

1 **Importance of Serpulid reef to the functioning of a hypersaline estuary**

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23 **Abstract**

24 Biogenic reefs provide important ecological functions and services to coastal and marine
25 environments, supplying high levels of biodiversity, providing refuge and foraging habitat, and
26 supporting fisheries. Serpulid reefs are a relatively uncommon habitat in coastal ecosystems
27 globally that provide habitat for a diverse community of organisms, and have become a target for
28 conservation and management efforts due to habitat degradation and loss. Baffin Bay, Texas, USA,
29 is known for exceptionally productive commercial and recreational fisheries that are thought to be
30 supported by Serpulid reef benthic macrofauna, particularly during regular periods of
31 hypersalinity. This study compared the functioning of Serpulid reef habitats with nearby soft
32 sediment areas using quantitative faunal and food web analyses. Serpulid reefs support a unique
33 benthic macrofaunal community with 191 times greater abundance, 97 times greater biomass, and
34 twice the number of species than in soft sediments. In contrast to soft-sediment macrofauna,
35 Serpulid reef macrofaunal abundance and biomass were not correlated with any measured water
36 quality variables. Isotope compositions of both suspension and deposit-feeding macrofauna from
37 both habitats (i.e. Serpulid reefs and soft sediments) were close to organic matter from the
38 sediment, demonstrating connectivity and the importance of primary production in the sediment
39 to both habitat types. Abundant macrofauna inhabiting Serpulid reefs likely serve as an important
40 food source for sport fish and other higher trophic-level fauna, particularly in hypersaline periods
41 when soft-sediment macrobenthic food resources are scarce. Given the substantial loss of Baffin
42 Bay's Serpulid reef habitat compared to historic levels, conservation actions may be warranted to
43 protect and restore Serpulid habitat and food resources. The results of this study can be used to
44 increase the success of such efforts.

45 **Key Words**
46 salinity; stable isotopes; trophic relationships, Baffin Bay, Texas, Gulf of Mexico

47 **1. Introduction**

48 Estuaries across the Gulf of Mexico are dominated by soft-sediment habitats, yet the bulk of
49 benthic faunal biomass is associated with biogenic reefs (Enochs 2012, Davis 2017, La Peyre et
50 al. 2019). A relatively uncommon reef type in coastal ecosystems is built by Serpulid worms
51 (Serpulidae, Polychaeta) that settle on hard substrates and secrete a calcareous tube around
52 themselves as they grow (Bastida-Zavala et al. 2017). In rare circumstances, millions of small (<
53 2 cm) Serpulid worms can aggregate via gregarious larval settlement (Ippolitov et al. 2014),
54 forming extensive reefs (Andrews 1964; Bosence 1973; Bianchi and Morri 2001). These Serpulid
55 reefs supplement marine complexity by increasing the three-dimensional relief of the bottom,
56 providing refuge and foraging habitat for fish and invertebrate species (Haines and Maurer 1980,
57 Zühlke et al. 1998; Obenat et al. 2001), and influencing sediment and organism transport processes
58 (Obenat and Pezzani 1994). Through their suspension feeding activities, Serpulid worms can also
59 improve water quality and minimize algal blooms (Leung and Chueng 2017 and references
60 therein).

61 Baffin Bay, a secondary bay within the Upper Laguna Madre Estuary, Texas, USA, is famous
62 locally for its extensive Serpulid reefs. The predominantly hypersaline conditions in Baffin Bay
63 (Orlando et al. 1993) make it uninhabitable for the Eastern Oyster (*Crassostrea virginica*), the
64 dominant reef-building species in northern Gulf of Mexico estuaries. *Hydroides dianthus*, a
65 common Serpulid (Bastida-Zavala et al. 2017), is the only species currently building reef structures
66 in Baffin Bay. *H. dianthus* has a wide recorded tolerance to both salinity (1-51.7) and temperature
67 (3-30 °C and higher; maximum summer temperature for Baffin Bay (May 2013-March 2021) is

68 31.2 °C (Wetz unpublished data)), enabling it to successfully invade disparate waters of the world
69 (e.g., Northern Yellow Sea, China, salinity 33, Dong et al. 2018; Tyrrhenian Sea, Italy, salinity 13-
70 48, Bianchi and Morri 2001; Delaware Bay, USA, salinity 23-28, Maurer et al. 1979; Haines and
71 Maurer 1980). However, sizeable Serpulid reef structures to the extent of those found in Baffin
72 Bay (last estimated at 16 km²; Brown et al. 1977) are rare and relatively understudied (Ardbear
73 Lough, Ireland, <1 km² (Bosence 1973); Ellis Fjord, Antarctica, >8 km long (Kirkwood and Burton
74 1988); Delaware Bay, USA, 1 km² (Haines and Maurer 1980); see ten Hove and van den Hurk
75 1993 for review).

76 The diverse and abundant benthic macrofauna that occur on Baffin Bay’s Serpulid reefs
77 are potential forage for higher trophic-level animals. Therefore, the Serpulid reefs may serve as an
78 important nursery area for Spotted Seatrout (*Cynoscion nebulosus*), with Baffin Bay hosting the
79 highest occurrence of juveniles (Froeschke and Froeschke 2011), and high densities of large
80 “trophy”-sized adults (McKee 2008) relative to elsewhere along the Texas coast, making Serpulid
81 reefs a unique habitat that is targeted by local anglers. Similarly, commercially important Black
82 Drum (*Pogonias cromis*), are three to six times more abundant in Baffin Bay than elsewhere along
83 the Texas coast (Martinez-Andrade et al. 2005; Olsen 2014). On the contrary, benthic macrofauna
84 in Baffin Bay’s soft sediments are sparse, particularly during periods of hypersalinity (Montagna
85 and Kalke 1995; Rubio et al. 2018; Breaux et al. 2019), and Serpulid reefs are thought to contribute
86 much of the biomass critical to supporting the exceptionally productive commercial and
87 recreational fisheries (McKee 2008; Bohannon et al. 2015). However, evidence indicates that
88 Serpulid reefs have been reduced in size and distribution compared to historic levels, primarily
89 due to wave action, prop damage from boats, and trampling from fishermen (Hardegree 1997;

90 Tunnell et al. 2001; Smith et al. 2005; Chapman et al. 2012), and conservation actions may be
91 needed to protect and restore habitat.

92 Given their limited distribution and evidence of decline, there is a need to better understand
93 Serpulid reef ecological structure and function to inform conservation, restoration, and
94 management efforts. This study aimed to assess the importance of Serpulid reef as habitat for
95 benthic macrofauna and to investigate the role of these reef-resident species as prey for
96 commercially and recreationally important fish species. Comparing carbon and nitrogen isotope
97 compositions of primary producers, macrofauna of known feeding modes, and fish allows for
98 determining the origin of the main food sources and assessing the structure and functioning of the
99 food web. Specifically, we sought to: (1) quantify differences in benthic macrofaunal communities
100 between Serpulid reefs and soft sediments, (2) determine the influence of varying hydrological
101 conditions on Serpulid reef benthic macrofaunal communities, and (3) investigate the role of
102 Serpulid reef benthic macrofauna in the Baffin Bay food web using stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$),
103 with a focus on commercially and recreationally important fish species.

104 **2. Methods**

105 **2.1 Study Area**

106 Baffin Bay is a shallow (0.9 - 2.3 m), 248-km² secondary bay of the Upper Laguna Madre
107 Estuary, located in the northwestern Gulf of Mexico in a semi-arid region of South Texas, USA
108 (Figure 1; Diener 1975; Tunnell et al. 2001). Serpulid reefs were last estimated in 1977 to cover
109 approximately 6% (16 km²) of Baffin Bay's otherwise soft bottom (Breuer 1957; Brown et al.
110 1977). Freshwater enters the bay through several small ephemeral streams at an average rate that
111 does not keep up with average evaporation rates. Residence time in Baffin Bay and the Upper
112 Laguna Madre exceeds one year, much longer than any other major estuary in Texas (< 0.5 yr;

113 Solis and Powell 1999; Wetz et al. 2017). Salinity conditions in the Upper Laguna Madre,
114 including Baffin Bay, are on average hypersaline (mean \pm standard deviation = 35.9 ± 7.0 ;
115 Montagna et al. 2011). Salinity in Baffin Bay specifically is generally higher and has more
116 spatiotemporal variability (2013-2016 mean \pm standard deviation = 41.2 ± 10.4 ; Montagna et al.
117 2018) than the Upper Laguna Madre as a whole (2015-2017 = 39.1 ± 6.4 ; Breaux et al. 2019).

