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Recommended Citation

Failon, Caroline Mackenzie; Wittingham, Serina Sebilian; and Johnson, David S., Ecological Associations of *Littoraria irrorata* with *Spartina cynosuroides* and *Spartina alterniflora* (2020). *Wetlands*.
doi: 10.1007/s13157-020-01306-4

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1 Ecological associations of *Littoraria irrorata* with *Spartina cynosuroides* and
2 *Spartina alterniflora*

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7 **Abstract**

8 It is well-documented that marsh periwinkles (*Littoraria irrorata*) consume and inhabit smooth
9 cordgrass (*Spartina alterniflora*), but their interactions with big cordgrass (*Spartina*
10 *cynosuroides*) remain unknown. Plant communities in mesohaline marshes will change as sea-
11 level rise shifts species from salt-intolerant (e.g., *S. cynosuroides*) plants to salt-tolerant (e.g., *S.*
12 *alterniflora*) ones. Therefore, understanding how *L. irrorata* interacts with different habitats
13 provides insight into this species' generalist nature and allows us to predict the potential impacts
14 of changing plant communities on *L. irrorata*. We show, for the first time, that *L. irrorata*
15 inhabits, climbs, and grazes *S. cynosuroides*. We compared both habitats and found snails were
16 larger, plant tissue was tougher, and sediment surface temperatures were higher in *S. alterniflora*
17 than *S. cynosuroides*. Snails had greater survivorship from predators in *S. cynosuroides* than in *S.*
18 *alterniflora*. Further, snails grazed *S. cynosuroides* more than *S. alterniflora*, evidenced by a
19 greater number of radulation scars. Despite these differences, snail densities were equal between
20 habitats suggesting functional redundancy between *S. cynosuroides* and *S. alterniflora* for *L.*
21 *irrorata*. Our results indicate *L. irrorata* is a habitat generalist that uses both *S. alterniflora* and
22 *S. cynosuroides*, which may allow it to gain an ecological foothold as sea-level rises.

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24
25
26
27 Keywords: brackish marsh, mesohaline marsh, salt marsh, ecological equivalence, sea level rise

34 **Introduction**

35 Tidal marshes cover approximately 45,000 km² globally (Greenberg et al. 2006) and contribute
36 ecologically and economically to human well-being by providing erosion and flood control,
37 recreation, improved water quality, carbon sequestration, and nursery habitat for commercially
38 important fishes and invertebrates (Boesch et al. 2000; Beck et al. 2001; Shepard et al. 2011).
39 There are 16,000 km² of tidal marshes in North America alone, with high concentrations on the
40 South Atlantic coast and Gulf of Mexico (Greenberg et al. 2006). The Chesapeake Bay in the
41 United States contains an estimated 1,240 km² of tidal marshes, with brackish marshes making
42 up one-third of this area (Stevenson et al. 2000). A mesohaline marsh is a type of estuarine
43 brackish marsh where saline and fresh waters mix, leading to salinities between 5 and 18 ppt on
44 average (Odum 1988). Despite their abundance, mesohaline marshes are relatively understudied
45 compared to their polyhaline counterparts (i.e., salt marshes, 18-30 ppt), especially regarding
46 their flora and fauna.

47 Mesohaline marshes tend to have higher plant diversity than that of polyhaline marshes
48 (Odum 1988) because a greater abundance of vascular plant species can tolerate lower salinities
49 (Anderson et al. 1968; Wass and Wright 1969; Perry and Atkinson 1997). On the Atlantic coast
50 of the United States, the lowest elevations of mesohaline marshes are dominated by two co-
51 occurring species: the smooth cordgrass, *Spartina alterniflora*, and the big cordgrass, *Spartina*
52 *cynosuroides*. Both species have similar growth forms, with leaves growing from a single tall
53 stem (culm) and rhizomatous belowground biomass (Silberhorn 1992; McHugh and Dighton
54 2004). However, in the Chesapeake Bay region, *S. cynosuroides* ranges from 2 to 4 meters tall,
55 whereas *S. alterniflora* ranges from 1 to 2 meters tall (Silberhorn 1992). Both species are flood
56 tolerant, however *S. alterniflora* has a wider salt tolerance than *S. cynosuroides* (Penfound and

57 Hathaway 1938). *Spartina alterniflora* commonly dominates polyhaline marsh communities due
58 to its ability to outcompete salt-sensitive species, however it can also thrive in lower salinity
59 marshes (Stribling 1997; White and Alber 2009). In contrast, *S. cynosuroides* prefers oligohaline
60 (0.5-5 ppt) environments but can tolerate freshwater to mesohaline conditions (Odum et al. 1984;
61 Constantin et al. 2019). The co-occurrence of these plant species creates distinct habitat types
62 with qualities that may attract similar fauna to each.

63 The marsh periwinkle (*Littoraria irrorata*) is an abundant and herbivorous gastropod
64 found in tidal marshes along the Gulf of Mexico and Atlantic coast of the United States. It
65 thrives in salinities ranging from 5 to 30 ppt; however, it can survive shorter periods of time (less
66 than a week) in salinities from 0 to 5 ppt (Crist and Banta 1983; Henry et al. 1993). It is a critical
67 component of saltmarsh food webs (McCann et al. 2017) as prey for fishes and crustaceans
68 (Hamilton 1976) and as a consumer of live and dead *S. alterniflora*, marsh sediment, algae,
69 diatoms, nematodes, foraminifera, ostracods, mites, copepods, and other microorganisms
70 (Alexander 1979). *Littoraria irrorata* climbs plant stems to avoid rising tides and aquatic
71 predators (Warren 1985; Carroll et al. 2018), as well as to cultivate fungus colonies on plant
72 leaves for consumption (Silliman and Zieman 2001; Silliman and Newell 2003). At
73 extraordinarily high densities, this fungal farming by *L. irrorata* can lower aboveground biomass
74 of *S. alterniflora* (Silliman and Zieman 2001). During low tide, some snails move back to the
75 sediment surface to feed and to avoid the threat of desiccation (Bingham 1972).

