

## Predation on oysters is inhibited by intense or chronically mild, low salinity events

Timothy J. Pusack,<sup>1,2\*</sup> David L. Kimbro,<sup>3</sup> J. Wilson White,<sup>4,5</sup> Christopher D. Stallings<sup>1</sup>

<sup>1</sup>College of Marine Science, University of South Florida, St. Petersburg, Florida

<sup>2</sup>Williams Mystic Maritime Studies Program, Williams College, Mystic, Connecticut

<sup>3</sup>Department of Marine and Environmental Sciences, Northeastern University, Marine Science Center, Nahant, Massachusetts

<sup>4</sup>Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, North Carolina

<sup>5</sup>Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Oregon State University, Newport, Oregon

### Abstract

Environmental stress gradients can affect species distributions and interspecific interactions. Because environmental stress depends on both intensity and duration, understanding the consequences of stress requires experiments that simultaneously manipulate both dimensions. In Apalachicola Bay, Florida (U.S.A.) the southern oyster drill (*Stramonita haemastoma*) is a major predator of the eastern oyster (*Crassostrea virginica*). Drill predation appears to be salinity-dependent: in a recent field study, predation rates were positively correlated with salinity. Salinity in the bay is typically high (> 20) during the dry summer months, conditions that favor both oysters and the drill. However, periodic freshets can dramatically reduce salinity, which inhibits (or kills) drills, but not oysters. In this study, we used field measurements of salinity and drill densities to inform mesocosm experiments. We investigated the specific combinations of intensity and duration of low-salinity stress that inhibit drill predation. In these experiments, more intense salinity reductions reduced feeding both during and after the low-salinity stress event. During the event, longer durations (15 d) were necessary for mild salinity reductions (−5) to reduce the feeding rate by the same amount as a short (5 d) exposure of more intense (−10 or −15) salinity reduction. Both conditions may create a predation refuge for oysters, consistent with field observations. Given that the recent collapse of the Apalachicola Bay oyster population was preceded by several years without low-salinity events to inhibit predation, our results provide a mechanism by which a predator may have contributed to the loss of a historically productive and sustainable fishery.

Zones of high environmental stress can limit species distributions (Louthan et al. 2015) and modify interspecific interactions in both aquatic (Wellborn et al. 1996) and marine systems (Menge and Sutherland 1987). As a classic example, Connell (1961a,b) found that competitive interactions between barnacle species were stronger in the low-stress subtidal zone than the high-stress intertidal zone. Similarly, and in accordance with the *consumer stress model*, high-stress conditions are likely to reduce predation on prey, because mobile predators often tolerate a narrower range of stress than their less mobile prey (Menge and Sutherland 1987; Menge and Olson 1990). Consequently, a prey refuge can be created when and where the environmental stress is severe enough to reduce predation, but not prey maintenance and growth (Menge and Sutherland 1987; Witman and Grange 1998; Petes et al. 2008).

Given that stress-induced refuges can enhance prey persistence (Sih et al. 1985), describing the mechanisms by which environmental stressors modify species interactions is fundamental to understand and manage key natural systems.

Environmental stress gradients that promote predation refuges can undergo temporal fluctuations that are both predictable (e.g., tidal cycles, seasonal changes) and stochastic (e.g., storms). For example, bivalves in the middle to upper intertidal zones of rocky shorelines typically enjoy a refuge from predation by sea stars (*Pisaster ochraceus*), because the latter require frequent immersion. However, this predation refuge can temporarily extend down to lower intertidal and subtidal locations during intense coastal upwelling events, when extremely cold water reduces the sea star's feeding rate. Importantly, the degree to which sea star feeding is suppressed depends on both the intensity and the duration of the temperature reduction (Sanford 1999). Thus, the interplay among intensity and duration of a stress likely determines how a stressor affects species interactions and the effectiveness of a predation refuge.

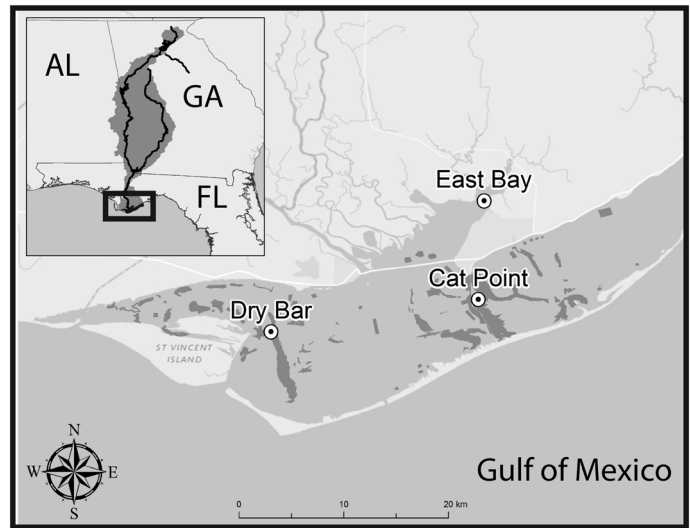
\*Correspondence: tjp3@williams.edu

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Estuaries are high-stress systems due to large fluctuations in abiotic conditions: oxygen, temperature, and salinity can change rapidly as a result of ocean tides and freshwater discharge from rivers (Mann and Lazier 2006). Many sessile estuarine prey species exist in the brackish mid-estuary where they can benefit from feeding on marine plankton and from relatively low densities of marine predators that cannot physiologically tolerate the dynamic salinity fluctuations (Kimbrot et al. 2009; Rogers et al. 2016). However, freshwater flow regimes are changing globally due to both anthropogenic water use (e.g., dams, industry, agriculture) and altered precipitation patterns attributed to climate change (Scavia et al. 2002). As climate change progresses, regional precipitation is likely to be characterized by extreme temporal variability (Min et al. 2011; Yoon et al. 2015; Cheng et al. 2016). In areas with extreme precipitation reductions, brackish zones of estuaries will likely receive less freshwater input, and experience consistently higher salinities (Scavia et al. 2002; Cloern et al. 2011; but see Najjar et al. 2010 for an example of decreasing salinity in Chesapeake Bay). If the salinization of brackish zones increases the access of marine predators to estuarine prey, then key spatial refugia from predators will be compromised.