118 **2.3 Study Design**

119 Three Serpulid reefs (R1-R3) and three soft sediment stations (SS1-SS3) were sampled
120 quarterly from June 2018 to March 2019 (Figure 1; Table S1). A fourth soft sediment station (SS4)
121 was also sampled in December 2018 and March 2019 to increase spatial coverage of soft sediment
122 communities. Samples were collected during sampling events for quantitative faunal community
123 analysis and assessment of food web structure. Soft sediment stations SS3 and SS4 were previously
124 sampled for benthic macrofaunal community analysis from 1989 to 1993 (as stations 24 and 6,
125 Montagna *et al.* 1993; Montagna and Kalke 1995). All soft sediment stations (SS1-SS4) were
126 previously sampled from 2014 to 2017 (as stations BB40, AL1, BB24, BB6, Rubio et al. 2018;
127 Breaux et al. 2019).

128 **2.4 Water Quality**

129 During each sampling event, water temperature, salinity, dissolved oxygen (DO)
130 concentration, and pH were measured at each station using a YSI Pro DSS multiparameter
131 instrument (YSI Incorporated 2014). Measurements were taken from approximately 0.1 m below
132 the water surface and 0.2 m above the sediment bottom.

133 **2.5 Quantitative Fauna Analyses**

134 *Sampling*

135 Three replicate pieces (approximately 3 cm³) of Serpulid reef were collected by hand at
136 each of the three Serpulid reef stations. Reef pieces were immediately transferred to a 500 µm
137 mesh bag to prevent loss of benthic macrofauna (henceforth “macrofauna”) that live within and
138 between the worm tubes. At soft sediment stations, macrofauna were collected using a 6.7-cm
139 diameter core tube (35.4 cm² area) to a depth of 3 cm (modified from Street et al. 1997). Three
140 replicate cores were collected from each station on each sampling date. All samples taken for
141 quantitative analysis were preserved in 10% buffered formalin.

142 *Laboratory analysis*

143 In the laboratory, the volume of Serpulid reef samples were determined by water
144 displacement, then molluscs and other hard-shelled organisms were counted and identified.
145 Serpulid reef samples were then placed in 12 mol L⁻¹ HCl for 24 hours to dissolve the calcium
146 carbonate reef substrate. Organisms from Serpulid reef and soft-sediment samples were extracted
147 on a 500 µm sieve, sorted using a dissecting microscope, identified to the lowest practical
148 identifiable level (usually species), and enumerated. A Folsom plankton splitter was used to obtain
149 a subsample of reef samples when macrofaunal abundance was too great to be practically counted.
150 Dry-weight biomass measurements for both Serpulid reef and soft-sediment organisms were
151 obtained for individual species or family groups after drying at 55 °C for 24 hours. Mollusc shells
152 were removed with 1 mol L⁻¹ HCl prior to drying and weighing.

153 Organisms were classified by feeding mode (suspension feeder, deposit feeder, or
154 predator/scavenger; Bruggeman 2020) and taxa group (e.g., Crustacea, Bivalvia, Polychaeta).
155 Suspension feeders were defined as macrofauna possessing filter feeding structures that generally

156 feed on particles in the water column. Deposit feeders were defined as organisms that consume
157 particulate matter in or on the sediment. Predator/scavengers were defined as carnivorous
158 organisms that consume other fauna.

159 *Statistical Analysis*

160 Spearman rank correlation analyses were run between water quality variables (salinity,
161 temperature, DO, pH) and both Serpulid reef and soft sediment macrofaunal abundance and
162 biomass. Spatio-temporal differences in biomass-based macrobenthic community composition
163 were determined using non-metric multi-dimensional scaling (nMDS) and cluster analysis (group
164 average method; Clarke 1993). Multivariate analyses were performed on a Bray–Curtis similarity
165 matrix on $\log_e(x+1)$ transformed data using Primer 7 software (Clarke and Gorley 2015).

166 **2.6 Stable Isotope Analyses**

167 *Sampling*

168 Surface sediment organic matter (SSOM) and suspended particulate organic matter
169 (SPOM) were collected at all stations via benthic coring (3 cm deep, 35.4 cm² area) and surface
170 water collection, respectively, during each sampling event. Samples were stored on ice until
171 returning to the laboratory. Triplicate Serpulid reef pieces and sediment cores were sampled at
172 each station during each sampling event to collect macrofauna for stable isotope analyses using
173 the same methods as for quantitative fauna analysis. The stable isotope cores were sieved in the
174 field using a 500 μ m mesh bag. Retained items and reef pieces were stored in containers filled
175 with local water inside a cooler until the end of the field day, when they were transported to the
176 laboratory.

177 Fish were collected in two ways: Reef-dwelling fish (Pinfish [*Lagodon rhomboides*] and
178 Sheepshead [*Archosargus probatocephalus*]) were collected from Serpulid reef stations using

179 hook and line, or speargun. Sport fish (Black Drum [*Pogonias cromis*], Red Drum [*Sciaenops*
180 *ocellatus*], and Spotted Seatrout [*Cynoscion nebulosus*]) were collected through partnerships with
181 commercial and recreational fishermen. Up to 15 sport fish (including at least five *P. cromis*) were
182 collected from Baffin Bay six to eight weeks after each benthic sampling event. *Pogonias cromis*
183 were purchased from local trotline fishermen, while tissue samples from other species (particularly
184 the non-commercial species *S. ocellatus* and *C. nebulosus*) were collected from anglers at a
185 recreational boat launch. Sport fish were caught in Baffin Bay, but not necessarily around Serpulid
186 reefs. All fish tissue was stored on ice until returning to the laboratory to be stored at -20 °C.

187 *Laboratory Sample Preparation*

188 Water samples for SPOM analysis were sieved through a 250 µm-mesh to remove large
189 zooplankton and detritus, then filtered through pre-combusted (4 hours at 450 °C) glass fiber filters
190 (Whatman GF/F glass fiber filters, 0.7 mm porosity) which were then freeze dried, generally for
191 24-72 hours, until dry (Labconco Freezone). Carbonates were removed from filters for $\delta^{13}\text{C}$
192 measurements by contact with HCl fumes for 4 hours in a vacuum-enclosed system. Nitrogen
193 isotope compositions were analyzed using raw filters.

194 Samples of SSOM were sieved through a 500-µm mesh to remove macrofauna, large
195 detritus, and large pieces of shell hash, then freeze dried and ground using a mortar and pestle.
196 Samples to be analyzed for carbon were decarbonated by adding 1 mol L⁻¹ HCl drop by drop until
197 cessation of bubbling. These samples were then dried in a dry-block heater, rinsed with deionized
198 water, freeze-dried and manually ground again.

199 Macrofauna collected for stable isotope analyses were sieved live on a 500 µm mesh within
200 24 hours of sample collection, separated by taxa, and placed in aquaria in artificial seawater for 36
201 hours to allow evacuation of gut contents. For each species identified, three individuals of differing

202 size classes were reserved when possible. Soft tissues were collected from macrofauna. Mollusk
203 shells were manually removed prior to stable isotope analysis. Lipids were not extracted from
204 macrofauna because entire prey items are ingested by fish and therefore all tissues (including
205 lipids) can be assimilated into predators (Newsome et al. 2014; Wolf et al. 2015). Mathematical
206 corrections to $\delta^{13}\text{C}$ values to account for variations in prey lipid concentrations were not used in
207 this study because corrections on a large range of prey (with a large range of tissue compositions;
208 Table S2) in habitat-scale assessments such as these can lead to larger biases than when not using
209 any correction (Arostegui et al. 2019). Epaxial fish muscle tissue samples were removed from the
210 anterior portion of the fillet. Any adhering skin, scales, or bones were removed from the tissue
211 samples. Lipid removal was not needed on fish tissues prior to stable isotope analysis as C/N ratios
212 (by mass) were lower than 3.5 (Table S2; Post et al. 2007). All fish and macrofauna samples were
213 stored at $-20\text{ }^{\circ}\text{C}$, freeze-dried and then ground (Retsch MM 400 ball mill) to a homogenous fine
214 powder.

215 Appropriate amounts of each sample type were encapsulated in tin capsules, except
216 acidified sediment samples. Those were encapsulated in silver capsules (to prevent corrosion of
217 the capsule by acidified material) and then packed into tin capsules (to improve their combustion
218 during the elemental analysis). The surface of the filters (i.e. acidified and non-acidified) was
219 scraped using flat tweezers to collect the maximum amount of SPOM and the smallest amount of
220 glass fibers, to improve the quality of combustion in the elemental analyzer. Samples were
221 prepared in Texas A&M University-Corpus Christi laboratories for stable isotope analysis before
222 sending off to be analyzed with a Flash EA 1112 elemental analyzer equipped with the Smart EA
223 option (Thermo Scientific, Milan, Italy), coupled with a Delta V Advantage isotope ratio mass
224 spectrometer with a ConFlo IV interface (Thermo Scientific, Bremen, Germany) at the University

225 of La Rochelle, France (Littoral, Environment and Societies Joint Research Unit stable isotope
226 facility, LIENSs). Isotope compositions are reported in the δ notation as deviations from standards:
227 atmospheric N_2 for $\delta^{15}N$ and Vienna Pee Dee Belemnite for $\delta^{13}C$ using the formula:

$$228 \quad \delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

229 where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Calibration was conducted using reference materials (USGS-24, -
230 61, -62, IAEA-CH6, -600 for carbon; USGS-61, -62, IAEA-N2, -NO-3, -600 for nitrogen). The
231 analytical precision of the measurements was $<0.15\%$ for carbon and nitrogen based on analyses
232 of USGS-61 and USGS-62 used as laboratory internal standards.