76 *Littoraria irrorata* is frequently studied in polyhaline marshes and therefore associated
77 primarily with *S. alterniflora* (e.g., Hamilton 1976; Silliman and Zieman 2001; Silliman and
78 Newell 2003; Deis et al. 2017; Zengel et al. 2017; Rietl et al. 2018). In the mesohaline marshes
79 of the Chesapeake Bay, we have observed *L. irrorata* in both *S. alterniflora* and *S. cynosuroides*

80 habitats. Here, we document, for the first time to our knowledge, the ecological use of *S.*
81 *cynosuroides* by *L. irrorata* in a mesohaline marsh. Our goals were to compare the
82 environmental characteristics, predation pressure, palatability of plant tissue, and algal-food
83 availability between *S. alterniflora* and *S. cynosuroides* habitats in relation to *L. irrorata* use. We
84 expected that *L. irrorata* climbed *S. cynosuroides* to avoid predation, similar to its behavior in *S.*
85 *alterniflora*. However, we hypothesized that *S. alterniflora* was more palatable than *S.*
86 *cynosuroides*, as the use of *S. alterniflora* as a preferred food source for *L. irrorata* is well-
87 documented (e.g. Hendricks et al. 2011; Sieg et al. 2013). We also expected the difference in
88 plant height between *S. alterniflora* and *S. cynosuroides* to influence the foraging behavior of *L.*
89 *irrorata*. For example, taller *S. cynosuroides* may limit access to leaves or light penetration to the
90 substrate, thus decreasing benthic diatom growth, an additional food for *L. irrorata* (Alexander
91 1979).

92

93 **Methods**

94 *Study Site*

95 Our study focused on the mesohaline marsh surrounding Taskinas Creek (37° 24' 54.79" N; 76°
96 42' 52.74" W; Fig. 1), within the Chesapeake Bay watershed in James City County, Virginia,
97 USA. Access to this York River State Park site was possible through the Chesapeake Bay
98 National Estuarine Research Reserve of Virginia (CBNERR-VA), which maintains marsh
99 monitoring stations within the York River estuary. Taskinas Creek has an average salinity of 6 to
100 7 ppt (VECOS Database, accessed: July 16, 2019) with a semidiurnal tidal range of 0.85 m on
101 average. The low marsh exists below the mean high-water level and is dominated by distinct,
102 side-by-side, monotypic stands of *S. alterniflora* and *S. cynosuroides*, with *L. irrorata* found in

103 both habitats. The high marsh above the mean high-water level is made up of mostly salt hay
104 (*Spartina patens*) and saltgrass (*Distichlis spicata*).

105

106 *Snail & Environmental Data*

107 We established two, 20-meter transects one meter from the creek bank, one in a monotypic stand
108 of *S. alterniflora*, and the other in a monotypic stand of *S. cynosuroides*. Along each transect, we
109 haphazardly placed twenty 0.0625 m² quadrats (total of forty quadrats) to estimate stem heights
110 and densities. Plant height was measured for all live plants within quadrats and the tallest plant
111 from each quadrat was clipped from the base and stored in a -80°C freezer to await plant trait
112 analysis. The second tallest plant from each quadrat was clipped from the base and processed
113 with a penetrometer immediately for tissue toughness (see below). To evaluate *L. irrorata*
114 densities in *S. alterniflora* and *S. cynosuroides*, thirty 0.0625 m² quadrats per habitat (total of
115 sixty quadrats) were haphazardly sampled and all snails within each quadrat were counted. In a
116 separate sampling effort, adult snails were haphazardly collected along each transect within each
117 habitat (*S. alterniflora*, n=184; *S. cynosuroides*, n=128) and measured in the lab for height and
118 width using digital calipers to determine average snail size. Height was measured from the tip of
119 the shell spire to the bottom of the shell aperture. Width was measured diagonally from the
120 widest part of the shell aperture to the body whorl. To assess leaf damage from snail grazing,
121 fifteen 0.0625 m² quadrats were haphazardly placed within each habitat type. In each quadrat,
122 five plants were chosen at random to measure heights and to count radulations. In addition, four
123 Onset HOBO pendants were deployed from July 11th to August 6th, 2018 to measure light
124 intensity and temperature in *S. alterniflora* and *S. cynosuroides* habitats, with two pendants per
125 habitat. To estimate benthic algal biomass, a benthic chlorophyll *a* sample was taken to a depth

126 of 3 mm from the sediment surface (volume = 0.29 mL) and placed in a cooler of ice. The
127 samples were then stored in a -80°C freezer to await further processing. Chlorophyll *a* was
128 extracted in 10 mL of 90% acetone for 24 hours and filtered through a 0.45µm Acrodisc with
129 absorbance measured at 630, 647, 664, 665, and 750 nm against a 90% acetone blank (Brush MJ,
130 *personal communication*). An additional acidification step allowed for phaeophytin correction.
131 Chlorophyll *a* concentration was calculated using the following equation where V is the volume
132 of extractant in mL (10 mL), SA is the core area in cm² (0.95 cm²), and L is the light path length
133 in cm (1 cm, UV-1601 Shimadzu UV Visible) (Lorenzen 1967; Jeffrey and Welschmeyer 1997).

$$134 \quad \text{Chl}_a(\text{mg} \cdot \text{m}^{-2}) = \frac{26.7 \times (\lambda_{665} - \lambda_{665_{\text{acid}}})}{(L)} \times \frac{V}{SA} \times \frac{1 \text{ mg}}{1000 \mu\text{g}} \times \frac{10000 \text{ cm}^2}{1 \text{ m}^2}$$

135

136 *Predation Assays*

137 To examine predation pressure between the two habitats and the effect of distance from the creek
138 bank, three predation trials were conducted on successive tides. Each trial consisted of tethers in
139 both habitats positioned 1 m, 2 m, and 3 m from the creek. Each tether consisted of one adult
140 snail attached with super glue to a 15 cm segment of 1.8 kg monofilament fishing line tied to a
141 30 cm clear plastic rod. For each distance from the creek bank, 8 snails were tethered and
142 separated by at least 0.5 m from each other for a total of 24 snails per habitat. This design
143 allowed us to assess predation pressure in relation to distance from the creek, as predators of *L.*
144 *irrorata* arrive with the incoming tide. Within the vegetated habitats, each rod was placed near a
145 single plant stem and pushed into the sediment until the tether and snail were flush with the
146 sediment surface. The tether was long enough to allow snails to climb the adjacent plant stem to
147 avoid predation, but short enough that they could not get tangled with any other nearby
148 vegetation. The tethers were deployed at low tide and were retrieved after 24 hours.