Oyster reefs are a common feature of estuaries that serve as an important foundation species by creating habitat for many vertebrates and invertebrates and providing key ecosystem services (Wells 1961; Peterson et al. 2003, 2008; Grabowski and Peterson 2007). Despite worldwide declines, oyster populations in the northern Gulf of Mexico (nGOM) have remained relatively robust (Beck et al. 2011). In that region, the eastern oyster (*Crassostrea virginica*, hereafter “oysters”) is prey for a variety of predators. One of the most important predators is the southern oyster drill (*Stramonita haemastoma*, hereafter “drills”; Butler 1985; FFWCC 2013), which is a stenohaline species found predominately on subtidal oyster reefs (Brown 1997). In recent years, drought conditions and increased upstream demand for freshwater have changed the amount of river discharge into many of the estuaries in the nGOM (McKee et al. 2004; Strzepek et al. 2010). As salinity has increased in those estuaries, oyster populations have declined (Petes et al. 2012), potentially due to the deterioration of the predation refuge in brackish areas and the rapid increase in the populations of stenohaline predators such as drills and stone crabs (*Menippe mercenaria*; Menzel et al. 1966; Livingston et al. 2000; FFWCC 2013) as well as Dermo disease caused by *Perkinsus marinus* (Burreson and Ragone-Calvo 1996; Ray 1996).

In the nGOM estuary of Apalachicola Bay, Florida (U.S.A., Fig. 1), a regional drought and reduced river discharge caused elevated salinity conditions in the summers of 2012 and 2013 (FFWCC 2013). By fall 2012, oyster populations had declined dramatically, which resulted in a federal fishery disaster declaration (FFWCC 2013). While the high salinity conditions that favor drills are normal during the late summer dry season, it is



**Fig. 1.** Map of Apalachicola Bay, Florida, U.S.A., with the areas of oyster reefs shaded in dark gray. The inset shows the total watershed (dark gray) of the Apalachicola-Chattahoochee-Flint (ACF) river system that spans Alabama (AL), Georgia (GA), and Florida (FL), U.S.A.

also normal for occasional low salinity events to stress or kill drills (Findley et al. 1978; Roller and Stickle 1989). However, the specific characteristics of freshwater discharge (i.e., intensity and duration of low-salinity events) that inhibit drill predation are not well understood. With respect to management of water resources, a quantitative description of these characteristics could enhance restoration efforts by suggesting freshwater discharge patterns that could promote predation refugia for oysters.

Here, we combined field observations with laboratory experiments to test how dynamic changes in salinity of Apalachicola Bay affect drill feeding behavior and mortality. Specifically, we used a 21-yr time series and multiyear field surveys to quantify salinity profiles and drill densities, respectively. We used these data to quantify the historical pattern (intensity and duration) of salinity fluctuations in the bay, and to test whether drill abundance within the estuary was associated with average salinity. Based on the historical pattern of low-salinity events and field data of drill densities, we then designed a laboratory experiment to test whether drill survival and predation on oysters changed during simulated freshwater discharges, with variable intensities and durations of exposure to salinity reductions. In this experiment, we addressed two major questions: (1) How do intensity and duration of salinity reductions directly affect drill predation on oysters? (2) Does the stress of salinity reduction produce prolonged effects on drill predation that persist when conditions return to less stressful salinities? By considering both the intensity and the duration of exposure, our goal was to provide a more comprehensive description of how the stress of low salinity conditions affects an important predator of oysters and therefore a spatial refuge for oysters from drills.

## Methods

### Study system

Apalachicola Bay, Florida (U.S.A.), is located at the terminus of the large (50,000 km<sup>2</sup>), Apalachicola-Chattahoochee-Flint (ACF) watershed (Fig. 1). Because Apalachicola Bay is a shallow, coastal plain estuary, salinity is determined by river input and can vary from 3 to 33 (Livingston et al. 2000; Petes et al. 2012; note that we report salinities using the dimensionless practical salinity scale). Low salinity conditions usually occur during the late winter/early spring months when rainfall is at the highest in the watershed, while low flows and higher salinities occur during the late summer and early fall when rainfall is at the lowest (Livingston et al. 2000; Petes et al. 2012). As with all well-mixed estuaries, a low-to-high salinity gradient occurs from the mouth to the ocean.

### Field observations

We collected field data on both salinity patterns and drill abundance throughout the year at various locations through Apalachicola Bay using two methods. To describe the relationship between drill density and salinity, we conducted seven rounds of predator surveys on six pre-existing experimental plots (*plot* in data analysis) found on oyster reefs throughout the bay during 2014–2016. Each plot was surrounded by a protective frame (120 × 90 × 60 cm) made of steel rebar (1.27 cm thickness). These relatively open rebar frames were used to prevent disturbances due to harvesting and boating activities. For each 3-month round of surveys, we surveyed each plot every month and then calculated the mean drill density. At these same sites, we used a Sea-Bird Electronics SBE 19plus V2 (Sea-Bird Scientific) to collect conductivity–temperature–depth (CTD) profiles of the water column. We then averaged the monthly median salinities and temperatures to obtain a mean salinity and temperature value for each site. We employed a hurdle method (*see* “Data analysis of laboratory experiment and drill field data” section for full description) using generalized linear mixed models (GLMM) to analyze the field data, which had repeated measurements on the six experimental plots. For this analysis, we chose to use a seasonal time scale (*i.e.*, average of three monthly data points) rather than a monthly time scale because the drill and salinity data were not collected during the same week each month. This would allow a coarse description of the effect of salinity on drill abundances across a large bay.