233 *Statistical Analyses*

234 Kruskal-Wallis rank sum tests followed by multiple comparisons were used to investigate
235 seasonal or spatial-related fluctuations in isotope compositions of SPOM, SSOM, macrofauna, and
236 fish muscle tissue. All tests were carried out with the R software (R Core Team 2013). Multiple
237 comparisons of means were completed using the *pgirmess* package (Giraudoux 2011).

238 **3. Results**

239 **3.1 Water Quality**

240 Water quality was similar at the Serpulid reef and soft sediment stations (Figure 2). Mean
241 salinity decreased from 45.6 ± 3.8 (mean \pm standard deviation) in June 2018 to 27.8 ± 0.7 in
242 December 2018 before slowly increasing back to 28.9 ± 0.3 in March 2019. Temperature followed
243 a typical seasonal pattern with a high of 29.1 ± 0.3 °C in June and a low of 14.0 ± 0.6 °C in
244 December. Trends in DO concentration were also seasonal, and inversely related to temperature
245 (5.7 ± 0.2 and 9.6 ± 1.1 mg L⁻¹ in June and December, respectively). Mean pH was highest during

246 the study period in September 2018 (8.5 ± 0.0) and then decreased to a low of 7.8 ± 0.1 in March
247 2019. Water quality measurements were within the range of historic averages (Bugica et al. 2020).

248 **3.2 Quantitative Fauna Analyses**

249 Mean abundance of macrofauna was 191 times greater per volume of Serpulid reef than
250 the same volume calculated from the top 3 cm of soft sediment (Figure 3). Forty-three species
251 occurred in Serpulid reef samples, as opposed to twenty-two taxa in the soft sediment samples
252 (Table S3). Serpulid reef macrofauna were dominated in abundance by crustaceans and
253 polychaetes. The most abundant taxa were the amphipod *Apocorophium louisianum* (formerly
254 *Corophium louisianum*; $18,837 \text{ n L}^{-1}$, 62.9% of total abundance), the polychaetes *Polydora ligni*
255 (1601 n L^{-1} , 5.4%), *Syllis cornuta* (1565 n L^{-1} , 5.2%) and *Nainereis laevigata* (1203 n L^{-1} , 4.0%),
256 the tanaid *Hargeria rapax* (1227 n L^{-1} , 4.1%) and the barnacle *Balanus eburneus* (1218 n L^{-1} ,
257 4.1%). The serpulid *H. dianthus* (539 n L^{-1} , 1.8%) was most abundant and temporally variable at
258 station R1 (966 n L^{-1}), with peaks occurring in September 2018 (2272 n L^{-1}) and March 2019 (1214
259 n L^{-1}). The most abundant taxa in the soft sediment were the polychaete *Mediomastus ambiseta*
260 (55 n L^{-1} , 35.2%), the bivalve *Mulinia lateralis* (49 n L^{-1} , 31.2%) and unidentified amphipods from
261 the Ampeliscidae family (27 n L^{-1} , 17.3%).

262 Mean macrofauna biomass was 97 times greater per volume of Serpulid reef than the same
263 volume calculated from the top 3 cm of soft sediment (Figure 3). The most dominant taxa by
264 weight on the Serpulid reefs were *B. eburneus* (3968 mg L^{-1} , 46.7% of total biomass), *A. louisianum*
265 (1100 mg L^{-1} , 12.9%), the bivalve *Brachidontes exustus* (992 mg L^{-1} , 11.7%), unidentified
266 Actinaria (485 mg L^{-1} , 5.7%) and the polychaete *Nereis riisei* (433 mg L^{-1} , 5.1%) (Table S4). The
267 most dominant taxa by weight in the soft sediment were the bivalves *M. lateralis* (67 mg L^{-1} ,

268 77.3%) and *Lyonsia hyalina* (3 mg L⁻¹, 3.7%), the polychaetes *Pectinaria gouldii* (8 mg L⁻¹, 9.3%)
269 and *M. ambiseta* (3 mg L⁻¹, 3.1%), and unidentified Ampeliscidae (3 mg L⁻¹, 3.1%).

270 Overall, Serpulid reef macrofauna abundance increased down-estuary toward the mouth of
271 Baffin Bay from R1 (18,984 n L⁻¹) to R3 (42,132 n L⁻¹) (Figure 3 and Figure 4). Abundance
272 increased down-estuary for crustaceans (from 10,993 to 32,598 n L⁻¹) and polychaetes (from 6,432
273 to 8,068 n L⁻¹), while bivalves decreased in abundance (from 736 to 170 n L⁻¹; Table S3). There
274 was no consistent spatial trend in macrofauna biomass among Serpulid reef stations. No spatial
275 trend was observed in soft-sediment macrofauna abundance or biomass. The highest abundance of
276 crustaceans (11 n L⁻¹) was at station SS4, located closest to the mouth of Baffin Bay near the
277 Laguna Madre.

278 Deposit feeders were the most abundant feeding type, contributing 69,873 n L⁻¹ (78%) of
279 total abundance for Serpulid reef and 386 n L⁻¹ (62%) for soft sediments (Table S3). Suspension
280 feeders were the next most abundant in both Serpulid reef (9,289 n L⁻¹; 10%) and soft-sediment
281 (225 n L⁻¹; 36%) stations. Macrofauna biomass was dominated by suspension feeders in both
282 Serpulid reef (17.3 mg L⁻¹; 68%) and soft-sediment (0.32 mg L⁻¹; 91%) stations (Figure 5, Table
283 S4). Deposit feeders were the next most dominant, constituting 5.8 mg L⁻¹(22%) of total biomass
284 for Serpulid reef and 0.03 mg L⁻¹ (9%) for soft sediments.

285 Macrofauna communities differed greatly between Serpulid reef and soft sediment stations
286 (Figure 6). Macrofauna community composition from all stations was at least 3% similar to one
287 another. Among Serpulid reef stations, macrofauna community composition was 53% similar.
288 There was a change in community composition and increase in diversity at Serpulid reef stations
289 moving down-estuary from R1 to R3. Soft sediment macrofauna community composition had

290 higher variability among stations and over time compared to macrofauna from Serpulid reef
291 stations.

292 Macrofauna abundance in soft sediments was negatively correlated with salinity ($r = -$
293 $0.499, p \leq 0.069$), temperature ($r = -0.473, p \leq 0.088$) and pH ($r = -0.550, p \leq 0.042$; Table 1). Soft
294 sediment biomass was also negatively correlated with pH ($r = -0.682, p \leq 0.007$). Abundance and
295 biomass of Serpulid reef macrofauna were not correlated with any measured water quality
296 variables ($r \leq |0.459|, p \geq 0.134$).

297 **3.3 Isotope compositions**

298 The isotope compositions of SPOM ($\delta^{13}\text{C}$: -24.5‰ , $\delta^{15}\text{N}$: 3.5‰) were more depleted than
299 SSOM ($\delta^{13}\text{C}$: -20.8‰ , $\delta^{15}\text{N}$: 4.4‰) (paired t -tests, $\delta^{13}\text{C}$: $p < 0.001$; $\delta^{15}\text{N}$: $p = 0.029$; Table 2).
300 Isotope compositions of SPOM and SSOM were similar among sampling stations (Kruskal-Wallis
301 tests, $p \geq 0.063$; Figure 7). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of SSOM were stable throughout the study
302 (Kruskal-Wallis tests, $\delta^{13}\text{C}$: $p = 0.652$; $\delta^{15}\text{N}$: $p = 0.491$), while SPOM $\delta^{13}\text{C}$ values decreased over
303 time (Kruskal-Wallis test, $p < 0.001$; Table S5; Figure S1). $\delta^{15}\text{N}$ values of SPOM peaked in
304 December 2018 (Kruskal-Wallis test, $p = 0.009$). Algae presented relatively large ranges of $\delta^{13}\text{C}$,
305 with means ranging from -20.5 (March 2019) to -16.9‰ (June 2018) and $\delta^{15}\text{N}$ values, ranging
306 from 3.9 (September 2019) to 6.2‰ (March 2019; Table S5).

