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2 **Consumption rates vary based on the presence and type of oyster**
3 **structure: a seasonal and latitudinal comparison**

4 Jonathan S. Lefcheck^{1*}, Bruce W. Pfirmann², F. Joel Fodrie³, Jonathan H. Grabowski⁴, A. Randall
5 Hughes⁴, Ashley R. Smyth⁵

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7 ¹Tennenbaum Marine Observatories Network, MarineGEO, Smithsonian Environmental Research
8 Center, Edgewater, Maryland 21037 USA

9 ²Baruch Marine Field Laboratory, University of South Carolina, Georgetown, SC 29442 USA

10 ³Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557
11 USA

12 ⁴Department of Marine and Environmental Sciences, Northeastern University, Nahant, MA 01908
13 USA

14 ⁵Soil and Water Sciences Department, Tropical Research and Education Center, University of
15 Florida, Homestead, FL 33031 USA

16

17 *Corresponding author: LefcheckJ@si.edu

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19 **Running head:** Consumption in oyster habitats

20

21 **Abstract**

22 As oyster reefs continue to decline worldwide, interest has turned to restoration and aquaculture as
23 ways to sustain the services derived from these ecologically and economically valuable habitats.

24 While biogenic oyster reefs support a variety of ecological functions, it remains unclear whether
25 aquaculture and its associated infrastructure can provide equivalent levels of functioning. Here, we
26 compare consumption rates by fish and invertebrate predators, a key indicator of energy transfer
27 between trophic levels, between reef and aquaculture habitats for the Eastern oyster (*Crassostrea*
28 *virginica*) in the Western Atlantic. We deployed a standardized dried squid prey item ('Squidpops')
29 in three different structured settings: biogenic oyster reefs, on-bottom aquaculture, and off-bottom
30 aquaculture. For each habitat treatment, we also implemented an adjacent control in nearby bare
31 (unstructured) sediment. These assays were repeated across three seasons at twelve locations
32 spanning 900 km of coastline. We found that consumption rates were contingent on the presence
33 and type of structure: they were highest near off-bottom floating bags, and the difference between
34 structured habitats and unstructured controls was also greatest for this treatment. Moreover, at
35 large temporal and spatial scales, consumption rates increased with increasing temperature, and
36 independently declined with increasing latitude. Our study revealed that certain types of
37 aquaculture support comparable or greater consumption rates than natural reefs, suggesting an
38 important role for this novel structured habitat in maintaining coastal food webs.

39 **Keywords:** predation; foraging; *Crassostrea virginica*; aquaculture; restoration; Squidpops

40

41 **Highlights**

- 42 • Shellfish aquaculture is increasing to meet global demands for oysters.
- 43 • Can oyster aquaculture provide similar ecosystem services as oyster reefs?
- 44 • We measured bait loss on reefs and two types of aquaculture at 12 sites.
- 45 • We show certain aquaculture types can increase consumption beyond that on reefs.
- 46 • Novel aquaculture infrastructure may contribute to coastal ecosystem functioning.

47

48 **1. Introduction**

49 Once a prominent feature of nearshore ecosystems, oyster reefs have declined by an
50 estimated 85% worldwide in the last century, making them among the most imperiled coastal
51 habitats (Beck et al., 2011; Zu Ermgassen et al., 2012). Oysters function as both a fishery and a
52 habitat, so their decline has both economic and ecological impacts (Grabowski et al., 2012; Newell,
53 2004). To the latter point, oyster reefs provide complex structure that serves as refuge for juvenile
54 and adult organisms, many of which recruit to commercially important fisheries (Lowery et al.,
55 2007; Wells, 1961). Furthermore, the oysters themselves improve water quality by filtering
56 suspended material from the water column (Kellogg et al., 2014) and counter the effects of nutrient
57 pollution by promoting denitrification (Hoellein et al., 2015; Piehler and Smyth, 2011).
58 Consequently, restoration is underway throughout much of the world as a way to enhance local
59 populations, revitalize oyster fisheries, and safeguard the economic and ecosystem services
60 provided by healthy reefs (Beck et al., 2011; Bersoza Hernández et al., 2018).

61 At the same time, bivalve aquaculture has experienced tremendous growth over the last 50
62 years, now accounting for more than half of all aquaculture production, which itself accounts for
63 46% of all fisheries production worldwide (FAO, 2020). As this practice continues to expand, there
64 arises a potential conflict for available space and resources: aquaculture operations often occupy
65 bottom area that is suitable for restoration of biotic habitats—including foundational species such
66 as oysters and submersed aquatic vegetation (Dumbauld et al., 2009; Orth et al., 2017). Moreover,
67 with growing interest in oyster restoration for purposes other than biomass production, such as
68 water quality management (Bricker et al., 2017), there is an urgent need to understand whether
69 aquaculture operations can provide comparable services as the natural systems they potentially
70 replace. For example, denitrification rates can be significantly higher at aquaculture sites compared

71 to natural reefs (Humphries et al., 2016), although this has not been observed everywhere
72 (Lunstrum et al., 2018).

