Geographic variation in intertidal oyster reef properties and the influence of tidal prism

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Abstract

Physical-biological coupling helps structure aquatic communities, yet physical factors can vary widely across large, biogeographic scales. The eastern oyster (*Crassostrea virginica*) is an ecosystem engineer that creates intertidal reefs, filters water, promotes denitrification, stabilizes shorelines, and provides habitat throughout the inner waters of the U.S. South Atlantic Bight (SAB). We quantified physical variables (temperature, salinity, duration and depth of water inundation), oyster reef properties (slope, vertical relief), and oyster recruitment, density, and biomass over a 1500 km scale across the SAB for one year. All oyster-level and many reef-level variables exhibited unimodal patterns with latitude that peaked in Georgia and South Carolina estuaries. Of the physical variables, salinity and duration of water inundation over reefs were similar across all sites, and temperature declined linearly with increasing latitude, except during summer when it had no relationship with latitude. Depth of water inundation over reefs was the only physical variable with a prominent unimodal distribution that may explain the oyster's biological responses. Similar durations of water inundation across all reefs coupled with higher water depths in the mid-latitude sites collectively indicate that these sites experience higher flow velocity, energy and net water volume delivery per unit time. The resultant higher accumulation of oyster biomass and heightened reef structure in areas of higher tidal energy emphasize that the physical forcing of the SAB (especially large cross-shelf gradients in tidal amplification) affects the biology of the eastern oyster, including its reef properties, with potential implications for community structure and ecosystem service delivery across a biogeographic scale.

In estuarine environments, physical-biological coupling is often pronounced due to the high amount of physical forcing and biological productivity that is typical at the land-sea interface (Mann and Lazier 1991). Much attention has focused on how organisms interact with and alter the flow, salinity, temperature, and dissolved oxygen of water (Kinne 1963; Vogel 1981; Nowell and Jumars 1984; Diaz and Rosenberg 1995). Species that are central to these interactions, such as ecosystem engineers, often interact heavily with such physical processes (Crooks 2002, 2009). Through such interactions, ecosystem engineers alter the abiotic, physical environment, in turn affecting the attendant biotic community (Jones et al. 1994). In coastal estuaries, prominent examples of ecosystem engineers include marsh grasses that baffle currents and trap sediment (Bouma et al. 2010), infau-

nal tube worms that buttress the benthos from shear stress stabilizing the environment for other infaunal species (Rhoads et al. 1978; Woodin 1978), and reef-building species that alter flow and thus feeding rates of reef-dwelling species (Lenihan 1999).

Sometimes the engineers themselves (including their engineering properties) are shaped by the interactions with the physical processes (Jones et al. 2010). For example, *Acropora* coral reefs grow oriented to the prevailing wave direction (Shinn 1963), trees grow slanted in the wind (Ennos 1997), oysters grow taller in higher flow (Lenihan et al. 1996), and tubes of infaunal worms achieve integrity with proper sediment grain size and rates of deposition (Myers 1972; Pinedo et al. 2000). Because ecosystem engineers are of primary importance in many systems, especially those heavily influenced by physical processes, identifying what shapes and constrains the engineers themselves is essential to understanding community structure and ecosystem functioning (Byers et al. 2006; Hastings et al. 2007).

Additional Supporting Information may be found in the online version of this article.

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At the scale of an estuary, much is known about how physical factors interact with organisms and biological processes. For example, marsh plants accrete sediment, elevating the surface of the marsh and in turn affecting competitive interactions and resultant species zonation patterns (Morris 2006). Also, the height of an oyster reef off of the benthos causes a quantifiable intensification of water flow speeds and resultant differences in feeding opportunities for seston-feeding organisms (Lenihan 1999; Gutierrez et al. 2003). However, the effects of variability in physical processes on estuarine biology at the scale of biogeographic provinces have seldom been explored. Understanding such regional-scale connections is of increasing importance as estuarine habitats are vulnerable to a number of intensifying large-scale stressors, including eutrophication and bottom-water hypoxia; degradation from fishing; dredging and erosion; invasive species; disease; and sea level rise (Byers and Grabowski 2014).

Although sometimes simplistically inferred to have relatively homogeneous abiotic factors and habitats, biogeographic regions often exhibit sizable variability and gradients in physical factors such as tidal amplitude, freshwater inputs, temperature, and sediment loading (Meade et al. 1975; Narvaez et al. 2004; Tapia et al. 2009; Walsh 2008, Kimbro et al. 2014). These physical variables can substantively affect species abundance, ecosystem function, and biotic habitat either directly or indirectly by modifying the function, properties, and interaction strengths of ecosystem engineers. The relatively similar species pool within a biogeographic region may provide a key opportunity to isolate the influence of physical factors from biological ones in shaping a system.

The eastern oyster (*Crassostrea virginica*) creates reefs that occur in the intertidal zone throughout much of its southern range from the mid-Atlantic states in the U.S. through the Gulf of Mexico and the Caribbean (Galtsoff 1964; Ahmed 1975; Bahr and Lanier 1981). Oysters substantially influence the integrity and health of southeastern estuaries by filtering water, promoting denitrification, stabilizing shorelines, and offering habitat for juvenile fish and crustaceans (Newell 1988; Meyer et al. 1997; Coen et al. 2000; Peterson et al. 2003; Newell 2004; Piehler and Smyth 2011; Grabowski et al. 2012). These reefs have been studied extensively in many areas, and there is substantial variation in oysters (e.g., density, biomass) and reef properties (i.e., slope, vertical reef, rugosity, elevation) on local to regional spatial scales (Grabowski et al. 2005; Luckenbach et al. 2005; Powers et al. 2009; Fodrie et al. 2014; Rodriguez et al. 2014). For instance, in localized studies, the influence of some physical variables, like tidal range, has been shown to be strongly related to individual reef size and overall areal coverage within an estuary (Bahr and Lanier 1981; Grizzle 1990). However, there has yet been no effort to evaluate systematically the simultaneous influence of multiple physical variables on critical reef attributes and ecological processes over a wide geographic scale. Understanding how large scale processes affect oysters should improve our ability to conserve, restore, and manage this foundation species and its associated species diversity.