307 Serpulid reef suspension feeders had mean $\delta^{13}\text{C}$ values ranging from -21.6 (*B. exustus*) to
308 -19.3‰ (*B. eburneus*) and mean $\delta^{15}\text{N}$ values from 5.3 (*B. exustus*) to 7.9‰ (*B. eburneus*, Table 2).
309 $\delta^{13}\text{C}$ values of *B. eburneus* were lower in December 2018 compared to June 2018 and March 2019
310 (Kruskal-Wallis test, $p < 0.001$; Table S5). Otherwise, carbon isotope compositions of the three
311 major species of suspension feeders (*B. eburneus*, *B. exustus* and *H. dianthus*) in the reefs were
312 stable over time (Figure S1) and did not follow any spatial pattern. The $\delta^{15}\text{N}$ values of these three

313 consumers were similar between stations (Kruskal-Wallis tests, $p \geq 0.391$) with no clear temporal
314 pattern. Serpulid deposit feeding species had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values similar to those of suspension
315 feeders; mean $\delta^{13}\text{C}$ values ranged from -20.4 (*A. louisianum*, Terebellidae) to -18.7‰ (*Cerapus*
316 *tubularis*) and mean $\delta^{15}\text{N}$ values ranged from 6.4 (*H. rapax*) to 7.6‰ (Terebellidae; Table 2).
317 Carbon isotope composition of the major species of deposit feeder (*A. louisianum*) was stable over
318 time (Kruskal-Wallis test, $p = 0.182$; Figure S1). Predators/scavengers had mean $\delta^{13}\text{C}$ values
319 ranging from -20.8 (Cnidaria) to -17.9‰ (Xanthidae) and mean $\delta^{15}\text{N}$ values from 8.4 (Nereididae)
320 to 10.0‰ (Cnidaria), with the upper limits of these ranges being higher than those of suspension
321 and deposit feeders.

322 Soft sediment suspension and deposit feeders' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were similar over
323 space and time. Mean $\delta^{13}\text{C}$ values of soft sediment suspension feeders ranged from -21.1
324 (Pectinariidae) to -20.5‰ (*M. lateralis*), and mean $\delta^{15}\text{N}$ values ranged from 5.8 (*M. lateralis*) to
325 7.1‰ (Pectinariidae; Table 2). Deposit feeders had mean $\delta^{13}\text{C}$ values ranging from -22.1
326 (Ampharetidae) to -15.0‰ (*N. vibex*) and mean $\delta^{15}\text{N}$ values ranged from 5.6 (Ampeliscidae) to
327 9.7‰ (Goniadidae). Soft sediment predators/scavengers had mean $\delta^{13}\text{C}$ values ranging from -21.8
328 (Nemertea) to -19.7‰ (*A. canaliculata*) and mean $\delta^{15}\text{N}$ values from 7.5 (Turbellaria) and 10.1‰
329 (Nemertea).

330 Comparisons between habitats demonstrated that suspension and deposit feeders collected
331 at Serpulid reef and soft sediment stations had similar $\delta^{13}\text{C}$ values (Kruskal-Wallis test, $p = 0.180$;
332 Figure 7). $\delta^{15}\text{N}$ values for these two groups of primary consumers were also similar, except
333 suspension feeders from the Serpulid reef which were slightly more ^{15}N -enriched than suspension
334 feeders from the soft sediment (means of 6.8 vs. 6.0‰; Kruskal-Wallis test, $p = 0.026$).

335 *Pogonias cromis* collected by commercial fishermen throughout Baffin Bay had similar
336 isotope compositions to *L. rhomboides* and *A. probatocephalus* collected at Serpulid reef sampling
337 stations (Kruskal-Wallis tests, $\delta^{13}\text{C}$: $p = 0.690$, $\delta^{15}\text{N}$: $p = 0.883$; Figure 7). Mean fish $\delta^{13}\text{C}$ values
338 ranged from -18.9 (*A. probatocephalus*) to -15.7‰ (*S. ocellatus*). No difference was observed
339 between $\delta^{13}\text{C}$ values of fish species (Kruskal-Wallis test, $p = 0.359$). Mean fish $\delta^{15}\text{N}$ values ranged
340 from 9.9 (*L. rhomboides*) to 13.5‰ (*C. nebulosus*), with *C. nebulosus* being more enriched in ^{15}N
341 than other fish species.

342 The range of fish $\delta^{13}\text{C}$ values overlapped those of suspension and deposit feeders from soft
343 sediment and Serpulid reefs (Figure 7). The mean $\delta^{13}\text{C}$ values of suspension (-20.7‰) and deposit
344 feeders (-20.1‰) from both habitats were in the range of mean SSOM $\delta^{13}\text{C}$ values (-21.0 to -
345 20.8‰) and were much more ^{13}C -enriched than SPOM (-24.7 to -24.4‰; Table 2).

346 **4. Discussion**

347 **4.1 Biomass enhancement and Serpulid reef macrofauna**

348 Baffin Bay's Serpulid reefs increase habitat complexity and support specific macrofauna
349 assemblages with enriched abundance, biomass, and diversity. Macrofauna inhabiting Serpulid
350 reefs occur in considerably higher densities (191x), have substantially higher biomass (97x), and
351 are more diverse (2x) than those occurring in soft sediments. Macrofaunal community composition
352 differed between habitat types, with crustaceans and polychaetes dominating at Serpulid reef
353 habitat and bivalves and polychaetes dominating in soft sediments. While the population dynamics
354 and community composition of Baffin Bay's soft sediment macrofauna has fluctuated greatly over
355 time (Montagna and Kalke 1995; Rubio et al. 2018; Breaux et al. 2019), Serpulid reef macrofauna
356 communities characterized in the current study are similar to those recorded historically, in
357 particular compared to the most recent and probably most comprehensive study of Serpulid reefs

358 in Baffin Bay, conducted two decades ago (Hardegee 1997). The deposit-feeding amphipod *A.*
359 *louisianum* was the most abundant reef organism observed in both studies (Hardegee 1997: 71%
360 of total abundance; current study: 60% overall, 70% at station R3), and the eight most abundant
361 macrofauna collected in 1997 were among the most numerous (8 of the 10 most abundant species)
362 in the current study.

363 Whereas soft sediment macrofauna decreased in abundance with increases in salinity,
364 temperature and pH, Serpulid reef macrofauna abundance and biomass were stable over time,
365 indicating that they are more consistently available to higher-level consumers than soft sediment
366 communities. Indeed, Baffin Bay experiences large and frequent fluctuations in water quality
367 variables including salinity and pH, as well as frequent algal blooms (Cira and Wetz 2019; Cira et
368 al. 2021), and numerous studies have documented the effects on soft sediment macrofauna
369 (Montagna et al. 1993; Montagna and Kalke 1995; Street et al. 1997; Rubio et al. 2018; Breaux et
370 al. 2019). While the role of salinity and temperature in structuring macrofauna communities is
371 generally well understood (Ritter et al. 2005; Beseres Pollack et al. 2009; Palmer and Montagna
372 2015; Van Diggelen and Montagna 2016), the mechanism for the response to pH is less well
373 known. Fluctuations in pH can affect marine organisms in various ways including reductions in
374 metabolism and growth, solubility of calcium carbonates, and bioavailability of metals (Knutzen
375 1981; Guinotte and Fabry 2008), which may have contributed to variability in soft sediment
376 macrofauna community.

377 Although Serpulid reef macrofaunal abundance and biomass were unrelated to salinity
378 fluctuations in the current study, persistent hypersalinity could have a negative effect on Serpulid
379 reef macrofaunal richness, as occurs in nearby soft sediment communities (Simmons 1957;
380 Montagna et al. 2002). A greater number of reef taxa were identified in the current study (43 in

381 this study versus 29 in Hardegee 1997) despite similar sampling efforts, which may be related to
382 the relatively moderate salinity range in this study (monthly salinity range of 28 to 47) as compared
383 to the consistently hypersaline conditions (salinity range of 40 to 65) occurring during the
384 Hardegee study. In contrast, the number of reef taxa in this study (43) is comparable to that found
385 in a limited study of Baffin Bay under similar salinity conditions conducted three decades ago (38
386 species, Cole 1981). The proposed link between hypersalinity and decreasing Serpulid reef
387 macrofauna richness is speculative, as factors such as other changes in water quality could be
388 responsible. There are likely to be long-term fluctuations in Serpulid reef macrofauna communities
389 over time, but community stability relative to the surrounding soft sediment macrofauna is evident
390 and important to the functioning of this dynamic system.

391 **4.2 Role of macrofauna from Serpulid Reefs in the Food Web**

392 Baffin Bay supports a uniquely large *P. cromis* population (Olsen 2014), and Serpulid reef
393 macrofauna are likely a key contributor to fish success in this environmentally stressed system.
394 Isotope analyses indicate that *P. cromis* and other sport fish likely rely on macrofauna from both
395 Serpulid reef and soft sediment habitats (directly for *P. cromis*, *A. probatocephalus* and *L.*
396 *rhomboides*, and indirectly for higher-trophic level consumers like *C. nebulosus*). Although it is
397 not possible to distinguish Serpulid reef macrofauna from macrofauna in soft sediments based on
398 their isotope compositions, quantitative analyses from this and other studies demonstrate that these
399 food sources are present in much higher numbers, with much greater biomass, and have less
400 variability, at Serpulid reefs than in soft sediments (Montagna et al. 1993; Montagna and Kalke
401 1995; Hardegee 1997; Rubio et al. 2018; Breaux et al. 2019).