73 A well-recognized service of oyster reefs is the provision of habitat. The complex three-
74 dimensional structure provided by reefs supports a diverse and abundant assemblage of
75 invertebrates and small fishes, providing them refuge and concentrating their forage base (Tolley
76 and Volety, 2005). The addition of reef structure in systems otherwise dominated by soft-sediments
77 also increases nekton biomass and enhances fishery production and value (Coen et al., 1999;
78 Humphries and La Peyre, 2015; Peterson et al., 2003; Ziegler et al., 2018; zu Ermgassen et al.,
79 2016). Although aquaculture does not produce identical biogenic structure to reefs, the addition of
80 fixed cages on shallow bottoms or off-bottom floating bags in relatively deeper water an increase
81 the availability of hard structure in soft sediment habitats. These structures may mimic that of
82 oyster reefs in offering refuge and/or foraging habitat. Indeed, both invertebrate epi- and
83 macrofauna (Dealteris et al., 2004; Dumbauld et al., 2009; Erbland and Ozbay, 2008) and their fish
84 predators (Tallman and Forrester, 2007) have all been observed at similar or greater densities on
85 oyster aquaculture gear than on biogenic reefs (reviewed in Callier et al., 2018).

86 The concentration of both predators and prey on oyster reefs might be expected to lead to
87 higher rates of predation and greater trophic transfer, as has been observed across many
88 structured marine ecosystems (Aronson and Heck, 1995; Lefcheck et al., 2019). Alternately, the
89 three-dimensional habitat may provide increased refuge, reducing consumption relative to open
90 areas where prey are more exposed and therefore more vulnerable (Crowder and Cooper, 1982;
91 Summerson and Peterson, 1984). Whether either of these expectations are associated with
92 aquaculture infrastructure remains relatively unexplored (but see Clarke 2017), although
93 differences in predation between artificial structures and natural coastal habitats have recently
94 been observed for docks and piers (Rodemann and Brandl, 2017).

95 Historically, experiments to test the relationship between structure and ecological
96 processes such as predation, competition, and trophic transfer have been challenging to implement
97 in the field at large scales. For example, traditional methods such as tethering may lead to issues
98 with prey availability, create artifacts by impeding prey behavior in ways that varies across
99 habitats, and result in mismatch of prey identities at scales that cross whole-estuary, regional, or
100 even biogeographic realms (Peterson and Black, 1994). One recently proposed solution is the
101 ‘Squidpop,’ which is a standardized assay of relative consumption using a dried squid bait (Clarke,
102 2017; Duffy et al., 2015; Rodemann and Brandl, 2017) (Fig. 1A). In contrast to traditional tethering
103 assays, dried squid presents a standard prey (or carrion) item, and thus is advantageous for large-
104 scale comparative experiments where the same prey species may not be available in each location
105 (Duffy et al., 2015; Whalen et al., 2020). It is also of marine origin, resistant to degradation in the
106 water, and is easily shipped and stored for long periods. The loss of bait from Squidpops through
107 time has positively correlated with the abundance, length, composition, and diversity of
108 mesopredators in the vicinity (Duffy et al., 2015; Rhoades et al., 2019; Whalen et al., 2020),
109 including a range of fishes and invertebrates (Musrri et al., 2019; Whalen et al., 2020), thus making
110 Squidpops a useful method for the aims of our study.

111 Here, we investigated whether the addition and type of structure modifies consumption
112 rates across shallow oyster-dominated subtidal habitats. Specifically, we deployed Squidpops at
113 multiple kinds of aquaculture operations and biogenic reefs of the Eastern oyster, *Crassostrea*
114 *virginica*, along the east coast of the US. These assays were repeated over several seasons to further
115 evaluate trends in consumption through time. We also paired each assay with an adjacent soft-
116 sediment location to serve as an unstructured control. We aimed to broadly test whether and how
117 artificial and natural structure affects consumption rates in oyster-dominated habitats.

118 **2. Materials and Methods**

119 *2.1 Study Sites*

120 We selected twelve locations in three states along the east coast of the US (Fig. 2). In North
121 Carolina (abbreviated NC), we conducted the experiments at an off-bottom floating bag aquaculture
122 operation (Cedar Island: 35.00 N, -76.30 W) and two oyster reefs (North River Marsh: 34.72 N, -
123 76.61 W). In Virginia (VA), we deployed our assays at three sites within the York River estuary: a
124 floating bag oyster aquaculture operation (Big Island Aquaculture Company: 37.27 N, -76.39 W), an
125 on-bottom rack-and-bag aquaculture site (Virginia Institute of Marine Science: 37.25 N, -76.50 W),
126 and a restored oyster reef (Timberneck Creek: 37.29 N, -76.54 W). Finally, in Rhode Island (RI), we
127 selected three on-bottom rack-and-bag operations (Narragansett Bay: 41.65 N, -71.26 W; Ninigret
128 Pond: 41.36 N, -71.67 W; and Winnapaug Pond: 41.32 N, -71.79 W) with adjacent biogenic reefs
129 (Narragansett Bay: 41.64 N, -71.24 W; Ninigret Pond: 41.35 N, -71.69 W; and Winnapaug Pond:
130 41.33 N, -71.80 W). Examples of each habitat type are given in Figure S1. We deployed the Squidpop
131 assays in July, August, October, and December 2016 in NC; in June, July, August, October, and
132 November 2016 in VA; and in July and October 2016 in RI.