Second, we obtained a 21-yr (1992–2012) daily record of salinity up to the most recent oyster population crash, which was measured at three locations in the bay (Fig. 1). These data were obtained from the National Estuarine Research Reserve System’s Centralized Data Management Office (<http://cdmo.baruch.sc.edu/>) for stations in the Apalachicola National Estuarine Research Reserve (<http://apalachicolareserve.com/>). We described salinity patterns in Apalachicola Bay from the 21-yr time series using a series of analyses. Our goal was to quantify

the range of salinities and duration of extreme low-salinity events that have occurred in Apalachicola Bay. Because salinity varies naturally throughout the year, we defined extreme events not as absolute salinity levels but relative to the climatological mean salinity expected for each week of the year. We quantified the frequency of weeks in the time series in which there was a minimum daily mean salinity that was 5, 10, or 15 units lower than the weekly climatological mean. We also estimated the return time of low salinity events (*i.e.*, the expected long-term frequency of occurrence of weeks in which the minimum daily mean salinity was lower than the climatological mean by a particular threshold) following the maximum likelihood procedure of Gaines and Denny (1993). We then used these estimated return times to predict the minimum daily mean salinities expected at annual and semiannual frequencies (*i.e.*, minima expected once or twice per year). Because we were interested in effects on drill predation behavior, we restricted this analysis to the summer months (April–September) when water temperatures are high enough for drills to be active. We also compared the frequency of salinity reductions of different magnitudes (5, 10, or 15 below the weekly climatological mean) and durations (5 d, 10 d, or 15 d) between two time periods: a historical period (1992–2005) when drought conditions were less common, and a more recent period (2006–2012) when two rounds of seasonal drought preceded the 2012 oyster collapse. We used Chi-square tests to test the null hypothesis that the distribution of frequencies of low-salinity-events was the same between the two time periods for each duration of disturbance. Maximum likelihood estimation and Chi-square testing were performed using MATLAB R2017a (MathWorks).

