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Local and regional stressors interact to drive a salinization-induced outbreak of predators on oyster reefs

David L. Kimbro,[1,]† J. Wilson White,[2] Hanna Tillotson,[3] Nikkie Cox,[3] Megan Christopher,[3]
Owen Stokes-Cawley,[1] Samantha Yuan,[3] Timothy J. Pusack,[4] and Christopher D. Stallings[4]

[1]*Department of Marine and Environmental Sciences, Northeastern University, Marine Science Center, Nahant, Massachusetts 01908 USA*
[2]*Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA*
[3]*Apalachicola National Estuarine Research Reserve, East Point, Florida 32328 USA*
[4]*College of Marine Science, University of South Florida, St. Petersburg, Florida 33701 USA*

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Abstract. Predator outbreaks are predicted to increasingly decimate economically and ecologically important prey populations because global climate change and food-web modifications frequently facilitate predators and stress prey. Natural systems are organized hierarchically, with processes operating at multiple scales giving rise to patterns of biodiversity, so predicting and managing outbreaks requires a framework that accounts for the effects of both local and regional stressors. Here, we used the comparative experimental approach to investigate whether the collapse of a nationally important oyster fishery in the Gulf of Mexico (Apalachicola Bay, Florida) could have been (1) caused proximally by a predator outbreak and (2) whether this outbreak was mediated by local- and/or regional-scale forces. During the fishery collapse, we paired experiments with monitoring in Apalachicola Bay and found elevated water salinity, high abundance of predatory snails, and intense oyster mortality due to predation. By repeating these experiments over 4 yr, we found that periods of reduced water salinity inhibited predation on oysters. To partition the influence of local-versus-regional factors on this predator outbreak, we simultaneously replicated the paired experiments and monitoring in a nearby bay (Ochlockonee Bay) that shares the same regional-scale rainfall conditions. Increasing freshwater withdrawals from the watershed that drains into Apalachicola Bay have increased salinities in that bay, but there have not been similar withdrawals in the Ochlockonee Bay watershed. Therefore, Apalachicola Bay experienced a localized anthropogenic stress, while both bays experienced regional stress from drought. In Ochlockonee Bay, our experiments demonstrated that the river maintained sufficiently low salinity to provide ~50% of oyster reefs with a refuge from predation. In contrast, salinity-dependent predation in Apalachicola Bay extended up to the river mouth. Given the stark differences in upstream water withdrawals between these watersheds, it is reasonable to surmise that these withdrawals exacerbated the stress of regional drought, created the difference in predation between the two bays, and thus may have precipitated the oyster fishery collapse. Our study provides empirical support for recent theory about the hierarchical organization of ecosystems, which predicts that stressors will interact across scales to cause localized predator outbreaks.

Key words: Apalachicola Bay; climate change; consumer front; drought; environmental stress; meta-ecosystem; oyster fishery; predation refuge; predator–prey; scale; water withdrawals.

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† **E-mail:** d.kimbro@northeastern.edu

INTRODUCTION

Predators can maintain the community structure and ecosystem functioning of natural systems (Paine 1966, Schmitz 2008). However, under certain conditions, outbreaks and fronts of predators (or herbivorous consumers) can form, resulting in runaway consumption of important resources (Silliman et al. 2013). For instance, a prolonged drought associated with climate change promoted an outbreak of pine beetles that caused a regional loss of forest trees in Canada (Kurz et al. 2008). Likewise, nutrient-rich coastal runoff events triggered outbreaks of crown-of-thorns seastars on the Great Barrier Reef, which decimated living corals (Fabricius et al. 2010). Because the effects of predation on community structure can quickly shift from beneficial to detrimental, understanding the underlying cause(s) of such outbreaks is fundamental to conserving key resources such as hardwood forests and coral reefs.

Recently, the initiation of predator outbreaks was linked to environmental stressors that exceed a certain threshold and in turn either increase prey susceptibility to predation, increase the local density of the predator, or both (Silliman et al. 2013). But to understand how ecosystems will respond to environmental stressors, we must consider the relative influence of local- and regional-scale processes (Gouhier et al. 2010, Menge et al. 2015). For instance, the American Dustbowl of the 1930s involved a broad drought and catastrophic loss of topsoil that was associated with—yet could not be completely explained by—La Niña conditions of warmer sea surface temperatures in the tropical eastern Pacific (Cook et al. 2009). To accurately explain the location and magnitude of drought, models had to include the effect of local-scale devegetation and enhancement of dust aerosols, which were caused by the replacement of drought-tolerant prairie grasses with drought-sensitive wheat (Cook et al. 2009). If predator outbreaks result from an interaction between regional-scale (e.g., La Niña, drought) and local-scale stressors (e.g., devegetation), then our ability to mitigate outbreaks depends on understanding the relative roles of multi-scale processes in exceeding stress beyond critical thresholds (Scheffer and Carpenter 2003).