149

150 *Plant Traits*

151 To determine tissue toughness of fresh leaves, we used a penetrometer consisting of an insect pin
152 attached to a plastic tray which was suspended above leaf material (Pennings et al.1998; Siska et
153 al. 2002). A plastic cup was placed on the tray and dry sand was added to the cup until the pin
154 pierced the tissue. The mass of sand in kilograms required to pierce the tissue was indicative of
155 leaf toughness. This was then converted into a measure of force in newtons (N). Toughness was
156 assessed for each leaf and an average was determined for each plant. Frozen plants were freeze
157 dried in a Labconco Freezone system for 72 hours. Dry mass was recorded, and plants were
158 ground to a fine powder using a mini Wiley mill fitted with a 40-mesh sieve. Total soluble
159 protein content was measured using a modified Bradford assay with absorbance read at 595 nm
160 and compared to a Bovine Serum Albumin (BSA) standard curve. Total phenolic concentrations
161 were determined using a modified Folin-Ciocalteu assay with absorbance measured at 760 nm
162 and compared to a ferulic acid standard curve. Carbon [C] and Nitrogen [N] content were
163 analyzed using a Fisher Scientific FlashEA system.

164

165 *Statistical Analysis*

166 All statistical analyses were conducted using R software (Version 3.5.1, R Core Team, 2018).
167 The response variables snail height and width, C:N, %N, tissue toughness, benthic chlorophyll *a*,
168 temperature, and light intensity were analyzed using one-way ANOVAs with habitat type as the
169 factor, while protein content and phenolic concentration were analyzed with ANCOVA, with
170 plant biomass serving as the covariate. For all responses the assumptions of normality and
171 homogeneity of variance were tested; if data did not meet these assumptions, responses were

172 transformed via Box-Cox transformations. For ANCOVA, the assumptions of linearity and
173 equality of slopes were also tested. If there was no relationship between the response and the
174 covariate, the covariate was removed from the model. Predation data was analyzed with a
175 binomial logistic regression, while generalized linear models with a negative binomial
176 distribution were used for radulations and snail count data. To account for differences in size
177 between *S. alterniflora* and *S. cynosuroides*, the covariate, plant height, was included in the
178 analysis of radulation data.

179

180 **Results**

181 *Snail & Environmental Data*

182 Habitat type had no significant effect on snail density ($p=0.43$), with an average of 42.15 ± 8.15
183 standard error (se) snails per m^2 across habitats. However, habitat type did influence snail height
184 ($p \ll 0.01$; *S. alterniflora*, mean= 19.27 ± 0.15 se; *S. cynosuroides*, mean= 18.40 ± 0.10 se) and
185 width ($p \ll 0.01$; *S. alterniflora*, mean= 14.94 ± 0.11 se; *S. cynosuroides*, mean= 14.35 ± 0.08 se),
186 with larger snails found in *S. alterniflora*. One snail from *S. alterniflora* habitat was excluded
187 from analysis as an outlier due to small size. There was a wider distribution of both heights and
188 widths in *S. alterniflora* than *S. cynosuroides* (Online Resource 1). Habitat type also had a
189 significant effect on the number of radulations ($p=0.05$, Fig. 2), with more found on *S.*
190 *cynosuroides* than on *S. alterniflora*. There was no significant effect of the covariate, plant
191 height, on the number of radulations ($p=0.84$). Additionally, habitat type had a significant effect
192 on daily temperature ($p=0.03$, Online Resource 2a), with higher temperatures in *S. alterniflora*
193 (Online Resource 2a), but no significant effect on daily light intensity ($p=0.86$, Online Resource

194 2b). Benthic chlorophyll *a* was similar between habitats ($p = 0.69$), for a combined mean of
195 36.19 ± 4.07 se mg/m^2 .

196

197 *Predation Assays*

198 Trial number had no significant effect on survival ($p=0.67$), therefore data from each trial was
199 pooled. We found that habitat type ($p=0.02$, Fig. 3a) had a significant effect on survival, with
200 greater survival in *S. cynosuroides* than in *S. alterniflora*. In addition, distance from the creek
201 also had a significant effect on survival ($p=0.01$, Fig. 3b), with the highest survival farthest from
202 the creek (3 m away), and the lowest survival closest to the creek (1 m away).

203

204 *Plant Traits*

205 Plant type had a significant effect on both tissue toughness ($p \ll 0.01$, Fig. 4a) and total soluble
206 protein content ($p < 0.01$, Fig. 4b), with the covariate, biomass, having no significant effect on
207 protein content ($p=0.41$). *Spartina cynosuroides* had higher protein content while *S. alterniflora*
208 tissues were tougher. In addition, plant type had no significant effect on either %N ($p=0.32$; *S.*
209 *alterniflora*, mean= 0.89 ± 0.03 se; *S. cynosuroides*, mean= 0.94 ± 0.04 se) or C:N molar ratio
210 ($p=0.59$; *S. alterniflora*, mean= 54.25 ± 2.00 se; *S. cynosuroides*, mean= 52.56 ± 2.33 se). Plant
211 type and biomass had a significant interactive effect on total phenolic concentration ($p=0.03$, Fig.
212 5). Due to this significant interaction, main effects were not explored further.

213

214 **Discussion**

215 We demonstrate, for the first time to our knowledge, that *L. irrorata* will use *S.*
216 *cynosuroides* in addition to *S. alterniflora* as habitat. Between the two habitats, we found

217 significant differences in the size of *L. irrorata*, environmental characteristics, predation
218 pressure, and palatability of plant tissue. In *S. alterniflora* habitat, we found significantly larger
219 snail height and width, higher daily surface temperatures, and tougher plant tissues. In *S.*
220 *cynosuroides* habitat, we found significantly higher plant protein content, safer habitat from
221 predation, and a higher number of radulations. Despite these differences, snails were seen
222 climbing the stems of both *S. alterniflora* and *S. cynosuroides* at high tide and densities were
223 equal between habitats. This suggests that, from a population level, snails use both habitats
224 similarly. Thus, from the perspective of *L. irrorata*, *S. cynosuroides* and *S. alterniflora* habitats
225 may be functionally redundant. Research is needed in additional marshes to confirm these
226 results, as this study was conducted in a single marsh.