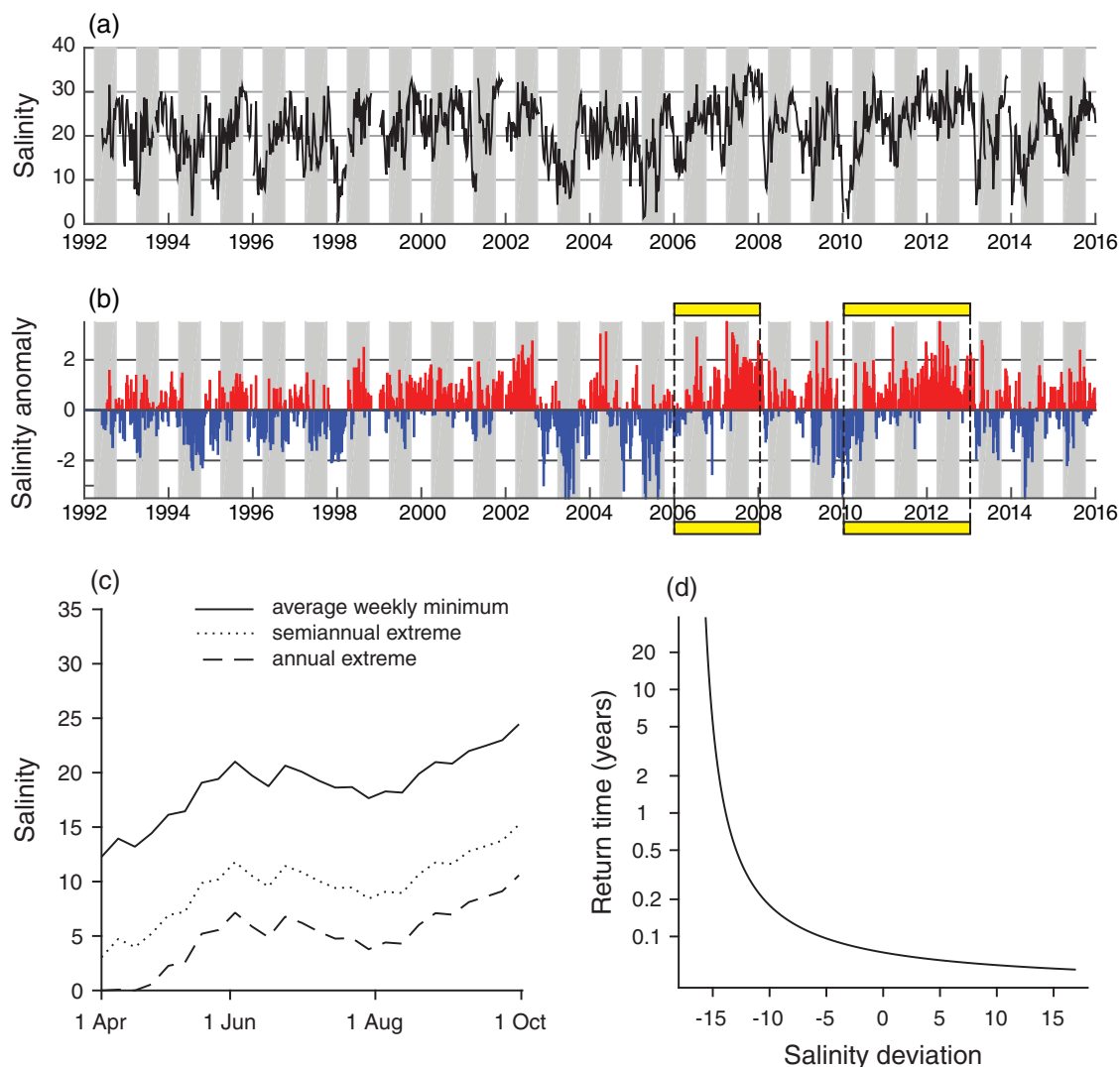
### Design of laboratory experiment

In this experiment, drills and oysters were exposed to different levels of simulated freshwater discharges based on our analysis of the long-term salinity data (*see* “Field observations” section). From that analysis, we chose intensities and durations of low-salinity events that were, on average, observed at least annually in Apalachicola Bay. We orthogonally crossed four intensities of salinity reduction (–5, –10, –15, and –20) with three durations (5 d, 10 d, and 15 d), and for each treatment we had 4–5 replicates, with some exceptions (Supporting Information Table S1). Due to logistical constraints, the experiment was run in three rounds. Rounds one and three had salinity reductions of –5 and –10 for all three durations and round two had salinity reductions of –15 and –20 for all three durations. Each round used a new set of oysters and drills to prevent any potential acclimation or residual effects. Within each round, an experimental trial comprised four time periods: (1) a 5-d drill starvation period to standardize hunger (based on the daily consumption rate of drills on oysters; Pusack et al. 2018), (2) a 10-d feeding period at the baseline salinity (“pre-period”), (3) a 5-, 10-, or 15-d feeding period at the reduced salinity (“treatment period”),

and (4) a return to the baseline salinity 10 d (“post-period”) (Supporting Information Fig. S1; Supporting Information Table S1). The lowest target salinity was 5 (Supporting Information Fig. S1; Supporting Information Table S1), approximately the lowest semiannual, weekly mean salinity reached during the summer months (Fig. 2c). In each round there was also a control treatment where salinity was maintained throughout experiment at the pre-period salinity.

For each round, we collected new oysters and drills from subtidal reefs in Apalachicola Bay during summer months, June to September. Experimental trials were conducted at the University of South Florida, College of Marine Science in three separate, closed seawater systems, each comprising 10 experimental aquaria (47.3 L; 68 × 40 × 27.5 cm), for a total of 30 total aquaria. Within each system, a large sump (633 L;

76 × 45.5 × 183 cm) recirculated ~ 950 L of saltwater through the experimental aquaria. Each system also had a canister filter with physical, chemical, and biological filtration (Penn Plax Cascade 1500, Penn-Plax) to reduce the accumulation of ammonia/nitrite. Additionally, at least a 10% water change occurred between periods. Temperature was maintained at 25°C using two 800-watt titanium heating rods (Finnex TH-800 Plus, Finnex) and temperature controller (Reef Octopus, Honya, Shenzhen, China) per system, which is a typical temperature for this area during the summer months (Kimbro et al. 2017). Each salinity level was maintained by mixing deionized water with Instant Ocean sea salt (Instant Ocean Spectrum Brands), and we adjusted salinities within 0.5 of the target level during daily checks using a YSI 85 (Xylem). During the experiment, oysters were fed daily with Instant Algae



**Fig. 2.** (a) The average weekly salinity from 1993 to 2016 for Apalachicola Bay, Florida, U.S.A. (b) The weekly salinity anomaly, which is the deviation of salinities compared to the mean weekly salinity. Yellow bars indicate years when the oyster populations collapsed. (c) The average weekly minimum salinity (solid line) relative to the semiannual (dotted line) and annual (dashed line) extreme minimum. (d) The return time of extreme minimum salinities relative to the average minimum salinity for each week.

Shellfish Diet 1800 (Reed Mariculture), following the manufacturer's instructions of 3.6 mL per ~ 100 g of oyster wet weight.

Within each of the 30 aquaria, there were two distinct areas: a restricted-access area and an open-access area. The restricted-access area consisted of a small, perforated container made of clear plastic (1.2 L; 15.5 × 15.5 × 5.6 cm) suspended from the lid of the experimental aquaria, which protected a single oyster from drill predation to estimate oyster survival in the absence of predation (in-aquaria control). The open-access area of each aquaria held one drill and five oysters that were randomly selected from the full range of collected oyster shell lengths (25–99 mm), yielding one large (75–99 mm), one medium (50–74 mm), and three small (25–49 mm) oysters available to each drill. These size distributions were used to ensure consistent presentation to the drills based on natural oyster demographic patterns. We randomly arranged oysters in an "X" pattern to isolate the predator-prey interactions while controlling for the effects of reef complexity. Drills ranged in length from 57 mm to 82 mm, with a mean ( $\pm$  standard deviation) length of  $65.9 \pm 6.6$  mm. This size range spanned the upper mode (i.e., adults) of the drill size distribution we observed in the field (Supporting Information Fig. S2).

During the starvation period, drills were housed in aquaria without oysters at the target baseline salinity level. Subsequently, salinity was slowly reduced to the target reduction intensity (–5, –10, –15, or –20) at a rate of 1–2 units per hour. This rate was based on observations of salinity change preceding low-salinity events from the Apalachicola National Estuary Research Reserve monitoring data. After the treatment period, we increased salinity at the same rate back to the baseline and maintained those conditions during the post-treatment period. We checked aquaria twice daily (except on weekends when they were checked once daily) for gaping oysters without any tissue present in the shell (i.e., dead) for each of the three feeding periods (pre, treatment, and post). If an oyster was gaping, we recorded it as a predation event and replaced it with an oyster from the same size class. We decided to identify predation in this way, rather than by checking for a drill borehole, because drills often attack between the valves using proteolytic enzymes rather than boring a hole into one valve with their radula (Brown and Alexander 1994). Because no oysters died in the in-aquaria controls, and all dead oysters lacked tissue between their two shells, we attributed all gaping oysters to drill predation. From these data, we calculated the daily feeding rate of drills during each of the three feeding periods (pre, treatment, and post). To assess drill survival, we probed each drill operculum to test for a response. If a drill was nonresponsive and did not close upon touching with a metal probe, then the drill was scored as dead and was removed from the experiment, with its feeding rate calculation referring only to the time prior to death.

