Stark differences in spatial gradients of Eastern oyster (*Crassostrea virginica*) productivity in two Florida, USA, estuaries

Laura S. Storch [a],[*], David L. Kimbro [b], Nikki Dix [c],[d], Pamela Marcum [e], Jason Garwood [f], Christopher D. Stallings [g], J. Wilson White [h]

[a] *Department of Mathematics, Bates College, Lewiston, ME, United States of America*
[b] *Department of Marine & Environmental Science, Northeastern University, Boston, MA, United States of America*
[c] *Guana Tolomato Matanzas National Estuarine Research Reserve, Florida Department of Environmental Protection, Ponte Vedra Beach, FL, United States of America*
[d] *Department of Biology, University of North Florida, Jacksonville, FL, United States of America*
[e] *South Carolina Department of Natural Resources, Charleston, SC, United States of America*
[f] *Apalachicola National Estuarine Research Reserve, Florida Department of Environmental Protection, Eastpoint, FL, United States of America*
[g] *College of Marine Science, University of South Florida, St Petersburg, FL, United States of America*
[h] *Department of Fisheries, Wildlife, & Conservation Sciences, Coastal Oregon Marine Experiment Station, Oregon State University, Newport, OR, United States of America*

ARTICLE INFO

ABSTRACT

The eastern oyster (*Crassostrea virginica*) is a foundation species in U.S. Atlantic and Gulf coast estuaries because of its numerous ecosystem services and importance to local fisheries. Concerns about the persistence and sustainable harvesting of oysters in the state of Florida is growing due to environmental factors (e.g., increased predation, salinity, and disease) and increased harvesting pressure. Thus, we need to understand which estuary locations are best suited for conservation or restoration efforts. Here, we use a combination of field experiments and modeling to assess the potential oyster productivity at sites throughout two estuaries at the same latitude but in different ocean basins: Apalachicola Bay (Gulf of Mexico coast) and the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM, Atlantic coast). Our population model used the per-recruit approach from fisheries science, allowing us to combine field data on growth and mortality to estimate productivity (measured as lifetime spawning output) in an elegant way, without requiring assumptions about unknown larval supply processes. Subtidal Apalachicola Bay oysters exhibit an expected pattern, with greater productivity in the inner estuary nearer the river mouth and predation reducing productivity in the seaward direction. In contrast, intertidal GTM oysters do not exhibit strong spatial gradients, with little effect of predators and slightly higher productivity near the river mouth; intertidal oysters in Apalachicola exhibited similar productivity and lack of predator effect. We attribute these differences in oyster productivity to differences in tidal exposure, the predator community, and hydrology of oyster reefs at the two study sites. Thus, we would give diverging recommendations for spatial prioritization of restoration and conservation efforts. Additionally, these results lead us to caution against generalized statements about spatial patterns of oyster productivity within estuaries without consideration of the predation context.

1. Introduction

Large-scale spatial variation in life history traits such as body size, growth, reproductive output, and lifespan, is prevalent in ecology (Brown, 1995). Examples include Bergmann's rule (Blackburn et al., 2008), the center-periphery hypothesis for geographic ranges (Sagarin and Gaines, 2002), and patterns of countergradient evolution (Conover and Schultz, 1995). Nonetheless, there is a desire to generalize about species' ecology across their range. For example, fishery stock assessments and species distribution models typically assume common demographic rates across large swaths of a species' range, and modelers often rely on demographic parameter estimates or abiotic reaction norms from particular study sites in order to make broader predictions about population dynamics, leading to a variety of potential biases (Barry and Elith, 2006). For declining populations, incorrect spatial generalizations regarding species' size, growth, and

---

mortality may impair our ability to manage sustainably or conduct habitat restoration. In particular, assessments of habitat suitability for restoration frequently neglect spatial variation in biotic factors such as predator effects.

In some environments, variability may be greater over scales much finer than the scale of the species' range. Estuaries are a good example, with large variability in salinity, flow, temperature, and other factors over scales of only hundreds of meters and with sub-hourly variability. This scale can be even finer in the vertical plane, e.g., significant changes in salinity over a vertical meter of water. The physiology and ecology of sessile subtidal and intertidal invertebrates in estuaries is heavily influenced by those abiotic environmental gradients (Menge and Sutherland, 1976, 1987; Kennedy et al., 1996; Kimbro et al., 2019). For example, in eastern oysters, (*Crassostrea virginica*, hereafter, "oysters") – a commercially important, foundation (i.e., habitat-forming) species in U.S. Atlantic and Gulf of Mexico estuaries – larval recruitment and survival are lowest and susceptibility to diseases is highest at very high or low salinities or temperatures (Livingston et al., 2000; Kennedy et al., 1996; Powell et al., 1996; Lough, 1975). Oyster growth, in turn, is dependent on myriad abiotic and biotic factors such as water flow, salinity levels, oyster reef height, and whether the reef is subtidal or intertidal. For example, oysters tend to have the highest growth rates at intermediate salinity levels (e.g., Tolley et al., 2005; Wang et al., 2008; Kimbro et al., 2009), and oysters located on intertidal reefs with extreme aerial exposure have slower growth (Kimbro et al., 2020; Bishop and Peterson, 2006).

Understanding these environmental gradients and the resulting spatial patterns of oyster productivity is essential for successful spatial management of oysters, for example, by planning sites for effective restoration (Hernandez et al., 2018; Smith et al., 2023) and setting appropriate harvest zones and sanctuary locations (Puckett and Eggleston, 2012). By "productivity" in this context we refer to the lifetime reproductive output of an oyster, as the product of survival, growth, and fecundity over its lifetime, which determines an oyster's contribution to the demographic replacement of the population (Botsford et al., 2019). Previous research in this area has lead to many examples of habitat suitability indices for different oyster species and study sites (e.g., Barnes et al., 2007; Beseres Pollack et al., 2012), as well as dynamic models that include these factors to project the effects of different spatial management schemes on oyster population sustainability (e.g., Barille et al., 2011; Dekshenieks et al., 2000; Grangeré et al., 2009; North et al., 2010). Such models often use environment-performance functions, such as a salinity-growth relationship, to model effects of predicted temperature and salinity across an estuary (e.g., North et al., 2010) or use site-specific demographic rates estimated at each location in the domain (e.g., Puckett and Eggleston, 2012). However, modeling efforts do not always consider across-estuary spatial variability. In some cases, a single set of demographic parameters are used to represent the oyster population in an entire estuary or region (e.g., Ray et al., 1994), and so quantifying the relative importance of spatial variation in productivity within and across estuaries is necessary.

Spatial variability in predator effects is also frequently neglected. Predator effects include (1) consumptive effects, i.e., direct mortality due to consumption, (Kimbro et al., 2017b), (2) non-lethal effects, i.e., changes in behavior/morphology due to presence of predators (Lima and Dill, 1990; Robinson et al., 2014; Scherer et al., 2016; Kimbro et al., 2017a), and (3) trait-mediated indirect interactions, i.e., trophic cascade effects due to higher level predators acting on oyster predators (Werner and Peacor, 2003; Grabowski, 2004; Grabowski and Kimbro, 2005; Kimbro et al., 2014). There can also be spatial variability in predator effects on prey due to environmental heterogeneity, such as increased salinity-dependent predator attack rates or mortality rates, (Garland, 2015; Pusack et al., 2019), leading to greater predation on subtidal reefs than on intertidal reefs, and in higher-salinity regions of estuaries (Kimbro et al., 2017b; Fodrie et al., 2014). There is also variability in predator density and activities within estuaries and

biogeographically across regions (Weissburg et al., 2014; Kimbro et al., 2014, 2017b). Here, we focus on consumptive effects (due to the type of data collected), which evidence suggests has a stronger effect on oyster populations than non-consumptive effects (Kimbro et al., 2017a, 2020).

Eastern oysters are an important commercial species and ecosystem service provider, but many populations have experienced substantial declines in population abundance over the past several decades, due to both environmental effects and harvesting pressures (Beck et al., 2011; Grabowski et al., 2012; Zu Ermgassen et al., 2012). In this study, we examined spatial variation in oyster productivity within and across two estuaries that lie at the same latitude but vary hydrologically, in the tidal height of oyster reefs, and in the density, identity, and distribution of oyster predators. We conducted a series of predator-excluding outplant experiments across both estuaries in order to estimate growth and mortality rates. We then used a population modeling approach to examine how the effects of predators and environment jointly determine productivity patterns, and how those patterns vary within and among estuaries. This information could ultimately be useful to inform spatial selection of restoration and conservation efforts.

2. Methods

2.1. Overview

In our investigation, we used field experiments to estimate growth and mortality rates (including with and without predator consumptive effects) at each of our study sites, which were then used to parameterize a size-structured population model which produced estimates of per-recruit lifetime spawning biomass at each site. Lifetime spawning biomass (explained in more detail below) is an estimate of the expected lifetime productivity of a single new juvenile oyster on a reef (Botsford et al., 2019). Thus it is useful for estimating the relative value of enforcing harvest limits or conducting restoration at different sites. The outcome of this analysis is a description of the spatial variance in productivity both within and between the two estuaries, and the portion of that variance due to consumption by predators.

Oyster population dynamics can be highly variable and depend not only on abiotic and biotic factors affecting adult oysters on the reef, but also on the transport and settlement of larval oysters, which can be highly variable in space and time (White et al., 2019). A spatially explicit representation of the full population dynamics of oysters within an estuary would therefore require assumptions regarding larval connectivity among locations, which can be both highly structured and temporally variable (Puckett and Eggleston, 2012). There are also great uncertainties about larval connectivity within estuaries, with some recent genetic studies suggesting highly limited dispersal, despite the potential for transport throughout an estuary by tidal flushing (Adrian et al., 2017). Given these uncertainties, we adopted an approach widely used in fisheries science to estimate productivity (or fishery yield) independent of recruitment variability, and calculated spawning biomass per recruit (SBPR).

In fisheries, yield per recruit is used to represent how much fishery yield is obtained – on average – from one individual recruit to the fishery (or a cohort of recruits). Yield per recruit is calculated by taking the product of the expected probability of survival from recruitment to age *a*, biomass at *a*, fishery selectivity (the probability of being in a targeted size or age class) at *a* and the harvest rate, then summing that product for each age *a* (Beverton and Holt, 1957; Botsford et al., 2019). We take the same approach, but for spawning biomass; essentially the product of survival-to-age, biomass-at-age, and probability of (female) reproductive maturity at age, summed over age (note that this presumes egg production is proportional to biomass, which has been shown to be the case for oysters; Kennedy et al., 1996). This provides an estimate of the expected relative total lifetime egg spawning output of one oyster recruit (spat). The utility of this approach is that it is agnostic with respect to uncertain larval processes, focusing only on the post-larval

Table 1

Average depth (m) plus/minus one standard deviation for each subtidal site in Apalachicola Bay, averaged over the study period.

Site	Average depth (m)
West 2	0.88 ± 0.56
West 1	0.79 ± 0.30
East 1	0.82 ± 0.41
East 2	0.99 ± 0.70
East 3	1.01 ± 0.78

factors affecting productivity of a site. This could be useful in spatial management contexts (i.e., which reefs should be protected from harvest?) or restoration contexts (i.e., which locations could support more productive oyster populations if habitat were restored?). Although we have described these per-recruit quantities in an age-structured context, we calculated them using a size-structured model, because the demographic quantities of interest are largely determined by size, not age (mortality, maturity, and biomass). Fortunately, the distribution of spawning biomass-at-age in the spawning biomass calculation is identical to the equilibrium distribution of spawning biomass in a population (akin to the stable age distribution in an age-based model; Botsford et al., 2019). Thus, we can simply obtain the equilibrium spawning biomass distribution over size with constant recruitment and integrate to obtain spawning biomass per recruit.

