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Consumption rates vary based on the presence and type of oyster structure: A seasonal and latitudinal comparison

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ABSTRACT

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

1. Introduction

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

At the same time, bivalve aquaculture has experienced tremendous growth over the last 50 years, now accounting for more than half of all aquaculture production, which itself accounts for 46% of all fisheries production worldwide (FAO 2020). As this practice continues to expand, there arises a potential conflict for available space and resources: aquaculture operations often occupy bottom area that is suitable for restoration of biotic habitats—including oyster reefs and other foundational species such as submersed aquatic vegetation (Dumbauld et al. 2009; Orth et al. 2017). Moreover, with growing interest in oyster restoration for purposes other than biomass production, such as water

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quality management (Bricker et al. 2017), there is an urgent need to understand whether aquaculture operations can provide comparable services as the natural systems they potentially replace. For example, denitrification rates can be significantly higher at aquaculture sites compared to natural reefs (Humphries et al. 2016), although this has not been observed everywhere (Lunstrum et al. 2018).

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

The concentration of both predators and prey on oyster reefs might be expected to lead to higher rates of predation and greater trophic transfer, as has been observed across many structured marine ecosystems (Aronson and Heck 1995; Lefcheck et al. 2019). Alternately, the three-dimensional habitat may provide increased refuge, reducing consumption relative to open areas where prey are more exposed and therefore more vulnerable (Crowder and Cooper 1982; Summerson and Peterson 1984). Whether either of these expectations are associated with