Here, we comprehensively examine the population properties (density, biomass, and recruitment) and reef structural characteristics (slope and vertical relief) of oysters throughout the South Atlantic Bight (SAB). We were interested broadly in the shaping influence of many physical variables, especially those that may vary widely and/or systematically across large spatial scales, such as water temperature, salinity, and the duration and depth of water inundation. Water temperature and salinity correlate positively with oyster growth (Shumway 1996; Kraeuter et al. 2007). However, because water temperature is correlated with air temperature, and because high air temperatures can be lethal for intertidal oysters (Malek *unpublished data*), the positive effect of water temperature may be bounded. The duration of water inundation, which is usually studied through the proxy of intertidal elevation, also influences oyster growth and survivorship. On a reef, longer inundation duration (lower intertidal elevation) increases oyster submergence, which prolongs feeding and enhances growth (e.g., Bahr 1976; Roegner and Mann 1995; Bartol et al. 1999). However, higher growth is not simply a direct function of increased submergence time; other factors such as lower desiccation stress clearly contribute (Crosby et al. 1991; Peterson and Black 1988). Very long submersion can also negatively affect oyster survival in the SAB. For instance, Fodrie et al. (2014) found that subtidal oysters experience higher rates of predation and biofouling than do those in the intertidal. Finally, greater water depth (tidal amplitude) likely has a positive effect on oysters. Although it is not often a variable examined directly for its effect, several of its derivatives are. For instance, for a given inundation duration, higher tidal amplitude implies more water volume delivery per unit time, that is, higher flow and energy. Higher flow benefits oysters because of concomitant increases in the flux of seston and oxygen and decreases in sedimentation, all of which positively affect oyster growth and survivorship (Lenihan et al. 1996; Grabowski et al. 2005; Fodrie et al. 2014). Even apart from flow effects, the higher volume of tidal water can boost allochthonous inputs of oxygen and nutrients, enhance mixing, and deliver more planktonic oyster recruits (Monbet 1992).

As oysters individually respond to these four physical variables (water temperature, salinity, and the duration and depth of water inundation), their emergent reef structural properties (e.g., slope, vertical relief) are influenced. Due to oysters' role as ecosystem engineers, alterations of their reef properties by physical processes are likely to affect dozens of species dependent on oyster reefs as habitat and the ecosystem services that the reefs provide. Specifically, the different structural properties of reefs across geographic scale may affect their performance of ecosystem services like fish habitat, provisioning energy attenuation, and shoreline stabilization.

Given that much is known about the influence of these physical variables on oyster performance at local scales, we ask "how do these variables differ across space, and what is their relative importance on oyster and reef properties across large scales?." Only temperature has a readily predictable pattern and is expected to decrease with latitude. Salinity is often influenced by localized factors like riverine inputs and the size of the local watershed (e.g., Lane et al. 2007); however, our study design standardized selection of studied reefs from within polyhaline areas, thus limiting the range of variability we expected to capture in this variable. The duration and depth of inundation are largely driven by tidal processes which differ throughout the SAB, but not in linear fashion. Tides vary considerably in this region with tidal ranges spanning from 1.5 m to 3 m, peaking in the central part of the SAB (Fig. 1). The potential accompanying variation in inundation duration and depth (with its associated aspects of tidal volume, tidal velocity, and energy) could dramatically influence physical-biological coupling, with particularly strong effects on oysters. Here, we examine relationships that have previously been considered largely in isolation of each other, and we do so over a very large scale using a multivariate approach that allows us to identify potential drivers of oyster reef properties.

Methods

Study species and area

Our study focuses on the SAB, extending along the southeastern coast of the United States between Cape Hatteras, North Carolina to Cape Canaveral, Florida (Fig. 1). This section of the U.S. coastal plain is characterized by extensive lagoon-marsh systems and estuaries that are bound on their eastern extent by barrier islands (Bahr and Lanier 1981). In general, the SAB is a mixed-energy coast (Hayes 1975) because coastal processes and morphologies are determined by the varying influence of both waves and tides, which in this area are largely a function of the changing profile of the inner continental shelf (Hayden and Dolan 1979; Hubbard et al. 1979). Most estuaries in the study area are vertically homogeneous (Pritchard 1967, 1971; Schubel 1971), where tidal mixing is the dominant physical process. These systems receive freshwater mainly from local precipitation via tidal creek drainage systems particularly during spring floods (Finley 1975; Bahr and Lanier 1981). Marshes, mudflats, and tidal creeks associated with estuaries throughout the SAB are the dominant habitat for the Eastern oyster, *Crassostrea virginica*. Within these habitats *C. virginica* larvae settle gregariously, cementing themselves to existing adult populations, thereby creating extensive, multi-generational reefs.

Study approach

To examine how variation in physical factors influences oysters and oyster reef properties across a regional scale, we surveyed 10 estuaries within the SAB that were approximately evenly interspersed along a 1500 km domain (Fig. 1). By working within a single biogeographic region, the species pool remains largely constant (Briggs 1974; Spalding et al. 2007; Pappalardo et al. 2014), helping to constrain possible sources of variation and isolate physical differences driving observed patterns.

Beginning in summer 2010, five oyster reef locations were chosen within each of the 10 estuaries. Reefs were selected to standardize certain influential variables; thus, all reefs were intertidal, located on tidal creek banks near the mouth of an estuary, had a summertime salinity greater than 25 ppt, and had cordgrass (*Spartina alterniflora*) habitat located immediately behind. The reefs in each estuary were separated by a minimum of 100 m and were chosen from at least two different tidal creeks. On each reef, we located and marked out one permanent 3 m $\times$ 3 m intertidal sampling area on the creek bank adjacent to the salt marsh habitat that had an oyster density of at least 30 adults/m^2 that were at least five centimeter in shell length.

We measured three inter-related aspects of the oysters and the environment including: (A) properties of the oysters themselves (density, biomass, and recruitment); (B) emergent structural properties of the oyster reefs (slope and vertical height); and (C) physical variables (temperature, salinity, and duration and depth of water inundation).

Oyster properties—density, biomass, and recruitment

In August 2010, during low tide, we randomly placed a 0.5 m $\times$ 0.5 m quadrat along the upper edge of our designated reef adjacent to the marsh above it. Within the quadrat, we excavated all oysters on the surface. Many oysters form clusters of two or more individuals (dead or alive) that are attached. If more than half of an individual oyster or oyster cluster was within the quadrat, then it was included. Single oysters and oyster clusters were rinsed of mud and weighed with a spring scale. We also counted all living oysters, including spat (newly recruited oysters). To minimize the impacts of the oyster harvesting on future variable measurements, we filled the sampled area with a plug of sediment and shell hash from a nearby area off of the reef and placed live oyster clusters from a nearby reef on top.