133 *2.2 Consumption Assay*

134 A Squidpop is a 1.3-cm diameter circle of dried squid (Golden Squid Brand, Hong Kong,
135 China) tethered to a 76-cm garden stake (EcoStake). Squids are attached using approximately 5-cm
136 of monofilament line affixed to the stake. These stakes are then inserted into the sediment so that
137 approximately 20-cm of stake is exposed above the surface (Fig. 1A). On oyster reefs, stakes were
138 deployed as close to the reefs as possible while still providing soft enough substrate to insert the
139 stake to the standard depth. For on-bottom aquaculture operations, stakes were deployed
140 immediately adjacent to the cages, and for off-bottom, directly underneath the floating bags. We
141 paired each structured assay with an unstructured control located in a bare substrate area 50-100
142 m distant and at approximately the same depth and exposure. For each deployment and treatment,

143 we set out $n = 25$ Squidpops per treatment at low tide. We checked the Squidpops after 1- and 24-
144 hours and scored them as present or consumed (absent). For each deployment, we also deployed
145 GoPro Hero 3+ video cameras aimed at a separate uncounted replicate to capture the identity of
146 any potential predators. Because of poor visibility across most sites, we did not formally analyze
147 any of the GoPro footage other than to provide some anecdotal examples of predators interacting
148 with the Squidpops (Fig. 1B-D). We used a data sonde (YSI Instruments) to record temperature and
149 salinity at each site during each sampling event, and a Secchi disk to measure turbidity at sites in
150 two regions (NC and VA).

151 2.3 Statistical Analysis

152 We analyzed our split-plot design using generalized linear mixed effects models as
153 implemented in the *lme4* package (Bates et al., 2015) in the R statistical software version 4.0.3 (R
154 Core Team, 2017). We modeled the two-way interaction between the within-plot treatment
155 (structured vs. unstructured habitat) and the between-plot treatment (reef, on-bottom, and/or off-
156 bottom aquaculture habitat), plus the additional main effects of latitude, temperature, and salinity.
157 We fit the binary response (presence or absence of squid bait) to a binomial distribution with a
158 logit link. We included crossed random effects of month and site to account for potential temporal
159 and spatial autocorrelation among sites and through time. We report marginal and conditional R^2
160 values reflecting the deviance explained by fixed effects alone and the fixed and random effects,
161 respectively, which were obtained using the *piecewiseSEM* package (Lefcheck, 2016). Because not
162 all treatments were present at all sites, we re-fit the same model within each region (NC, VA, RI),
163 removing latitude as a predictor and only including a random effect of month. For the within-region
164 models for NC and VA, we included an additional predictor of Secchi depth. For all models, we held
165 an experiment wide $\alpha = 0.05$. All data and code necessary to replicate all analyses and figures are
166 included in the supplementary materials.

167 3. Results

168 After 24 h and across all sites and months, we found that the average effect of structure on
169 consumption rates depended on the type of structure (Table 1). Specifically, the loss of Squidpops
170 underneath off-bottom floating bags was higher and enhanced to a greater degree relative to the
171 bare sediment than in the other two habitat treatments ($P < 0.001$) (Fig. 3A; see supplementary
172 code for reproduction using model-estimated means). This trend was dominated by the off-bottom
173 floating bag aquaculture site in VA, which exhibited 1.6x greater loss of Squidpops on average than
174 in the nearby unstructured control (Fig. 4). Consumption was lowest adjacent to on-bottom rack-
175 and-bags, which significantly but minimally increased consumption relative to the unstructured
176 control over the course of the study ($P = 0.002$) (Fig. 3A). This effect was driven primarily by sites
177 in RI (Fig. 4). In contrast to the two types of aquaculture, consumption rates were generally lower
178 immediately adjacent to biogenic reefs than in nearby bare sediment (Fig. 3A), driven by sites in
179 both NC and RI (Fig. 4). Consumption rates were maximal in the summer and declined through the
180 fall and winter in NC and VA, while in RI, consumption was greater in October than in July (Fig. 5).

181 In general, salinity and Secchi depth varied among sites and from month-to-month, while
182 temperature declined in all regions from June to December (Fig. S2). We found that consumption
183 rates significantly declined with latitude, independently increased with temperature, and declined,
184 but not significantly so, with salinity (Table 1, Fig. 6). While there are undoubtedly many other
185 constraints on foraging in these systems, our fixed effects alone (including the experimental
186 treatments and the three environmental covariates) explained nearly half of the deviance in
187 consumption rates (marginal $R^2 = 0.47$), with a further 22% explained by our random effects of
188 month and site (conditional $R^2 = 0.69$).