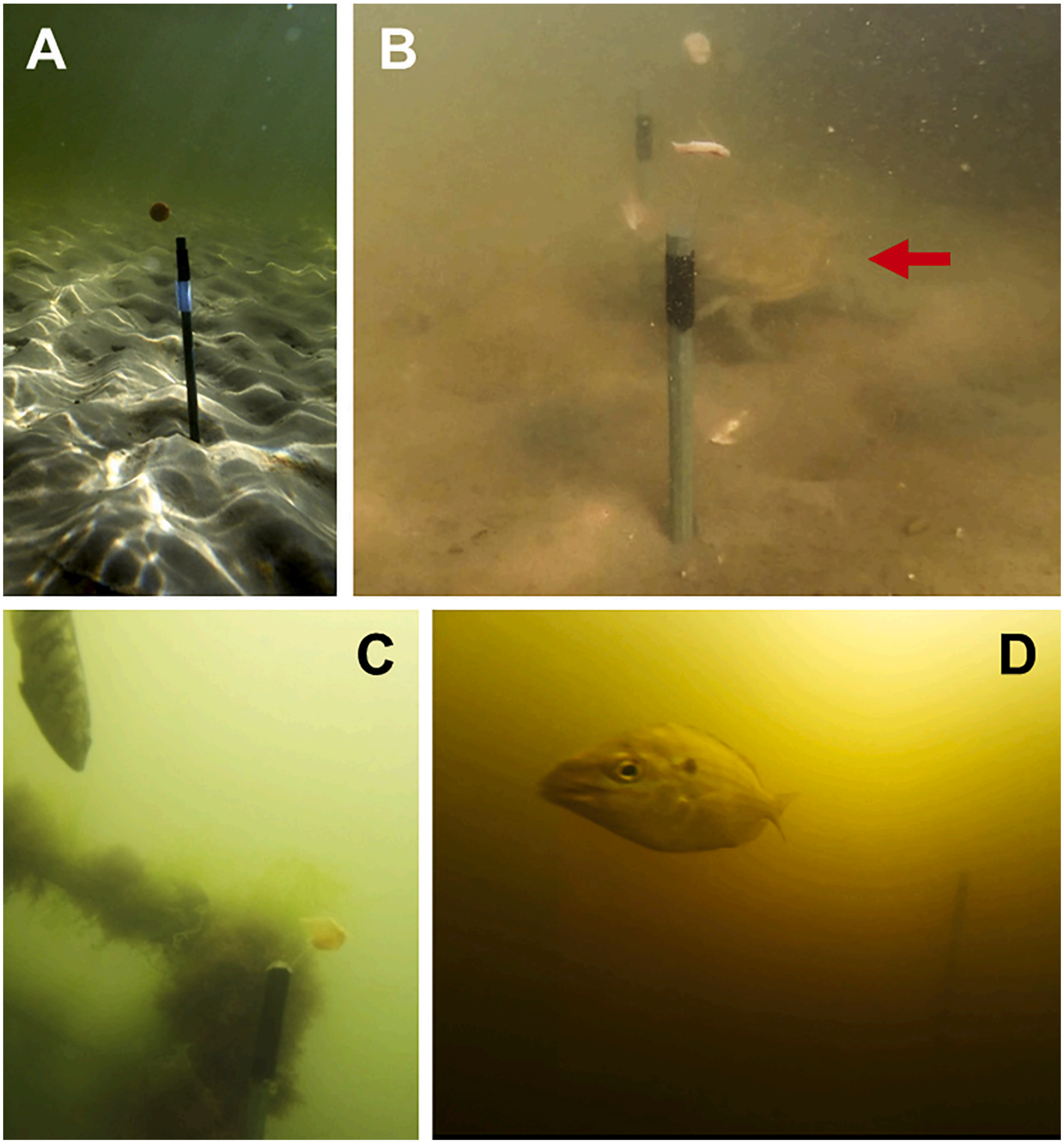

Fig. 1. (A) The Squidpop is a piece of dried commercial squid tethered to a garden stake inserted approximately 20 cm above the sediment surface. (B) The blue crab (*Callinectes sapidus*) interacting with Squidpops in Virginia (facing toward the rear Squidpop, arrow). (C) A juvenile black sea bass (*Centropristis striata*) before taking the bait in Rhode Island. (D) A pinfish (*Lagodon rhomboides*) after having consumed the squid in North Carolina. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

aquaculture infrastructure remains relatively unexplored (but see Clarke 2017), although differences in predation between artificial structures and natural coastal habitats have recently been observed for docks and piers (Rodemann and Brandl 2017).

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

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

2. Materials and methods

2.1. Study sites

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

2.2. Consumption assay

A Squidpop is a 1.3-cm diameter circle of dried squid (Golden Squid Brand, Hong Kong, China) tethered to a 76-cm garden stake (EcoStake). Squids are attached using approximately 5-cm of monofilament line affixed to the stake. These stakes are then inserted into the sediment so that approximately 20-cm of stake is exposed above the surface (Fig. 1A). On oyster reefs, stakes were deployed as close to the reefs as possible while still providing soft enough substrate to insert the stake to the standard depth. For on-bottom aquaculture operations, stakes were deployed immediately adjacent to the cages, and for off-bottom, directly underneath the floating bags. We paired each structured assay with an unstructured control located in a bare substrate area 50–100 m distant and at approximately the same depth and exposure. For each deployment and treatment, we set out $n = 25$ Squidpops per treatment at low tide. We checked the Squidpops after 1- and 24-h and scored them as present or consumed (absent). For each deployment, we also deployed GoPro Hero 3+ video cameras aimed at a separate uncounted replicate to capture the identity of any potential predators. Because of poor visibility across most sites, we did not formally analyze any of the GoPro footage other than to provide some anecdotal examples of predators interacting with the Squidpops (Fig. 1B–D). We used a data sonde (YSI Instruments) to record temperature and salinity at each site during each sampling event, and a Secchi disk to measure turbidity at sites in two regions (NC and VA).