We measured oyster recruitment from late summer 2010 through summer 2011. We deployed one oyster spat collection stick (PVC pipe infused with corrugated cement, 15 cm length, 2.5-cm diameter, 118 cm^2) on every reef in 2010 and two in 2011 in the same location the oyster quadrat sample had been taken. We mounted the spat sticks on an embedded rebar stake and to reduce post-settlement predation mortality we positioned the bottom end of the spat stick 10 cm above the top of the oysters and fastened cable ties below and above the stick to hold it in place. Spat sticks were replaced every 4–8 weeks in the spring through fall when recruitment was high. Over the winter, sticks were deployed for up to three months. Upon retrieval spat were counted
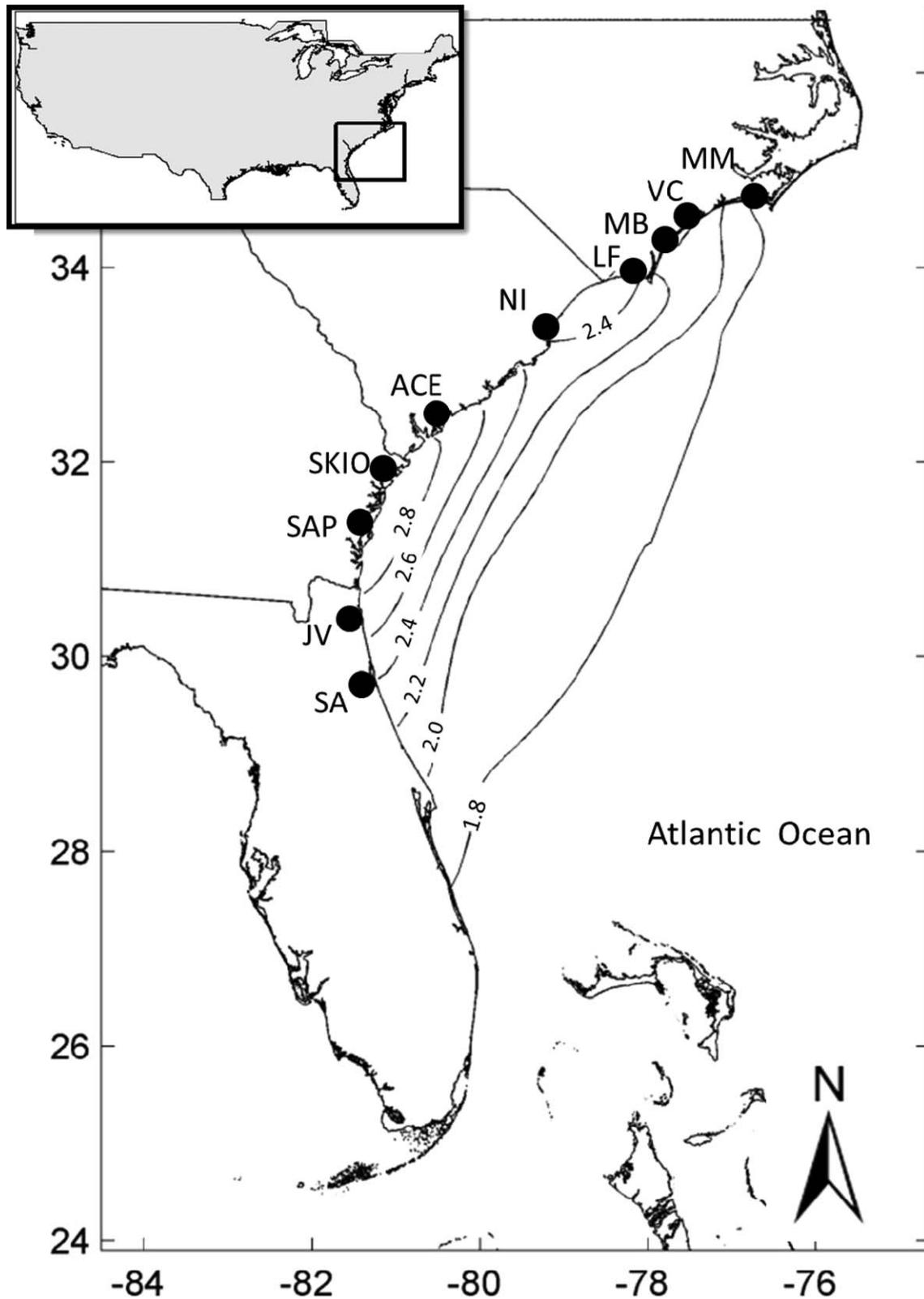
Fig. 1. The southeastern U.S. showing our 10 study sites (•).Table 2 lists the full names for each site code. Inset in upper left corner denotes the location of the U.S. South Atlantic Bight, which is shown in fuller detail in the larger map. Isoclines connect points of equal tidal range with numbers representing the mean maximum semimonthly spring tidal range in meters. Tidal data according to Egbert and Erofeeva (2002).

with a hand lens or a dissecting scope in the lab. Recruitment for each replicate reef was calculated as the total number of spat settled on spat sticks from August 2010 to October 2010 and April 2011to mid September 2011. Recruitment was extremely low to none in the intervening months across all sites.

Reef properties—slope and vertical relief

Slope

In summer 2011, on each reef, a laser level was set on top of a PVC post which was embedded into the sediment at the top, marsh-ward edge of the 3 m × 3 m reef and leveled. A meter stick was held upright at the bottom edge of the reef to measure the height intersected by the laser beam. This measurement represents the vertical drop (x) across the 3 m reef. The angle of inclination (Θ), or slope, of the reef was calculated using the equation: $\sin \Theta = x/3$ m. We took two replicate slope measurements (spaced at least 1-m apart) on each reef and averaged these two values.

Vertical relief

At a distance of 0.5 m below the marsh-ward (and typically higher elevation) edge of our 3 m × 3 m reef section, we measured the vertical height of the aboveground reef. Starting at the side of the reef and moving parallel to the water line, every one meter we measured to the nearest cm the distance from the sediment to the top of the oysters at that point. To characterize vertical relief as a function of reef zone (tidal height), we took two more sets of relief measurements, one along a transect across the middle of reef and the other across the water-ward (low elevation) end of the reef (0.5 m in from the bottom edge).