#### Data analysis of laboratory experiment and drill field data

We first calculated the feeding rate (no. oysters consumed/day) for each drill in each of the three experimental periods (pre, treatment, and post). For each experimental period (pre,

treatment, and post), we used a generalized linear model (GLM) to test for the effects of three predictor variables: *intensity*, *duration*, and *drill size*, and an interaction term between *intensity* and *duration*. Additionally, because numerous replicates resulted in no feeding during the treatment and post-period (Supporting Information Fig. S3b,c), we had to account for the large number of zeros present in the data. To address this issue, we used the two-step hurdle method to analyze the data, a common technique for zero-inflated data (also known as Delta models, Stern and Coe 1984; Stefánsson 1996; Martin et al. 2005; Zuur et al. 2009). The analysis first evaluates the binomial probability of feeding as a function of the predictors (step 1) and then quantifies the feeding rates greater than zero as a function of the three predictors (step 2). We used a GLM for each of these analyses, but with different error distributions for each step. In step 1, we used a binomial error distribution (logit link) and for step 2 we used a gamma error distribution (log link) because our data were continuous, strictly positive, and expected to have variance increasing with the mean. We chose the gamma error distribution, instead of Poisson distribution with an offset for duration, because we were interested in the effect of duration and how it may interact with intensity. If we used an offset, this technique would have prevented us from estimating a coefficient for the effect of duration (Anderson et al. 2004; Zuur et al. 2009). We visually checked the residuals of our data and used Cook's distance to quantify potential outliers, but all models had favorable performance. We used a similar hurdle model (also with binomial and gamma error distributions), but used a mixed-model (GLMM) approach and included *plot* as a random effect because we visited the same experimental plots in each of the seven rounds. We described the drill field density as a function of two fixed effects, *salinity* and *temperature*, the interaction term between *salinity* and *temperature*, and *plot* as our random effect as our full model.

For both the experimental and field analyses, we undertook a backwards stepwise model selection procedure to identify the model that had the fewest predictor terms but a goodness of fit that was not statistically different from the full model. To accomplish this, we started with the full model, then sequentially removed the term with the smallest *t*-statistic. After each removal, we tested the difference in goodness-of-fit between the reduced model and the full model using a likelihood ratio test. The best model was identified as the one with the fewest terms but not significantly different from the full model ( $p > 0.05$  in the likelihood ratio test). We used the *base* and *lme4* (Bates et al. 2015) packages for these analysis and *ggplot2* (Wickham 2009) for visualizations in R version 3.4.3 (R Core team 2017).

## Results

### Field observations

Salinities in Apalachicola Bay fluctuated over a wide range (0–30) during the summer months of 1992–2012 (Fig. 2a).

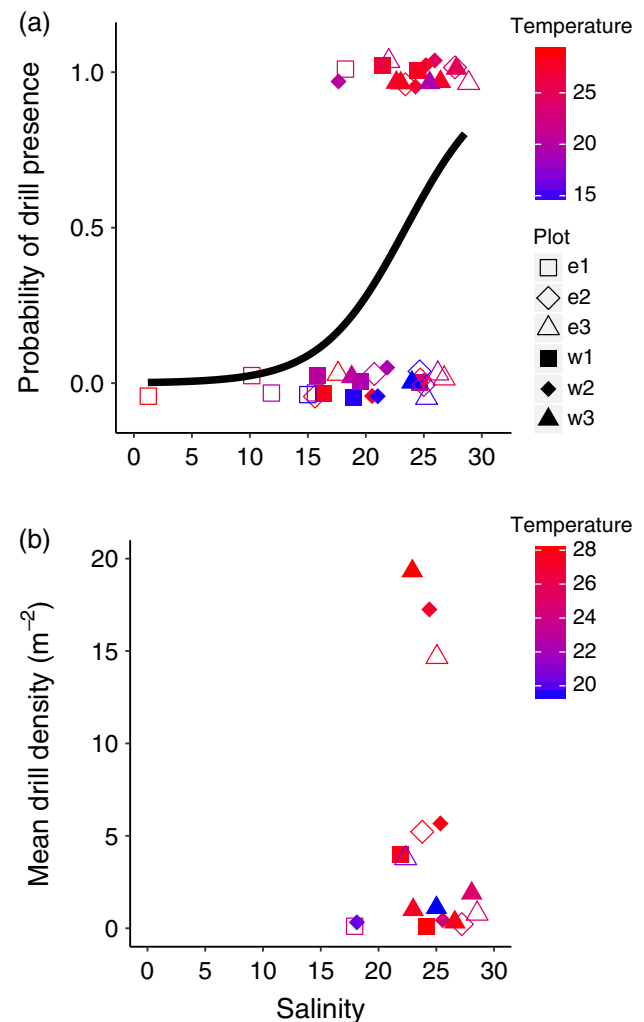
During this time period, the average weekly minimum salinity ranged from 13 to 25. There were annual and semiannual extreme minimums when salinity dropped below 10, and even down to 0 in the in the late spring (Fig. 2c). Calculation of return times for low-salinity events indicated that days with mean salinity reductions of 10 below the weekly average were expected multiple times per year, while reductions of greater than 15 below the weekly average were extremely infrequent (Fig. 2d). The frequency of salinity reductions and their durations differed between recent (2006–2012) and older (1992–2005) time periods (Supporting Information Fig. S4). While East Bay stayed relatively constant and fresh, likely due to its close proximity to the mouth of the Apalachicola River, we documented differences at both of the primary commercial oyster reefs, Cat Point and Dry Bar (Fig. 1, Supporting Information Fig. S4). Between the post-2006 and pre-2006 time periods, there were fewer occurrences of salinity reduced below 15 for 5 d ( $\chi^2 = 6.12$ ,  $df = 2$ ,  $p = 0.047$ ) at Cat Point, and at Dry Bar there were fewer occurrences below a salinity of 15 for 5 d ( $\chi^2 = 10.75$ ,  $df = 2$ ,  $p = 0.005$ ), 10 d ( $\chi^2 = 11.13$ ,  $df = 2$ ,  $p = 0.004$ ), and 15 d ( $\chi^2 = 6.18$ ,  $df = 2$ ,  $p = 0.046$ ), as well as fewer occurrences below a salinity of 10 for 5 d ( $\chi^2 = 7.08$ ,  $df = 2$ ,  $p = 0.029$ ). Across the entire 1992–2012 period,  $\leq 75\%$  of low-salinity events (daily mean salinity reductions of  $> 5$  from the weekly climatological mean) had durations  $\leq 15$  d (Supporting Information Fig. S4).