One important resource vulnerable to predator outbreaks is the oyster. Oysters form reefs that provide habitat for juveniles of commercially important invertebrates and finfishes, stabilize shorelines, filter coastal water, and remove excess nitrogen (Grabowski et al. 2012). Unfortunately, habitat degradation, overharvesting, and eutrophication have decreased the global abundance of this habitat by 85%, with most of the remaining reefs concentrated in six ecoregions, five of which are located in the United States (Beck et al. 2011). These remaining reefs continue to face a variety of threats, including environmentally triggered predator outbreaks. For example, eastern oyster (*Crassostrea virginica*) reefs began to decline in the southern reach of the Matanzas River estuary (northern Florida, USA) in 2008 (Garland and Kimbro 2015). The underlying cause of this decline was increased water salinity, due in part to a regional drought, which facilitated the reproductive success of the crown conch (*Melongena corona*), a gastropod predator responsible for the proximal cause of oyster loss (Garland and Kimbro 2015).

Regional drought alone, however, could not entirely explain the conch outbreak in the southern Matanzas River estuary. Oyster reefs in the northern reach of the same estuary lacked conchs and remained healthy, despite experiencing the same regional stress. To reconcile this contradiction, Garland and Kimbro (2015) observed that the southern reach of the estuary was flushed only by the Matanzas inlet (Sheng et al. 2008), while the northern reach was influenced by flushing of both the Matanzas inlet and the St. Augustine inlet. Because the Matanzas inlet has constricted by 63% since 1995 (Garland and Kimbro 2015), the southern reach now experiences less tidal flushing than the waters of the northern reach. Thus, the combination of regional drought and a local stress (reduced tidal flushing) was necessary to explain why southern reefs—but not northern reefs—were affected by a salinity-induced conch outbreak.

More recently, oysters in Apalachicola Bay, Florida (Fig. 1), experienced catastrophic mortality. The Apalachicola oyster fishery was one of the healthiest in the nation, consistently providing 10% of U.S. oyster landings (Beck et al. 2011). But sharp oyster declines between the summer of 2012 and the spring of 2013 resulted in the declaration of a federal fishery disaster (FFWCC 2013). The southern oyster drill (*Stramonita haemastoma*, hereafter "drill") is known to cause high oyster