Physical variables

We measured water temperature, salinity, and the duration and depth of water inundation on the reefs from the end of summer 2010 through summer 2011. At the four NC sites, measurements began in fall 2010. On one reef within each estuary, we deployed a pressure gauge (Onset HOBO, U20-001-04) in a waterproof pouch on the benthos in the middle of each reef that recorded pressure at 20-min intervals. At each site, an additional gauge was secured above the water at a known elevation to simultaneously record atmospheric pressure. Subtracting data of the latter from the former yielded site-specific measurements of hydraulic pressure. Hydraulic pressure was divided by the temperature-corrected density of water (also recorded by the Onset gauges) to yield water depth, which we could use to compute a profile of the duration and depth of reef submergence. The same loggers also quantified the water temperature while submerged. Both temperature and submersion data were binned into two-week intervals that matched the spring-neap tidal cycle. These binned data were averaged and used as site-specific measures of tidal submergence and water temperature. Mean temperatures were calculated seasonally. For summer tem-

peratures, with the exception of NC sites, the few data points we had from summer 2010 were averaged with the 2011 summer data. Gauges failed at Jacksonville, Florida during the winter and at the two northern-most North Carolina sites for all seasons except fall, so the physical dataset is avaiable for all 10 sites in fall, at seven sites in winter, and at eight sites for spring and summer. Salinity was measured manually with a YSI meter or a handheld refractometer in each tidal creek once a month, or more frequently when possible.

Analyses and predictive models

To examine patterns in oysters (recruitment, density, biomass), reef properties (slope, relief), and physical factors (temperature, salinity, depth of inundation, inundation duration), we analyzed each variable singly as a function of latitude, with each latitude represented by measurements from the five replicate reefs. Vertical relief was measured on each reef four times per zone in each of the low, mid, and high zones. For initial analysis of vertical relief, reef zone was nested within reef, and reef within site. Because reef zone was significant as a nested factor, subsequent statistics on vertical relief were run on each reef zone individually using latitude as a continuous variable. Given that our response variables may be influenced by regional factors that do not vary linearly with latitude, we also tested for nonlinear patterns with latitude. Thus, for all analyses, a second-order polynomial was fit and tested for significance; if it was not significant, the polynomial term was dropped from the model and only the linear model was fit. Residuals of all analyses were examined for trends that would indicate heteroscedascity; if not uniformly distributed, the variables were transformed. Vertical reef height and oyster recruitment were both ln ($x + 1$) transformed.

Latitude was significant for almost every response variable in the above analyses, so we next investigated which physical response variables that differed with latitude potentially mediated oyster and reef properties at a biogeographic scale. Specifically, once all univariate models had been examined, we built statistical models to explore the relative importance of physical variables (temperature, salinity, duration of water inundation, and depth of water inundation) to explain oyster properties (density, recruitment, biomass) and reef properties (slope, vertical relief). We first examined the seasonal measures of temperature for collinearity. Finding much ($R > 0.7$), we chose to use fall water temperatures for which we had the most complete dataset. Also, as opposed to summer, fall was a season where temperature varied significantly with latitude. Next we examined duration of water inundation and depth of water inundation for collinearity and found none ($R = 0.35$).

Using an information-theoretic approach, we examined each of the five oyster and reef response metrics in its own model. For each, we identified all possible models and
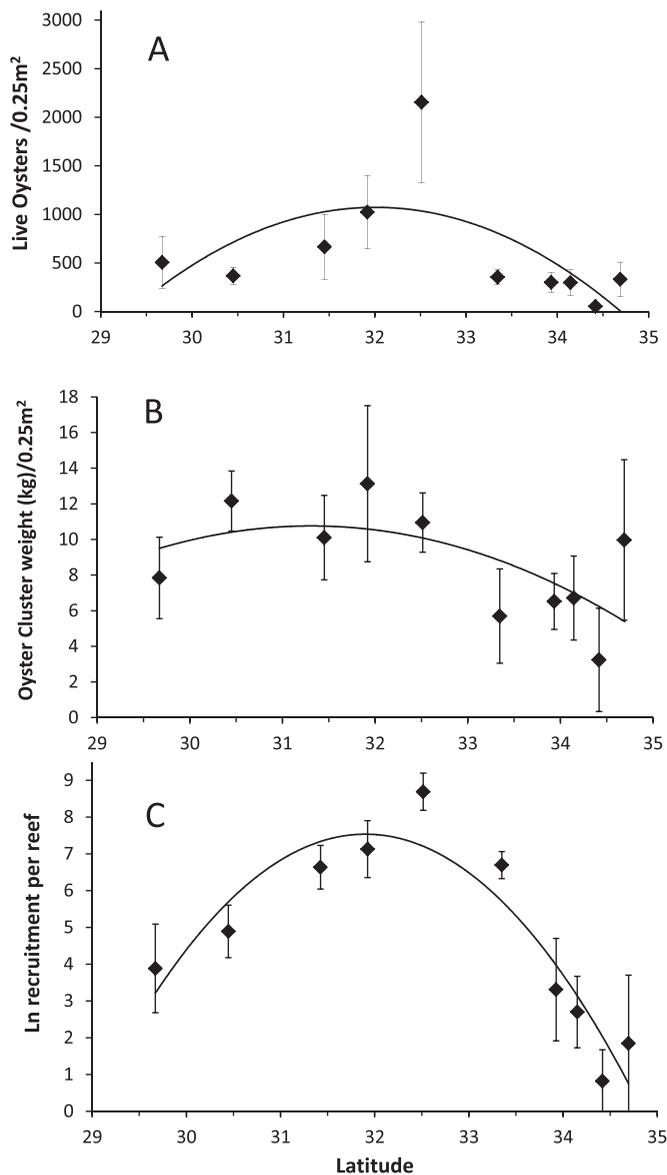
Fig. 2. Relationship of latitude on (A) live oyster density (# per 0.25 m²), (B) oyster cluster weight per 0.25 m², and (C) indexed oyster recruitment per reef [ln (*x* + 1) transformed]. Indexed recruitment is the total spat settled on spat sticks (*n* = 8 spat sticks replaced and counted monthly) from August 2010 to October 2010 and April 2011 to mid September 2011 (214–239 d). Each panel A–C depicts the average across all five reefs at each latitude (±SD) with the best fitting second-order polynomial curve.

examined the Akaike's Information Criterion corrected for small sample sizes (AIC$_c$), which provides a relative measure of model performance for a given set of data and is designed to balance complexity (i.e., the number of model parameters included) and goodness of fit. We calculated the difference between AIC$_c$ for a given model *i* and the minimum AIC$_c$ value in the set, where *i* = 1, 2,…*R*. Models were ranked according to their Akaike weight (*w$_i$*), which was calculated

as the model likelihood normalized by the sum of all model likelihoods; values close to 1 indicate greater confidence in the selection of the best model. Typically models with *w$_i$* < 0.02 are not shown. We examined the best performing model (i.e., lowest AIC$_c$, highest *w$_i$*), for each oyster response metric. All statistical analysis was performed using JMP v10 (SAS 2010).