The further advantage of the spawning biomass per recruit approach is that it integrates the effects of different demographic processes that could exhibit competing spatial gradients. For example, because they spend a portion of every day exposed to air, unable to feed but also unavailable to subtidal predators, we expect intertidal oysters to have lower mortality rates but also slower growth rates than subtidal oysters (e.g., Fodrie et al., 2014; Bishop and Peterson, 2006). Yet it is not intuitive how those factors would combine to make intertidal or subtidal oysters more productive. The modeling approach we took combines those factors to understand gradients in overall demography.

2.2. Study species

Eastern oysters are suspension-feeding bivalves that form subtidal and intertidal reefs in estuaries in the southeast United States. They are protandrous hermaphrodites (i.e., they typically mature as male first, then change sex to female) that reproduce by broadcast spawning; larvae remain in the water column for several weeks before settling back to the benthos as spat, preferentially settling on the shells of living or dead adult oysters (Kennedy et al., 1996). Historically oysters have supported productive fisheries and provided numerous ecosystem services (Grabowski et al., 2012), although most oyster populations have suffered from overharvesting and habitat degradation on a global scale (Beck et al., 2011; Zu Ermgassen et al., 2012). In our study systems, oysters are vulnerable to a variety of predators that we describe below.

2.3. Study areas

2.3.1. Apalachicola Bay

The Apalachicola Bay estuary is contained within the Apalachicola National Estuarine Research Reserve, one of 30 NERR sites in the United States. The estuary is located at the terminus of the Apalachicola River in the Florida panhandle (Fig. 1). In past studies (Kimbro et al., 2017b) we divided the bay into six study regions based on proximity to the river mouth (close, mid, and far, where salinity increases as distance from the river mouth increases) and position relative to the river (east or west). Note that the color scheme denoting different regions of the estuary in Fig. 1 are used to color-code results throughout the rest of the paper. There are both intertidal and subtidal oyster reefs in

Apalachicola Bay, although the subtidal reefs are more extensive and supported a commercial fishery prior to its collapse in 2012 (Kimbro et al., 2017b). The subtidal reefs are shallow, on the order of 1 m deep (Table 1). Oyster predators in Apalachicola Bay include mud crabs (predominantly *Panopeus herbstii* and *Eurypanopeus depressus*), which are the primary predators of small, juvenile oysters < 25 mm, crown conchs (*Melongena corona*), which are restricted to the intertidal reefs, stone crabs (*Menippe mercenaria*), which were not present during the study period because they require reef habitat and the reefs were in too poor condition to maintain stone crab populations (D. Kimbro, personal observation), blue crabs (*Callinectes sapidus*), and a different gastropod predator, the southern oyster drill (*Stramonita haemastoma*; hereafter "drill"). Drills have a preference for medium-sized oysters (50–75 mm; Pusack et al., 2018) and for higher-salinity conditions further from the river mouth; in the experiments we describe here, evidence from the shells of dead outplanted oysters suggests that the drill is the primary predator of subtidal oysters > 25 mm (Kimbro et al., 2017b; Pusack et al., 2019).

2.3.2. Guana Tolomato Matanzas (GTM)

The Guana Tolomato Matanzas estuary is located in northeastern coastal Florida, within the Guana Tolomato Matanzas National Estuarine Research Reserve. The reserve spans an area beginning just south of Palm Valley, Florida and ending just north of Palm Coast, Florida, and connects to the Atlantic Ocean at the St. Augustine Inlet and the Matanzas Inlet. During the time of data collection, the Matanzas Inlet was only partially open and did not contribute significantly to flow; thus the primary inlet was at St. Augustine. The GTM comprises seven distinct regions (Fig. 1), which are differentiated based on water bodies, harvesting areas, and tidal flows.

Oyster reefs in the GTM are intertidal and primarily located along the Intracoastal Waterway and the brackish reaches of its tributaries. Previous work by Garland (2015) documented large variability in oyster size and density among the three southern regions (Butler, Matanzas, and Pellicer). Salinity gradients in the estuary are set by proximity to the ocean inlets (primarily the St. Augustine inlet) and to the freshwater inflows. The GTM watershed is long and narrow surrounding the bar-build estuary, and freshwater enters from a variety of small creeks and tributaries throughout its length. There is also a gradient in the oyster predator community. Mud crabs are ubiquitous in the estuary, as are blue crabs. However, crown conchs, which primarily consume larger oysters (> 25 mm), are only found in high densities in the southern reach of the estuary, south of the Matanzas Inlet.

2.4. Field data

2.4.1. Apalachicola Bay

Apalachicola Bay experiments ran from July 2013 to September 2016 in several rounds. The longest continuous data collection effort occurred between November 2014 and September 2016 and so we used this round of experiments to obtain growth and mortality estimates.

For each of the six predefined regions, one subtidal reef was randomly selected. Average reef depths ranged from 0.73 to 0.94 m (averaged over the study period). On each reef, nine protective frames made of steel rebar were spaced 3 m apart along a transect. The frames were 1.2 × 0.9 × 0.6 m and designed to protect the experiment from boating and fishing activities. Within each frame, we placed nine experimental units made of vinyl coated mesh (0.2 × 0.2 meter tiles within 0.2 meter cubes) and randomly assigned one of three treatments: (1) placed in mesh cages so the spat were completely protected from predators, (2) placed on the reef in the open so the spat were fully susceptible to predation, and (3) placed in mesh cages with two open sides to assess possible effects of diminished water flow in the cages (caged, uncaged, and cage-control, respectively). The Apalachicola Bay experiments used hatchery spat epoxied to ceramic tiles. This method was also used for the GTM 2018 outplant experiment
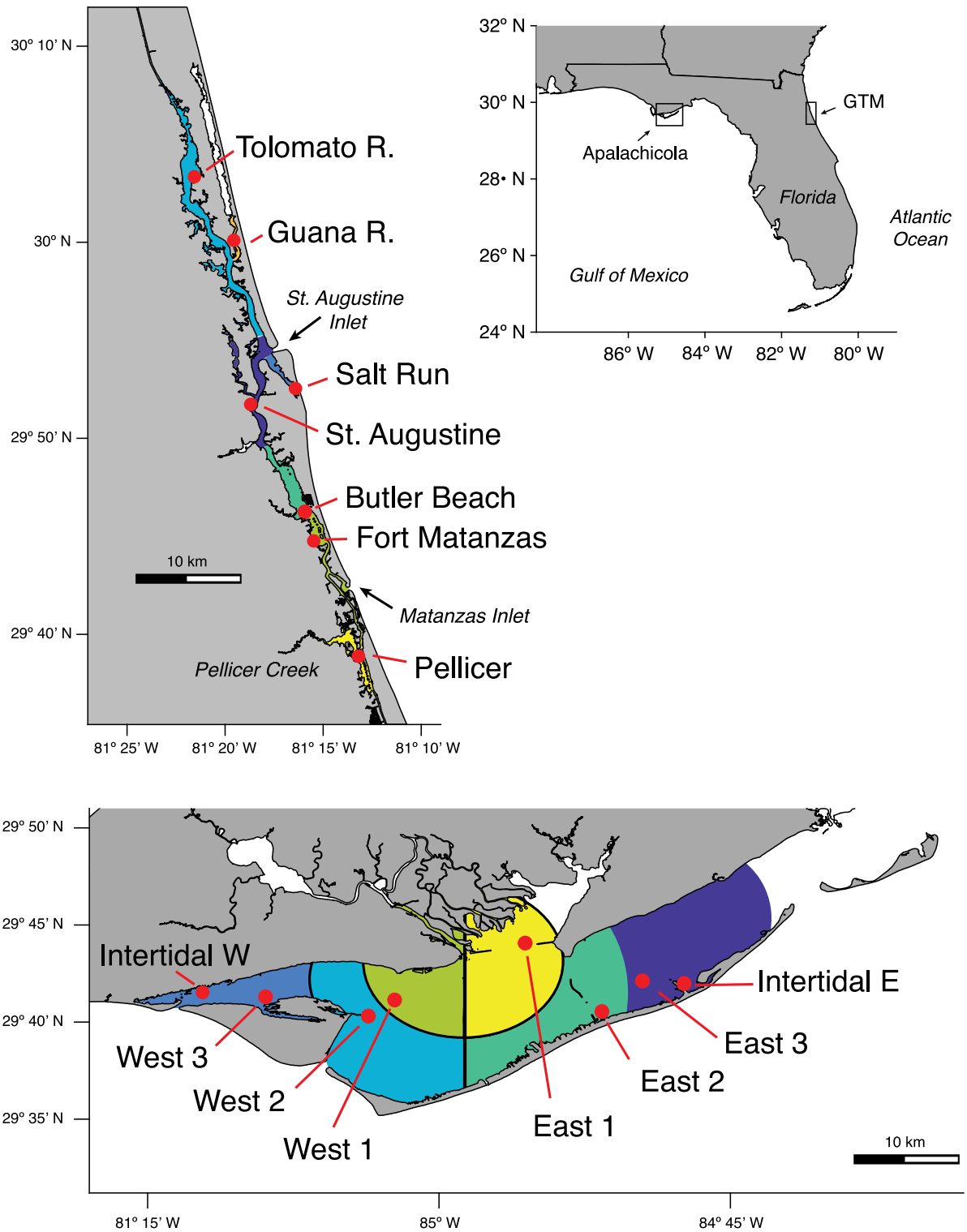
Fig. 1. Maps of the GTM estuary and the seven regions that comprise it (top left) and Apalachicola Bay and the six regions that comprise it (bottom). Red circles indicate reef locations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(see below). These juvenile-focused experiments co-occurred with adult (wild oyster) experiments of the same design, featured in Kimbro et al., 2017b.

During this outplant experiment, the density of oyster predators was estimated by visual counts within each of the rebar frames during monthly sampling visits. Blue crabs are too mobile to count in this manner, and we assume they are ubiquitous in the estuary. We also collected data on water conditions on the subtidal reefs via a

monthly conductivity-temperature-depth (CTD) profile at each reef using a SeaBird Electronics profiler (SBE 19plus V2). For each cast we took the median salinity and temperature across depth. At the intertidal sites, we deployed a HOBO salinity logger (model no: U24–002) and a HOBO pressure gauge logger (model no: U20–001-04) at the on the centermost rebar frame on each reef. Subtracting pressure 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 used to estimate the duration and depth of reef submergence. We did not collect salinity data on the intertidal reefs but we assume that conditions are similar to nearby subtidal sites.

2.4.2. GTM

Outplant experiments in the GTM were initiated in the summers of 2018 and 2019. In July 2018, juvenile hatchery oysters (spat) were attached to ceramic tiles using epoxy resin and deployed on the reefs in each region in three separate treatments. As in Apalachicola Bay, one reef was randomly selected, and tiles were (1) placed in mesh cages so the spat were completely protected from predators, (2) placed on the reef in the open so the spat were fully susceptible to predation, and (3) placed in mesh cages with two open sides to assess possible effects of diminished water flow in the cages (again labeled as caged, uncaged, and cage-control). As in Apalachicola Bay, cages were 0.2 meter cubes constructed of Vexar mesh netting and string trimmer line.

Each reef had four replicates (tiles) for each of the three treatments, spaced evenly along 12 meter transects with 12 spat per tile. We oriented transects along the main axis of each reef, approximately parallel to the shoreline, and situated transects at the midpoint between reef crest and the seaward edge of the reef. In this way, experimental units were at relatively the same reef height across sites, regardless of exact elevation. We marked spat with colored nail polish for unique identification. Once per month, we collected size and mortality data, beginning June 2018 and ending August 2019.