402 During hypersaline periods, when soft sediment macrofauna become scarce, Serpulid reefs
403 likely become an essential source of macrofaunal prey for higher trophic level consumers. Breaux

404 et al. (2019) found that *P. cromis* diets in Baffin Bay consist primarily of deposit-feeding
405 macrofauna, which were rare or absent in soft sediment habitats during high salinity conditions.
406 *Pogonias cromis* have limited motility during hypersaline conditions, foraging primarily within
407 the boundaries of the bay rather than migrating to adjacent systems (Ajemian et al. 2018; Rubio et
408 al. 2018; Breaux et al. 2019). In these situations, Serpulid reefs are the primary source of
409 macrofauna prey. An increased understanding of the *P. cromis* diet is important because up to 76%
410 of annual commercial landings for the region are harvested from Baffin Bay (Olsen et al. 2018),
411 and because periodic emaciation events with significantly underweight *P. cromis* have plagued
412 this relatively small estuarine system (Olsen 2014; 2016). Additional research to estimate *P.*
413 *cromis* population size and carrying capacity would help further elucidate the importance of
414 Serpulid reef macrofauna to maintaining fish populations in Baffin Bay.

415 While Baffin Bay's Serpulid reefs host considerably more macrofauna than do soft
416 sediments, there is a clear and strong connection between the two habitat types, with soft sediments
417 playing an important trophic role. Macrofauna biomass was dominated by suspension feeders in
418 both Serpulid reef (68%) and soft sediment (91%) habitats. Suspension feeders generally rely on
419 food sources suspended in the water column, but in the current study their isotope compositions
420 were close to those of SSOM, indicating that a large part of their food resources originate from the
421 sediment, likely due to the shallow depth (average ~1 m) and predominant wind-driven mixing
422 (Tunnell 2001). The role of SSOM as a food source for suspension feeders has been demonstrated
423 in similarly shallow, well-mixed estuaries (Blomberg et al. 2017), and in other estuarine habitats
424 such as seagrass beds, and intertidal and subtidal mudflats (Riera and Richard 1996; Lebreton et
425 al. 2011; Kang et al. 2015). Our results highlight the connectivity between these two major

426 habitats: soft sediments where primary production and/or storage of this production occurs, and
427 Serpulid reefs where macrofaunal consumers make this resource available to higher trophic levels.

428 **4.3 Implications for Conservation and Restoration**

429 Serpulid reefs are limited in their global distribution and at risk from anthropogenic
430 disturbance yet are highly valued for their ecological and conservation importance owing to their
431 high levels of biodiversity (Haines and Maurer 1980). Loss of biogenic reef structure has negative
432 implications for both reef-associated macrofauna and for higher trophic level organisms foraging
433 in these habitats (Kaiser et al. 1999). The only Serpulid found on the reef in the current study, *H.*
434 *dianthus*, is known to exhibit gregarious settlement (Haines and Maurer 1980) and rapid growth
435 (up to 66 mm yr⁻¹; Grave 1933). However, it is plausible that *H. dianthus* reef-building activities
436 are affected by the predominantly hypersaline conditions (Cole 1981), reducing the rate of
437 biogenic reef recovery from physical disturbances, e.g., those associated with fishing activities
438 (Kaiser et al. 1999). Biochemical mechanisms may also contribute to reef decline, with common
439 and extreme changes in pH in the bay potentially altering calcification rates and changing the
440 mechanical properties of Serpulid tubes (Chan et al. 2012; Smith et al. 2013; Díaz-Castañeda et
441 al. 2019) and reducing their effectiveness against external attacks and bioerosion by predators
442 (Waldbusser et al. 2011; Wisshak et al. 2012; Hossain and Rahman 2017). Additional research is
443 warranted to understand how Serpulids will respond to environmental change.

444 Restoration is increasingly being used as a tool to ameliorate the effects of habitat loss for
445 biogenic reef builders (Jaap 2000; De Santiago et al. 2019). For habitats that are rare or limited in
446 distribution, ecological knowledge is needed to promote efficient, effective, and successful
447 restoration efforts (Cook et al. 2021). Although the current extent and size of Baffin Bay's Serpulid
448 reefs are unknown, observations indicate substantial reductions in habitat have occurred from the

449 16 km² reported from surveys conducted in the 1970s (Brown et al. 1977; Hardegee 1997; Tunnell
450 et al. 2001). Additional effort is warranted to update maps of Serpulid reef in Baffin Bay using
451 approaches that have been successful in other systems, including lidar (Noernberg et al. 2010) and
452 side-scan sonar surveys (Moore et al. 2009; Raineault et al. 2012). Our results indicate that
453 Serpulid reef macrofauna abundance increased up-estuary, and that *H. dianthus*, the only reef-
454 builder in Baffin Bay, was most numerous at the furthest up-estuary station. Updated maps could
455 be used in combination with these results to help select suitable locations to create restored reefs
456 or protected areas to reestablish lost Serpulid habitat and food resources. Also, restoration success
457 may be enhanced by selecting locations where *H. dianthus* are found in abundance because *H.*
458 *dianthus* settlement relies on chemical cues associated with adults as indicators of habitat
459 suitability (Toonen and Pawlik 1996). Additional information on hydrodynamics and larval
460 dispersal could further help improve restoration planning and protected area design. The creation
461 of short-term (< week) hydrodynamic transport models would be particularly useful for Serpulid
462 management because *H. dianthus* larvae settle approximately five days after fertilization in the
463 water column (Scheltema et al. 1981).

464

465 **5. Conclusion**

466 We have shown that Serpulid reefs play a critical role in the functioning of the Baffin Bay
467 ecosystem, supporting specific macrofauna assemblages and providing increased macrofauna
468 biomass. In contrast to macrofauna from soft sediments, Serpulid reef macrofauna abundance and
469 biomass were stable over time, indicating they are more consistently available to higher-level
470 consumers. In periods of hypersalinity common to the bay, when soft sediment macrofauna are
471 limited, Serpulid reefs likely become an essential source of prey supporting *P. cromis* and other

472 sport fish populations. Stable isotope analysis results demonstrate trophic connectivity between
473 Serpulid reef and soft sediment habitats and highlight the importance of sediment organic matter
474 as a food source for the dominant suspension feeders. Previous evidence has shown substantial
475 reductions of Serpulid reef habitat in Baffin Bay compared to historic levels. Our results indicate
476 that further reef degradation and loss will undoubtedly have cascading effects for higher trophic
477 level organisms. Conservation actions may be needed to reestablish lost Serpulid habitat and food
478 resources, and results from the current study could help in selecting suitable locations for
479 restoration or protection. An improved understanding of the ecological structure and function of
480 Serpulid reef habitats is important because it will increase the probability of restoration success of
481 this rare and vulnerable habitat.

482

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722

723 **Tables**
 724

725 **Table 1.** Spearman rank correlation coefficients and p-values among macrofaunal community
 726 measurements and water quality parameters. Analyses included four soft sediment and three
 727 Serpulid reef stations sampled between June 2018 and March 2019.

Habitat	Variable (unit)		Salinity	Temperature (°C)	pH	Dissolved Oxygen (mg L ⁻¹)
Serpulid Reef	Abundance (n L ⁻¹)	rho	0.112	0.046	0.098	0.056
		p	0.729	0.888	0.762	0.863
	Biomass (mg L ⁻¹)	rho	-0.238	-0.459	-0.203	0.385
		p	0.457	0.134	0.527	0.217
Soft Sediment	Abundance (n L ⁻¹)	rho	-0.499	-0.473	-0.550	0.389
		p	0.069	0.088	0.042	0.169
	Biomass (mg L ⁻¹)	rho	-0.341	-0.292	-0.682	0.134
		p	0.233	0.311	0.007	0.648