227 Predation pressure on *L. irrorata* was higher in *S. alterniflora* than in *S. cynosuroides*,
228 indicating that *S. cynosuroides* serves as better predation refuge for snails. One possible
229 explanation for this trend is plant size. *Spartina cynosuroides* is much larger, in terms of biomass
230 and height, than *S. alterniflora* and potentially provides more structure to impede incoming
231 predators of *L. irrorata*, such as the blue crab (*Callinectes sapidus*), during tidal flooding.
232 Although we found greater survivorship in *S. cynosuroides* than in *S. alterniflora*, snail densities
233 did not differ between the habitats, suggesting that there is limited predator control of snail
234 populations or that the effects of predation are ultimately offset by recruitment. While *L. irrorata*
235 larvae settle over wide portions of the marsh, they do not move far from their settlement site over
236 the course of their life (Hamilton 1978; Vaughn and Fisher 1992). Distance from the creek
237 enhanced *L. irrorata* survival in both habitats, likely because plant shoots impede benthic
238 predators such as crabs (Schindler et al. 1994; Lewis and Eby 2002). This indicates that snails
239 are most susceptible to predators at the edge and that the interior provides a predation refuge, a

240 trend seen for *L. irrorata* in mixed marshes of *J. roemarianus* and *S. alterniflora* (Hughes 2012)
241 and for other mollusks in tidal marshes (ribbed mussels, *Geukensia demissa*, Lin 1989, coffee-
242 bean snails, *Melampus bidentatus*, Johnson and Williams 2017).

243 We found that benthic chlorophyll *a* concentration was similar between the two habitats,
244 which means that each habitat could provide comparable levels of algae for *L. irrorata* to
245 consume. Although it is well-documented that *L. irrorata* will graze and fungal farm on *S.*
246 *alterniflora* (Vaughn and Fisher 1992; Silliman and Zieman 2001), we found that they will also
247 graze *S. cynosuroides*, as it had more radulations than *S. alterniflora*. In our study, *S.*
248 *cynosuroides* had higher forage quality than *S. alterniflora*, as indicated by weaker tissues and
249 higher protein content. Further, *S. alterniflora* produces Dimethylsulphoniopropionate (DMSP),
250 a known deterrent to herbivores, whereas *S. cynosuroides* does not (Otte et al. 2004). The lack of
251 DMSP production and higher forage quality of *S. cynosuroides* may be responsible for
252 promoting more grazing on *S. cynosuroides*. Despite our finding that *L. irrorata* grazes more on
253 *S. cynosuroides* than *S. alterniflora*, *L. irrorata* is a generalist feeder (Alexander 1979) and both
254 plants may ultimately serve as a source of food for *L. irrorata*.

255 Our work contributes to the evidence that *L. irrorata* is a habitat generalist that will use
256 marsh vegetation other than *S. alterniflora* as habitat (Lee and Silliman 2006; Hendricks et al.
257 2011; Hughes 2012; Sieg et al. 2013; Kicklighter et al. 2018). For instance, *L. irrorata* will use
258 *Juncus roemarianus* as a refuge from predation over *S. alterniflora* in mixed-species marshes
259 (Hughes 2012), however it remains unknown whether *J. roemarianus* can also serve as a food
260 source. *Littoraria irrorata* prefers to inhabit and consume *S. alterniflora* over *Phragmites*
261 *australis*, *Bolboschoenus robustus* (Kicklighter et al. 2018), *Batis maritima*, *Borrichia*
262 *frutescens*, *Sarcocornia* sp., and *Iva frutescens* (Sieg et al. 2013), due to its low chemical defense

263 and greater palatability (Hendricks et al. 2011; Sieg et al. 2013; Kicklighter et al. 2018). Further,
264 both *P. australis* and *B. robustus* were better at inhibiting fungal growth than *S. alterniflora*,
265 leading to a greater density of *L. irrorata* on *S. alterniflora* stems than these other species
266 (Kicklighter et al. 2018).

267 Our results have implications for periwinkles adjusting to changing plant communities in
268 mesohaline marshes due to sea-level rise. Mesohaline marsh vegetation is resilient to acute
269 pulses of salinity from spatial and temporal changes in tidal salinity gradients (Jarrell et al. 2016;
270 Li and Pennings 2018), however, chronic saline presses from sea-level rise could result in a shift
271 in plant communities in mesohaline marshes from salt-intolerant (e.g., *S. cynosuroides*) to salt-
272 tolerant plant species (e.g., *S. alterniflora*). In marshes where *S. cynosuroides* and *S. alterniflora*
273 co-occur, this disparity in salt tolerance could lead to monotypic stands of *S. alterniflora*, as salt-
274 water intrusion via sea-level rise drives salinity above the threshold for *S. cynosuroides*. Our
275 results suggest that *L. irrorata* is a habitat generalist, one that will use both *S. alterniflora* and *S.*
276 *cynosuroides* as functionally redundant habitats, which may allow it to gain an ecological
277 foothold in brackish marshes as sea-level rises.

278

279 **Acknowledgements**

280 We thank the following people for help in the field and laboratory: Manisha Pant, Catherine
281 Wilhelm, Kayla Martínez-Soto, Emily Goetz, Anna Ledwin, Leah Scott, Mark Brush, and Sarah
282 Blachman. Many thanks go to the Chesapeake Bay National Estuarine Research Reserve of
283 Virginia (CBNERR-VA) and York River State Park for access to our study site, Taskinas Creek.
284 We are thankful to the Virginia Institute of Marine Science for funding this project. This work
285 was funded, in part, by the National Science Foundation (grant number 1832221) and the

286 Virginia Institute of Marine Science. This paper is Contribution No. 3899 of the Virginia
287 Institute of Marine Science, William & Mary. Lastly, we thank the snails for their persistent
288 efforts to escape.