In May 2019 a new outplant experiment began. The 2019 outplant experiment used natural spat that had settled onto living oyster reef. Each reef had six replicates for each of the three treatments spaced along 18 meter transects, with three to four spat per tile. As in the 2018 experiment, we collected size and mortality data monthly, beginning May 2019 and ending May 2020.

For each of the seven GTM regions we calculated average growth and mortality rates using the 2018 and 2019 outplant data. In 2018 there were experimental errors with initial placement of spat (some spat were accidentally glued shut) and so we used the 2018 outplant data to estimate growth rates for the viable spat (because the 2018 outplant data provides the longest time series) but used the 2019 outplant data to estimate mortality rates.

We quantified predator abundance at these sites in May 2019. We deployed a transect along the crest of the reef. For each reef, that transect was then partitioned into 6 intervals. In the center of each interval, a second transect was deployed from the reef crest to the seaward edge of the reef. At the midpoint of the reef within each interval, we deployed a 1 x 1 m quadrat and searched for all mud crabs and crown conchs within each quadrat (n = 6 quadrats per reef). Because crown conchs were concentrated on the seaward edge of the reef at low tide, we also placed the quadrat at the seaward edge of each of the reef intervals to count and measure size of crown conchs, which resulted in 12 quadrat samples per reef: half from the interior (as describe above) and half from the reef edge.

To quantify spatial variation in environmental conditions, we deployed a HOBO salinity logger (model no: U24–002) and a HOBO pressure gauge logger (model no: U20–001-04) at the center of one oyster reef within each site, and calculated submergence time as described above.

2.5. Parameter estimation

We estimated age-length relationships (growth curves) by fitting the von Bertalanffy growth function to the size-age data at each study site using nonlinear least squares. The estimated parameters are the asymptotic maximum average length L_∞ (mm), the growth rate k

(1/year), and the age at size zero, t_0. The von Bertalanffy expression for effective size at time t, $L(t)$, is:

$$L(t) = L_\infty(1 - e^{-k(t-t_0)}) \tag{1}$$

We estimated L_∞ and k for oysters in each region of the GTM via this method, using data pooled across all treatment types (i.e., age-length data from caged, uncaged, and cage-control treatments were combined; although over time there were more surviving oysters in the cage treatment). There were insufficient data in the Pellicer region to estimate L_∞ and k and so that site was excluded from our analysis (there were no surviving oysters far enough into the adult stage to estimate maximum size). In two of the GTM regions, Salt Run and Tolomato, there were both harvested and unharvested sites. For Salt Run we used information from the unharvested site to match the other unharvested GTM regions. For Tolomato, we calculated parameter estimates using data from the harvested site, as the unharvested site had insufficient data for parameter estimations (but harvest was not considered in our analysis).

In Apalachicola Bay, the growth curves failed to converge on biologically reasonable estimates for L_∞, because there were few data for large, old oysters. To resolve this we fixed L_∞ at the average length of the oldest oysters in the data for each region (> 600 days), then estimated k only. There were insufficient data to calculate parameter estimates in the West 3 region and so we excluded it from our analysis. We computed variance in L_∞ by taking the standard error of the average oldest oyster lengths.

We calculated mortality rates for each Apalachicola Bay and GTM region for each of the three treatment types (caged, uncaged, and cage-control) using a generalized linear model with Poisson error and log link function. We estimated the instantaneous mortality rate, M (1/year), such that survival from time t to $t + 1$ is e^{-M}. Thus, the regression uses the number of surviving oysters as the dependent variable and time as the independent variable; given a log link function, the slope parameter is an estimate of M. We calculated a single mortality rate across all size classes. Although adult oyster mortality is typically significantly lower than juvenile oyster mortality and there are ontogenetic shifts in vulnerability, we frequently could not make separate juvenile and adult mortality estimates due to too few surviving oysters in the larger size classes. For the intertidal Apalachicola sites, we found that the Poisson GLM consistently failed to converge, so we instead used a linear model on log-transformed data, which produces the same slope estimate as the GLM approach.

We tested for caging artifacts by comparing parameter estimates of the cage-control treatment with the uncaged treatment and determined there were no significant caging effects. Specifically, a post-hoc Tukey test on models that included treatment as a factor had p-values >0.74 in both study regions, indicating very weak evidence of any caging artifacts. Therefore, we focus on effects of predation by comparing the caged vs uncaged treatments in subsequent sections.

2.6. Model structure and uncertainty estimation

We used an Integral Projection Model (IPM, Easterling et al., 2000; Ellner et al., 2016; Kimbro et al., 2019) to represent size-based oyster population dynamics and estimated spawning biomass. For a population with constant external recruitment (as we assume in the per-recruit framework), an IPM describes the population density of size x individuals at time t, $N(x, t)$, as a function of density at size y in the prior time step, $N(y, t - 1)$, multiplied by $K(x, y)$, the kernel, which defines the probability density of surviving and growing (or shrinking) from size y to size x in one time interval. The density of new recruits of size x at t is $R(x, t)$. $R(x, t)$ is added to the integrated product of $K(x, y)$ and $N(y, t - 1)$, giving a model of form:

$$N(x, t) = \int_\Omega [K(x, y)N(y, t - 1)]dy + R(x, t) \tag{2}$$

For this study, the kernel $K(x, y)$ incorporated the size-dependent growth and mortality rate estimates from the field experiments at each study site. We obtained the survival portion of $K(x, y)$ by converting the mortality rates M to single-time-step survival probabilities e^{-M} (where a single time step in the model is one month).

We created the growth portion of the kernel via a normal probability density function, where the mean growth for size y is the mean of the von Bertalanffy function $\mu(y) = L_\infty - (L_\infty - y)e^{-k}$ (see Eq. (1)) and the standard deviation is calculated from the residuals of the function fit to the data. Standard deviations are calculated individually for each site. We modeled $R(x, t)$ as a normal probability density function with mean $\mu = 7$ mm and $\sigma = 5$ mm, where μ is the mean spat size of the Apalachicola Bay field experiments and σ is the standard deviation in spat size (D. Kimbro, unpublished data).

To obtain the stable size distribution, we iterated the model for 100 time steps (after initializing at arbitrary conditions) with constant recruitment $R(x, t)$ in each time step, which was sufficient to ensure that the model reached equilibrium ($N(x, t + 1) = N(x, t)$, for all x). We then multiplied the stable size distribution by a function giving the probability of being a mature female oyster at size x (oysters are protandrous hermaphrodites, maturing first as males and then changing sex to female). We obtained the estimates of fraction female-at-length by averaging the fraction female-at-length curves from Powell et al., 2013. We then multiplied the female-only stable size distribution by an allometric function for the ash-free dry weight as a function of length (Kennedy et al., 1996), then integrated with respect to length to obtain the estimate of spawning biomass per recruit (SBPR, in grams).

We estimated SBPR for five of the six subtidal Apalachicola sites, the two intertidal Apalachicola sites, and six of the seven GTM sites, for uncaged groups (oysters are unprotected and subject to predation) and caged groups (oysters are protected from predation via mesh cages), in order to assess the effects of predation on productivity in different regions of Apalachicola Bay and the GTM.

To estimate uncertainty in SBPR, we generated 10^5 random parameter combinations using draws from a multivariate normal distribution defined by the mean parameter estimates and their covariance matrix, for the three estimated parameters (M, L_∞, and k; M has no dependence on L_∞ and k). We then used these 10^5 random parameter combinations to produce a distribution of spawning biomass per recruit estimates for each site and treatment (caged/uncaged) in Apalachicola Bay and the GTM.

2.7. Statistical analysis

In our analysis, we wanted to determine how much of the variation between SBPR distributions (i.e., productivity) was explained by spatial variation within the estuary (site to site variability) versus predation (caged or uncaged) effects. To address this goal, we performed two separate analysis of variance (ANOVA) on the Apalachicola Bay and GTM model outputs to obtain the partial R^2 for each of those factors, providing estimates of the variability in spawning biomass per recruit explained by each factor. We built linear models with site, treatment, and site × treatment interaction effects as the independent variables and SBPR as the dependent variable (and we constructed separate linear models for Apalachicola Bay and the GTM). Due to the large, order-of-magnitude variation in the spawning biomass per recruit distributions, we analyzed log-transformed SBPR values. We do not report p-values from this analysis because the sample size was arbitrarily large in the simulated data, but this does not affect the R^2 calculation (White et al., 2014). We performed statistical analyses using R version 4.1.2 (R Core Team, 2021).

2.8. Data availability

Field collected data and codes for estimating M, L_∞, and k, along with the integral projection model, are publicly available in the GitHub repository https://github.com/jwilsonwhite/NERR_science.

Table 2
Proportion of time exposed to air, calculated for the two intertidal Apalachicola Bay reefs. These values were calculated using the total hours over the entire study period vs the total hours of time exposed to air.

Site	Proportion exposed
Intertidal W	0.17
Intertidal E	0.18

Table 3
Proportion of time exposed to air, calculated for the six intertidal GTM reefs. These values were calculated using the total hours over the entire study period vs the total hours of time exposed to air.

Site	Proportion exposed
Tolomato	0.23
Guana	0.25
St. Augustine	0.24
Salt Run	0.32
Butler	0.19
Matanzas	0.24

3. Results

We observed striking differences in the levels of spatial variation with respect to growth, mortality, and SBPR estimates between the two estuaries and between subtidal and intertidal reefs. Subtidal Apalachicola Bay oysters followed expected patterns of spatial variation across the estuary, with strong effects of predation and greater productivity farther from the river mouth. In contrast, the intertidal GTM oysters exhibited minimal effects of predation and minimal spatial gradients. It was not possible to test for any sort of gradient in the intertidal Apalachicola reefs, as only two reefs had sufficient data to make SBPR calculations. However in general SBPR on those reefs matched the pattern in the GTM. We now explain these findings in detail.

3.1. Water conditions and tidal exposure

During the study period, salinity in Apalachicola bay followed a consistent spatial pattern, with lower salinity in the river mouth and near-seawater conditions nearest the inlets (at sites West 2 and East 3; Fig. 2). There was also a seasonal pattern of lower salinity during winter at the sites closer to the river mouth, and generally more variability in salinity at those sites. Temperature was similar at all sites and followed a typical seasonal pattern (Fig. 2). There were similar spatial differences in salinity in the GTM estuary, with much lower salinity at the more upstream sites such as Guana, Tolomato, and Butler, relative to the sites near the main inlet at St. Augustine and Salt Run. Although the Matanzas inlet was not fully open during this study period, there was enough exchange there to have near-seawater salinities there (Fig. 3). Water temperature followed a similar pattern as at Apalachicola, and temperatures were similar across GTM study sites (Fig. 3). For the intertidal sites, the proportion of time spent exposed to air was similar among the sample sites at both estuaries, ranging from 0.18–0.19 in Apalachicola (Table 2) and 0.19–0.34 in GTM (Table 3).