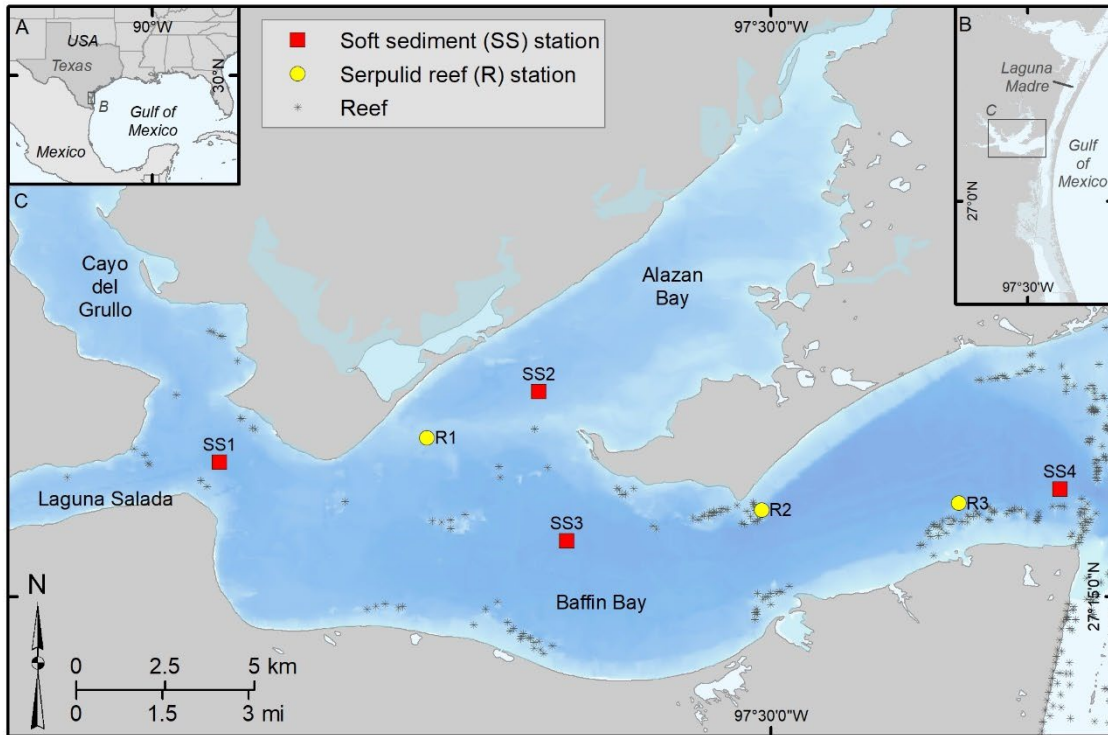
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730 **Table 2.** Stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) of taxa and organic matter samples
 731 collected from June 2018 to March 2019. SPOM = suspended particulate organic matter, SSOM
 732 = surface sediment organic matter.

Location Collected	Sample Type	Species Name	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
				Mean	Std. Dev.	Mean	Std. Dev.
Soft Sediment	Organic matter	SPOM	25	-24.7	1.6	3.5	2.4
		SSOM	14	-21.0	0.7	4.6	0.3
	Suspension feeder	<i>Mulinia lateralis</i>	19	-20.5	0.8	5.8	1.0
		Pectinariidae	10	-21.1	0.5	7.1	1.2
	Deposit feeder	<i>Armandia agilis</i>	1	-21.6		7.9	
		Ampeliscidae	2	-19.6	1.0	5.6	0.5
		Ampharetidae	3	-22.1	2.2	7.7	0.3
		Amphipoda	1	-20.8		7.3	
		Goniadidae	4	-20.9	1.1	9.7	1.1
		<i>Nassarius vibex</i>	1	-15.0		6.1	
		Predator/scavenger	<i>Acteocina canaliculata</i>	2	-19.7	1.0	7.6
	Nemertea		1	-21.8		10.1	
	Turbellaria		2	-20.9	0.4	7.5	0.0
	Primary producer / Organic matter	Algae	20	-18.4	4.0	5.0	1.6
		SPOM	20	-24.4	1.6	3.4	1.7
SSOM		12	-20.8	2.0	4.2	0.7	
Serpulid Reef	Suspension feeder	<i>Balanus eburneus</i>	36	-19.3	1.1	7.9	0.9
		<i>Brachidontes exustus</i>	29	-21.6	0.6	5.3	0.6
		<i>Hydroides dianthus</i>	29	-21.1	0.9	7.0	0.9
	Deposit feeder	<i>Apocorophium louisianum</i>	33	-20.4	1.2	6.5	0.7
		<i>Cerapus tubularis</i>	2	-18.7	1.5	7.2	1.6
		<i>Hargeria rapax</i>	1	-19.8		6.4	
		Orbiniidae	4	-20.3	0.5	7.0	0.3
		Terebellidae	3	-20.4	0.2	7.6	0.1
	Predator/scavenger	Cnidaria	6	-20.8	0.3	10.0	0.9
		Nereididae	29	-19.7	1.2	8.4	1.0
Xanthidae		4	-17.9	0.8	8.5	0.7	
Baffin Bay	Fish	<i>Archosargus probatocephalus</i>	1	-18.9		11.0	
		<i>Cynoscion nebulosus</i>	13	-17	1.5	13.5	0.7
		<i>Lagodon rhomboides</i>	8	-16.4	2.5	9.9	1.1
		<i>Pogonias cromis</i>	23	-16.8	2.8	10.2	1.7
		<i>Sciaenops ocellatus</i>	4	-15.7	2.8	12.2	0.6

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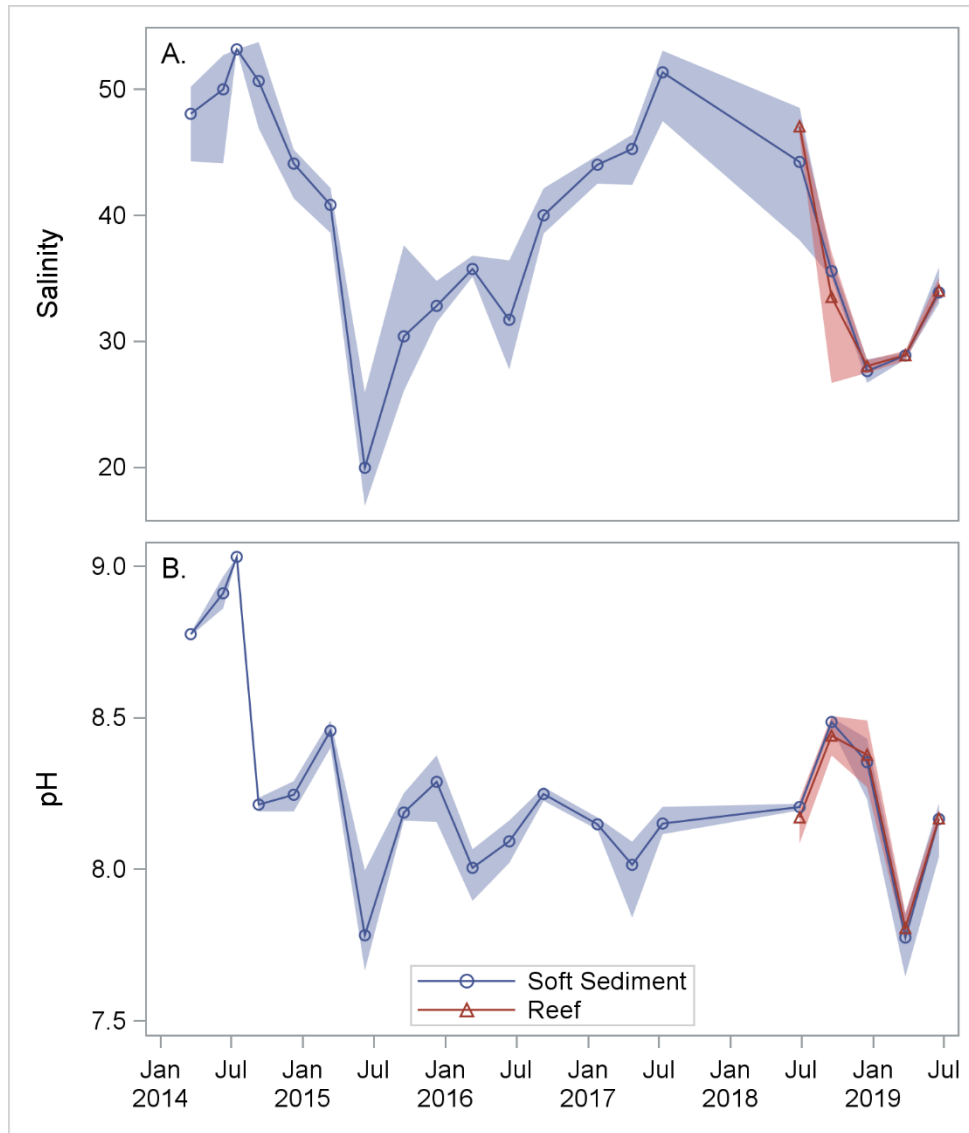
734 **Figure Captions**



735

736 **Figure 1.** Map of the Baffin Bay complex showing reef (R) and soft sediment (SS) sampling
737 locations. Approximate locations of reef are derived from NOAA electronic navigation charts
738 (NOAA 2018). Almost all reefs in the map are Serpulid reefs (some in the Laguna Madre are rock
739 reefs).