Results

Oyster properties: density, biomass, and recruitment

Oyster density peaked in the central part of the study domain in Georgia and southern South Carolina (Fig. 2A). Oyster density was boosted in this mid-latitude region by a large number of recently settled individuals (*see* below), but the density of adults was also high. A second-order polynomial fit of latitude explained 32% of the variation in oyster density ($R^2 = 0.32$; $F_{2, 49} = 10.97$; $p < 0.0001$; Supporting Information Appendix A). The site with the highest oyster density (Ace Basin, South Carolina) had nearly 40 times the density as the lowest site (VC, North Carolina; Fig. 2A).

Oyster biomass likewise peaked in the central part of the domain ($R^2 = 0.23$; $F_{2, 49} = 6.89$; $p = 0.0024$; Fig. 2B). Although biomass exhibited a significant unimodal-shaped distribution with latitude (Supporting Information Appendix A), its effects were not symmetrical on either end, with the North Carolina sites exhibiting far lower mass than Florida (Fig. 2B). The reefs in Jacksonville, Florida, Georgia, and southern South Carolina had very large biomass, with an average of over 10 kg of oyster per 0.25 m² and a few quadrats at SKIO exceeded 16 kg/0.25 m².

The most extreme hump-shaped pattern was exhibited by oyster recruitment ($R^2 = 0.76$; $F_{2, 49} = 72.93$; $p < 0.0001$; Supporting Information Appendix A). Over nearly two full annual recruitment periods, the spat count spanned several orders of magnitude across the study domain, and was far greater on Georgia and South Carolina reefs, especially at Ace Basin (Fig. 2C). Recruitment at the NC sites was extremely low, with as few as two recruits per reef observed at VC and 17 at MM over a nearly two-year period. Recruitment was extremely low to none at all sites from November through March.

Reef properties: slope and vertical relief

The slopes of oyster reefs were significantly greater at the mid-latitude sites in our study domain (Supporting Information Appendix A; Fig. 3A). Latitude and its polynomial term explained a significant portion of the variability in slope ($R^2 = 0.73$; $F_{2, 49} = 64.19$, $p < 0.0001$). Slope was 4 − 5X greater in the mid latitudinal range than at either end; reefs in North Carolina were extremely flat.

Vertical relief, or height of the oyster reef from the ground, differed significantly by reef zone which was a nested factor within reef and within site ($R^2 = 0.38$; $F_{149, 599} = 1.90$; $p < 0.001$; Table 1). Because of the significance of
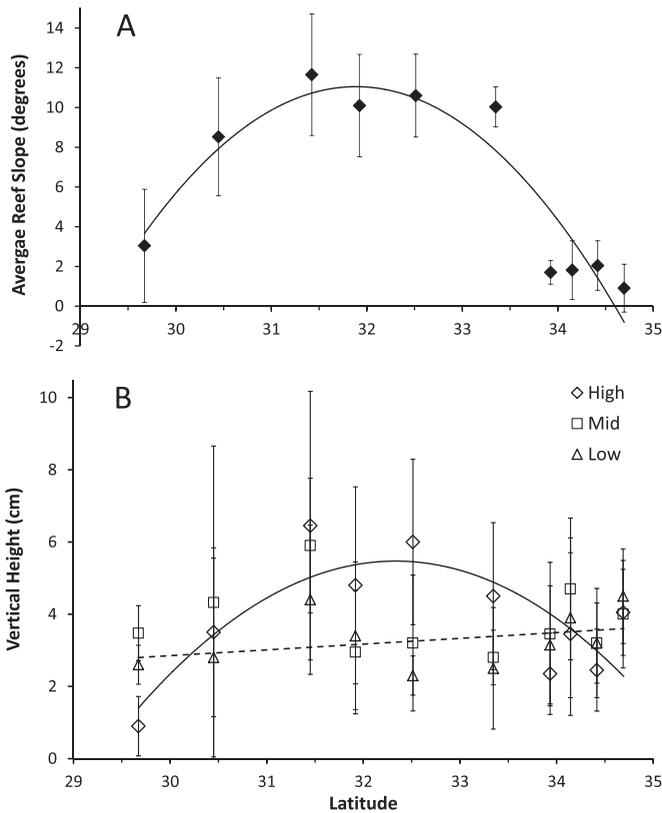
Fig. 3. Relationship of latitude on (A) the average slope of reefs at each latitude (± SD) and (B) the average vertical height of oyster reef (± SD) by reef zone [High (◇), mid (☐), and low(△)]. High zone data fit significantly better with a polynomial curve (—); low zone data was best fit with a linear curve (---); and mid zone heights did not vary significantly with latitude.

reef zone as a nested factor, further analyses were conducted on separate models to examine the effect of latitude within each zone. Analyses of latitude for each reef zone separately revealed interesting differences. Within the high reef zone, vertical relief peaked in the center of the study domain ($R^2 = 0.12$; $F_{2, 199} = 14.0$; $p < 0.0001$; Supporting Information Appendix B; Fig. 3B). Vertical relief within the low zone on reefs had a slight, linear increasing relationship with latitude ($R^2 = 0.023$; $F_{1, 199} = 4.64$; $p = 0.033$), while within mid

Table 1. Vertical relief of oyster reefs [ln ($x + 1$) transformed] as a function of site, reef nested within site, and reef zone nested within reef and site. Data fit with all four measurements from each of the three reef zones from all five replicates from each site.