3.2. Predator density

The predator survey data in Apalachicola were highly overdispersed, with a preponderance of zeros (Fig. 4). We did not test for statistical differences among the sites, but the southern oyster drill, that caused the majority of oyster mortality in our experiments, was most common further from the river mouth at sites West 2 and East 2. (Fig. 4). Crown conchs were not observed on any of the subtidal
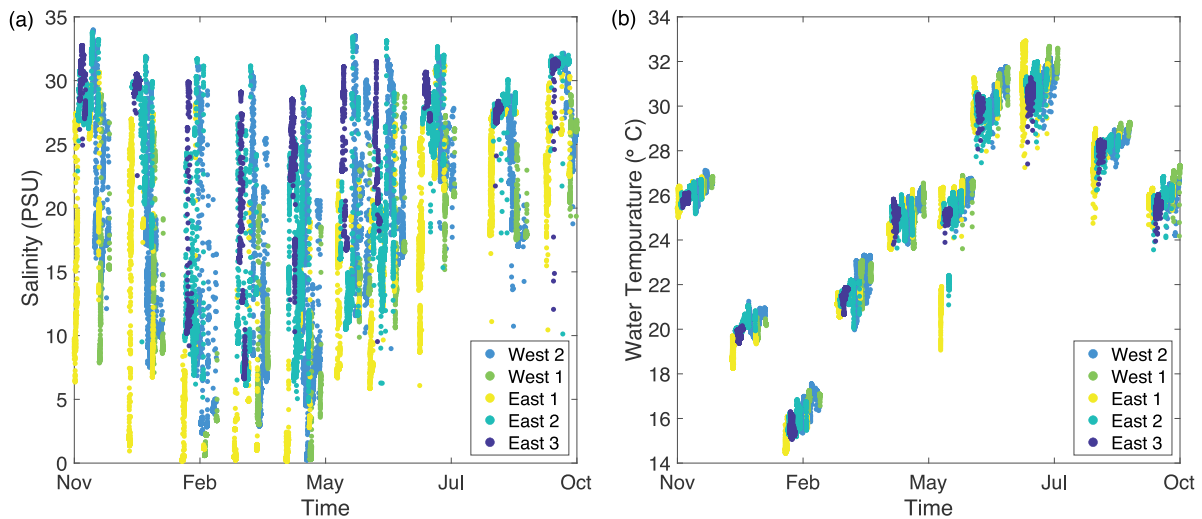
Fig. 2. A representative year (November 2015 to October 2016) of (a) salinity and (b) water temperature data for the five study regions in Apalachicola Bay. Each point is one sample at one sample rebar frame.
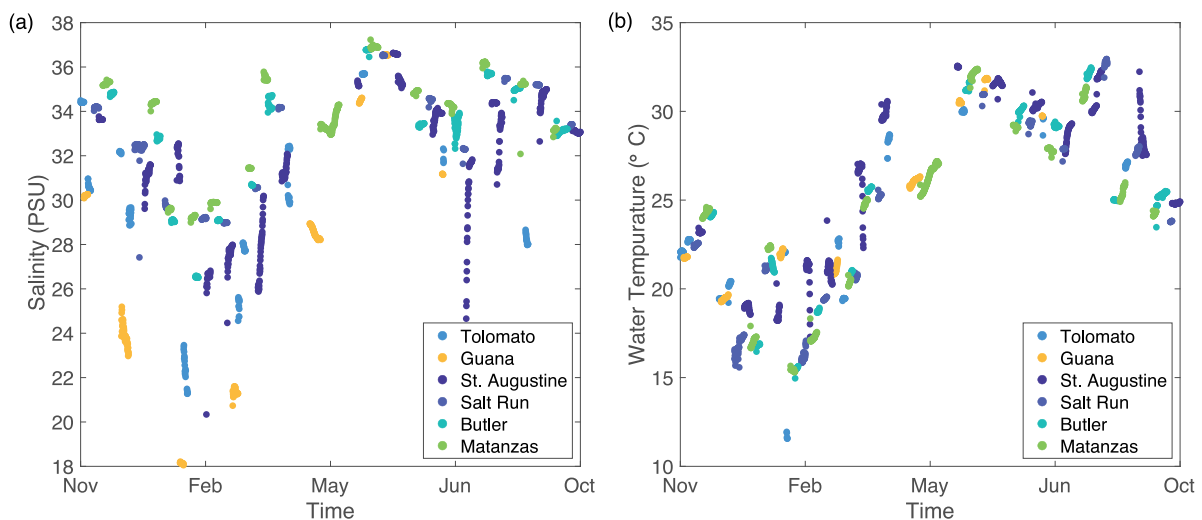

Fig. 3. A representative year (November 2018 to October 2019) of salinity and water temperature data for the six study regions of the GTM. Each point is one sample at one quadrat.

reefs. In the GTM, there was no clear gradient in the abundance of the mud crab predator among sites, and we did not observe the crown conch at any of the study sites (historically it had only been observed at Pellicer, which we had excluded from our analysis because the outplanted oysters did not survive; Fig. 5).

3.3. Oyster size and growth

We calculated estimates of the von Bertalanffy growth parameters k and L_∞ at five of the Apalachicola subtidal sites (excluding West 3, Table 4, Fig. 6), the two intertidal sites (Table 5, Fig. 7), and six of the GTM sites (excluding Pellicer, Table 6, Fig. 8).

In Apalachicola Bay, L_∞ ranged between $87.81 \le L_\infty \le 72.67$ mm, with the greatest values in the most seaward site, East 3, and the lowest values in the west-most site, West 2 (Fig. 6). There was little variation in asymptotic maximum size across sites, especially in comparison to the GTM (Tables 4 and 6). Growth rates were positively related to the asymptotic maximum size, with the fastest growth in East 3 (1.10 y^{-1}) and the slowest in West 2 (0.77 y^{-1}). We observed relatively little variation in k values, suggesting a high level of homogeneity in growth patterns among the Apalachicola Bay sites. At the Apalachicola Bay

intertidal sites, L_∞ was highest at Intertidal West (73.00 mm) and lowest at Intertidal East (62.56 mm). Growth rates at the two sites were similar (0.83 and 0.89 y^{-1} respectively, Table 5).

In the GTM estuary, the asymptotic maximum length, L_∞, ranged between $34.64 \le L_\infty \le 100.30$ mm, with the highest value at Matanzas, the southernmost site for which we analyzed data, and the lowest value at Guana River, in the northern reach of the estuary (Fig. 8). In contrast with Apalachicola Bay, the estimated growth rates, k, were generally negatively correlated with estimates of L_∞, and those sites had the lowest (0.55 y^{-1}, Matanzas) and highest (4.27 y^{-1}, Guana River) values, respectively. Oysters at Salt Run and St. Augustine, the two sites nearest to the St. Augustine Inlet, had intermediate values of both growth parameters and grew to large sizes relatively quickly. In comparison to Apalachicola Bay, the GTM generally had higher levels of heterogeneity in L_∞ and k across sites.

3.4. Oyster mortality

We calculated estimates of the natural mortality M for the same five Apalachicola Bay and six GTM sites (Tables 4 and 6, Figs. 9 and 11).

Yearly uncaged mortality in the subtidal Apalachicola Bay sites ranged between $6.02 \le M_{uncaged} \le 33.47 y^{-1}$ with West 2 having the
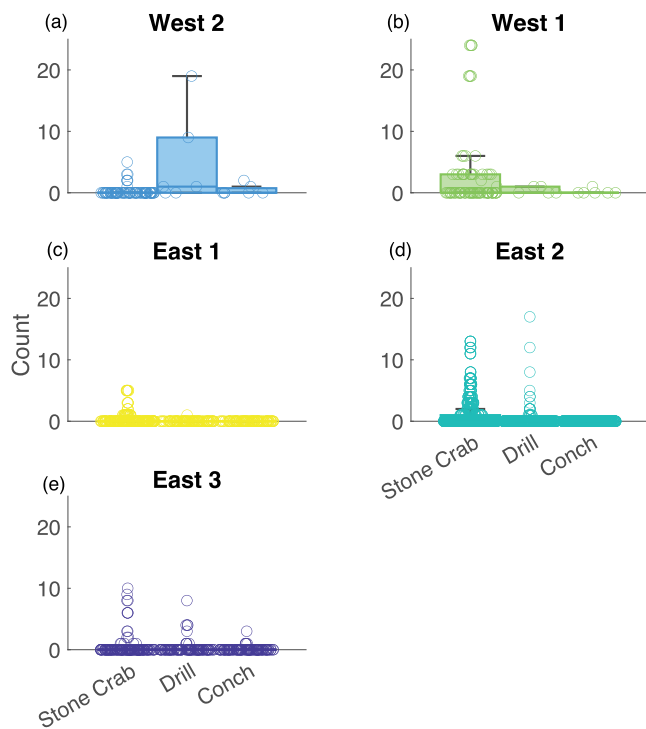
Fig. 4. Abundance of oyster predators at the Apalachicola Bay sites during the study period. Each point reflects one count in one rebar frame during a monthly survey during the outplant experiment.
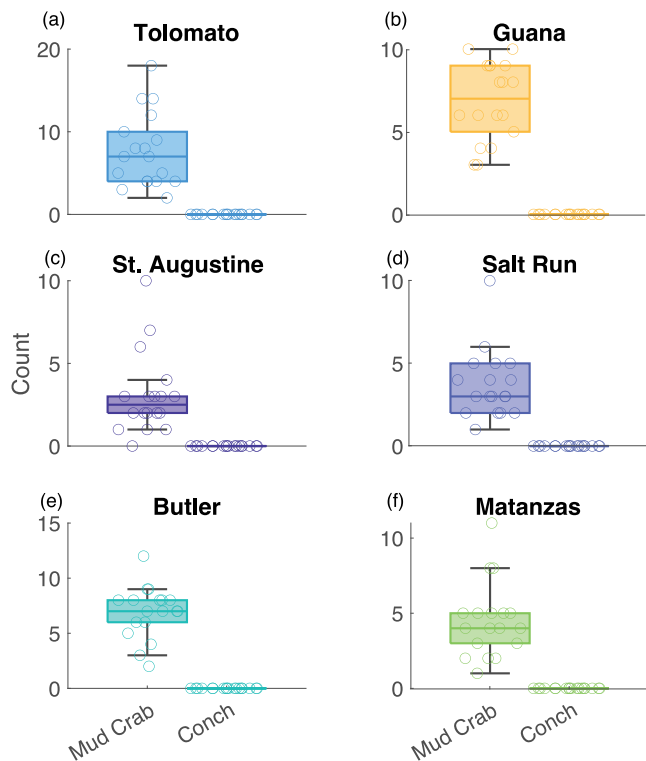

Fig. 6. Growth curves for the five Apalachicola Bay subtidal regions with length in mm (y-axis) over time in days (x-axis). For the growth analysis, caged and uncaged data were pooled together.

Fig. 5. Abundance of oyster predators at the GTM sites during the study period. Each point reflects one count in one quadrat during a monthly survey during the outplant experiment.

highest and East 1 the lowest. Yearly caged mortality varied between $0.62 \leq M_{caged} \leq 1.68y^{-1}$ with West 2 having the highest and East 3 the
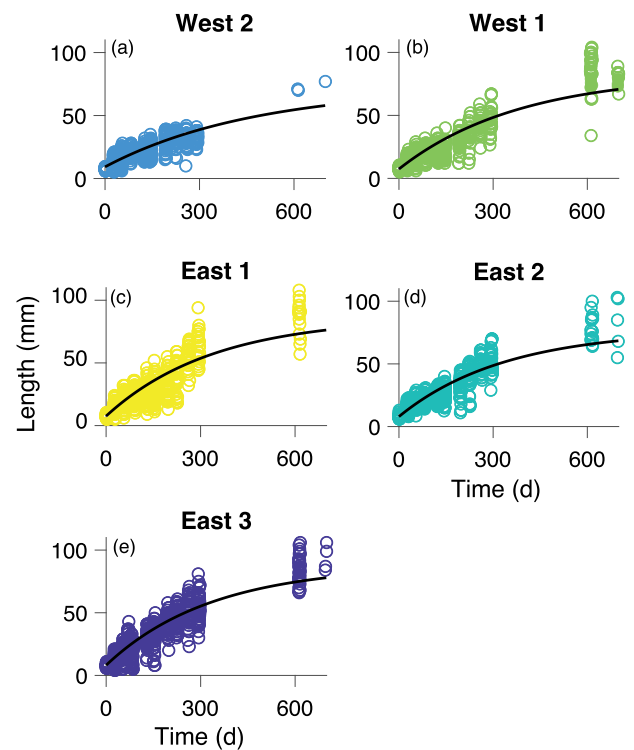
lowest (Fig. 9). Across all Apalachicola Bay subtidal sites, caged mortality rates were an order of magnitude lower than uncaged mortality rates, suggesting a significant influence of predation on Apalachicola Bay oyster populations. Conversely, higher mortality was observed in the cages at both intertidal sites (Table 5, Fig. 10).