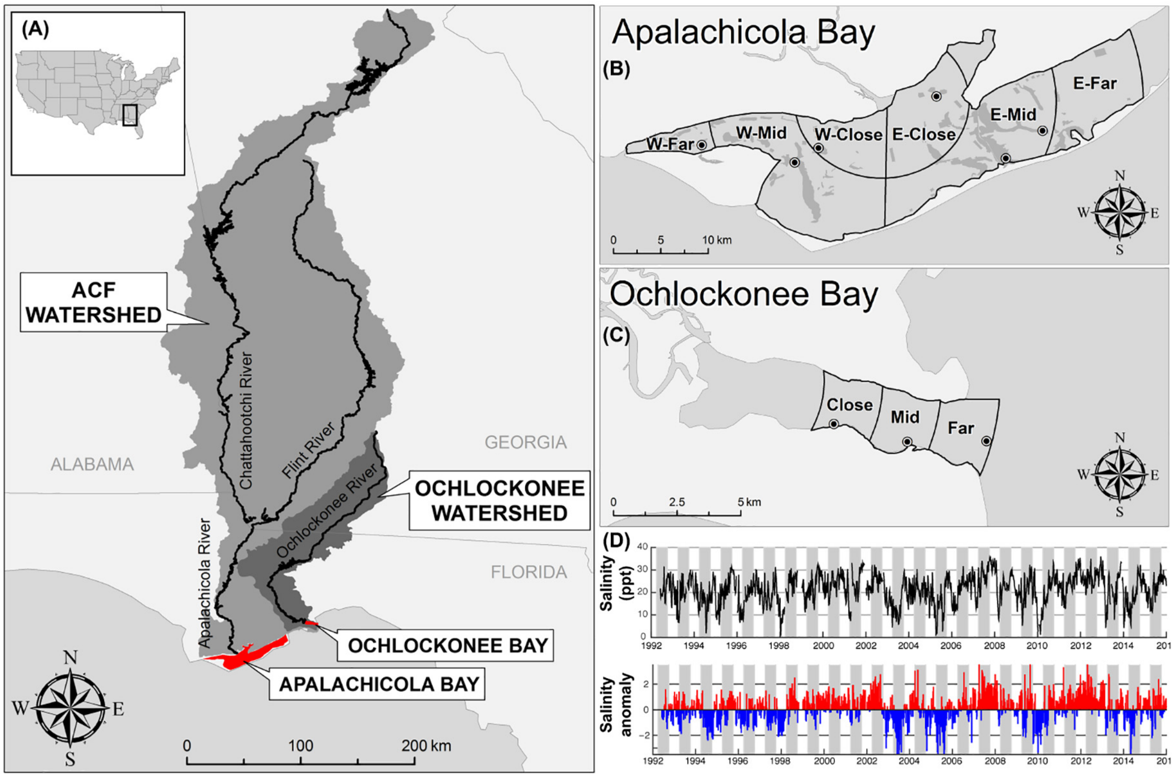

Fig. 1. (A) Map of study sites along the Florida panhandle. Apalachicola Bay and Ochlockonee Bay are highlighted in red. Shading distinguishes the watersheds of the Apalachicola River (dark gray) and the Ochlockonee River (darker gray). Map of Apalachicola Bay (B) and Ochlockonee Bay (C). In Apalachicola, dark shading illustrates distribution of oyster reefs. In both estuaries, concentric circles illustrate proportional distances (close, mid, far) of oyster reefs from river discharge. In Apalachicola, proportional distances extend west (W) and east (E) of the river. (D) Time series of weekly mean salinity and weekly salinity anomaly at Cat Point oyster bar in Apalachicola Bay from 1992 to 2016. Anomaly was calculated based on the climatological mean from 1992 to 2002; data obtained from Apalachicola National Estuarine Research Reserve (http://cdmo.baruch.sc.edu).

mortality, especially under high-salinity conditions (Menzel et al. 1966), and could have contributed to the oyster population collapse that occurred during anomalously high-salinity conditions of 2011–2013 (Fig. 1D). However, there is debate as to the contribution of local-versus-regional factors that produce high-salinity conditions favoring drill outbreaks in Apalachicola Bay. A regional drought in 2011–2013 may have increased the salinity of estuaries throughout northern Florida (i.e., a regional factor), but freshwater input into Apalachicola Bay also depends on flow from the Apalachicola-Chattahoochee-Flint (ACF) watershed, which lies mostly within the state of Georgia (Fig. 1A). Georgia's withdrawals from the ACF river system have increased over time (Marella and Fanning 2011), which may have also increased salinity in Apalachicola Bay (i.e., a factor local to the bay). Understandably, legal disputes have developed between Florida and Georgia over these freshwater withdrawals (Florida v. Georgia, 2014).

We used the comparative experimental approach (Menge et al. 2003) to address two questions about the cause(s) of drill outbreaks in Apalachicola Bay, Florida, that may have contributed to the oyster fishery collapse. First, are drill abundance and predation on oysters controlled by water salinity? Second, is the spatial distribution of drill outbreaks, and the ensuing predation, similar between two bays sharing the same regional drought stressor but with different local stressors via freshwater withdrawal rates? If upstream freshwater withdrawals enhance the intensity and spatial distribution of drill predation, then future management could reduce freshwater withdrawals from the ACF watershed. This is a challenging resource management scenario, because we lack data on drill predation in Apalachicola Bay prior to the collapse, and therefore cannot conduct a traditional Before-After-Control-Impact (BACI) assessment (Underwood 1993). Instead, we used manipulative field experiments in two estuaries to separate the contribution of local-versus-regional factors on drill outbreaks.