From our field observations, drills were more likely to be observed at higher temperatures and salinities (Fig. 3a; Supporting Information Table S2a). Holding the other variable constant, increasing the temperature by  $1^\circ\text{C}$  increased the probability of drill presence by 24.8% when the temperature ranged  $14.4\text{--}29.1^\circ\text{C}$ , and an increase in salinity by 1 increased the probability of the drill presence by 32.0% when salinity ranged from 1.2 to 28.5 (Fig. 3a; Supporting Information Table S2a). When present, drill density increased with increasing temperatures, but we did not detect an effect of salinity on the overall density (Fig. 3b; Supporting Information Table S2b).

### Laboratory experiments

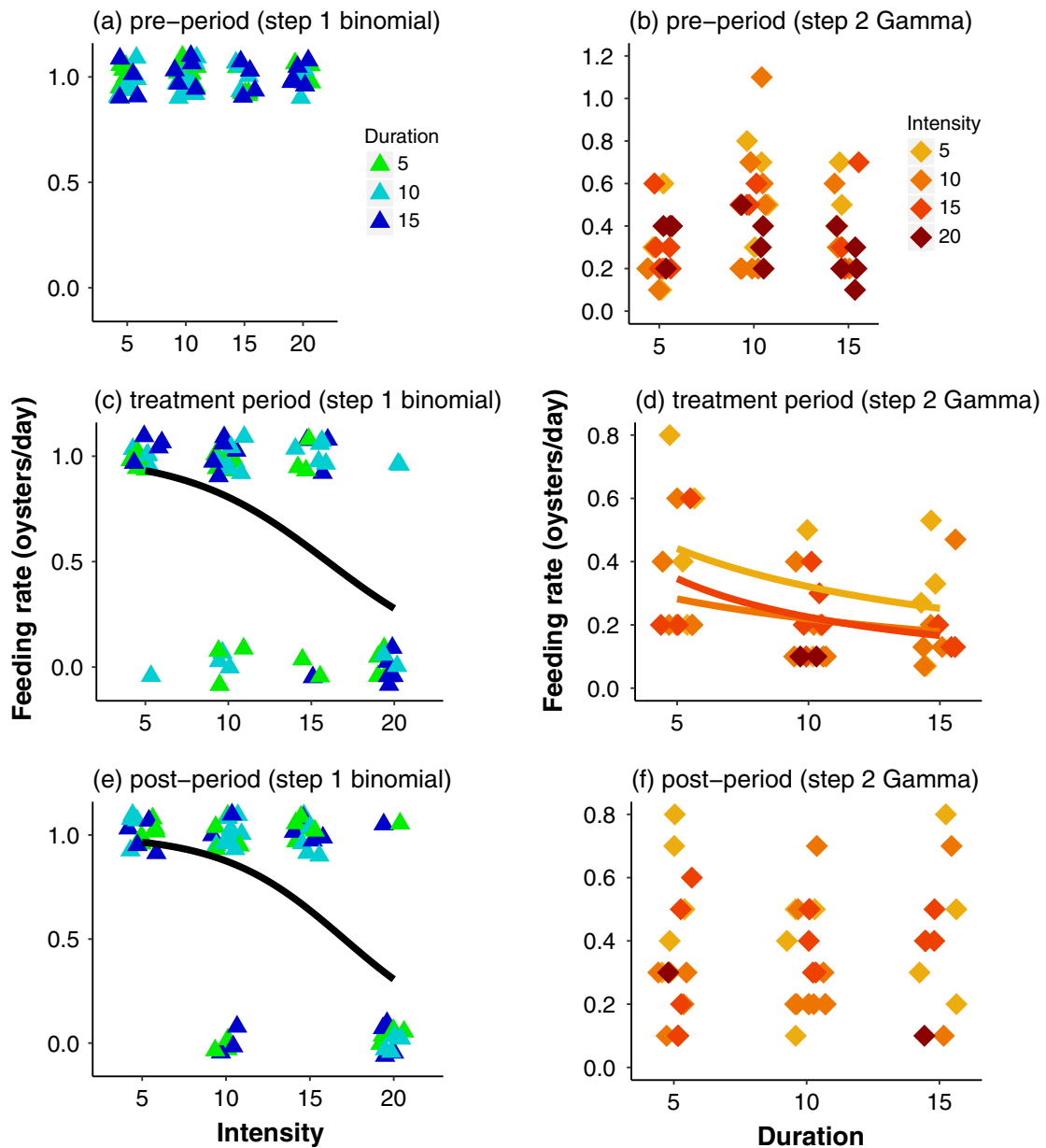
During the pre-period, there was no effect of intensity, duration, or drill size on the feeding rate (Supporting Information Table S3a). All drills fed (Fig. 4a) and there was not any variation in feeding rate among treatment levels (Fig. 4b). On average the feeding rate was  $0.39$  oysters  $\text{d}^{-1}$  (95% Confidence Interval [CI]:  $0.34\text{--}0.44$ ).