Source	df	SS	F	p
Site	9	21.34	4.63	<0.0001
Reef[Site]	40	27.12	1.32	0.095
Reef zone [Site, Reef]	100	96.89	1.89	<0.0001
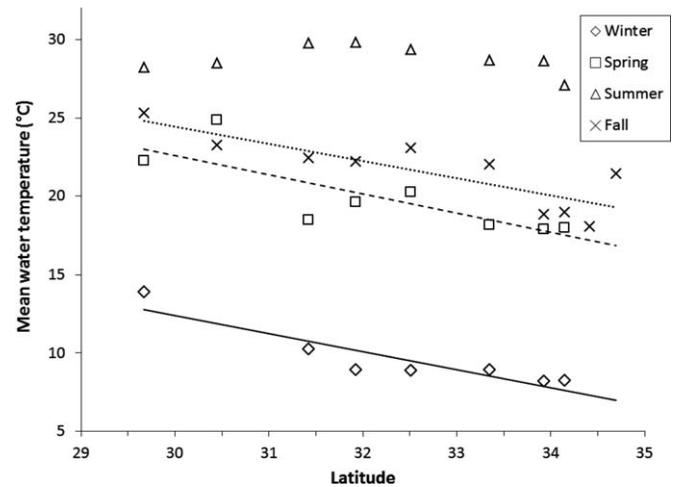
Fig. 4. The effect of latitude on mean water temperature by season. Temperature varied significantly with latitude during winter (—) [winter temperature = − 1.15 × latitude + 47.0]; spring (---) [spring temperature = −1.23 × latitude + 59.5]; and fall (•••) [fall temperature = −1.1 × latitude + 57.4]. During summer, temperatures did not vary with latitude (summer temperature = −0.15 × latitude + 33.6).

zone heights it did not vary significantly with latitude ($R^2 = 0.007$; $F_{1, 199} = 1.33$; $p = 0.25$; Supporting Information Appendix B). Reefs had similar vertical height across all three measured reef zones at both the northern and southern ends of our domain; however, in the mid latitudes, the highest tidal elevations of the reef had $2 − 3X$ more vertical oyster reef height than anywhere else, including at other zones on the same reefs. Because the mid-latitude reefs also had the steepest slopes, the differences in vertical relief from the high to low zones on these 3 m wide reefs occurs across a large gradient of tidal height—typically 0.5 m.

Physical variables: salinity, temperature, inundation duration, depth of inundation

Summertime salinity was consistently high at all sites, averaging 34.4 ppt ± 3.25 (SD) (Table 2). There was no effect of latitude on salinity ($R^2 = 0.12$; $F_{1, 9} = 1.07$, $p = 0.33$). Replication was not sufficient for formal analysis of salinity in other seasons, but seasonal means were never below 25 ppt at any site. Mean water temperatures showed significant patterns with latitude that varied by season. Temperatures declined just over 1°C with every one degree north in latitude in winter ($R^2 = 0.83$; $F_{1, 6} = 24.12$, $p = 0.0044$), spring ($R^2 = 0.64$; $F_{1, 7} = 10.76$, $p = 0.017$), and fall ($R^2 = 0.70$; $F_{1, 9} = 19.0$, $p = 0.0024$; Fig. 4). However, in summer, temperatures were high everywhere with no significant latitudinal pattern ($R^2 = 0.07$; $F_{1, 7} = 0.47$, $p = 0.52$; Fig. 4).

Our reefs spent a consistently high proportion of time inundated (0.52–0.84) at all sites (Table 2). There was no effect of latitude on duration of water inundation ($R^2 = 0.003$; $F_{1, 9} = 0.024$, $p = 0.88$). Conversely, the depth of water inundation on reefs varied nonlinearly with latitude

Table 2. Coordinates of each study site along with the average proportion of time reefs are inundated. Because inundation values are computed as a proportion across the entire logger deployment they have no computed standard deviation. Also reported are the average summer salinity (ppt) and its standard deviation and sample size at each estuary.

Site	Site code	Latitude (°N)	Longitude (°W)	Inundation duration	Salinity	SD	*n*
St. Augustine, FL	SA	29.67	81.22	0.68	35.7	1.53	6
Jacksonville, FL	JV	30.45	81.42	0.67	35.0	0.96	6
Sapelo Is., GA	SAP	31.42	81.30	0.67	28.7	1.54	6
Skidaway Is., GA	SKIO	31.92	80.99	0.76	31.2	1.21	6
Ace Basin, SC	ACE	32.51	80.45	0.64	31.9	4.62	5
North Inlet, SC	NI	33.35	79.17	0.61	39.3	3.50	6
Lockwoods Folly, NC	LF	33.93	78.22	0.63	35.0	0.64	6
Masonboro Is., NC	MB	34.15	78.86	0.69	33.0	2.55	6
Virginia Creek, NC	VC	34.42	77.59	0.52	37.6	0.14	4
Middle Marsh, NC	MM	34.70	76.62	0.84	37.0	0.48	6

(Supporting Information Appendix A), with a marked peak in the center of the domain ($R^2 = 0.73$; $F_{2, 9} = 9.44$, $p = 0.010$; Fig. 5). Measuring from the moment of submersion on the rising tide to the moment of emergence on the falling tide, water averaged almost 1-m deep over our mid latitude reefs and only ~ 0.25 m at the high and low latitudes.

Predictive models

Oyster density had no single model that clearly emerged as the best; none of the models outperformed the null, intercept-only model (Table 3). Salinity and depth of water inundation individually provided the second and third best fitting models, respectively.

Oyster biomass was highly and positively correlated with the depth of water inundation ($R^2 = 0.61$; oyster biomass = 11.8 (depth of inundation) + 2.0; Fig. 6; Supporting Information Appendix C). With a model weight of 0.36, this single variable model had the strongest fit in our AIC model

comparison. However, the second and third best models, which provided reasonable fits, included depth of water inundation along with duration of water inundation ($w_i = 0.31$) and water temperature ($w_i = 0.14$), respectively, with all terms positively associated with biomass.

Oyster recruitment was strongly and positively correlated with the depth of water inundation ($R^2 = 0.60$; recruitment [$\ln(x + 1)$] = 9.6 [depth of inundation] – 0.70; Fig. 6; Supporting Information Appendix D). With a model weight of 0.63, this single variable model was nearly four times better than all other models in our AIC model comparison. Although there were interesting spatial patterns of other predictor variables, none of them was considered strong explanations of oyster recruitment (Supporting Information Appendix D).

Reef slope correlated most strongly with the depth of water inundation ($R^2 = 0.63$; slope = 16.9 [depth of inundation] – 3.44; Fig. 6; Supporting Information Appendix E). A model with depth and duration of water inundation also performed well ($w_i = 0.24$); duration of water inundation was also positively associated with slope.