In the GTM, uncaged yearly mortality ranged between $0.94 \leq M_{uncaged} \leq 2.36y^{-1}$ with the highest mortality estimates at Salt Run and the lowest in Tolomato River. Yearly caged mortality values were between $0.79 \leq M_{caged} \leq 3.04y^{-1}$, with the highest rate at Tolomato River and the lowest at Butler Beach, towards the south (Fig. 11). For many of the GTM sites, the difference between caged and uncaged mortalities was small. The greatest differences between mortality in and out of cages were at Tolomato River and Matanzas River sites, but in those cases mortality was higher inside the cages, contrary to expectation. In general, we observed negligible effects of predation on GTM oysters as compared to Apalachicola Bay.

3.5. Spawning biomass per recruit estimates

The spatial variation among sites in oyster growth and mortality lead to spatial differences in spawning biomass in each of the estuaries (Fig. 12). In the Apalachicola Bay subtidal sites, caged treatments had substantially higher spawning biomass per recruit estimates than uncaged treatments, with no overlap between the distributions of estimated SBPR between those treatments at any site. This is strong evidence for the importance of predation across the bay; the smallest difference was at site East 1, where the median value of caged estimates was ≈ 200 times larger than the median value of uncaged estimates. The West 2 uncaged site had the lowest spawning biomass estimates, with a median value ≈ 40 times smaller than the next lowest median at West 1 uncaged. The two intertidal sites had similar SBPR, with uncaged sites having higher SPBR than cages sites due to the lower mortality estimates.
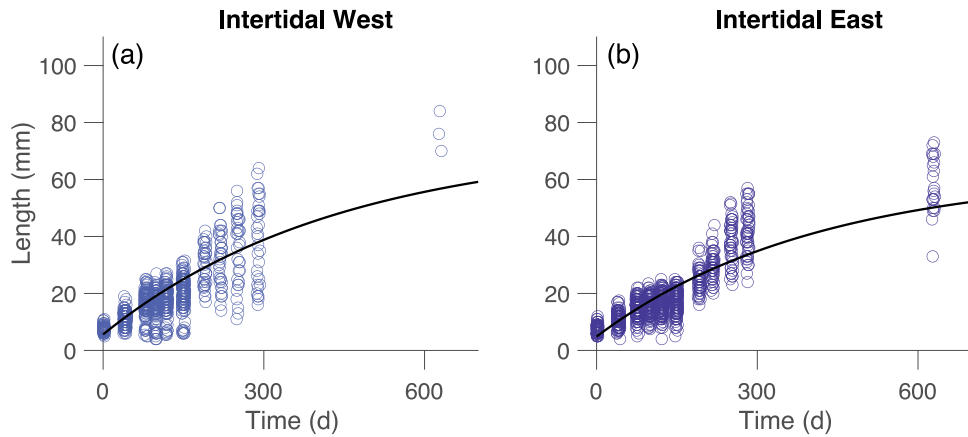
Fig. 7. Growth curves for the two Apalachicola Bay intertidal regions with length in mm (y-axis) over time in days (x-axis). For the growth analysis, caged and uncaged data were pooled together.
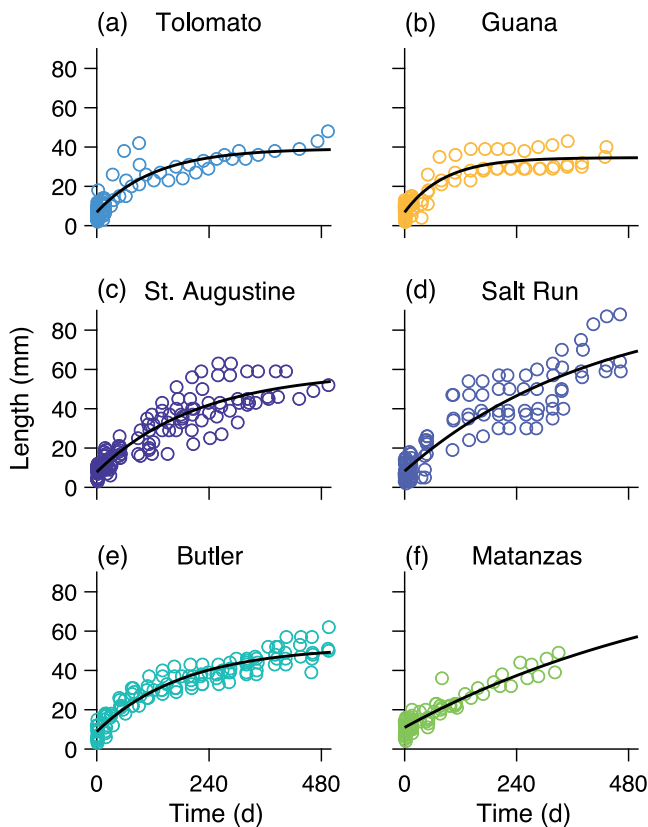

Fig. 8. Growth curves for the six GTM regions with length in mm (y-axis) over time in days (x-axis). For the growth analysis, caged and uncaged data were pooled together.

Fig. 9. Mortality curves for the five Apalachicola Bay subtidal regions with proportion surviving (y-axis) over time in days (x-axis). For the mortality analysis, separate parameters were obtained for uncaged (solid line) and caged (dashed line) data to determine the effects of predation.

Conversely, caged and uncaged SBPR distributions for the GTM estuary overlapped at all sites. Sites furthest from the primary inlet (Tolomato River and Matanzas River) had the least overlap in uncaged versus caged distributions (12% and 44% overlap, respectively). The remaining four sites had at least 59% overlap in the distributions of SBPR between caged and uncaged distributions.

The two estuaries differed in the main factor structuring the majority of spatial variability in spawning biomass per recruit (SBPR). For the Apalachicola Bay subtidal sites, the caging treatment explained 81% of the variance in SBPR (Table 7 and Supplementary Table 1), that is, the primary source of spatial variation in Apalachicola Bay oyster productivity was preda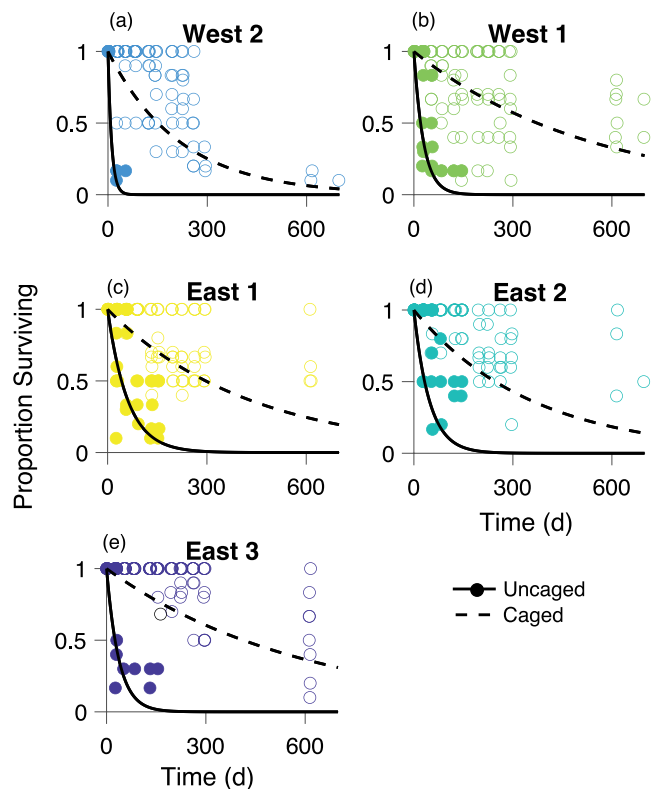tion. For the intertidal sites, treatment explained 93% of the variance in SBPR (Table 7 and Supplemental Table 2). In contrast, the variance in spawning biomass per recruit for the GTM was partially explained by site (partial R^2 = 30%), with little effect of the caging treatment (partial R^2 = 3.8%; Table 7 and Supplemental Table 3). The site*treatment effect had a partial R^2 of 12%, indicating some spatial variability in the importance of predation. Therefore, in the GTM estuary, environmental factors other than predation drove differences in oyster productivity among sites.

4. Discussion

Estuaries are by nature defined by gradients in physical conditions. The distribution, abundance, and productivity of sessile benthic
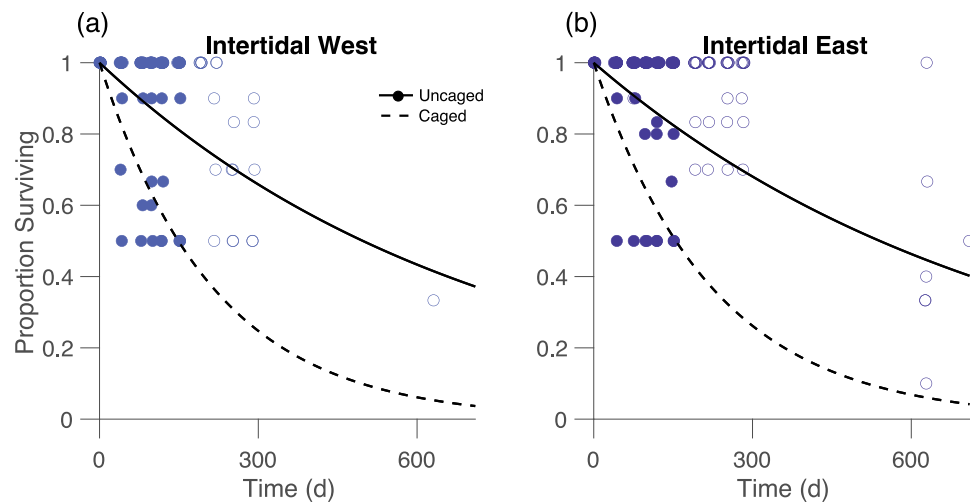
Fig. 10. Mortality curves for the two Apalachicola Bay intertidal regions with proportion surviving (y-axis) over time in days (x-axis). For the mortality analysis, separate parameters were obtained for uncaged (solid line) and caged (dashed line) data to determine the effects of predation.

Table 4

Estimated parameters for five of the six Apalachicola regions, plus minus the standard deviation. Data were insufficient to calculate parameter estimates for the West 3 region. L_∞ is the maximum size of adults in mm, k is the von Bertalanffy growth rate with units y^{-1}, and M is the mortality rate with units y^{-1}. Note that sites are ordered west to east.

	Apalachicola Bay Subtidal				
	West 2	West 1	East 1	East 2	East 3
L_∞	72.67 ± 2.19	82.91 ± 2.36	86.38 ± 3.53	77.20 ± 3.83	87.81 ± 2.11
k	0.77 ± 0.02	0.95 ± 0.02	1.06 ± 0.03	1.10 ± 0.02	1.10 ± 0.02
M uncaged	33.47 ± 5.73	12.45 ± 1.53	6.02 ± 0.80	7.77 ± 0.84	9.86 ± 1.31
M caged	1.68 ± 0.18	0.69 ± 0.11	0.84 ± 0.15	1.02 ± 0.11	0.62 ± 0.11

Table 5

Estimated parameters for the two intertidal Apalachicola regions, plus minus the standard deviation. L_∞ is the maximum size of adults in mm, k is the von Bertalanffy growth rate with units y^{-1}, and M is the mortality rate with units y^{-1}.