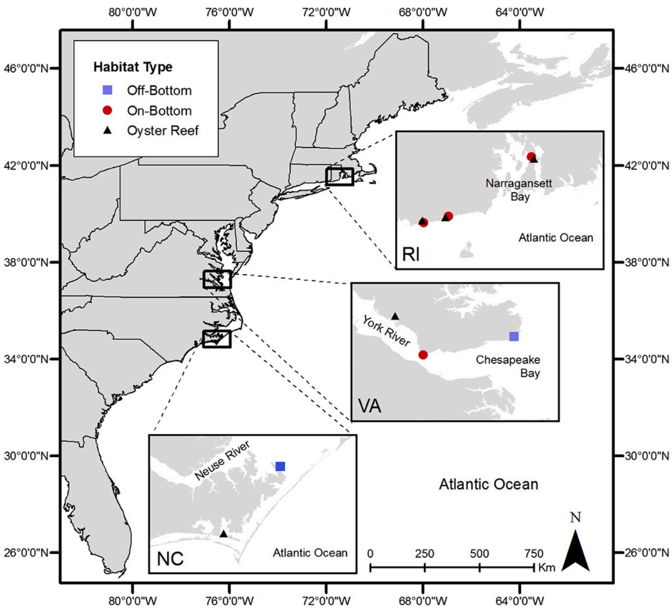

Fig. 2. A map of study sites, including biogenic oyster reefs (black triangles) and both on-bottom (red circle) and off-bottom (blue square) oyster aquaculture operations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Statistical analysis

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

3. Results

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

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

Examining loss of Squidpops after only 1 h revealed similar trends to the 24 h analysis, with a few distinctions. First, consumption rates were overall lower after 1 h (11–44% loss on average, compared to 37–75% after 24 h; Fig. 3B), leading to a slightly lower proportion of explained deviance (marginal $R^2 = 0.45$, conditional $R^2 = 0.64$). Second, the average consumption rate was approximately equivalent at biogenic reefs and on-bottom rack-and-bag aquaculture after only 1 h (Fig. 3B), leading to a non-significant interaction with structure involving these two habitat treatments (Table S1). Third, the enhancement in consumption beneath off-bottom floating bags relative to adjacent sediment was still significant and even stronger after 1 h than 24 h—a 2.2× increase (Fig. 3). Temperature was the only significant environmental covariate predicting consumption rates after 1 h (Table S1).

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

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

4. Discussion

Our study of consumption rates near artificial structures associated with oyster aquaculture versus those on biogenic reefs revealed a strong interaction between the presence and type of structure on loss of a standardized bait after both 1 and 24 h, an effect which also varied across locations. Variation in consumption pressure between the different structured habitats and bare sediment controls likely stem from differences in their water column position and the nature of the hard structure, which in turn affects the type and efficiency of predators and scavengers that forage on these habitats across the three biogeographic regions.

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

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

Oyster reefs were the only structured habitat where loss of squid bait was generally greater in the unstructured control. There are several potential explanations for this finding. First, habitat complexity and landscape context may alter foraging strategies: biogenic oyster reefs can vary considerably in height, aerial extent, exposure, and complexity, which contrasts the uniformity of aquaculture structure. In turn, larger, more complex or connected reef systems may provide more shelter for mesopredators who emerge to forage on the Squidpops surrounding the reef. For example, in situ measurements of rugosity at two of our sites