189 Examining loss of Squidpops after only 1 h revealed similar trends to the 24 h analysis, with
190 a few distinctions. First, consumption rates were overall lower after 1 h (11-44% loss on average,

191 compared to 37-75% after 24 h; Fig. 3B), leading to a slightly lower proportion of explained
192 deviance (marginal $R^2 = 0.45$, conditional $R^2 = 0.64$). Second, the average consumption rate was
193 approximately equivalent at biogenic reefs and on-bottom rack-and-bag aquaculture after only 1 h
194 (Fig. 3B), leading to a non-significant interaction with structure involving these two habitat
195 treatments (Table S1). Third, the enhancement in consumption beneath off-bottom floating bags
196 relative to adjacent sediment was still significant and even stronger after 1 h than 24 h—a 2.2x
197 increase (Fig. 3). Temperature was the only significant environmental covariate predicting
198 consumption rates after 1 h (Table S1).

199 Finally, we found qualitatively identical results to the main analysis when fitting within-
200 region models for NC and RI (Tables S2, S3), except we did not recover a significant two-way
201 interaction in VA due to similar levels of consumption observed near natural reefs and on-bottom
202 racks relative to their adjacent unstructured controls. Instead, in VA, consumption was significantly
203 increased under floating bags relative to the other two structured habitats (Table S4, Fig. 4).
204 Similarly, temperature remained significant in NC and RI but not VA. For the two regions where
205 Secchi depth was measured, it had significant but contrasting effects: consumption was greater at
206 greater Secchi depths (higher clarity) in VA (Table S4), but lower at greater Secchi depths in NC
207 (Table S2).

208 **4. Discussion**

209 Our study of consumption rates near artificial structures associated with oyster aquaculture
210 versus those on biogenic reefs revealed a strong interaction between the presence and type of
211 structure on loss of a standardized bait after both 1 and 24 h , an effect which also varied across
212 locations. Variation in consumption pressure between the different structured habitats and bare
213 sediment controls likely stem from differences in their water column position and the nature of the

214 hard structure, which in turn affects the type and efficiency of predators and scavengers that forage
215 on these habitats across the three biogeographic regions.

216 In the case of off-bottom floating bags, assays were deployed ~1 m below the bags at low
217 tide and slightly above the benthos, providing a greater three-dimensional volume over which
218 mobile consumers can forage. Like natural substrates, the sides and underside of the floating bags
219 support an abundant and diverse faunal community that can be exploited by predators. A previous
220 study on floating bag operations in Virginia reported faunal densities ranging from 12,000-92,000
221 individuals per 61-by-61 cm bag, comprised of worms, crustaceans, and small fishes also common
222 to biogenic reefs (O'Beirn et al., 2004), and similarly high faunal densities have been reported on
223 floating bag aquaculture in Delaware Bay (Marenghi et al., 2010) and New Brunswick, Canada
224 (Mallet et al., 2006). Moreover, the high animal biomass associated with the off-bottom floating
225 bags can potentially increase nutrient delivery to the sediments below the bags in areas with low
226 water velocities, supporting productive epibenthic and infaunal communities (Erbland and Ozbay,
227 2008; Mallet et al., 2006; Testa et al., 2015). It is likely then that predators and scavengers already
228 attracted to the high densities of prey both on and below the off-bottom aquaculture also honed in
229 on the Squidpops, leading to the overall highest consumption rate in this habitat treatment.

230 While on-bottom racks have similar capacity to enhance faunal communities (Mallet et al.,
231 2006; Marenghi et al., 2010), they are often positioned inshore in shallow areas as to improve
232 accessibility by growers. Consequently, the on-bottom infrastructure is periodically exposed by
233 tides and remains relatively inaccessible to predators for long stretches, unlike floating bags in the
234 water column which rise and fall with the tide. Periodic exposure may also explain lower rates
235 observed on intertidal reefs in NC, where access by small fishes is also limited (Ziegler et al., 2018).
236 Even when inundated by the tide, predators may have more difficulty locating and consuming the
237 Squidpop assays when they were hidden or restricted by structured habitats on the bottom than on
238 exposed bare substrate underneath the floating bags (Crowder and Cooper, 1982).

239 Oyster reefs were the only structured habitat where loss of squid bait was generally greater
240 in the unstructured control. There are several potential explanations for this finding. First, habitat
241 complexity and landscape context may alter foraging strategies: biogenic oyster reefs can vary
242 considerably in height, aerial extent, exposure, and complexity, which contrasts the uniformity of
243 aquaculture structure. In turn, larger, more complex or connected reef systems may provide more
244 shelter for mesopredators who target the Squidpops. For example, *in situ* measurements of rugosity
245 at two of our sites based on the 'chain-link method' suggest more heterogenous reefs in VA
246 compared to NC (60.7 cm per 0.5 m length in NC vs. 154.5 cm per 0.5 m in VA), potentially
247 explaining the higher rates of consumption adjacent to reefs there (Fig. 4). Second, the total
248 footprint of remaining biogenic reefs is perhaps less in the regions studied relative to bottom
249 covered by aquaculture, meaning that there is simply a lot less structure over which to forage on
250 reefs, forcing predators to forage in adjacent unstructured sediments.