	Apalachicola Bay Intertidal	
	Intertidal West	Intertidal East
L_∞	73.00 ± 3.00	62.56 ± 2.03
k	0.83 ± 0.02	0.89 ± 0.02
M uncaged	0.51 ± 0.06	0.47 ± 0.04
M caged	1.70 ± 0.21	1.63 ± 0.32

organisms such as oysters is typically thought to be determined by those gradients in environmental and consumer stress (Menge, 1992; Bergquist et al., 2006; Cheng and Grosholz, 2016; Kimbro et al., 2019). Because they are subjected to daily tidal fluctuations and salinity variability, such organisms are typically able to tolerate a range of salinities (even if they are most productive at intermediate salinity), whereas predators and pathogens typically have more narrow tolerances, leading to gradients in the growth and mortality of the oysters. The general perception is that the two key gradients are, first, a gradient of decreasing stress but increasing predation risk moving from intertidal to subtidal habitats (Fodrie et al., 2014; Johnson and Smee, 2014; Bishop and Peterson, 2006), and second, the salinity gradient from the freshwater input at the head of the estuary to seawater at the inlet, creating an area of oyster-preferred moderate salinity and predation risk in the mid-estuary (Livingston et al., 2000). Here, we used replicated outplant experiments to examine gradients in oyster productivity (i.e., lifetime spawning biomass) in two estuaries at similar latitudes but in different basins (Gulf and Atlantic) and tidal elevation (i.e., solely intertidal in the Atlantic, but both subtidal and intertidal in the Gulf). We found that gradients in oyster productivity – and the contribution of predation to those gradients – differed strikingly among

the oyster habitats. We attribute this result to differences in hydrology, tidal elevation, and the predator community in the two estuaries, and note the implication for the generality of statements about gradients in, or salinity-dependence of, oyster demography based on results from any given estuary.

Results from subtidal reefs in Apalachicola Bay followed the typical expected pattern of oyster demography (Livingston et al., 2000; Kimbro et al., 2019): caged oysters, protected from predation, had high and similar productivity throughout the bay (except for the westernmost study site where growth was slower). Predation had a strong effect, and uncaged oysters had nearly half the productivity of caged oysters due to high predation mortality, particularly in the western bay where predator densities were higher. There was also a gradient in mortality, with the lowest predator-caused mortality closest to the freshwater input at the mouth of the Apalachicola River. Additionally, the predator treatment explained a high proportion of the variability in productivity (Table 7). This aligns with the conclusions of Kimbro et al. (2017b) about the salinity dependence of predation in Apalachicola Bay, and the importance of freshwater flow in limiting the distribution and activity of the main predator, the oyster drill (Pusack et al., 2018, 2019).

In strong contrast, intertidal oyster reefs in the GTM estuary had no obvious spatial gradients in productivity, and only a very weak effect of predators on patterns of productivity. Indeed, at the two sites furthest from the primary inlet, exposure to predators had a slightly positive effect on survival and thus productivity; it is unclear how that effect would arise mechanistically, and it may be an artifact of small sample sizes affecting our estimates of survival and growth. Nonetheless, the distributions of estimated productivity generally had high levels of overlap between caged and uncaged treatments, and the effect size of predation was minimal (Fig. 12). With only two intertidal study sites in Apalachicola it was not possible to test for a gradient, but estimates of productivity at those sites closely matched the values calculated for caged subtidal Apalachicola reefs and the intertidal GTM reefs, and

Table 6

Estimated parameters for six GTM regions, plus minus the standard deviation. L_∞ is the maximum size of adults in mm, k is the von Bertalanffy growth rate with units y^{-1}, and M is the mortality rate with units y^{-1}. Note that sites are ordered north to south.

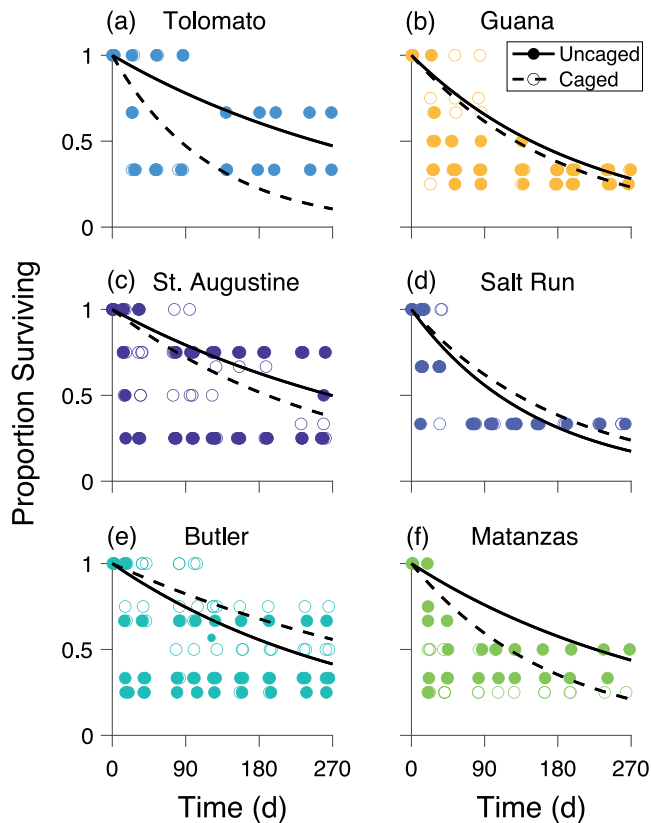|	GTM					
	Tolomato	Guana	St. Augustine	Salt Run	Butler	Matanzas
L_∞	39.29 ± 2.04	34.64 ± 1.16	59.13 ± 4.54	95.55 ± 18.23	52.21 ± 1.77	100.30 ± 46.31
k	2.92 ± 0.47	4.27 ± 0.58	1.68 ± 0.29	0.88 ± 0.29	1.97 ± 0.18	0.55 ± 0.33
M uncaged	1.01 ± 0.60	1.72 ± 0.55	0.94 ± 0.44	2.36 ± 0.91	1.19 ± 0.53	1.12 ± 0.65
M caged	3.04 ± 1.84	1.97 ± 0.58	1.33 ± 0.44	1.94 ± 0.73	0.79 ± 0.41	2.11 ± 0.83

Fig. 11. Mortality curves for the six GTM regions with proportion surviving (y-axis) over time in days (x-axis). For the mortality analysis, separate parameters were obtained for uncaged (solid line) and caged (dashed line) data to determine the effects of predation.

Table 7

Partial R^2 values for the residual variance by treatment (caged/uncaged) or site.

Estuary	Site R^2	Treatment R^2
Apalachicola Bay Subtidal	0.143	0.807
Apalachicola Bay Intertidal	0.000	0.934
GTM	0.301	0.038

shared with the latter the curious pattern of greater survival in the uncaged treatments.

Why do the spatial patterns of productivity across the whole-estuary gradient differ so dramatically between the two study sites? There are two clear factors at play. First is the different stressors facing subtidal (Apalachicola) versus intertidal (GTM) oysters. From prior studies we expected lower mortality but potentially slower growth on the intertidal reefs, but it was unknown how those two factors would balance; ultimately our results are similar to the findings of Fodrie et al. (2014), who found overall higher oyster productivity on restored intertidal reefs than on subtidal reefs. A likely second important factor is the difference in the predator communities at the two sites, with the GTM

estuary lacking a gastropod predator on large oysters. While the crown conch is present in high densities in the southernmost region of the GTM estuary (Pellicer), we excluded that site from our analysis because the outplanted oysters all died rapidly. Past studies consistently show high levels of conch predation on oysters in Pellicer (Garland, 2015; Booth et al., 2018; Kimbro et al., 2022), and therefore, if Pellicer had been included, we would expect to see strong predation on adult oysters there. This is a relatively new phenomenon in the GTM, as aquaculture of oysters was productive in this area until ~2008 (Garland, 2015). If crown conchs radiate northward over time, predation could become a more important factor structuring oyster productivity in GTM.

The differences in tidal elevation between the main oyster habitat in the two estuaries does not necessarily explain the lack of within-estuary gradients in GTM. We hypothesize that this is because the GTM estuary is fed by much smaller freshwater inputs than Apalachicola Bay and has a second, smaller inlet near one of those freshwater streams, creating weaker gradients in salinity, nutrients, and water velocity, and overall higher salinity throughout the bay. As a counter example, Ochlockonee Bay, a small estuary 30 km east of Apalachicola Bay, is also fed by a small local drainage but has a spatial gradient of predation pressure similar to that of Apalachicola Bay, likely because the predator community there also has the drill (Kimbro et al., 2017b).

Another difference in oyster productivity between the two estuaries is that oysters in the GTM estuary grew to larger sizes near the primary inlet (with productivity balanced by higher mortality there), as opposed to closer to the freshwater input as in Apalachicola Bay. It is possible that flow is more important to growth and productivity than salinity, and the more tidally influenced sites near the inlet in the GTM estuary have faster flows and shorter water residence times (Gray et al., 2022). Kimbro et al. (2020) found that flow velocity was the most parsimonious factor explaining variation in juvenile oyster growth at three sites in the southern GTM estuary. One might also expect to find differences in productivity between subtidal (Apalachicola Bay) and intertidal (GTM) oyster habitats, due to differences in temperature stress, feeding opportunities, and exposure to predation risk (Fodrie et al., 2014; Johnson and Smee, 2014). Yet, overall estimates of lifetime spawning biomass per recruit were similar in magnitude in caged treatments in both estuaries, suggesting that differences in stress versus safety in the two habitats may approximately balance.

In some ways, the patterns of oyster productivity at GTM more closely match those of intertidal Olympia oysters in U.S. Pacific coast estuaries fed by low-flow seasonal streams, such as Tomales Bay in California (Kimbro et al., 2009, 2019; see a similar example in Willapa Bay, Washington in Lowe et al., 2018). There, at a much higher latitude, the natural gradients appear to be high predation by native predators (crabs and native snails) in the outer bay (closer to the inlet), with higher recruitment at sites farthest from the inlet due to longer water residence times, and high growth in the middle of the bay due to the intersection of nutrient profiles and water residence times. But with the recent invasion of a stress-tolerant gastropod (*Urosalpinx cinerea*), this intertidal system, which prior to invasion would seem to have resembled the subtidal Apalachicola system with refuge from predation far away from inlet, now resembles the GTM, with growth driven by the spatial pattern of food availability and little spatial variation in predation pressure (Kimbro et al., 2019).