Vertical relief in the high reef zone of oyster reefs [$\ln (x + 1)$ transformed] was significantly and positively associated
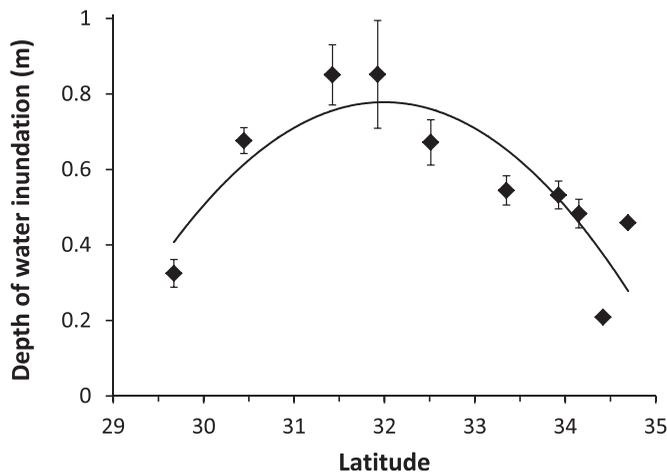
Fig. 5. Mean depth of water inundation (*m*) on oyster reefs when the reef was submerged. Points represent seasonal averages ± SD. The two northern-most sites lack error bars because we only have data from fall.

Table 3. Model selection results for regression analyses on oyster density at each site. The best model (shown in bold) as selected by the lowest AIC$_c$ is the null model.

No. predictors	Model	R^2	AIC$_c$	ΔAIC$_c$	w_i
0	**Null model [Intercept only]**	**—**	**161.1**	**0**	**0.37**
1	Salinity	0.28	162.1	1.03	0.22
1	Depth of inundation	0.25	162.5	1.41	0.18
1	Fall water temperature	0.19	163.3	2.21	0.12
1	Inundation duration	0.010	165.3	4.18	0.05
2	Salinity, fall water temperature	0.40	166.3	5.24	0.03
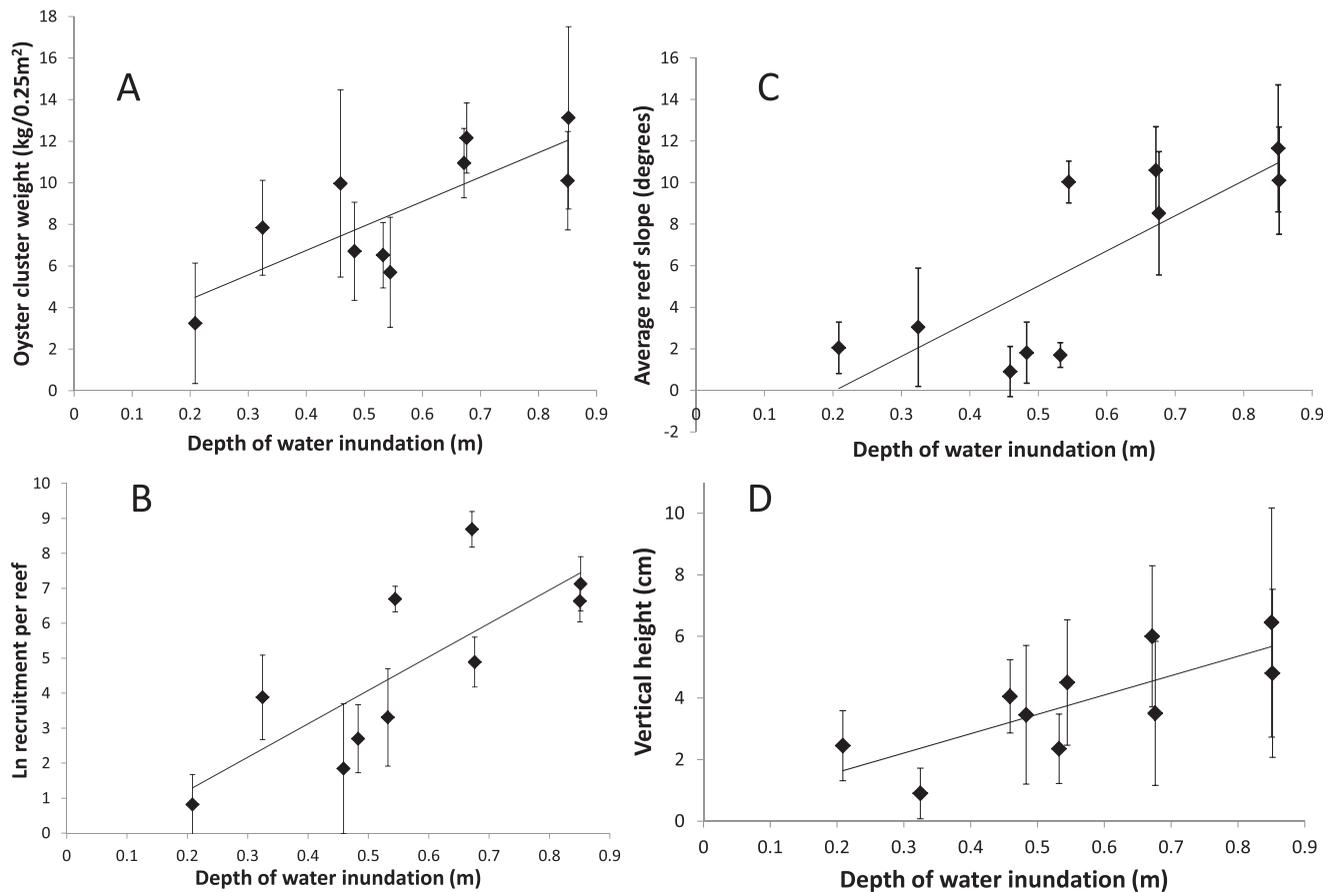
Fig. 6. Relationship of mean depth of water inundation on (A) oyster biomass, (B) oyster recruitment [ln (x + 1) transformed], (C) the average slope of reefs, and (D) the average vertical height of oyster reef within the high reef zone. Each panel A–D depicts the average across all five reefs at each site (±SD).

with depth of water inundation (R^2 = 0.60; vertical relief [ln(x + 1)] = 6.3 [depth of inundation] – 0.3; Fig. 6; Supporting Information Appendix F). For both mid and low reef zones, the null model performed best (Supporting Information Appendix F).