251 A final explanation for the differences in predation across structured habitats may be the
252 spatial distribution of our sites. Floating bag operations were only tested at the southern and
253 intermediate sites (NC and VA) while rack-and-bag operations were only tested at the intermediate
254 and northern sites (VA and RI) (Fig. 2), largely due to different adoption of these two gear types
255 across different states (Baillie et al., *in review*). Latitude emerged as a significant predictor of bait
256 loss from our mixed model, with higher consumption at lower latitudes (Table 1, Fig. 6A). In theory,
257 the effect of latitude is independent from habitat type in our statistical model, but this inference is
258 slightly conflated by the uneven implementation of habitats across the latitudinal gradient. Thus,
259 higher predation in certain gear types, like off-bottom floating bags, may be partially because this
260 gear type was only tested at low latitudes, and vice versa for on-bottom aquaculture.

261 Biogenic oyster reefs, however, were tested across all three regions, suggesting that the
262 latitudinal effect may still reflect ecological processes operating at broad scales. For example, biotic
263 interactions are typically stronger at lower latitudes due to greater productivity and diversity of

264 these communities (Schemske et al., 2009), echoing similar trends observed in seagrass bed fauna
265 (Reynolds et al., 2018) and terrestrial caterpillars (Roslin et al., 2017). GoPro footage revealed
266 potentially different consumers across the range of sites whose distribution and dominance differ
267 along the latitudinal gradient, such as pinfish (*Lagodon rhomboides*, Fig. 1D) which are rarely
268 present north of NC. Indeed, a recent paper demonstrated strong biogeographic differences in
269 resident food webs across oyster reefs south of our study area (Grabowski et al., 2020). Reef
270 properties may also change with latitude: live biomass, reef height and juvenile recruitment all vary
271 with increasing latitude which likely affects the amount of available habitat for prey and predators
272 (Byers et al., 2015), and could potentially explain why consumption rates were much lower in RI
273 than in the other two regions. Future studies could explore a wider gradient in reef properties using
274 the standard Squidpop assay to resolve these questions.

275 We also found a strong effect of temperature in our model: as temperature increased, so did
276 bait loss (Table 1, Fig. 6B). We note that this effect is independent of latitude: even though higher
277 latitudes are generally cooler, there was much greater variation in temperature through time than
278 across space, making temperature more of a seasonal rather than a spatial indicator. The
279 temperature effect likely stems from higher metabolic demands leading to greater resource
280 utilization in the summer (Brown, 2004) as well as seasonal turnover in the predator communities.
281 Demersal fish biomass and diversity peak in the early summer months in NC and VA (Lefcheck et
282 al., 2014; Ziegler et al., 2018) and in late summer and early fall in RI (Oviatt and Nixon, 1973),
283 tracking the observed consumptions rates through time in these regions (Fig. 5).

284 Finally, our model revealed that consumption rates were uncorrelated with changing
285 salinity (Table 1, Fig. 6C). One potential explanation is that the predator community (and/or their
286 preference for the squid bait) does not respond to or change drastically along the salinity gradient
287 captured during our survey (14-33 psu), especially for the more variable estuarine sites in NC and
288 VA. The blue crab (*Callinectes sapidus*), for example, was often found interacting with the Squidpops

289 in all three regions (Fig. 1B) and can be abundant at mesohaline salinities and higher. Furthermore,
290 the contrasting results of Secchi depth for in NC and VA suggest that the effect of water clarity is not
291 well resolved in the current study. Thus, environmental drivers in the form of both salinity and
292 water clarity are deserving of further attention with respect to their effects on consumption in
293 marine and estuarine systems.

294 **5. Conclusions**

295 That significant effects of habitat type (particularly off-bottom floating bags), structure,
296 latitude, and temperature on consumption emerged despite considerable spatial and environmental
297 variation suggests that, unlike other context-dependent functions such as denitrification
298 (Humphries et al., 2016; Lunstrum et al., 2018; Smyth et al., 2015), consumer pressure may be
299 reliably enhanced by floating-bag aquaculture. Such operations often occur in areas that are too
300 deep or muddy to allow for natural restoration or on-bottom aquaculture (Dumbauld et al., 2009),
301 and thus may subsidize trophic processes occurring in these unstructured habitats. While biogenic
302 reefs provide many additional services, such as nursery habitat and shoreline protection (Beck et
303 al., 2011), the finding that aquaculture may increase trophic transfer should inform guidance on the
304 placement of aquaculture leases and evaluation of their ecosystem impacts relative to natural
305 systems.

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480

481 **Table 1.** Output from a generalized linear mixed effects model predicting consumption (as the log
482 odds ratio) after 24 h as a function of within-plot (structured vs. unstructured) by between-plot
483 treatments (reef—as the reference level—compared to off-bottom floating bag and on-bottom rack-
484 and-bag aquaculture) and other covariates across all regions.

