Other forms of natural bioerosion of serpulid tubes, such as that caused by boring fungi, algae, sponges, small crabs, and polychaetes (Ten Hove and van den Hurk 1993, and references therein), may be occurring but were untested in this study.

Other untested factors that could decrease reef size and hinder future restoration success include dissolution from water acidification or decreased calcium concentrations, stresses from changes in temperature, and dissolved oxygen. Tubes of another serpulid species (*Mercierella enigmatica*, possibly an erroneous identification of *Ficopomatus uschakovi*; ten Hove and van den Hurk 1993) deteriorated faster when exposed to fast-flowing freshwater with lower calcium concentrations in the tidal portion of the Brisbane River, Australia (Straughan 1972). Decreases in pH from 8.1 to 7.6 (from increased $p\text{CO}_2$) in laboratory conditions caused a deterioration of tube hardness and elasticity in juvenile *H. elegans* by altering tube mineralogy (increasing amorphous calcium carbonate proportions and calcite/aragonite ratios; Chan et al. 2012), and decreases in pH from 8.1 to 7.9 compromised juvenile calcification of the same species (Lane et al. 2013). Long-term decreases in pH have occurred in Baffin Bay (1964 to 2010, 0.005 yr^{-1} ; Montagna and Palmer 2012), although no changes were detected more recently (≤ 1996 to 2016; Bugica et al. 2020). Baffin Bay has higher dissolved calcium concentrations (Ca^{2+} $11.3 \text{ mmol kg}^{-1}$) than three other large, less saline Texas estuaries that do not host serpulid reefs (6.0 to 9.8 mmol kg^{-1} ; Montagna et al. 2018), but it is uncertain if there have been temporal changes in calcium concentrations. Because of Baffin Bay's watershed mineralogy, higher freshwater inflow should lead to a greater buffering capacity of carbonates, with potential positive effects for shell-forming organisms such as serpulids (Montagna et al. 2018).

Another potential stressor, hypoxia, was not detected in this study. However, low dissolved oxygen concentrations ($\leq 4 \text{ mg L}^{-1}$) have been documented in multiple years between April and September (this study; Wang et al. 2018), and summertime hypoxia ($< 2 \text{ mg L}^{-1}$) has

been observed in areas away from serpulid reefs in parts of Baffin Bay in previous years (M. Wetz, personal communications). Despite *H. dianthus* adults being highly tolerant to hypoxia ($0.5 \text{ mg-O}_2 \text{ L}^{-1}$) at salinities of 16 to 23 and temperatures from 20 to $26 \text{ }^\circ\text{C}$ (Sagasti et al. 2001), effects on other life stages and in combination with other stressors are unknown. The larval development and settlement of the related *H. elegans* were impaired when subjected to continuous dissolved oxygen concentrations $< 1 \text{ mg L}^{-1}$ (Shin et al. 2013). However, survival tolerance of larval and adult *H. elegans* was not impaired when subjected to 24 h of dissolved oxygen concentrations of 0.75 mg L^{-1} and 48 h of dissolved oxygen concentrations of 1.5 mg L^{-1} (Leung et al. 2013). Although *H. dianthus* can tolerate a wide range of temperatures ($3\text{--}30 \text{ }^\circ\text{C}$; Bastida-Zavala et al. 2017), summer temperatures at the serpulid reefs in Baffin Bay are at the upper end of this range (up to $30.6 \text{ }^\circ\text{C}$ in this study) and synergistic and sublethal negative effects cannot be ruled out.

Conclusion

Provision of hard substrates to promote serpulid recruitment and restore degraded reef habitat over large scales will require substantial investment. An increased understanding of serpulid recruitment, water quality dynamics (e.g., physico-chemical variables, nutrients, phytoplankton communities), and hydrodynamics in low-inflow estuaries can help increase the likelihood of successful restoration efforts. In Baffin Bay, there appears to be sufficient larval supply of *H. dianthus* for substrate provision to be a viable restoration approach. *H. dianthus* recruitment occurred year-round, but with a temporal peak between September and December, indicating that substrate deployment should occur during the later months of the year. There were no consistent differences in serpulid recruitment among sites, but there was a preference for serpulids to settle on lower surface of horizontally oriented tiles and for barnacles to occupy the upper surface, indicating that restoration substrates with high structural complexity may help maximize serpulid (and barnacle) recruitment and facilitate reef development. The effects of bioerosion by large (> 1 cm) predators appear to be negligible, which means that predation will not be a major barrier to restoration. Quantifying percent cover of restoration substrates by serpulids and barnacles was a suitable proxy for abundance and can be used to conduct more efficient monitoring of recruitment. Given the ecological importance of serpulid reef habitat in hypersaline conditions, and recognition of population declines, knowledge gained from this study will be valuable in improving the success of future serpulid reef restoration efforts.

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Author Contribution N. B., T. A. P., and J. B. P. conceived and designed the research; A. A., J. G., N. B., and T. A. P. performed the data collection and laboratory analyses; T. A. P. analyzed the data and wrote the first draft of the manuscript; and N. B., J. B. P., and T. A. P. edited the manuscript.

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Data Availability Data will be available from 2024 at the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) data repository (<https://data.gulfresearchinitiative.org/HI.x846.000:0009>).

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