289

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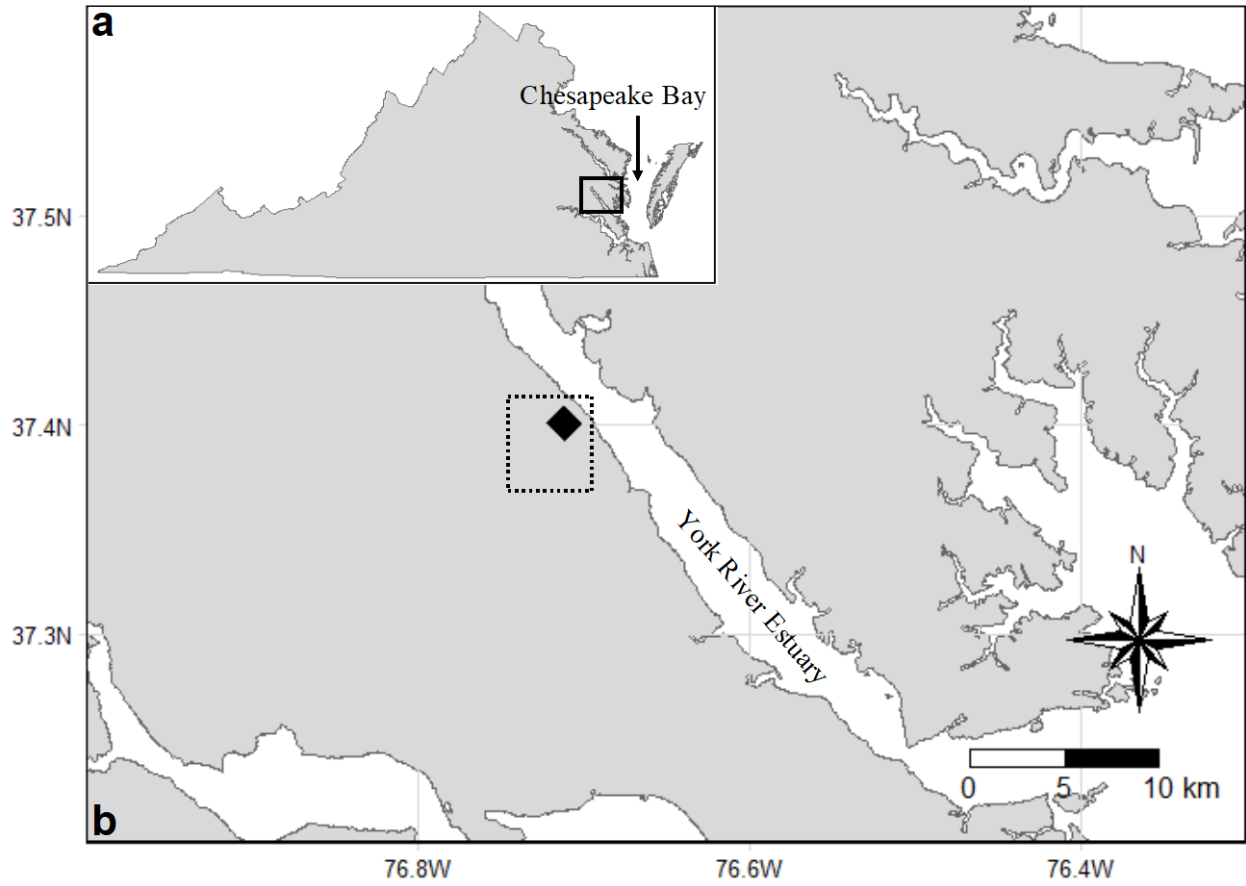
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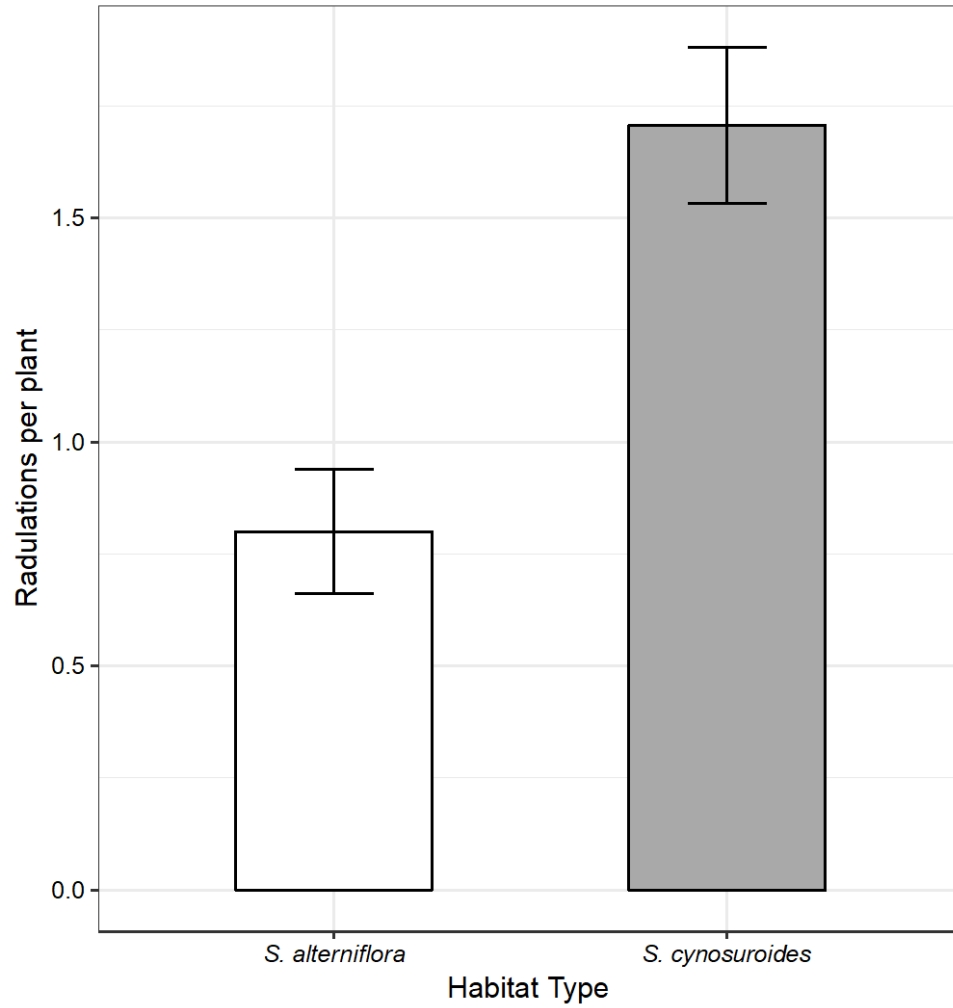
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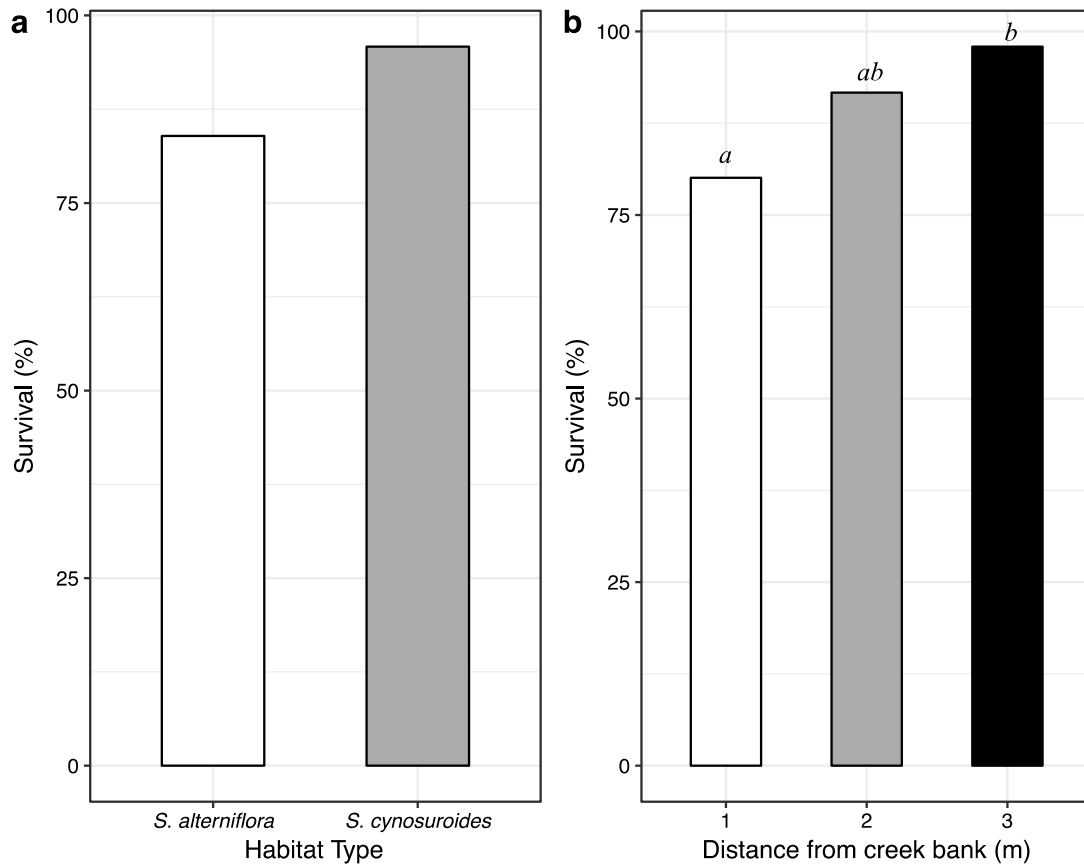
466 **Figure Captions**
467