During the treatment period, there was a significant effect of intensity on the probability of feeding, while duration and drill size did not have a significant effect (Fig. 4c; Supporting Information Table S3b). In addition, the  $-20$  reduction treatment involved the only occurrence of drill mortality (eight of the 13 drills died). When feeding did occur during the treatment period, all three predictors had an effect on the feeding



**Fig. 3.** (a) The probability of drill presence across a range of observed salinities. The black line is the prediction of a generalized linear mixed model with a binomial error distribution (Supporting Information Table S2a). (b) The mean density of drills ( $\text{m}^{-2}$ ) as a function of the mean weekly salinity in Apalachicola Bay, Florida from 2014 to 2016 for all non-zero densities (Supporting Information Table S2b). Color indicates the temperature with blue representing cooler temperatures and red warmer and each shape represents different plots, “e” stands for east and “w” stands for west.

rate. Larger drills had higher feeding rates across all intensities and durations, and the reduction in feeding rate increased with both intensity and duration (Fig. 4d; Table 1, Supporting Information Table S3c). In this model, long duration (15 d) at the lowest intensity ( $-5$ ) was required to produce a feeding reduction equivalent to that of drills in greater-intensity exposures at the shortest duration for drills of all sizes (Fig. 4d; Table 1). For example, mid-sized drills consumed  $0.25$  oysters  $\text{d}^{-1}$  when salinity was reduced by  $-15$  for 5 d. Compared to the mild intensity of  $-5$  salinity reduction, it was not until the longer duration of 15 d that the feeding rate was comparable,  $0.23$  oysters  $\text{d}^{-1}$  (Table 1).



**Fig. 4.** Drill predation on oysters during the pre-period (**a, b**), treatment period (**c, d**), and post-period (**e, f**). Panels (**a, c**, and **e**) show step 1 of the hurdle method to describe the probability of a drill feeding. In these panels, *duration* (no. of days) is represented by the triangles (5-d: green, 10-d: light blue, 15-d: dark blue). Panels (**b, d**, and **f**) show step 2 of the hurdle method wherein we modeled the feeding rates that were  $> 0$ . In these panels, *intensity* (reduction in salinity) is represented by the closed diamonds (a reduction by  $-5$ : yellow,  $-10$ : orange,  $-15$ : red,  $-20$ : dark red). Solid lines indicate a significant relationship. In panels (**c, e**), the black line is the prediction of a generalized linear model with a binomial error distribution, and in panel (**d**) the three solid colored lines are the prediction of a generalized linear model with a gamma error distribution (yellow:  $-5$  salinity reduction, orange:  $-10$  salinity reduction, red:  $-15$  salinity reduction,  $-20$ : not shown because only two drills feed). Note that points in all panels are jittered for visualization.

During the post-period, there was an effect of intensity but not duration or drill size on the probability of feeding (Fig. 4e; Supporting Information Table S3d), and there was no effect of intensity, duration, or drill size on the feeding rate of drills (Fig. 4f; Supporting Information Table S3e). During this period drills consumed 0.36 oysters/day (95% CI: 0.31–0.42%).

## Discussion

Here, we have shown that the average salinity levels on oyster reefs may predict the abundance of predatory drills, but it was not the only factor that affected the amount of oysters consumed by drills. Both duration and intensity of a salinity reduction (the stressor) mediated drill predation on oysters. While intense salinity reductions consistently reduced drill



**Table 1.** The feeding rate (no. oysters consumed/day) of drills at various sizes from a generalized linear model with a gamma error distribution where the feeding rate was a function of intensity (salinity reduction), duration (days), and drill size (Supporting Information Table S3c). The three sizes are the 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> percentile of the experimental size range of drills.

		Duration (days)	Intensity (salinity reduction)			
			-5	-10	-15	-20
Percentile (drill total length)	25 <sup>th</sup> % (62 mm)	5	0.39	0.30	0.23	0.17
		10	0.29	0.22	0.17	0.13
		15	0.21	0.16	0.12	0.09
	50 <sup>th</sup> % (65.9 mm)	5	0.43	0.32	0.25	0.19
		10	0.32	0.24	0.18	0.14
		15	0.23	0.18	0.13	0.10
	75 <sup>th</sup> % (69 mm)	5	0.48	0.36	0.28	0.21
		10	0.35	0.27	0.20	0.15
		15	0.26	0.20	0.15	0.11

predation across all durations, smaller intensities required longer duration to produce similar effects. For example, an intense reduction in salinity (-20) nearly eliminated predation by surviving drills and also caused a substantial amount of drill mortality regardless of duration. However, milder reductions (-5) required a longer duration—relatively chronic conditions—to decrease drill predation on oysters to the feeding rate exhibited by drills in more intense but shorter exposures. Additionally, only intense salinity reductions suppressed drill foraging after salinity returned to higher levels. These types of salinity events are common in the historical record, which contains both intense and mild reductions in salinity over 21 yr in Apalachicola Bay. Throughout a typical year, multiple chronic and mild reductions were accompanied by one to two acute and intense reductions. Thus, it is plausible that the persistence of widespread oyster reefs in Apalachicola Bay depends on both acute, intense events that create temporary refuges from drill predation, as well as chronic, mild reductions of salinity that can diminish predation. Our experiments suggest that predicting drill foraging rates requires a more nuanced understanding of how fluctuations in salinity affect drill feeding.

Describing how environmental stress affects interactions between species has been a central focus of ecology (Menge and Sutherland 1987; Crain et al. 2008; Todgham and Stillman 2013; Przeslawski et al. 2015; Gunderson et al. 2016). However, that literature has primarily focused on one component of stress, usually intensity, rather than simultaneously considering multiple dimensions of stress such as intensity and duration. In our study, a focus solely on short-duration salinity stress over a range of intensities would have led us to conclude that predation reductions rarely occur in the bay, because only very intense reductions would have had noticeable effects. Conversely, a simultaneous focus on the intensity and duration of salinity reductions suggested that a reprieve from intense predation may be a persistent feature of the bay due to chronic yet mild salinity reductions.