Predictor	Estimate	Std. Error	Z-value	P-value
Intercept	17.4880	6.9990	2.4986	0.0125
Structured vs. unstructured	-0.9187	0.2281	-4.0279	<0.001
Habitat (off-bottom)	-1.5400	1.1551	-1.3332	0.1825
Habitat (on-bottom)	-1.0575	0.8556	-1.2359	0.2165
Latitude	-0.5448	0.1810	-3.0094	0.0026
Temperature	0.2548	0.0417	6.1150	<0.001
Salinity	-0.0801	0.0412	-1.9440	0.0519
Structured-x-on-bottom	2.4023	0.3790	6.3381	<0.001
Structured-x-off-bottom	1.3615	0.3459	3.9358	<0.001

485

486 **Figure Captions**

487

488 **Figure 1. (A)** The Squidpop is a piece of dried commercial squid tethered to a garden stake inserted
489 approximately 20 cm above the sediment surface. **(B)** The blue crab (*Callinectes sapidus*)
490 interacting with Squidpops in Virginia (facing toward the rear Squidpop, arrow). **(C)** A juvenile
491 black sea bass (*Centropristis striata*) before taking the bait in Rhode Island. **(D)** A pinfish (*Lagodon*
492 *rhomboides*) after having consumed the squid in North Carolina.

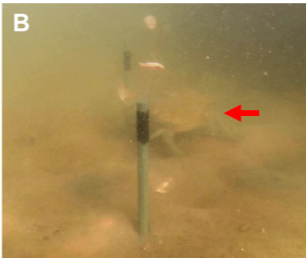
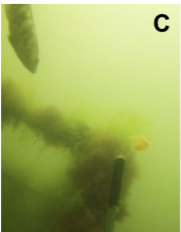
493 **Figure 2.** A map of study sites, including biogenic oyster reefs (black triangles) and both on-bottom
494 (red circle) and off-bottom (blue square) oyster aquaculture operations.

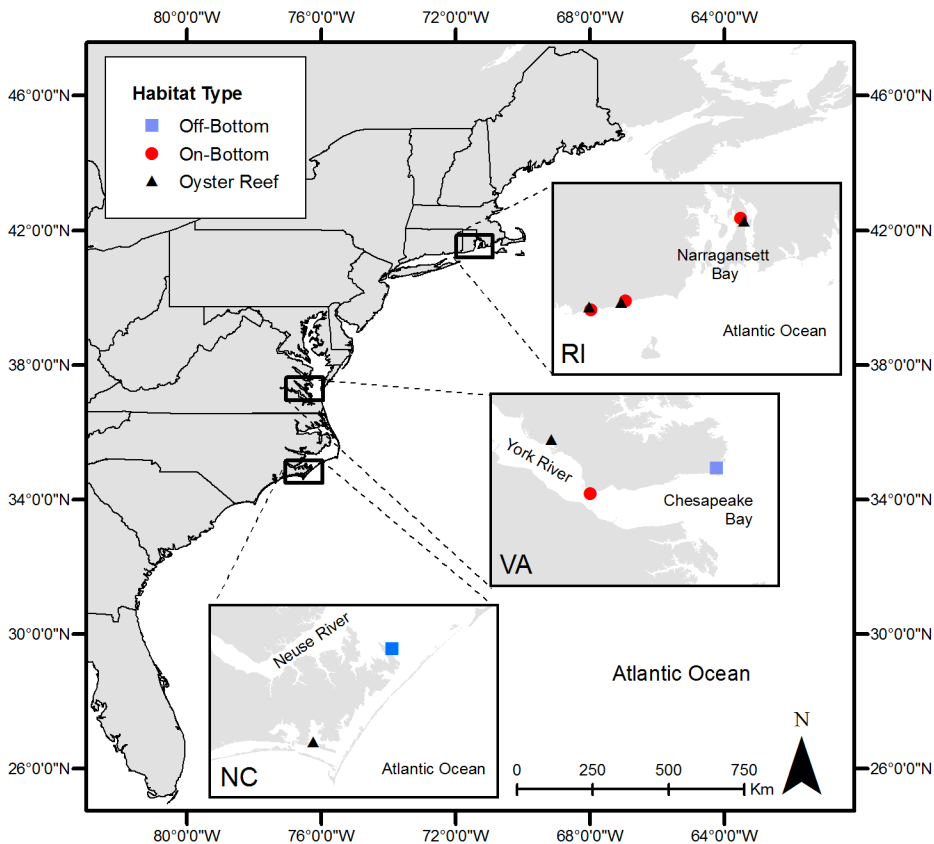
495 **Figure 3.** Plot of average consumption rate after **(A)** 24 h and **(B)** 1 h for within-plot (structured vs.
496 unstructured) and between-plot treatments (reef, off-bottom floating bag, and on-bottom rack-and-
497 bag aquaculture). Bars are means \pm 1 pooled standard deviation.