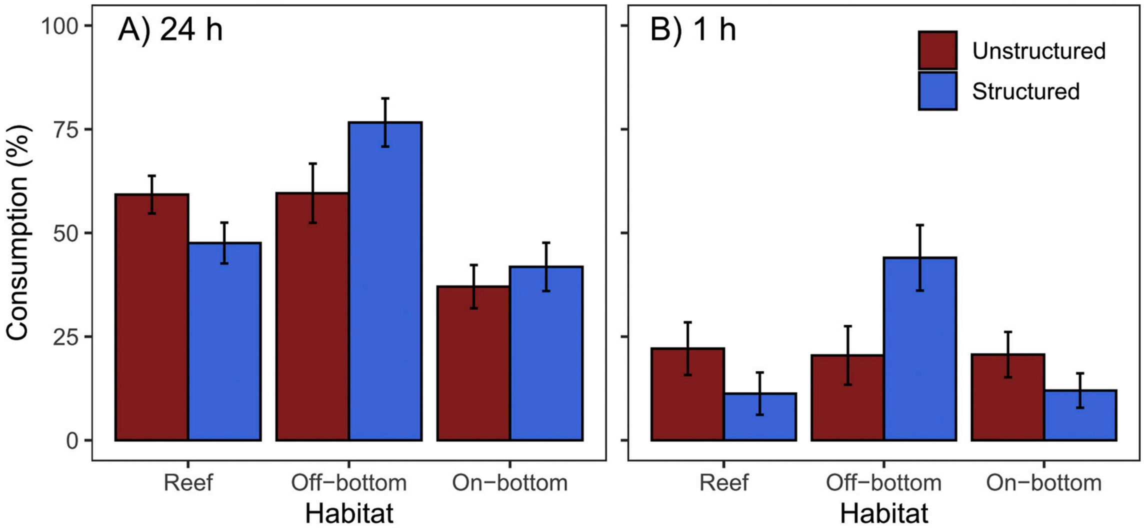

Fig. 3. Plot of average percentage of squid consumed ±1 standard deviation (pooled) after (A) 24 h and (B) 1 h for within-plot (structured vs. unstructured) and between-plot treatments (reef, off-bottom floating bag, and on-bottom rack-and-bag aquaculture).

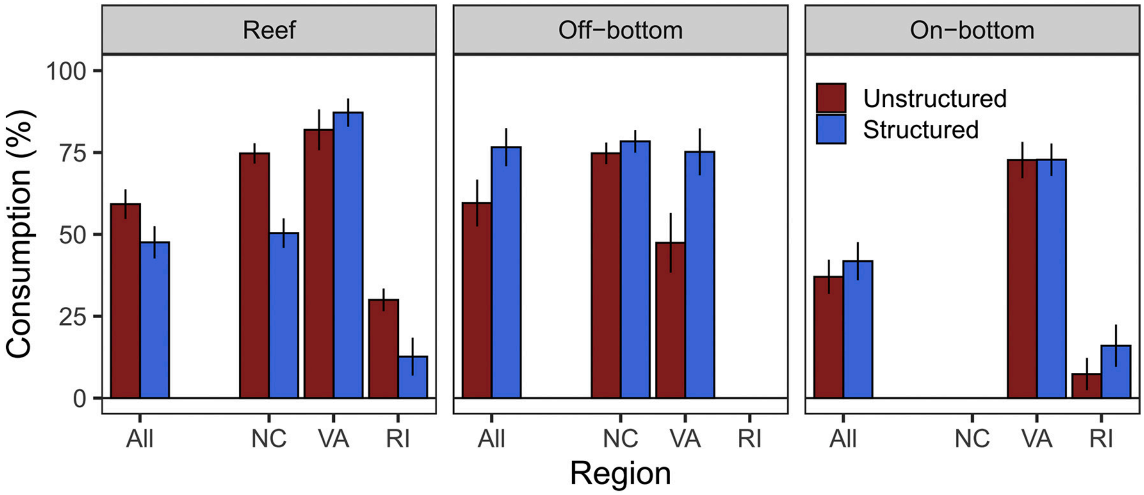

Fig. 4. Mean consumption across all months ±1 standard deviation (pooled) for each habitat across all regions, and for each individual region.

based on the 'chain-link method' suggest more heterogenous reefs in VA compared to NC (60.7 cm per 0.5 m length in NC vs. 154.5 cm per 0.5 m in VA), potentially explaining the higher rates of consumption adjacent to reefs there (Fig. 4). Second, the total footprint of remaining biogenic reefs is perhaps less in the regions studied relative to bottom covered by aquaculture, meaning that there is simply a lot less structure over which to forage on reefs, forcing predators to forage in adjacent unstructured sediments.

A final explanation for the differences in predation across structured habitats may be the spatial distribution of our sites. Floating bag operations were only tested at the southern and intermediate sites (NC and VA) while rack-and-bag operations were only tested at the intermediate and northern sites (VA and RI) (Fig. 2), largely due to different adoption of these two gear types across different states (Baillie et al., 2021). Latitude emerged as a significant predictor of bait loss from our mixed model, with higher consumption at lower latitudes (Table 1, Fig. 6A). In theory, the effect of latitude is independent from habitat type in our statistical model, but this inference is slightly conflated by the uneven implementation of habitats across the latitudinal gradient. Thus, higher predation in certain gear types, like off-bottom floating bags, may be partially because this gear type was only tested at low latitudes, and vice versa for on-bottom aquaculture.