METHODS

Study system

Apalachicola Bay is a large (400 km^2) and shallow (1.9 m average depth) estuary located in the Florida panhandle at the terminus of the ACF River system (Fig. 1A). The ACF watershed (50,000 km^2) has headwaters in northeastern Georgia and flows through west-central Georgia before entering Florida. The primary source of freshwater and nutrients to this bay is the Apalachicola River (Mortazavi et al. 2000, Putland et al. 2013). Consequently, it is the primary cause of salinity variation throughout the bay (Livingston et al. 2000). Maximum river flows occur during late winter months and reflect rainfall amounts in the upper basin; low flows occur during the late summer months (Morey et al. 2009). In Apalachicola Bay, oyster reefs cover approximately 5–13% of the bottom (16–24 km^2) and are distributed from areas close to the river mouth (lower salinity) to those far from it (higher salinity; Fig. 1B; FDEP and CAMA 2013, Zu Ermgassen et al. 2012).

Ochlockonee Bay is a shallow (1.0 m average depth) estuary located 30 km east of Apalachicola Bay (Kaul and Froelich 1984; Fig. 1C). Unlike the large ACF basin, the smaller watershed (6500 km^2) of this bay begins in southwest Georgia (Fig. 1C). Water salinity in Ochlockonee Bay (25 km^2 of water) is primarily influenced by flow from the Ochlockonee River, with maximum flows in late winter months and minimum flows in the late summer months (Kaul and Froelich 1984). Shellfish harvest area maps maintained by the state of Florida illustrate that this bay also has subtidal reefs both close to and far from the river (FDACS 2012*a*, *b*).

Hypothesis 1: Variation in salinity controls predation on Apalachicola Bay oysters

*Experiments.—*We conducted seven replicate rounds of a field experiment on oyster survival at multiple sites in Apalachicola Bay from 2013 to 2017, capturing both spatial and temporal variabilities in water salinity. These experiments are hereafter referenced as A1–A7 ("A" for Apalachicola) and are summarized in Table 1. Prior to the first experiment, we partitioned the subtidal oyster reefs of Apalachicola Bay into six zones that reflected spatial gradients in salinity. Specifically, reefs identified in a geophysical benthic habitat mapping program (Twichell et al. 2007) were assigned to a zone based on their relative distance from the river (close, mid, far) as well as their relative position to the river (east vs. west; Fig. 1B). In each zone, we randomly selected one reef to receive nine protective frames (1.2 m × 0.9 m × 0.6 m) constructed of steel rebar (13 cm thickness). On each reef, these relatively open rebar frames were deployed at 3.0-m linear increments from each other (9 frames × 6 zones = 54 total frames) and were used to protect the experiment from harvesting and boating activities (see Appendix S1 for further details).

One side of each rebar frame contained three posts separated by 0.4 m. Three experimental units were attached to these posts and randomly assigned among three treatments: (1) control, (2) cage, and (3) cage-control treatments. Thus, each experiment (A1–A7) consisted of 162 experimental units that were constructed from 0.2 m × 0.2 m squares of vinyl-coated wire mesh (5 mm × 5 mm mesh opening). The control treatment consisted of a single mesh panel to which adult oysters were attached; the panel was attached to a post and placed flat on the reef with oysters facing upwards. The cage treatment had the same orientation, but it was enclosed by additional mesh panels to form a 0.2 m × 0.2 m × 0.2 m cage. For the cage-control treatment, two mesh walls were removed from the full cage setup to maintain caging material effects, while also allowing access by predators. Adult oysters (mean ± SD length = 67.77 ± 17.21 mm) were collected from the east mid-zone of the bay (Fig. 1B). While final survival of these oysters in the cage treatment reflected the influence of the physiochemical environment and disease on oysters (e.g., Dermo, a disease caused by the protist *Perkinsus marinus*; Petes et al. 2012), survival in the

Table 1. Summary of repeated experiments conducted in Apalachicola Bay (AB) and Ochlockonee Bay (OB). For each experimental round (Apalachicola Bay, A1–A7; Ochlockonee Bay O1–O3), we provide the starting date, duration of the experiment (weeks), levels of oyster density tested, as well as the source and sample interval of the associated water salinity data.