The spawning biomass per recruit estimates (Fig. 12) provide several advantages for conveying important management information to
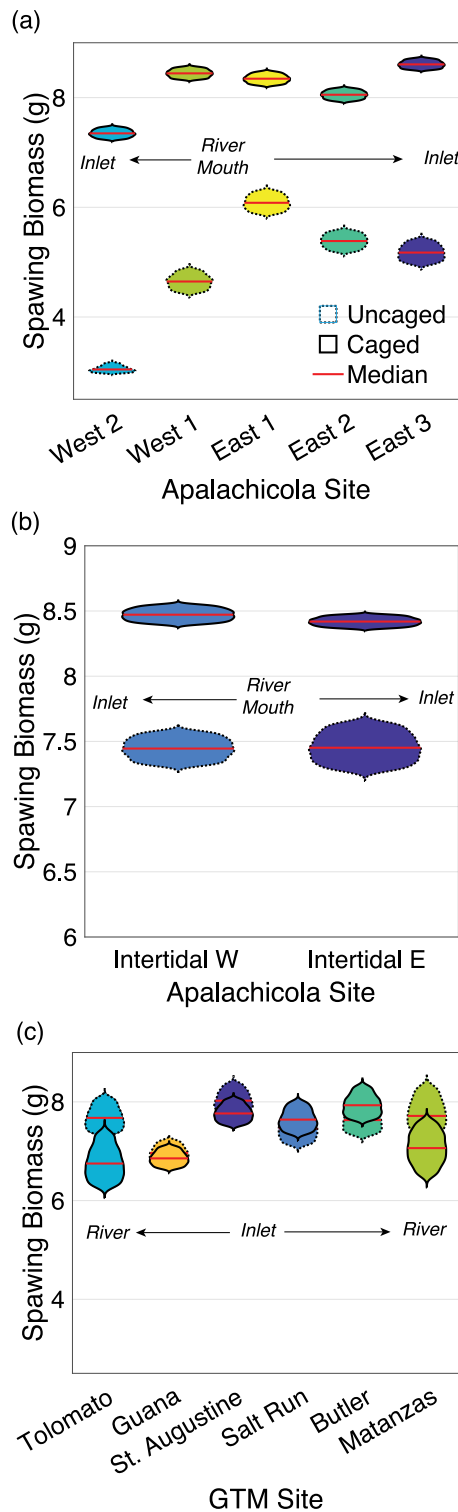
Fig. 12. *Log transformed* spawning biomass per recruit (SBPR) estimates for (a) Apalachicola Bay subtidal sites, (b) Apalachicola Bay intertidal sites, and (c) GTM intertidal sites. Units are grams. Violin plots display the middle 68% of model outputs (one standard deviation) out of 10^5 total spawning biomass per recruit estimates, produced from random parameter combinations (see Section 2.6). The mean and median of the distributions are displayed for each site. Uncaged and caged estimates are plotted separately to quantify the effect of predation on SBPR. Violin colors reflect the regions of each estuary, as in Fig. 1.

stakeholders. The spawning biomass estimates integrate both growth and mortality information into a single metric describing potential productivity, providing a means to resolve the joint influence of potentially competing spatial gradients in multiple abiotic and biotic factors (Kimbro et al., 2019). The typical assumption is that there is a life-history tradeoff between growth and mortality rates (Arendt, 1997), but the nature of that tradeoff varies among species (Schiesari et al., 2006). Different combinations of those two processes can interact to produce similar population size distributions, but with different consequences for population dynamics (Botsford et al., 2019), so the per-recruit metric provides more reliable information than that gleaned from surveys of population size structure alone. For example, in Apalachicola, oysters in site East 3 had a larger asymptotic maximum size but had a higher mortality rate than oysters at site East 1. It could be difficult to make an intuitive prediction about relative productivity given those competing patterns, but the spawning biomass per recruit estimate was considerably higher for East 1, resolving the dispute. Additionally, survey information alone can be misleading because high productivity sites may have low present-day abundance due to recent disturbances or lack of appropriate habitat. For example, much of Apalachicola Bay lost oysters in the 2012 fishery collapse, and has now lost much of its physical oyster habitat as well (D. Kimbro, unpublished data). Thus, we provide a single metric with a better picture of overall population health, which allows for easy comparison across sites and thus a simple means of prioritizing certain sites for restoration efforts that will potentially have the largest positive effects on population recovery.

We acknowledge one limitation in our approach is that we lacked site-specific information on maturation schedules and fecundity, instead relying on literature estimates. Additionally, small sample sizes in some of our treatments could explain our more counterintuitive results (such as higher mortality inside cages at some GTM sites and Apalachicola intertidal sites), and those patterns could be revisited in the future. Adding that information would likely improve the accuracy of our predictions, but it is difficult to imagine that it would outweigh the clear differences among the two estuaries in the importance of the predator community, and would likely amplify patterns driven by small spatial variation in growth rates. Future studies would also benefit from comparison of intertidal Apalachicola Bay reefs with intertidal GTM reefs, as well as a comparison of subtidal and intertidal reefs within Apalachicola Bay. Yet the management guidance we provide in this study represents the best available data at this time.

Our overall finding that the two estuaries, and two different tidal habitats, exhibited completely different spatial gradients in productivity leads to diverging recommendations for restoration and conservation. Different effects of flow on growth (higher growth near fresh water versus higher growth in tidal salt water) and differences in tidal elevation and predator communities led to a low-salinity refuge in Apalachicola, but not GTM. This means that guidance on general patterns of estuarine oyster ecology and demography are not necessarily generalizable: restoration should prioritize that low-salinity refuge in Apalachicola, but there are no clearly overperforming sites in GTM, and restoration could proceed based on other considerations, such as accessibility. While it is well established that oyster demography varies considerably with latitude (Kirby et al., 1998; Lord and Whitlatch, 2014; Kimbro et al., 2014; Byers et al., 2015; Hughes et al., 2017; Grabowski et al., 2020), we find that even at the same latitude, within-estuary patterns and gradients in demography and productivity are variable and context-dependent. Thus, we caution ecologists to take care in applying salinity-dependent relationships or generalities about estuarine gradients across locations with potentially very different predator communities and predator-environment interactions.

CRediT authorship contribution statement

Laura S. Storch: Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis. **David L. Kimbro:** Writing

– review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Nikki Dix:** Writing – review & editing, Funding acquisition, Conceptualization. **Pamela Marcum:** Investigation, Writing – review & editing. **Jason Garwood:** Writing – review & editing. **Christopher D. Stallings:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **J. Wilson White:** Writing – original draft, Visualization, Software, Methodology, Funding acquisition, Conceptualization.

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.

Data availability

Data and models are publicly available in the github repository: https://github.com/jwilsonwhite/NERR_science.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108602.

References

Adrian, A., Lack, C., Kamel, S., 2017. Kin aggregations in eastern oyster reefs crassostrea virginica despite limited regional genetic differentiation. Mar. Ecol. Prog. Ser. 584, http://dx.doi.org/10.3354/meps12361.

Arendt, J.D., 1997. Adaptive intrinsic growth rates: An integration across taxa. Q. Rev. Biol. 72 (2), 149–177. http://dx.doi.org/10.1086/419764.

Barille, L., Lerouxel, A., Dutertre, M., Barille, A.-L., Pouvreau, S., Alunno-Bruscia, M., 2011. Growth of the Pacific oyster (*Crassostrea gigas*) in a high-turbidity environment: Comparison of model simulations based on scope for growth and dynamic energy budgets. J. Sea Res. 66 (4), 392–402.

Barnes, T., Volety, A., Chartier, K., Mazzotti, F., Pearlstine, L., 2007. A habitat suitability index model for the eastern oyster (*Crassostrea virginica*), a tool for restoration of the Caloosahatchee estuary, Florida. J. Shellfish Res. 26 (4), 949–959.

Barry, S., Elith, J., 2006. Error and uncertainty in habitat models. J. Appl. Ecol. 43 (3), 413–423. http://dx.doi.org/10.1111/j.1365-2664.2006.01136.x, URL https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2664.2006.01136.x.

Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61 (2), 107–116. http://dx.doi.org/10.1525/bio.2011.61.2.5, arXiv:https://academic.oup.com/bioscience/article-pdf/61/2/107/19406950/61-2-107.pdf.

Bergquist, D.C., Hale, J.A., Baker, P., Baker, S.M., 2006. Development of ecosystem indicators for the Suwannee River Estuary: Oyster reef habitat quality along a Salinity Gradient. Est. Coasts 29 (3), 353–360, URL http://www.jstor.org/stable/3809756.

Beseres Pollack, J., Cleveland, A., Palmer, T.A., Reisinger, A.S., Montagna, P.A., 2012. A restoration suitability index model for the eastern oyster (Crassostrea virginica) in the mission-Aransas Estuary, TX, USA. PLOS ONE 7 (7), 1–11. http://dx.doi.org/10.1371/journal.pone.0040839.

Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations. Springer Science & Business Media.

Bishop, M.J., Peterson, C.H., 2006. Direct effects of physical stress can be counteracted by indirect benefits: Oyster growth on a tidal elevation gradient. Oecologia 147 (3), 426–433, URL http://www.jstor.org/stable/20445841.

Blackburn, T.M., Gaston, K.J., Loder, N., 2008. Geographic gradients in body size: a clarification of bergmann's rule. Divers. Distrib. 5 (4), 165–174. http://dx.doi.org/10.1046/j.1472-4642.1999.00046.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1472-4642.1999.00046.x.

Booth, H.S., Pusack, T.J., White, J.W., Stallings, C.D., Kimbro, D.L., 2018. Intraspecific predator inhibition, not a prey size refuge, enables oyster population persistence during predator outbreaks. Mar. Ecol. Prog. Ser..

Botsford, L.W., White, J.W., Hastings, A., 2019. Population Dynamics for Conservation. Oxford University Press, USA.

Brown, J., 1995. Macroecology. The University of Chicago Press, http://dx.doi.org/10.2307/1382661.

Byers, J.E., Grabowski, J.H., Piehler, M.F., Hughes, A.R., Weiskel, H.W., Malek, J.C., Kimbro, D.L., 2015. Geographic variation in intertidal oyster reef properties and the influence of tidal prism. Limnol. Oceanogr. 60 (3), 1051–1063. http://dx.doi.org/10.1002/lno.10073, URL https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.1002/lno.10073.

Cheng, B.S., Grosholz, E.D., 2016. Environmental stress mediates trophic cascade strength and resistance to invasion. Ecosphere 7 (4), e01247. http://dx.doi.org/10.1002/ecs2.1247, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1247.

Conover, D.O., Schultz, E.T., 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol. Evol. 10 (6), 248–252.

Dekshenieks, M.M., Hofmann, E.E., Klinck, J.M., Powell, E.N., 2000. Quantifying the effects of environmental change on an oyster population: A modeling study. Estuaries 23, 593–610.

Easterling, M.R., Ellner, S.P., Dixon, P.M., 2000. Size-specific sensitivity: Applying a new structured population model. Ecology 81 (3), 694–708, URL http://www.jstor.org/stable/177370.

Ellner, S.P., Childs, D.Z., Rees, M., 2016. Data-Driven Modeling of Structured Populations: A Practical Guide To the Integral Projection Model. Springer.

Fodrie, F.J., Rodriguez, A.B., Baillie, C.J., Brodeur, M.C., Coleman, S.E., Gittman, R.K., Keller, D.A., Kenworthy, M.D., Poray, A.K., Ridge, J.T., Theuerkauf, E.J., Lindquist, N.L., 2014. Classic paradigms in a novel environment: inserting food web and productivity lessons from rocky shores and saltmarshes into biogenic reef restoration. J. Appl. Ecol. 51 (5), 1314–1325. http://dx.doi.org/10.1111/1365-2664.12276, URL https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12276.

Garland, D.L., 2015. Drought increases consumer pressure on Oyster Reefs in Florida, USA. PLOS ONE 10 (8), 1–19. http://dx.doi.org/10.1371/journal.pone.0125095.

Grabowski, J.H., 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on Oyster Reefs. Ecology 85 (4), 995–1004. http://dx.doi.org/10.1890/03-0067, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/03-0067.

Grabowski, J., Brumbaugh, R., Conrad, R., Keeler, A., Opaluch, J., Peterson, C., Piehler, M., Powers, S., Smyth, A., 2012. Economic valuation of ecosystem services provided by Oyster Reefs. BioScience 632, 900–909. http://dx.doi.org/10.1525/bio.2012.62.10.10.

Grabowski, J.H., Gouhier, T.C., Byers, J.E., Dodd, L.F., Hughes, A.R., Piehler, M.F., Kimbro, D.L., 2020. Regional environmental variation and local species interactions influence biogeographic structure on oyster reefs. Ecology 101 (2), e02921. http://dx.doi.org/10.1002/ecy.2921, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2921.

Grabowski, J.H., Kimbro, D.L., 2005. Predator-avoidance behavior extends trophic cascades to refuge habitats. Ecology 86 (5), 1312–1319. http://dx.doi.org/10.1890/04-1216, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/04-1216.