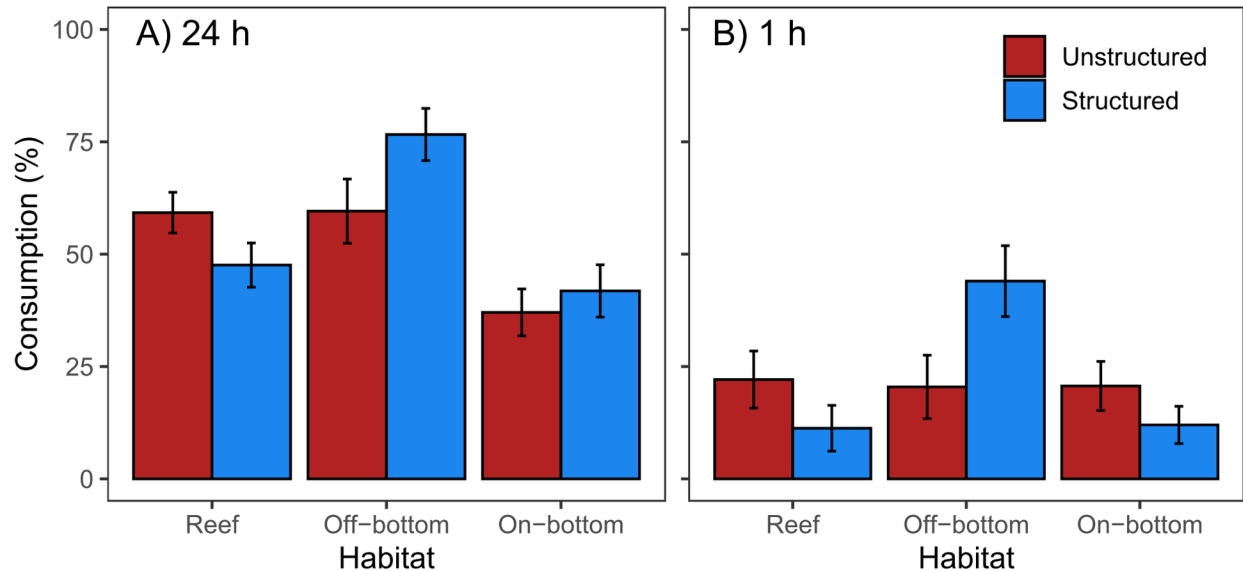
498 **Figure 4.** Mean consumption across all months \pm 1 standard deviation (pooled) for each habitat
499 across all regions, and for each individual region.

500 **Figure 5.** Time series of consumption (as proportional loss of Squidpops) by region, between-plot
501 (reef, off-bottom floating bag, and on-bottom rack-and-bag aquaculture), and within-plot
502 treatments (structured vs. unstructured). Note that in RI there are multiple structured and
503 unstructured locations.

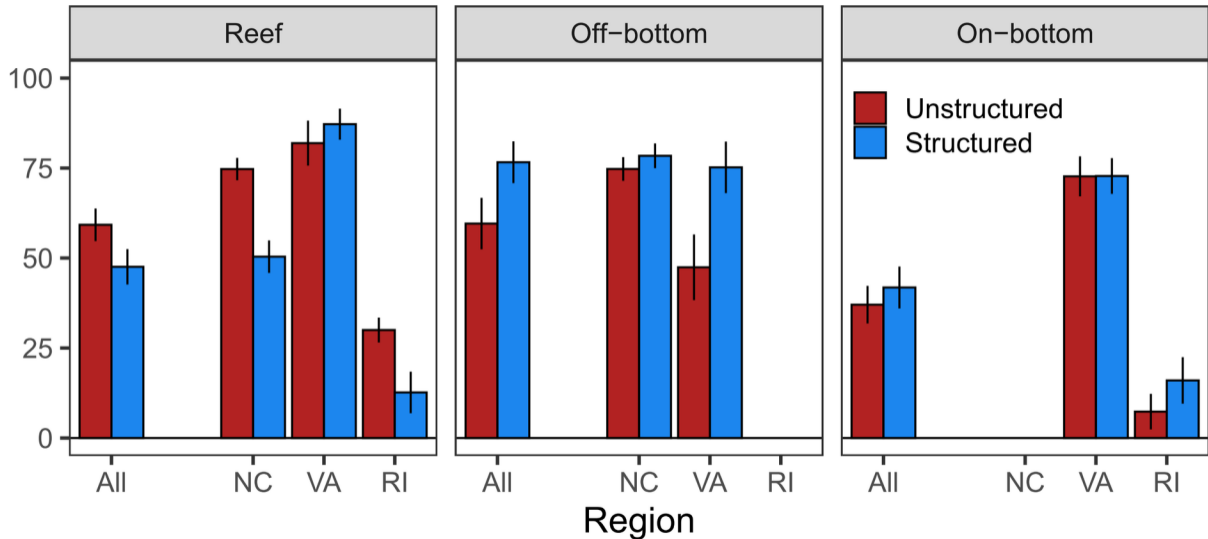
504 **Figure 6.** Predicted effects of environmental covariates on consumption rates from a generalized
505 linear mixed effects model (Table 1). Fitted lines represent the independent (partial) effects given
506 the contributions of other variables in the model (Z). Solid lines indicate significant trend ($P < 0.05$).
507 The distribution of raw data points is given by rug plots along the x-axis and colored by region.