Round	Start date	Duration (weeks)	Initial oyster density	Water salinity source	Interval of salinity samples
A1	May 2013	3	4	YSI Pro2030 Hydrodynamic model	Biweekly Daily
A2	August 2013	1	4	YSI Pro2030 Hydrodynamic model	Biweekly Daily
A3 O1	September 2014	12	1,3,5	Sea-Bird Electronics (A3) Hydrodynamic model (A3) Onset logger (O1)	Monthly Daily 15 min
A4	February 2015	14	1,3,5	Sea-Bird Electronics Hydrodynamic model	Monthly Daily
A5 O2	April 2015	14	1,3,5	Sea-Bird Electronics (A5) Hydrodynamic model (A5) Onset logger (O2)	Monthly Daily 15 min
A6 O3	October 2015	13	1,3,5	Sea-Bird Electronics (A6) Hydrodynamic model (A6) YSI Pro and Sea-Bird Electronics (O3)	Monthly Daily 8–10 d
A7	February 2016	11	1,3,5	Sea-Bird Electronics Hydrodynamic model	Monthly Daily

control treatment reflected the influences of both the environment and predators. Predation effects were calculated as the difference in survival between the cage treatment and the control treatment, standardized by survival in the cage treatment: ([cage − control]/cage; Trussell et al. 2006). We also quantified whether oysters in the control treatment died because of a destructive crushing predator (e.g., crab) or a non-destructive predator that attacks between the valves (e.g., drill).

The first two rounds of this experiment (A1 and A2) used an initial density of four adult oysters for each experimental unit, because average density per unit area of our cages (0.09 m^2) on the primary commercial reefs was 3.09 oysters in 2012 (FFWCC 2013). A1 lasted three weeks during the high-salinity conditions associated with the oyster fishery collapse (Fig. 1D). A2 followed the same procedure as A1, but occurred after two large precipitation events with lower-salinity conditions (Fig. 2C). A2 lasted one week due to logistical constraints. During each experiment, we quantified predator abundance within each rebar frame as well as the ambient salinity and temperature of each zone at the surface (1.0 m depth) and subsurface (1.0 m above benthos) with a handheld meter (YSI Pro2030; YSI, Inc., Yellow Springs, Ohio, USA; Table 1).

We repeated this experiment five times from 2014 to 2017 (A3–A7) to capture longer term variation in salinity and temperature (Table 1). In these additional rounds, we increased the experimental duration to three months to allow development of Dermo disease effects on oyster survival and introduced an additional factor: variation in initial oyster density. We manipulated oyster density because higher densities may increase predator attack rate (Sih 1984) and transmission of disease (Packer et al. 2003). Initial oyster density consisted of three levels (one, three, and five oysters), which were based on the minimum, average, and maximum densities of adult oysters (per unit area) on the primary commercial reefs in 2012 (FWCC 2013). The three levels of initial density were randomly assigned among the nine rebar frames within each zone of Apalachicola Bay so that each frame had the same initial density on all experimental units. Next, we randomly assigned the three experimental units of each rebar frame among the treatments: (1) control, (2) cage, and (3) cage-control.