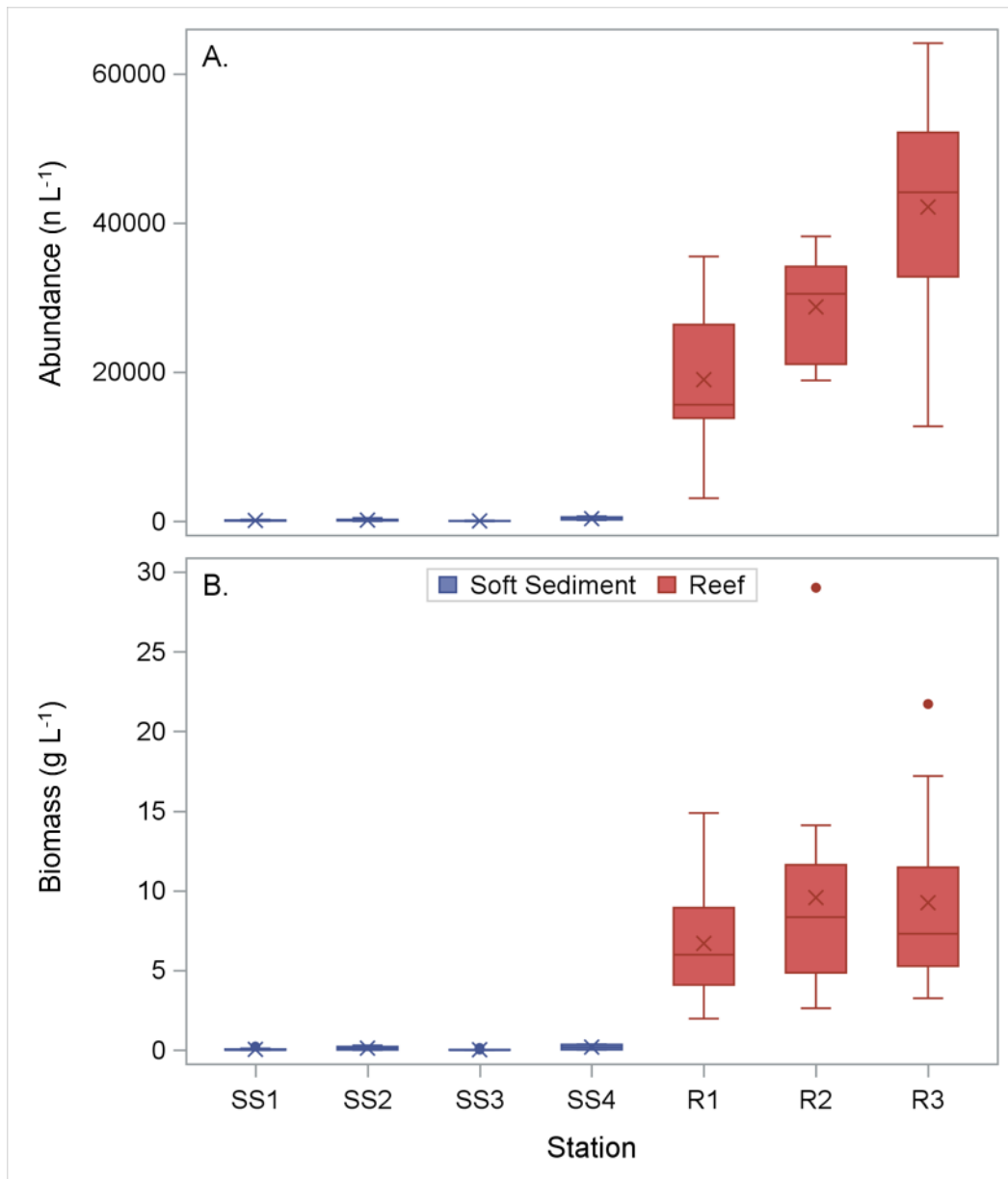
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742 **Figure 2.** Salinity and pH measured at soft sediment (blue) and Serpulid reef (red) stations.
 743 Shaded regions represent minimum and maximum salinities in each sampling period. Values
 744 before 2018 are plotted for reference only.

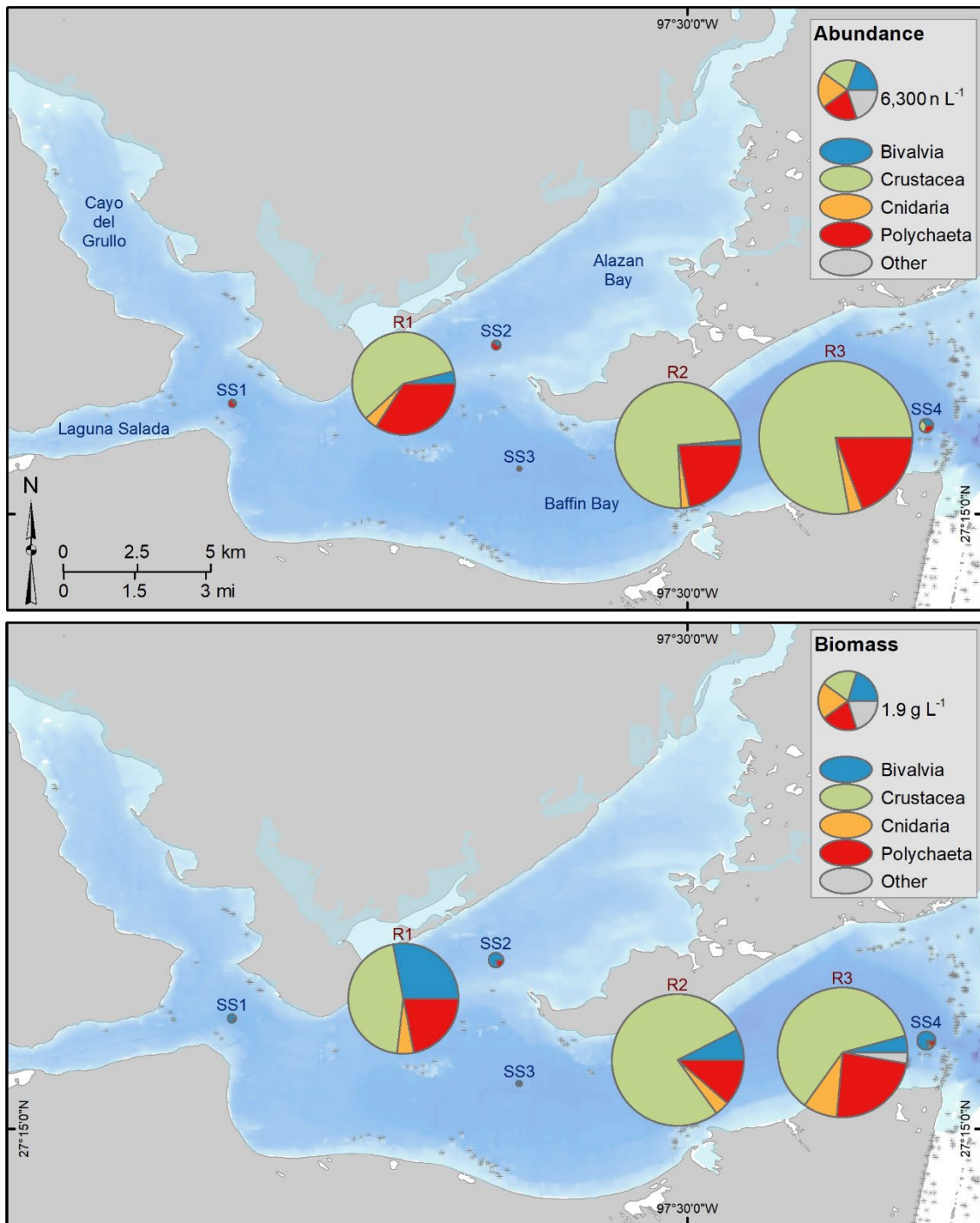
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747 **Figure 3.** Abundance (top), and biomass (bottom) of fauna ($n L^{-1}$) in the top 3 cm of soft
 748 sediment (blue) and 3 pieces (approximately $3 cm^3$) of Serpulid reef (red) from June 2018-March
 749 2019. In each boxplot, the line represents the median, x symbol represents the mean, the upper
 750 and lower box limits represent the upper and the lower quartile, upper and lower whiskers
 751 represent the minimum and maximum values (excluding outliers).