Biogenic oyster reefs, however, were tested across all three regions, suggesting that the latitudinal effect may still reflect ecological processes operating at broad scales. For example, biotic interactions are typically stronger at lower latitudes due to greater productivity and diversity of these communities (Schemske et al. 2009), echoing similar trends observed in seagrass bed fauna (Reynolds et al. 2018) and terrestrial caterpillars (Roslin et al. 2017). GoPro footage revealed potentially different consumers across the range of sites whose distribution and dominance differ along the latitudinal gradient, such as pinfish (*Lagodon rhomboides*, Fig. 1D) which are rarely present north of NC. Indeed, a recent paper demonstrated strong biogeographic differences in resident food webs across oyster reefs south of our study area (Grabowski et al. 2020). Reef properties may also change with latitude: live biomass, reef height and juvenile recruitment all vary with increasing latitude which likely affects the amount of available habitat for prey and predators (Byers et al. 2015), and could potentially explain why consumption rates were much lower in RI than in the other two regions. Future studies could explore a wider gradient in reef properties using the standard Squidpop assay to resolve these questions.

We also found a strong effect of temperature in our model: as temperature increased, so did bait loss (Table 1, Fig. 6B). We note that this effect is independent of latitude: even though higher latitudes are

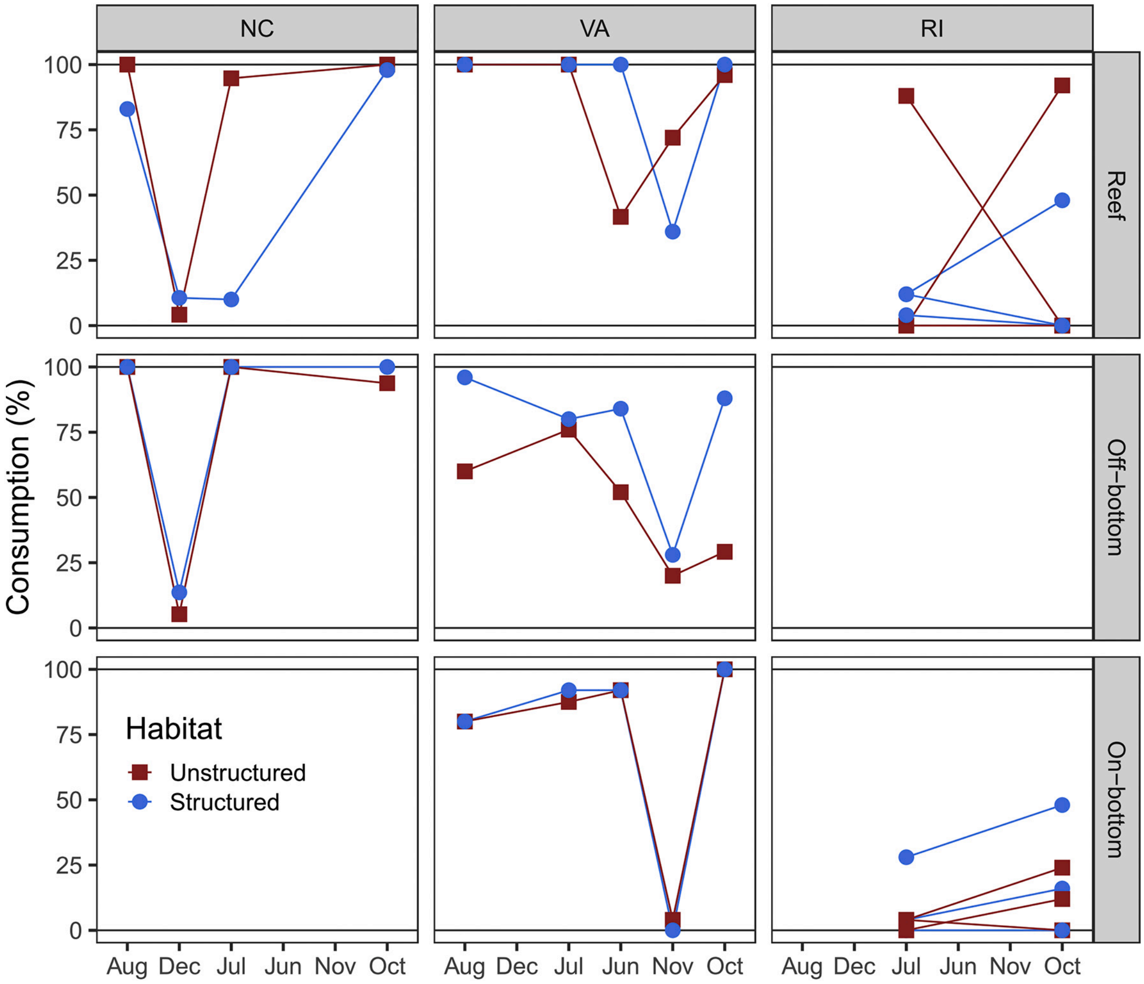

Fig. 5. Time series of consumption (as proportional loss of Squidpops) by region, between-plot (reef, off-bottom floating bag, and on-bottom rack-and-bag aquaculture), and within-plot treatments (structured vs. unstructured). Note that in RI there are multiple structured and unstructured locations.

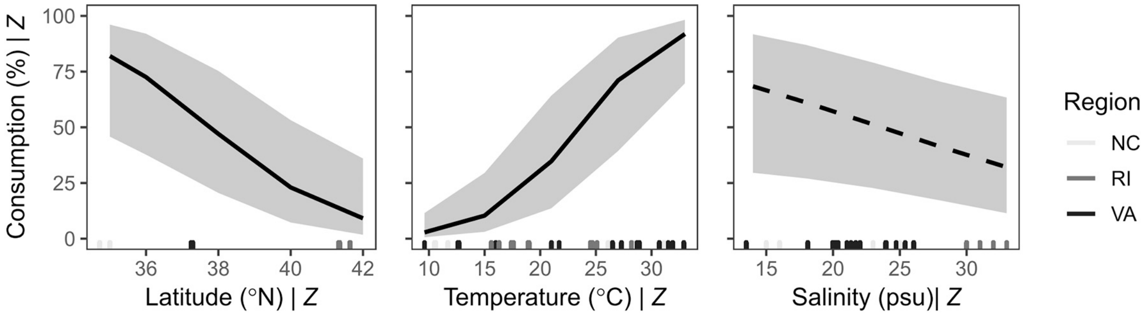

Fig. 6. Predicted effects of environmental covariates on consumption rates from a generalized linear mixed effects model (Table 1). Fitted lines represent the independent (partial) effects given the contributions of other variables in the model (*Z*). Solid lines indicate significant trend ($P < 0.05$).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