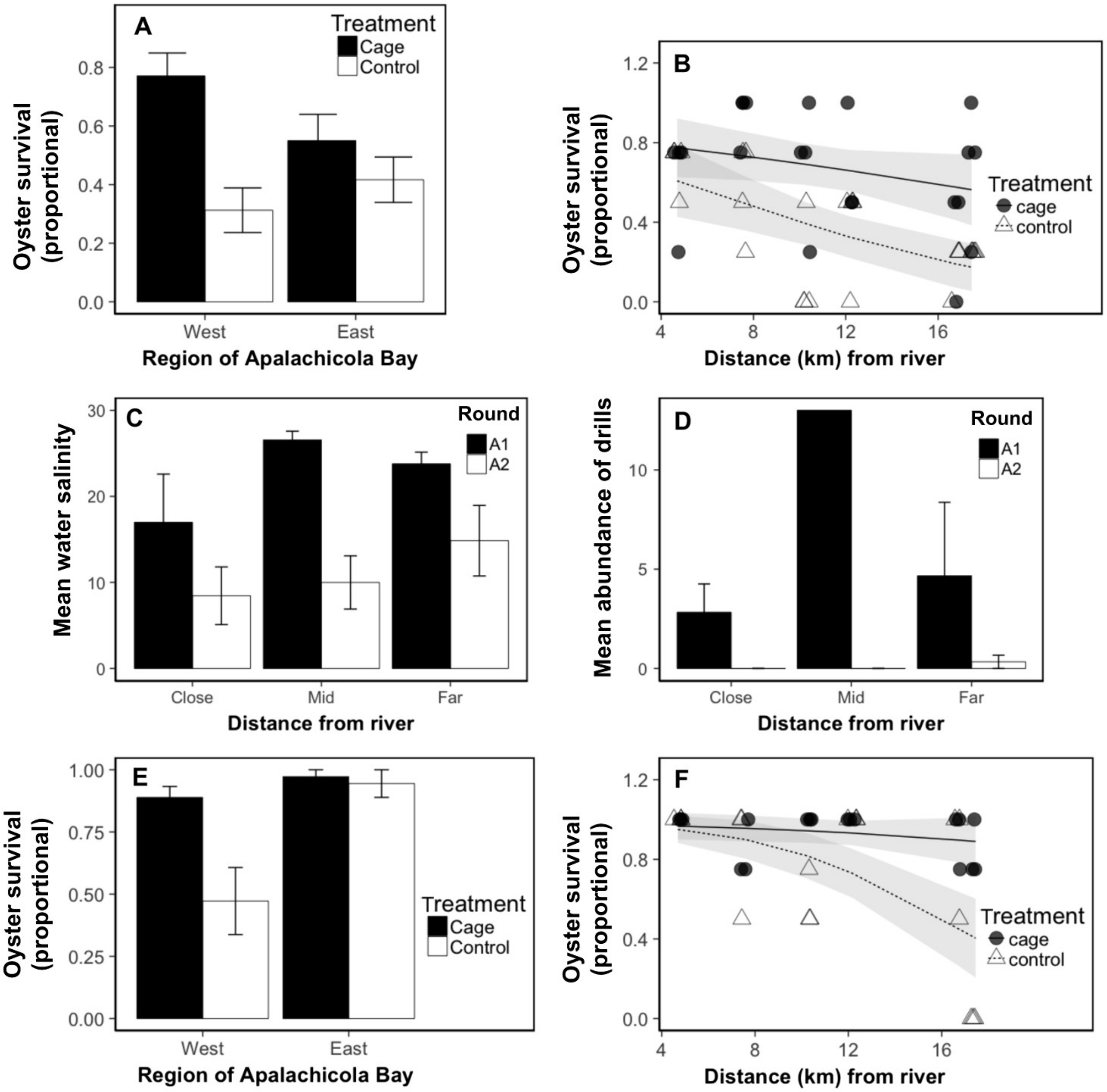

Fig. 2. Results of repeated field experiments and monitoring in Apalachicola Bay, Florida. Oyster survival in experiment A1 on reefs (A) toward the east and west of the Apalachicola River and (B) as a function of distance (km) from Apalachicola River as well as cage (closed circles) and control (open triangles) treatments. (C) Mean (±SE) of water salinity in Apalachicola Bay during experiment A1 (closed bars) and during a prolonged precipitation event prior to experiment A2 (open bars). (D) Mean (±SE) of drill abundance per rebar frame (1.2 m × 0.9 m × 0.6 m) in Apalachicola Bay during experiment A1 (closed bars) and experiment A2 (open bars). Oyster survival in experiment A2 on reefs (E) toward the east and west of the Apalachicola River and (F) as a function of distance (km) from Apalachicola River as well as cage (closed circles) and control (open triangles) treatments.

In experiments A3–A7, predator abundance within each rebar frame was monitored monthly and oyster survival was measured at the end. Water properties were quantified by conducting monthly conductivity–temperature–depth (CTD) profiles at each zone with a Sea-Bird Electronics (SBE 19plus V2; Table 1). For each CTD cast, we calculated the median for temperature and salinity across depths. Next, we calculated monthly median values of salinity and temperature at each zone. For each experiment, these monthly medians were averaged to create zone-specific values of salinity and temperature. The mean (± standard deviation, SD) salinity and temperature, as well as mean (±SD) number of drills per rebar frame, are presented in Appendix S2.

Data analysis for experiments A1–A7

Oyster survival.—We used a generalized linear model (GLM) with binomial error and logit link (i.e., logistic regression) to test whether final oyster survival in each experiment depended on treatment (cage vs. control), region (east or west), or distance (km) from the river mouth. Before proceeding with this analysis, we tested whether the control and cage-control treatments differed within any of the six zones (unique region × distance combinations). This analysis was performed by excluding the cage treatments and using a model with the factors "treatment" (levels = control or cage-control), "zone" (categorical, six levels), and their interaction. A procedural artifact of the caging material was identified if either the term for treatment or the treatment × zone interaction was statistically significant. We did not detect any significant procedural artifacts in experiments A1–A7. Thus, we excluded the cage-control treatments from each round and analyzed only the data from cage and control treatments.