Interactions among multiple components of stress may also dictate the persistence of species such as corals (e.g., Glynn and D’Croz 1990; Berkelmans et al. 2004), riverine insects and fish fry (e.g., Power and Stewart 1987; Power et al. 1996, 2008), and bivalves in the rocky intertidal (e.g., Helmuth and Hofmann 2001; Helmuth 2002; Somero 2002; Finke et al. 2007; Mislán et al. 2009; Iacarella and Helmuth 2012; Mislán et al. 2014). For example, sudden temperature changes, both hot (Hoegh-Guldberg et al. 2007) and cold (Hoegh-Guldberg and Fine 2004), can result in coral bleaching. However, whether a coral colony bleaches is determined by both the intensity and the duration of the temperature anomaly (Ridgway et al. 2016): small to moderate changes in temperature cause bleaching only when the temperature anomaly persists for an extended period of time (Glynn and D’Croz 1990; Winter et al. 1998; Saxby et al. 2003). Consequently, coral reef conservation efforts incorporated duration into monitoring of coral bleaching worldwide by calculating the number of Degree-Heating Weeks (DHW) (NOAA Coral Reef Watch 2013) to identify areas at risk. Similarly, incorporating duration into management of freshwater flows from watershed to estuary can help maximize efforts that balance the demands among user groups (e.g., upstream municipalities and agriculture, downstream fisheries). Specifically, understanding the role that mild, chronic freshwater flows play in sustaining estuarine oyster populations could better inform the tradeoffs between upstream usage and downstream flow that dominate watershed management debates.

According to a 21-yr time series, salinity changes frequently in Apalachicola Bay, with extended periods of both wetter and drier than average conditions (Fig. 2a). In the years of 2006–2008 and 2010–2013, Apalachicola Bay experienced extended dry periods, decreased river flow, and anomalously high salinity (Fig. 2b, identified by the yellow bars where there were numerous occurrences of anomalies above a salinity of 2; Petes et al. 2012; FFWCC 2013). The frequency of low salinity events during this period decreased from the previous 14 yr.



Notably, neither type of low-salinity event occurred in the summer and early fall of 2012, preceding the 2012 oyster fishery collapse. Recent research suggests that increased drill predation due to salinization of estuarine waters and absence of an effective predation refuge was likely the proximal cause of the 2010–2013 oyster collapse (Kimbrow et al. 2017). The results of our lab experiments provide some context to those field data, in that specific kinds of freshwater input may be necessary to create prey refuges or diminished drill predation. It is important to note that exposure to long (1+ month), extremely low salinities (< 5) can harm oysters (Turner 2006; Volety et al. 2009; La Peyre et al. 2013) and can result in their death (Schlesselman 1955). Thus, in accordance with the consumer stress model (Menge and Sutherland 1987; Menge and Olson 1990), periodic flushes that are either intense or long enough to decrease drill predation, but not long enough to harm the oysters, are critical to oyster reef persistence (Livingston et al. 2000; Cheng et al. 2017). An alternative possibility is that the population distribution of oysters may eventually shift toward the head of the bay to avoid high salinity conditions and predatory drills (e.g., Harding et al. 2010), if adequate hard substrate is available further upstream. However, to our knowledge, ecological monitoring efforts in Apalachicola Bay have not detected this response.

Although, we were able to describe in more detail how chronically mild salinities affected drills by combining field observations and controlled laboratory experiments, some questions still remain. Our field observations provided a coarse view of the relationship between salinity and drill abundances. Because we were only able to use monthly averages for temperature, salinity, and drill abundances, we could not detect subtle changes that may have occurred as salinity fluctuated in the bay over shorter time scales. Similar to our analysis on feeding rates, drill movement (and thus the resulting local abundances) may have also been affected by the duration and intensity of salinity reduction. Describing drill movement on either daily or weekly time scales throughout the bay with simultaneous monitoring of temperature and salinity would be required to address this issue. In addition, including other important factors, such as drill density (May 1971; Brown and Alexander 1994; Pusack et al. 2018), oyster population size structure (Pusack et al. 2018), or temperature (Kimbrow et al. 2017) to studies like ours will produce a more comprehensive understanding of drill predation on oysters in nature. Finally, mesocosms restrict movement of drills, which in the field may move from locations with mild salinity reductions. With the ability for snails to migrate and group feed, smaller salinity reductions of short duration may play a stronger role in predation refuge than we currently appreciate.

Resource management may benefit from the results of studies like this one, especially as managers adapt their strategies to account for the effects of climate change. Precipitation patterns, in particular, are changing rapidly such that certain locales have received increased rainfall and thus higher

freshwater input into estuaries, while others have experienced prolonged drought conditions (Poff et al. 2002; Whitehead et al. 2009). Moreover, increased anthropogenic consumption of freshwater from municipal, agricultural, and industrial uses has also altered hydrological flows and often leads to reduced abiotic variability (Jackson et al. 2001; Gordon et al. 2008). As such, it is vital to understand how variations in freshwater flow, i.e., intensity, duration, and frequency, affect salinity and mediate species interactions. Our results are the first to describe the way in which both the intensity and duration of exposure to salinity reductions due to changes in freshwater input over multiple days can either diminish or create refuges for adult oysters from drill predation (a prior study had examined typical diurnal fluctuations in salinity but not extreme events; Garton and Stickle 1980). There is an increasing realization that abiotic variability is the key to understanding ecological interactions, yet most ecological experiments are still performed using “average” conditions (Denny 2017). Here, we have shown that predation on oyster reefs depends on specific combinations of stress intensity and duration, rather than merely average salinity. This type of finer-scale assessment of abiotic stressors is key to planning oyster reef conservation and restoration efforts.

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#### Conflict of Interest

None declared.

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