generally cooler, there was much greater variation in temperature through time than across space, making temperature more of a seasonal rather than a spatial indicator. The temperature effect likely stems from higher metabolic demands leading to greater resource utilization in the summer (Brown 2004) as well as seasonal turnover in the predator communities. Demersal fish biomass and diversity peak in the early summer months in NC and VA (Lefcheck et al., 2014; Ziegler et al. 2018) and in late summer and early fall in RI (Oviatt and Nixon 1973), tracking the observed consumptions rates through time in these regions (Fig. 5).

Finally, our model revealed that consumption rates were uncorrelated with changing salinity (Table 1, Fig. 6C). One potential explanation is that the predator community (and/or their preference for the squid bait) does not respond to or change drastically along the salinity gradient captured during our survey (14–33 psu), especially for the more variable estuarine sites in NC and VA. The blue crab (*Callinectes sapidus*), for example, was often found interacting with the Squidpops (Fig. 1B) and can be abundant at mesohaline salinities and higher. Furthermore, the contrasting results of Secchi depth for sites in NC and VA suggest that the effect of water clarity is not well resolved in the current study. Thus, environmental drivers in the form of both salinity and water clarity are deserving of further attention with respect to their effects on consumption in marine and estuarine systems.

5. Conclusions

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

CRediT authorship contribution statement

Jonathan S. Lefcheck: Conceptualization, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization. **Bruce W. Pfirrmann:** Conceptualization, Investigation, Data curation, Writing - review & editing, Visualization. **F. Joel Fodrie:** Investigation, Resources, Writing - review & editing. **Jonathan H. Grabowski:** Investigation, Resources, Writing - review & editing. **A. Randall Hughes:** Investigation, Resources, Writing - review & editing. **Ashley R. Smyth:** Conceptualization, Investigation, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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