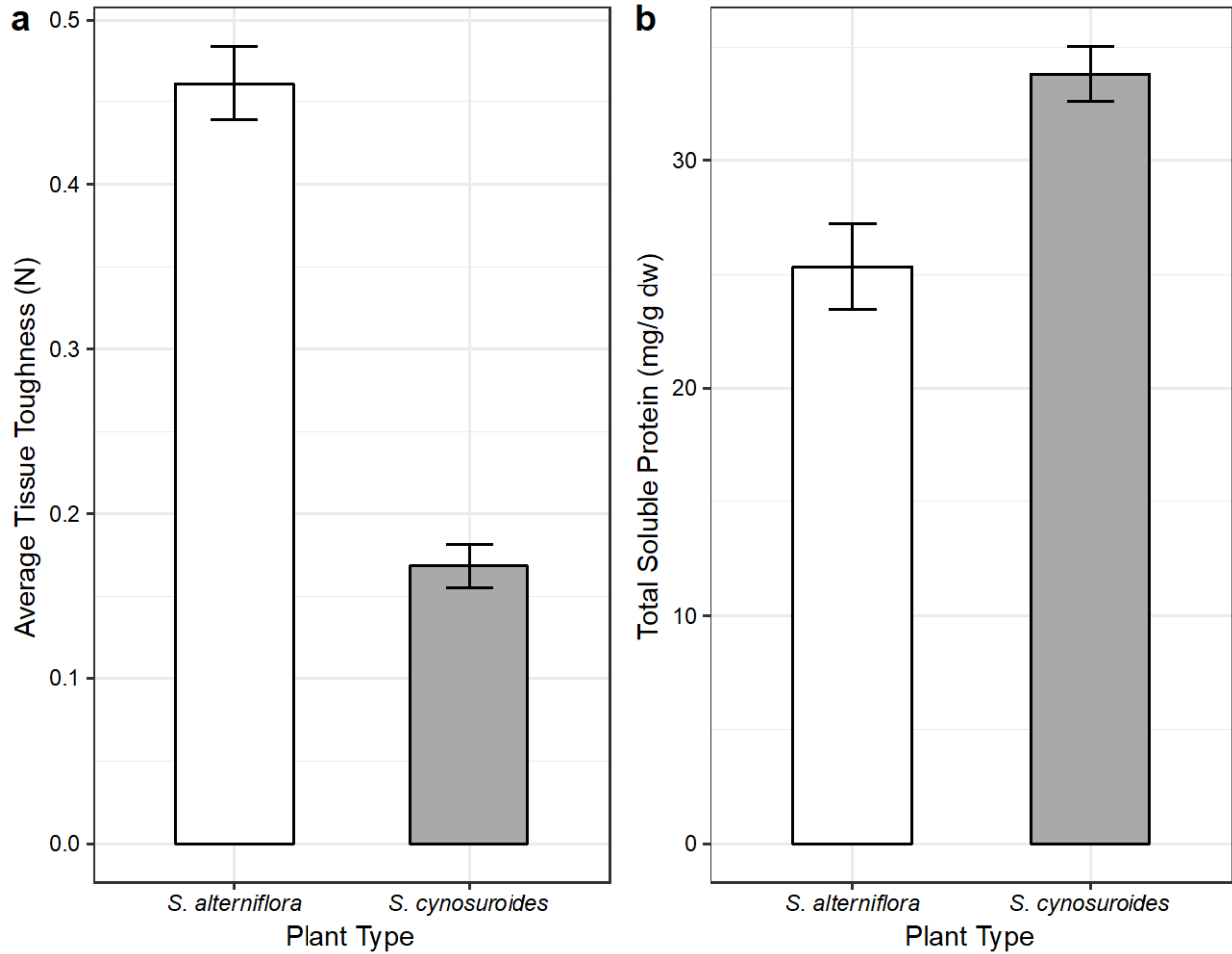
468 **Fig. 1** a) Inset map of the state of Virginia. Boxed area indicates study region and arrow points to
469 the Chesapeake Bay. b) Enlarged map of study region. Diamond is the location of Taskinas
470 Creek with dotted rectangular region representing York River State Park
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475 **Fig. 2** Mean number of radulations per *S. alterniflora* and *S. cynosuroides* habitat. Error bars
476 represent standard error
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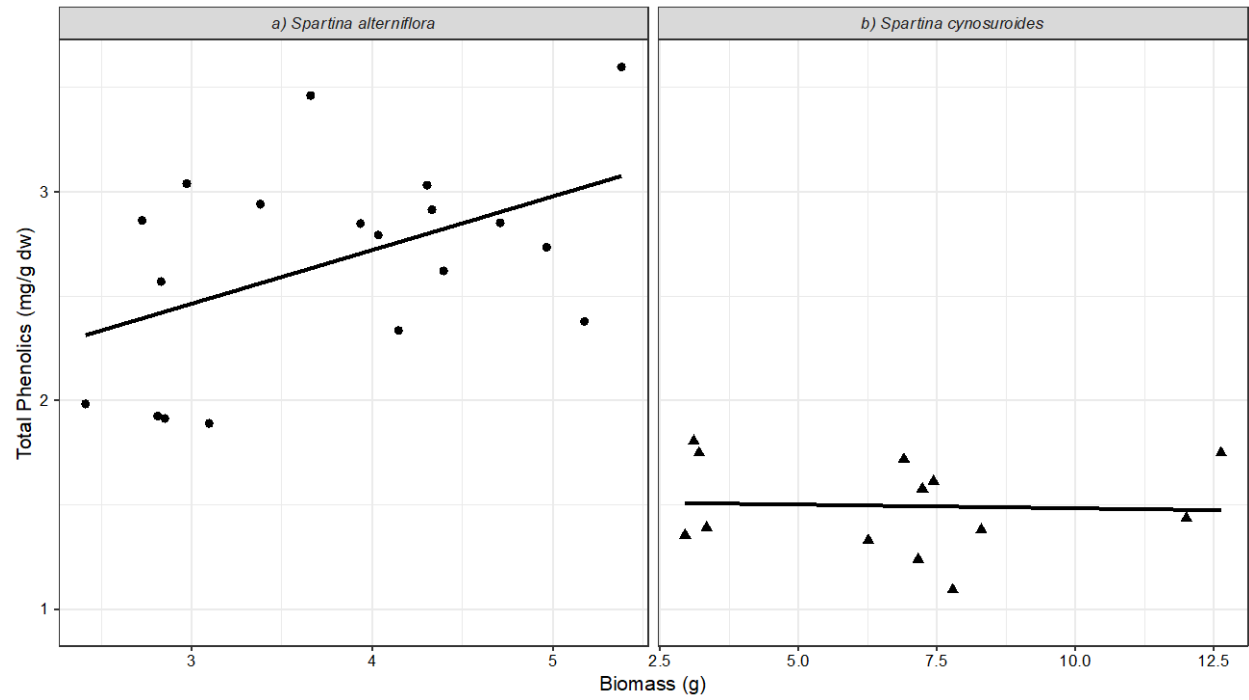