Grangeré, K., Ménesguen, A., Lefebvre, S., Bacher, C., Pouvreau, S., 2009. Modelling the influence of environmental factors on the physiological status of the Pacific oyster Crassostrea gigas in an estuarine embayment; the Baie des Veys (France). J. Sea Res. 62, 147–158. http://dx.doi.org/10.1016/j.seares.2009.02.002.

Gray, M., Pinton, D., Canestrelli, A., Dix, N., Marcum, P., Kimbro, D., Grizzle, R., 2022. Beyond residence time: Quantifying factors that drive the spatially explicit filtration services of an abundant native oyster population. Est. Coasts 45, 1343–1360.

Hernandez, A.B., Brumbaugh, R.D., Frederick, P., Grizzle, R., Luckenbach, M.W., Peterson, C.H., Angelini, C., 2018. Restoring the eastern oyster: how much progress has been made in 53 years? Front. Ecol. Environ. 16 (8), 463–471. http://dx.doi.org/10.1002/fee.1935, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/fee.1935.

Hughes, A.R., Hanley, T.C., Byers, J.E., Grabowski, J.H., Malek, J.C., Piehler, M.F., Kimbro, D.L., 2017. Genetic by environmental variation but no local adaptation in oysters (Crassostrea virginica). Ecol. Evolut. 7 (2), 697–709. http://dx.doi.org/10.1002/ece3.2614, URL https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.2614.

Johnson, K., Smee, D.L., 2014. Predators influence the tidal distribution of oysters (Crassostrea virginica). Mar. Biol. 161, 1557–1564. http://dx.doi.org/10.1007/s00227-014-2440-8.

Kennedy, V.S., Newell, R.I., Eble, A.F., 1996. The Eastern Oyster: Crassostrea Virginica. University of Maryland Sea Grant College.

Kimbro, D.L., Byers, J.E., Grabowski, J.H., Hughes, A.R., Piehler, M.F., 2014. The biogeography of trophic cascades on US oyster reefs. Ecol. Lett. 17 (7), 845–854. http://dx.doi.org/10.1111/ele.12293, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12293.

Kimbro, D.L., Grabowski, J.H., Hughes, A.R., Piehler, M.F., White, J.W., 2017a. Nonconsumptive effects of a predator weaken then rebound over time. Ecology 98 (3), 656–667. http://dx.doi.org/10.1002/ecy.1702, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.1702.

Kimbro, D.L., Largier, J., Grosholza, E.D., 2009. Coastal oceanographic processes influence the growth and size of a key estuarine species, the olympia oyster. Limnol. Oceanogr. 54 (5), 1425–1437. http://dx.doi.org/10.4319/lo.2009.54.5.1425, URL https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.4319/lo.2009.54.5.1425.

Kimbro, D.L., Tillotson, H.G., White, J.W., 2020. Environmental forcing and predator consumption outweigh the nonconsumptive effects of multiple predators on oyster reefs. Ecology 101 (7), e03041. http://dx.doi.org/10.1002/ecy.3041, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.3041.

Kimbro, D.L., White, J.W., Breef-Pilz, A., Peckham, N., Noble, A., Chaney, C., 2022. Evidence for local adaptation of oysters to a within-estuary gradient in predation pressure weakens with ontogeny. J. Exp. Mar. Biol. Ecol. 555, 151784.

Kimbro, D.L., White, J.W., Grosholza, E.D., 2019. The dynamics of open populations: integration of top–down, bottom–up and supply–side influences on intertidal oysters. Oikos 128 (4), 584–595. http://dx.doi.org/10.1111/oik.05892, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/oik.05892.

Kimbro, D.L., White, J.W., Tillotson, H., Cox, N., Christopher, M., Stokes-Cawley, O., Yuan, S., Pusack, T.J., Stallings, C.D., 2017b. Local and regional stressors interact to drive a salinization-induced outbreak of predators on oyster reefs. Ecosphere 8 (11), e01992. http://dx.doi.org/10.1002/ecs2.1992, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1992.

Kirby, M., Soniat, T., Spero, H., 1998. Stable isotope sclerochronology of pleistocene and recent oyster shells (Crassostrea virginica). Palaios 13, 560–569. http://dx.doi.org/10.2307/3515347.

Lima, S., Dill, L., 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canad. J. Zool. 68, 619–640. http://dx.doi.org/10.1139/z90-092.

Livingston, R., Lewis, F., Woodsum, G., Niu, X.-F., Galperin, B., Huang, W., Christensen, J., Monaco, M., Battista, T., Klein, C., Howell, R., Ray, G., 2000. Modelling Oyster population response to variation in freshwater input. Estuar. Coast. Shelf Sci. 50 (5), 655–672. http://dx.doi.org/10.1006/ecss.1999.0597, URL https://www.sciencedirect.com/science/article/pii/S0272771499905978.

Lord, J., Whitlatch, R., 2014. Latitudinal patterns of shell thickness and metabolism in the eastern oyster Crassostrea virginica along the east coast of North America. Mar. Biol. 161, http://dx.doi.org/10.1007/s00227-014-2434-6.

Lough, R., 1975. A reevaluation of the combined effects of temperature and salinity on survival and growth of bivalve larvae using response surface techniques. Fish. Bull. 73 (1), 86–94.

Lowe, A., Kobelt, J., Horwith, M., Ruesink, J., 2018. Ability of eelgrass to alter oyster growth and physiology is spatially limited and offset by increasing predation risk. Est. Coasts 42, 743–754. http://dx.doi.org/10.1007/s12237-018-00488-9.

Menge, B.A., 1992. Community regulation: Under what conditions are bottom-up factors important on rocky shores? Ecology 73 (3), 755–765, URL http://www.jstor.org/stable/1940155.

Menge, B.A., Sutherland, J.P., 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. Amer. Nat. 110 (973), 351–369. http://dx.doi.org/10.1086/283073.

Menge, B.A., Sutherland, J.P., 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Amer. Nat. 130 (5), 730–757, URL http://www.jstor.org/stable/2461716.

North, E., King, D., Xu, J., Hood, R., Newell, R., Paynter, K., Kellogg, M., Liddel, M., Boesch, D., 2010. Linking optimization and ecological models in a decision support tool for oyster restoration and management. Ecol. Appl. 20, 851–866. http://dx.doi.org/10.1890/08-1733.1.

Powell, E., Klinck, J., Hofmann, E., 1996. Modeling diseased oyster populations. II. Triggering mechanisms for Perkinsus marinus epizootics. J. Shellfish Res. 15, 141–165.

Powell, E.N., Morson, J.M., Ashton-Alcox, K.A., Kim, Y., 2013. Accommodation of the sex-ratio in eastern oysters crassostrea virginica to variation in growth and mortality across the estuarine salinity gradient. J. Mar. Biol. Assoc. United Kingdom 93 (2), 533–555. http://dx.doi.org/10.1017/S0025315412000215.

Puckett, B., Eggleston, D., 2012. Oyster demographics in a network of no-take reserves: Recruitment, growth, survival, and density dependence. Mar. Coast. Fish. 4, 605–627. http://dx.doi.org/10.1080/19425120.2012.713892.

Pusack, T.J., Kimbro, D.L., White, J.W., Stallings, C.D., 2019. Predation on oysters is inhibited by intense or chronically mild, low salinity events. Limnol. Oceanogr. 64 (1), 81–92. http://dx.doi.org/10.1002/lno.11020, URL https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.1002/lno.11020.

Pusack, T.J., White, J.W., Tillotson, H.G., Kimbro, D.L., Stallings, C.D., 2018. Size-dependent predation and intraspecific inhibition of an estuarine snail feeding on oysters. J. Exp. Mar. Biol. Ecol. 501, 74–82. http://dx.doi.org/10.1016/j.jembe.2018.01.005, URL https://www.sciencedirect.com/science/article/pii/S0022098117304392.

R. Core Team, 2021. R: A language and environment for statistical computing. URL https://www.R-project.org/.

Ray, S., Powell, E., Klinck, J., Hofmann, E., 1994. Modeling oyster populations. IV: Rates of mortality, population crashes, and management. Fish. Bull. 92.

Robinson, E., Lunt, J., Marshall, C., Smee, D.L., 2014. Eastern oysters Crassostrea virginica deter crab predators by altering their morphology in response to crab cues. Aqua. Biol. 20, 111–118. http://dx.doi.org/10.3354/ab00549.

Sagarin, R.D., Gaines, S.D., 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? Ecol. Lett. 5 (1), 137–147. http://dx.doi.org/10.1046/j.1461-0248.2002.00297.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1461-0248.2002.00297.x.

Scherer, A.E., Lunt, J., Draper, A.M., Smee, D.L., 2016. Phenotypic plasticity in oysters (Crassostrea virginica) mediated by chemical signals from predators and injured prey. Inverteb. Biol. 135 (2), 97–107. http://dx.doi.org/10.1111/ivb.12120, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ivb.12120.

Schiesari, L., Peacor, S., Werner, E., 2006. The growth-mortality tradeoff: Evidence from anuran larvae and consequences for species distributions. Oecologia 149, 194–202. http://dx.doi.org/10.1007/s00442-006-0440-1.

Smith, R.S., Cheng, S.L., Castorani, M.C.N., 2023. Meta-analysis of ecosystem services associated with oyster restoration. Conserv. Biol. 37 (1), e13966. http://dx.doi.org/10.1111/cobi.13966, URL https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.13966.

Tolley, S.G., Volety, A., Savarese, M., 2005. Influence of salinity on the habitat use of oyster reefs in three Southwest Florida estuaries. J. Shellfish Res. 24, 127–137. http://dx.doi.org/10.2983/0730-8000(2005)24[127:IOSOTH]2.0.CO;2.

Wang, H., Huang, W., Harwell, M.A., Edmiston, L., Johnson, E., Hsieh, P., Milla, K., Christensen, J., Stewart, J., Liu, X., 2008. Modeling oyster growth rate by coupling oyster population and hydrodynamic models for Apalachicola Bay, Florida, USA. Ecol. Model. 211 (1), 77–89. http://dx.doi.org/10.1016/j.ecolmodel.2007.08.018, URL https://www.sciencedirect.com/science/article/pii/S0304380007004267.

Weissburg, M., Smee, D.L., Ferner, M.C., 2014. The sensory ecology of nonconsumptive predator effects. Amer. Nat. 184 (2), 141–157. http://dx.doi.org/10.1086/676644, arXiv:DOI:10.1086/676644.

Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84 (5), 1083–1100. http://dx.doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2.

White, J.W., Carr, M.H., Caselle, J.E., Washburn, L., Woodson, C.B., Palumbi, S.R., Carlson, P.M., Warner, R.R., Menge, B.A., Barth, J.A., Blanchette, C.A., Raimondi, P.T., Milligan, K., 2019. Connectivity, dispersal, and recruitment: Connecting benthic communities and the coastal ocean. Oceanography 32 (3), 50–59, URL https://www.jstor.org/stable/26760082.

White, J.W., Rassweiler, A., Samhouri, J.F., Stier, A.C., White, C., 2014. Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123 (4), 385–388. http://dx.doi.org/10.1111/j.1600-0706.2013.01073.x, URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0706.2013.01073.x.

Zu Ermgassen, P.S.E., Spalding, M.D., Blake, B., Coen, L.D., Dumbauld, B., Geiger, S., Grabowski, J.H., Grizzle, R., Luckenbach, M., McGraw, K., Rodney, W., Ruesink, J.L., Powers, S.P., Brumbaugh, R., 2012. Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. Proc. R. Soc. B: Biol. Sci. 279 (1742), 3393–3400. http://dx.doi.org/10.1098/rspb.2012.0313, URL https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2012.0313.