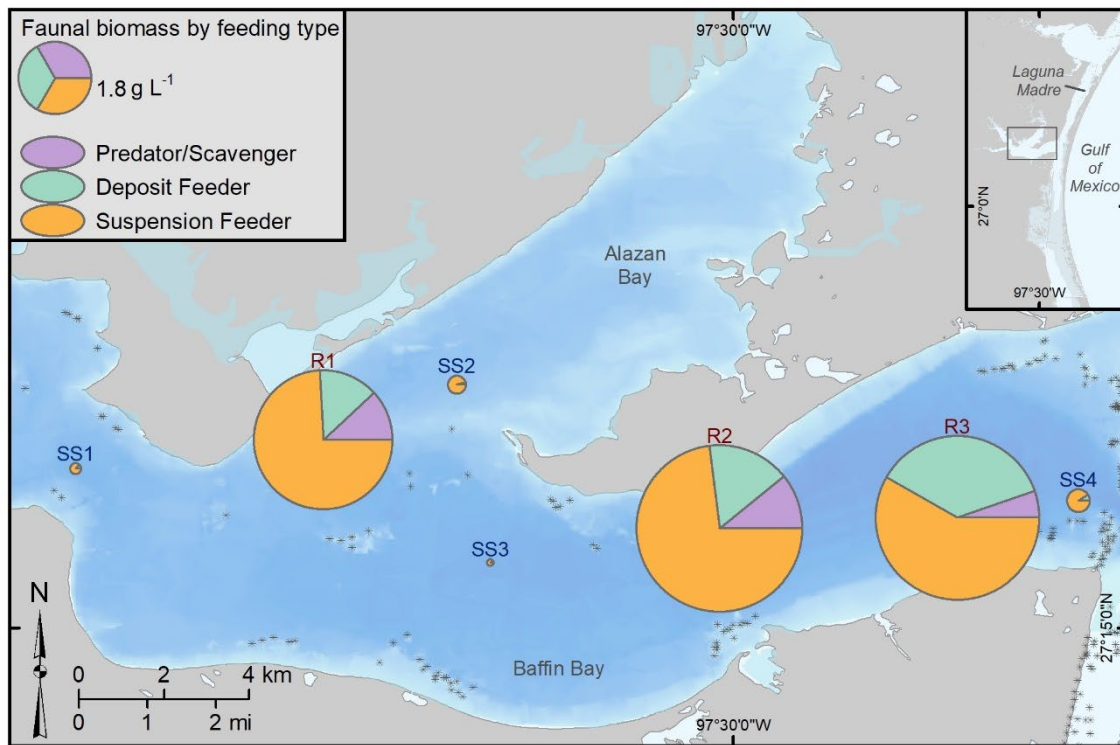
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755 **Figure 4.** Mean abundance (top) and biomass (bottom) of major faunal groups occurring in soft
 756 sediment and Serpulid reef stations from June 2018-March 2019. Pie graph size is indicative of
 757 relative macrofaunal abundance and biomass, respectively.

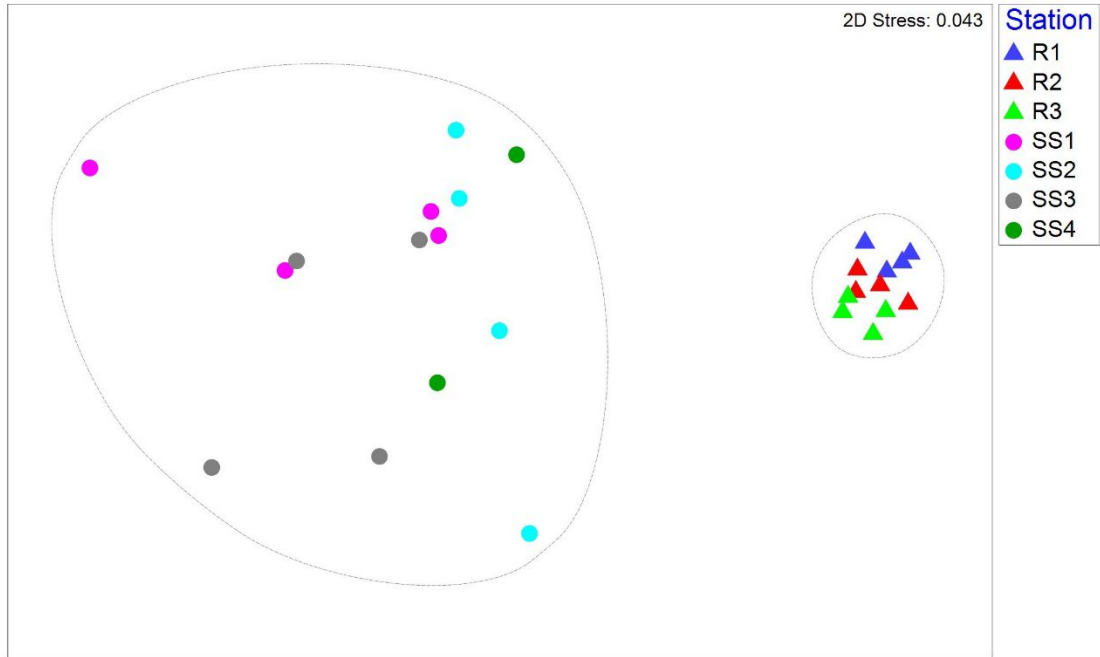
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760 **Figure 5.** Mean biomass of macrofauna by feeding type in soft sediment and Serpulid reef stations
 761 from June 2018-March 2019. Pie graph size is indicative of relative macrofaunal biomass.

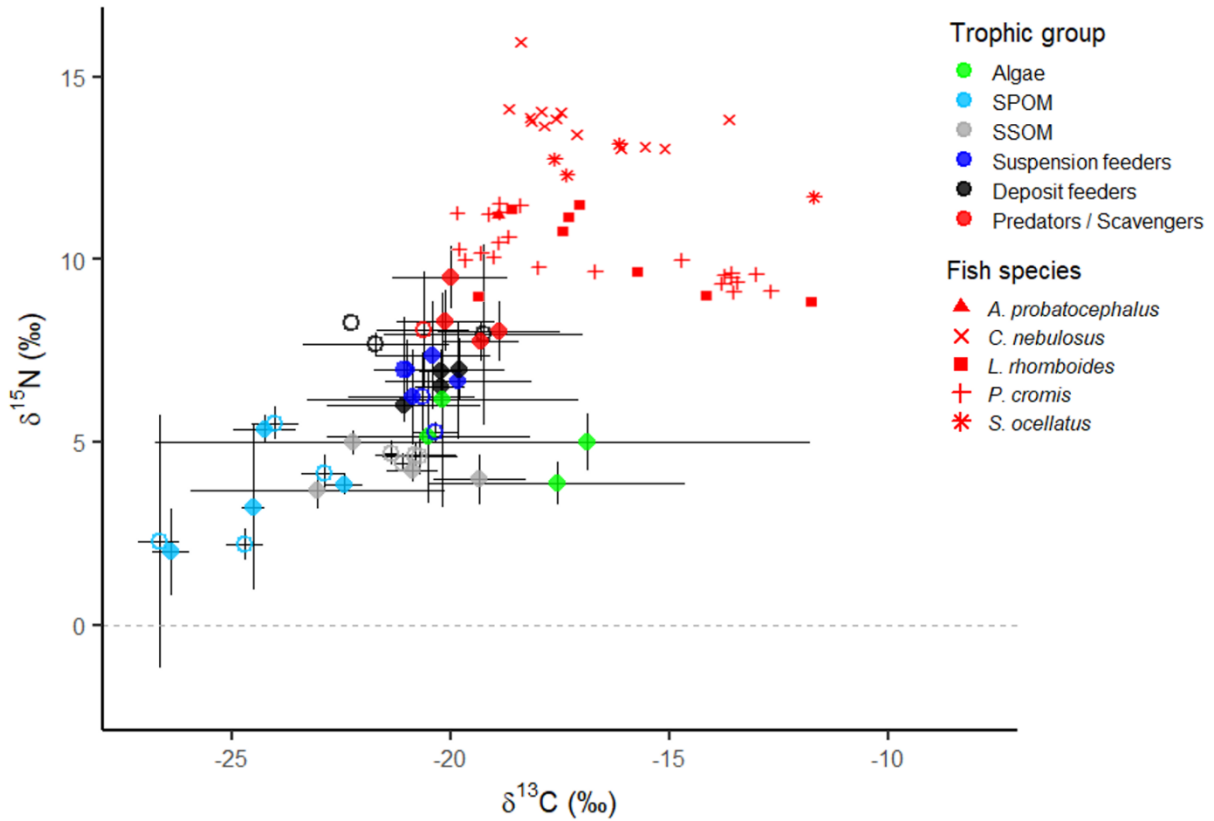
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764 **Figure 6.** Nonmetric multidimensional scaling plot of macrofaunal communities from Serpulid
 765 reef (R1-R3; triangles) and soft sediment stations (SS1-SS4; circles) from June 2018-March 2019.
 766 Ellipses represent 3% similarity groupings determined by cluster analysis.

767



769

770 **Figure 7.** Stable isotope compositions ($\delta^{13}C$ and $\delta^{15}N$, ‰) of potential food sources and fish. Fish
 771 are shown as individual samples. All other samples are averaged by season (mean \pm standard
 772 deviation). Sources from the Serpulid reef are represented by solid symbols and those from soft
 773 sediment by hollow symbols. SPOM = suspended particulate organic matter, SSOM = surface
 774 sediment organic matter.

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