478
 479 **Fig. 3** Mean percent snail survival by a) *S. alterniflora* and *S. cynosuroides* habitat types and b)
 480 distance from the creek bank (habitats combined). The italicized letters above bars indicate the
 481 significant differences between levels
 482



483
 484 **Fig. 4** Mean a) tissue toughness in Newtons and b) total soluble protein content in milligrams per
 485 gram dry weight for *S. alterniflora* and *S. cynosuroides* tissues. Error bars represent standard
 486 error

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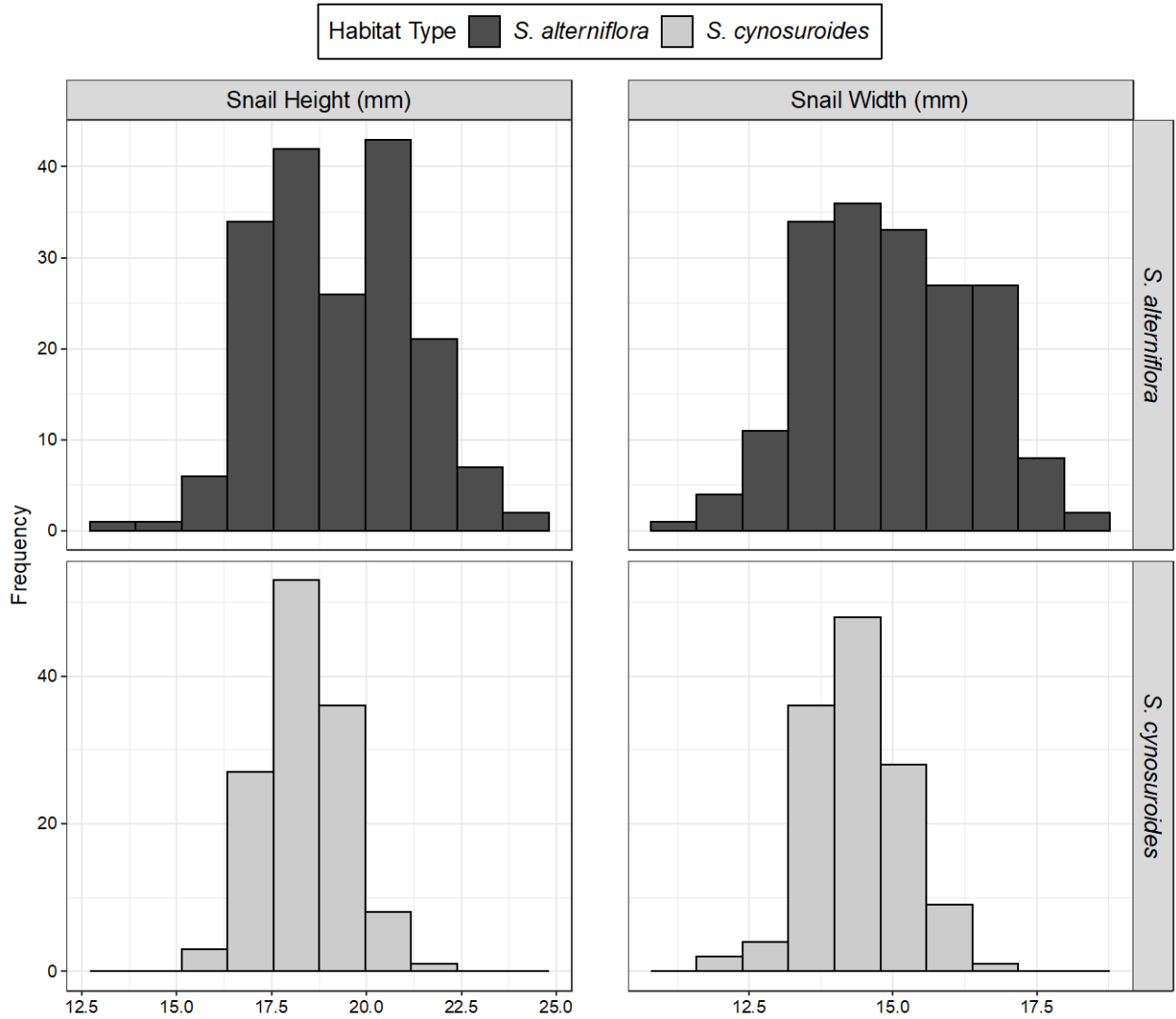