Because experiments A3–A7 included variation in initial density but A1–A2 did not (Table 1), we next tested for an effect of initial density on survival. Given that the full, four-factor GLM failed to converge to a maximum-likelihood solution (and would have also been difficult to interpret had it converged), we constructed three separate GLMs. Each GLM included the initial density factor, one other factor (region, distance, or experimental treatment), and their interaction so that all possible two-factor models with density were evaluated. Despite increasing the type I error rate by taking this approach, we never detected a significant effect of initial density ($P > 0.05$) either by itself or in an interaction term in any model. Therefore, we excluded the density factor, and the analysis of A3–A7 was thus the same as that for A1–A2.

After testing for procedural artifacts and density effects, we used GLM to test for the effects of region, distance (km), and treatment on oyster survival. If the treatment effect was significant either by itself or in interaction with region, then we used Tukey's post hoc test to compare means among treatment × region pairs. If there was a significant treatment × distance interaction, we used the coefficients of the model to predict the separate logistic relationships between oyster survival and distance for cages and controls. In some cases, the full model contained treatments with either 100% survival or 100% mortality, leading to perfect separation of that factor in the logistic regression (Heinze and Ploner 2002). To circumvent the bias in regression parameter estimates associated with separation, for those cases (i.e., experiment A2), we split our analysis into two simpler models consisting of either treatment and region or treatment and distance from the river; neither simpler model had perfect separation.

Salinity effects on predation.—For each experiment, we calculated the average strength of predation at each zone and used separate linear regressions to evaluate whether predation strength (calculated from survival as [cage − control]/cage) was related to distance from the river (km) and average salinity (generated from point samples, Table 1). Additionally, we conducted two more rigorous tests of the effects of salinity on predation by combining the standardized predation effect sizes across multiple experimental rounds. First, average effect sizes of predation at each zone during experiments A1–A2 were combined to evaluate whether the striking difference between the results of the two experiments was associated with salinity in a linear regression. Next, average effect sizes of predation at each zone from all seven experiments were combined into a single data set to evaluate the relationship between predation intensity and salinity as well as temperature over a four-year time frame. Because the predation effect sizes were constrained between values of 0 and 1, we applied an arcsine square root transformation to the effect sizes.

For both analyses, we obtained higher resolution (daily) salinity and temperature values for each experimental zone from a hydrodynamic model of Apalachicola Bay (see Appendix S3 for model validation details). We used these interpolated values to better represent the environmental conditions, which vary on tidal, daily, and weekly scales. For experiments A1–A2, we used hydrodynamic model output for year 2013 directly in our model. Hydrodynamic model outputs were not available for years 2014–2017, when experiments A3–A7 occurred, so we obtained zone-specific salinity estimates by interpolating from synoptic salinity and temperature data recorded daily at monitoring stations elsewhere in the bay (see Appendix S3 for further details). We then used regression to test whether predation strength depended on the mean daily salinity during experiments A1–A2 and on the interaction between mean daily salinity and temperature during experiments A1–A7. Because multiple experimental rounds differed in duration (Table 1), we tested the duration of each experiment (days) as a covariate. That covariate was non-significant ($P = 0.45$) so we excluded it from the final analysis.

Hypothesis 2: The spatial extent of drill predation differs between two bays that share the same regional drought but experience different freshwater withdrawals

Between-bay differences in drought and freshwater input.—To test for between-bay differences in precipitation, we obtained daily precipitation records from 1970 to 2016 from the National Climatic Data Center for three weather stations: the Apalachicola Regional Airport (GHCND: USC00080211), Panacea Florida (GHCND: USC00086828; a town adjacent to Ochlockonee Bay), and Smith Creek Florida (GHCND: USC00088290; a town adjacent to Ochlockonee Bay). Smith Creek data were available from 1970 to 1983, and Panacea data were available from 2000 to 2016; we combined the two to obtain a single data set for Ochlockonee Bay. For both bays, we summed daily precipitation totals at a monthly scale and calculated mean totals for August, September, and October of each year to produce an annual time series of average monthly precipitation rates for the late low-flow season, when bay salinities and drill abundance are highest. We focused on 1970–2016 because it was a period of pronounced growth in human population and water extraction from the ACF basin (Marella and Fanning 2011).