Discussion

All oyster-level responses measured in this study, including density, biomass, and recruitment, were unimodal patterns with latitude that peaked in Georgia and South Carolina estuaries. In fact, high recruitment seems requisite to setup the large values of the higher order oyster properties like density. Density and biomass patterns match the unimodal shape of the recruitment pattern, suggesting proportional decline over time of the high number of recruits that initially settle. At the highest recruitment site in Ace Basin, SC recruitment was nearly eight orders of magnitude greater than in our lowest site in NC. Similarly, many of the oyster reef characteristics, including slope and vertical relief of the high reef zone, peaked in Georgia and South Carolina estua-

ries. Reefs in the mid domain were the steepest, changing as much as 0.5 m in elevation over their 3-m width. Size and stature of oysters and oyster reefs often increase with aerial exposure in the intertidal zone (Bishop and Peterson 2006; Fodrie et al. 2014), so it is not surprising that we found the greatest differential in vertical relief where it coincided with high reef slope, that is, the largest intertidal gradient in elevation and aerial exposure. Thus, the mid latitudes of our study are where oysters along the salt marsh edge are seemingly thriving, creating the greatest differential in vertical relief across the intertidal zone. Moreover, this greater vertical relief generates habitat complexity, which can result in higher densities of reef-dwelling species (Humphries et al. 2011).

Of the physical variables examined, salinity and duration of water inundation were similar across all sites, and consequently exhibited no patterns with latitude. For salinity in particular, this result was not surprising as we standardized our site selection by picking high salinity areas (29–39 ppt). However, we had expected that water inundation duration would vary across sites. Low spatial variability in inundation

duration precludes a powerful test of its relative influence against the other physical variables in our models. Inundation duration is known from many previous studies to affect oyster performance (e.g., Crosby et al. 1991; Bartol et al. 1999, Malek 2010; Fodrie et al. 2014). Yet, because oyster reefs along the edges of salt marshes are largely constrained to a relatively narrow intertidal band at all of our sites, the low variation in inundation duration reflects the tidal height where fringing reefs are commonly found in the SAB. Thus, tidal duration largely cannot account for the biogeographical differences in oyster performance observed in our study.

Conversely, temperature and inundation depth varied considerably across our sites. Temperature showed a linear decline with increasing latitude in fall through spring, but no pattern in summer. The lack of latitudinal effect in summer could stem from less pronounced differences in solar insolation across the domain, or the fact that once seawater reaches near 30°C most extra added insolation presumably goes to heat of vaporization instead of raising the temperature. Despite the significant latitudinal trend in temperature in three seasons of the year, temperature was only slightly influential on oyster and reef properties. Only the depth of water inundation over reefs showed a prominent peaked distribution, and it was strongly correlated with oyster performance.

It is well known that the tide in the SAB exhibits the largest cross-shelf amplification at the widest part of the shelf, which occurs in Georgia (Redfield 1958; Blanton et al. 2004; Fig. 1). This essentially creates a wavelength resonant seiche that magnifies the tidal amplitude. However, we have systematically quantified how this tidal amplitude differentially affects the depth of water inundation on oyster reefs, and furthermore that the regional gradient in tidal amplitude does not differentially affect the duration of water inundation across our studied reefs. Most importantly, the physical forcing of the SAB, which drives deeper water on reefs in Georgia, seems to have important implications on oyster biology and reef properties (Fig. 6). In particular, we found that depth of water inundation explained variation in oyster recruitment, biomass, reef slope, and the vertical height of the high zones of reefs. We suggest there is support for a causative, mechanistic influence of the depth of water inundation on these variables that emphasizes the role of physical-biological coupling across the SAB.

Higher water inundation levels in our mid latitude sites, in combination with similar durations of water inundation across all our reefs throughout the SAB, suggest that mid latitude sites have a larger tidal prism and receive more flow speed, tidal energy, and/or net water volume delivery per unit time. These three physical aspects are highly interrelated, yet each one may be partially responsible for some of the oyster and reef differences we observed peaking in the mid SAB as they are known to positively affect the performance of oysters and resultant reef properties. First, higher flow and flux fosters higher density and faster growth and elongation in individuals, leading to more complex reef structure (Lenihan et al. 1996; Lenihan 1999; Grabowski et al. 2005). The large influx of water also increases oceanic influence and the possibility for higher allochthonous food inputs, sediment movement, and larval delivery, including oysters themselves (Roegner and Shanks 2001; Olaguer-Feliu et al. 2010; Fagherazzi et al. 2013; Byers et al. 2014). Second, higher tidal energy being channeled through tidal creeks possibly results in higher reef slopes at our sites and could also contribute to the high turbidity of the water column frequently observed in the mid-latitude areas and their subsequent high rates of sedimentation (Monbet 1992; Zheng et al. 2003; Ellis et al. 2004; Manning and Bass 2006). Third, water depth directly influences the volume of living space for large-bodied predators like bonnethead sharks (*Sphyrna tiburo*) that frequently forage on Georgia reefs for blue crabs (*Callinectes sapidus*) during high tide (Byers *unpublished data*; Graboswki *unpublished data*), potentially exerting strong top-down structuring forces on reef trophic structure. Collectively, these three physical factors associated with the higher tidal prism provide a possible mechanistic explanation for the differences in oyster biology and reef properties across the SAB. Moreover, the findings emphasize that biogeographic provinces are far from homogeneous and can contain influential physical gradients that mediate biological processes.

Oyster density was one of the only response variables that did not respond strongly to depth of water inundation. None of the explanatory models outperformed (exhibited a lower AIC score than) the null intercept-only model. Such an outcome suggests that other (perhaps biological) processes, such as predation, could be influential in shaping oyster abundance (Lenihan and Peterson 1998; Bartol et al. 1999; O'Beirn et al. 2000; Nestlerode et al. 2007; Knights et al. 2012; Johnson and Smee 2014, Kimbro et al. 2014). Similarly, the vertical relief of reefs at low and mid reef zones was not correlated strongly with any predictor variable. Rather, only at the highest reef zone at the top of the creek bank was vertical relief of the reef related to depth of water inundation. This high zone is where the reef is steepest (especially so in the mid-domain), and so oysters may be differentially and positively affected by tidal energy or aerial exposure there (Bishop and Peterson 2006; Fodrie et al. 2014).

That the physical-biological coupling apparent in this system can be accounted for with a single variable is appealing for its tractability, generalizability, and mechanistic underpinnings. That is, the depth of water inundation, or more generally, tidal amplitude, is an easily quantifiable variable that appears to have much predictive power at large spatial scales for biological processes on intertidal reefs. Understanding how physical factors influence ecosystem engineers is particularly important because of these species' disproportionately large effects on environmental variables and

habitat provisioning. In the case of oysters, their higher accumulation of mass and intensified reef structure in areas of higher tidal energy in turn can affect habitat quality, flow speeds, and sedimentation rates, which probably influence reef community dynamics and structure as well as the provisioning of ecosystem functions and services. Identification of physical factors with strong, deterministic influences on ecosystem engineers may help to explain substantial variation in biological communities even across large scales.

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