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 490 **Fig. 5** Interaction of biomass and mean total phenolic concentration for a) *S. alterniflora* and b)
 491 *S. cynosuroides*. Trend lines represent smoothed, linear regression lines

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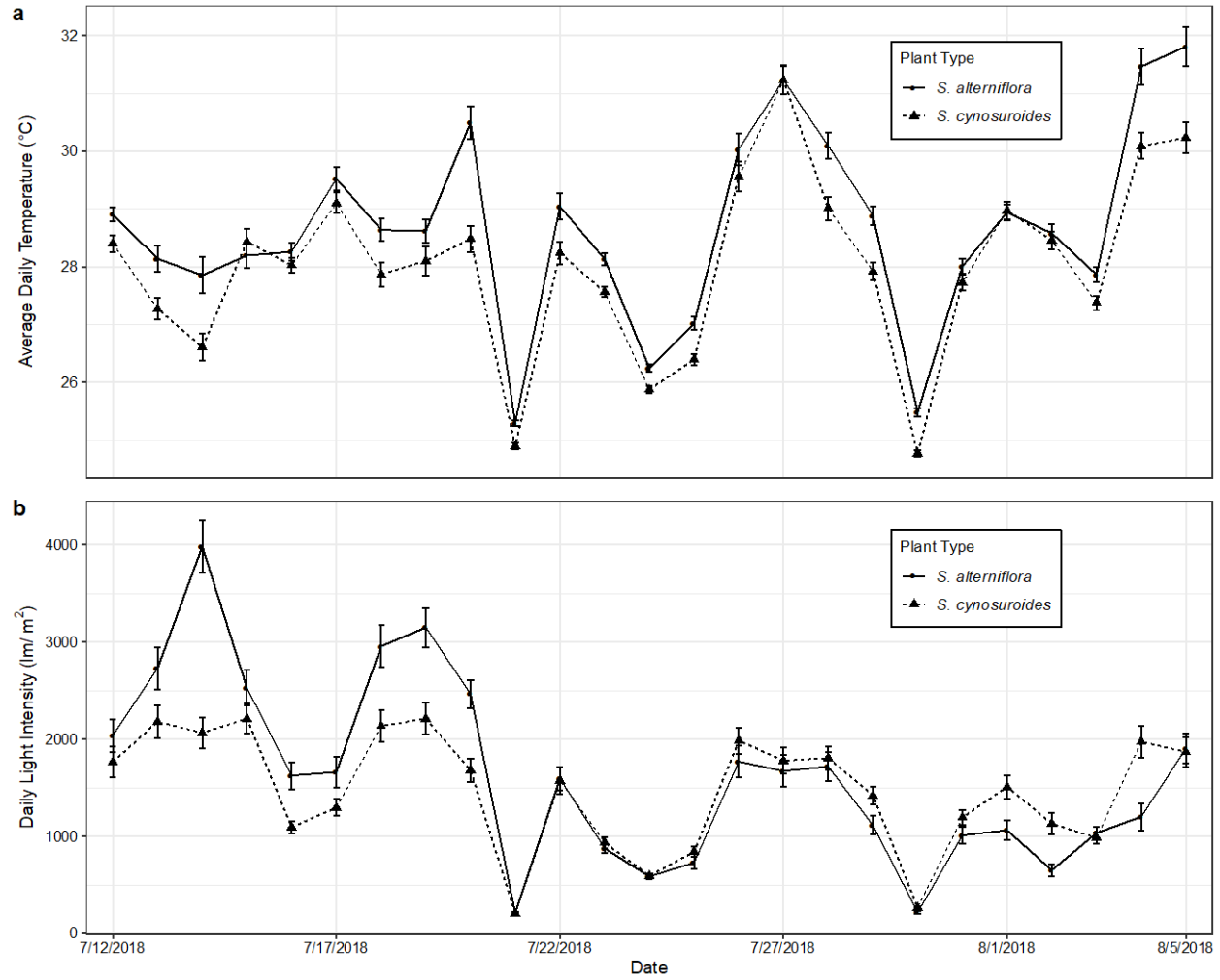
494 **Electronic Supplementary Material Captions**

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Online Resource 1 Size-frequency plots for shell height and width of *L. irrorata* found in a) *S. alterniflora* and b) *S. cynosuroides* habitats



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Online Resource 2 Mean a) daily temperature and b) daily light intensity in *S. alterniflora* and *S. cynosuroides* habitats from July 12, 2018 through August 5, 2018. Error bars represent standard error