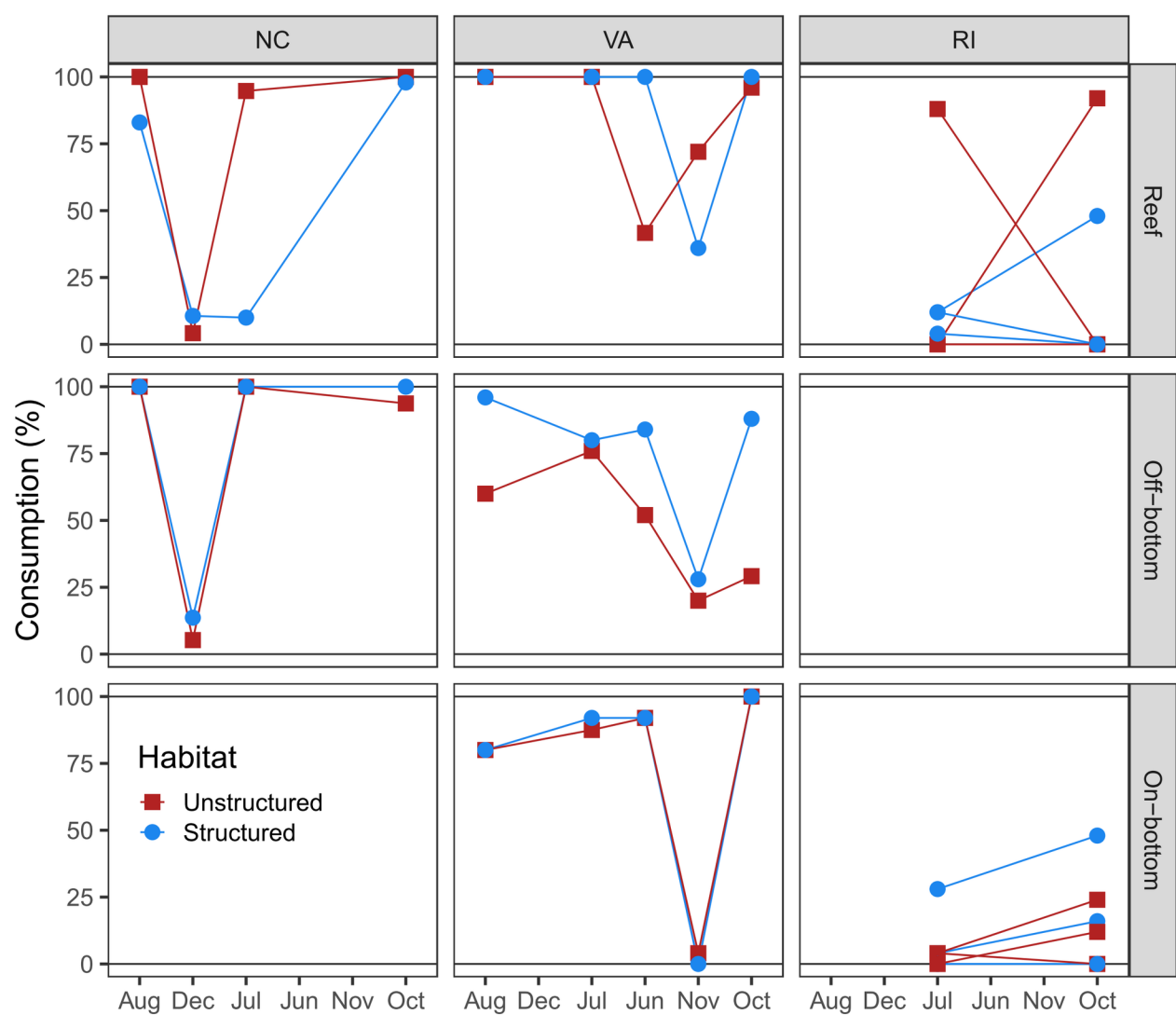
A**B****C****D**

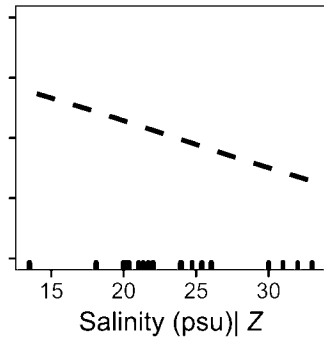
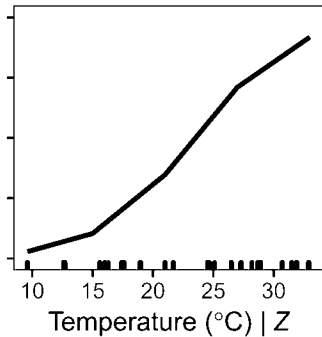
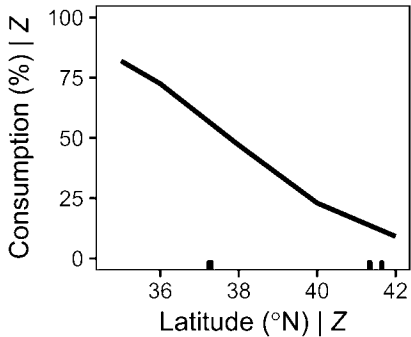




Consumption (%)







Region

- NC
- RI
- VA