To evaluate river flow, we obtained data for 1970–2016 at Chattahoochee, Florida (Apalachicola River, USGS station 02358000) and Bloxham, Florida (Ochlockonee River, USGS station 02330000). The Chattahoochee station is 173 km above the mouth of the Apalachicola River, and flow rates at this station are highly correlated with downstream river flow into Apalachicola Bay (Morey et al. 2009, Petes et al. 2012). The Bloxham USGS station is 67.1 km north of Ochlockonee Bay. For both data sets, we averaged daily flow rates to generate a mean daily flow rate for each month. We then averaged the monthly means for August, September, and October, producing an average daily flow rate for the late low-flow season of each year in each river. To compare temporal trends in flow between the two rivers, we standardized the seasonal average flow in each year by its long-term average ([seasonal average − long-term average]/long-term average), producing a data set of seasonal flow anomalies in each year for each river.

Experiments.—We replicated three rounds of our experiment in Ochlockonee Bay: O1 (fall 2014; “O” for Ochlockonee), O2 (summer 2015), and O3 (fall 2015), which corresponded to the timing of experiments A3, A5, and A6, respectively (Table 1). Before these experiments, we assigned subtidal reefs to a zone based on their distance from the river mouth (close, mid, far; Fig. 1C). Because Ochlockonee Bay is smaller and essentially limited to one dimension (i.e., east–west), we did not partition its reefs further in either east–west or north–south dimensions. Experiments in Ochlockonee only used oysters collected in that bay, and all methods were identical to those of experiments A3–A7.

Data analysis for experiments O1–O3.—The analysis of oyster survival proceeded as in experiments A3–A7 and involved the use of GLM with binomial error and logit link. We detected a significant caging effect in experiment O2 (summer 2015), so those data were excluded from further analysis. Because we failed to detect an effect of initial oyster density in experiments O1 and O3, we excluded that factor from future consideration. Next, we combined the results of experiments A3, A6, O1, and O3, which were conducted simultaneously (Table 1), into a single data set and proceeded with the main analysis. This analysis used a GLM with a binomial error distribution to test whether final survival depended on the fixed factors of bay (Apalachicola or Ochlockonee), distance from the river, round, and treatment. Instead of using raw distance (km), we used proportional distance of each zone from the respective river because of the size difference between Apalachicola Bay and Ochlockonee Bay. For instance, the "close" zones in Apalachicola Bay and Ochlockonee Bay were 4.69 km and 5.01 km from the river, respectively. To calculate the proportional distance of the reefs in these zones, we divided their raw distances by the raw distances from the river of the farthest reefs in the "far" zones (e.g., close reefs in Apalachicola 4.69 km/14.49 km = 0.32). Finally, we combined the predation effect sizes for experiments O1 and O3 with those of experiments A3 and A6 and used linear regression to evaluate the relationship between predation strength (arcsine square root transformed) and water salinity. Because we lacked a hydrodynamic model for Ochlockonee Bay, we deployed Onset HOBO conductivity loggers (model no: U24-002) to record salinity and temperature at 15-min intervals. These instruments failed during experiment O3. As a result, the mean salinity for the Ochlockonee sites during experiment O3 consists of point samples that were collected at an average frequency of 8–10 d for each site (Table 1). All analyses were performed in R 3.4.1 (R Core Team 2016).

RESULTS

Hypothesis 1

In A1, oyster survival depended on an interaction between the east–west region of Apalachicola Bay and treatment ($P = 0.01$; Appendix S4; Fig. 2A), with a significant difference between cage and control treatments in the west but not in the east (Tukey's HSD, $P < 0.001$ and $P = 0.60$, respectively). In addition, survival in the cage and control treatments decreased significantly with distance (km) from the river ($P = 0.005$; Appendix S4; Fig. 2B). Predation strength was high across sites so there was no difference in predation with increasing distance from the river ($F_{1,4} = 1.53$, $P = 0.28$; Appendix S5). However, there was a positive relationship between predation strength and salinity ($F_{1,4} = 3976.9$, $P < 0.01$; $y = 0.05x - 0.54$; $R^2 = 0.99$; Appendix S5). In A1, dead oysters in the control treatments were not damaged by a crushing predator (e.g., stone crab). Therefore, predation was attributed to the abundant drills.

Prior to experiment A2, precipitation had caused 55–61% reductions in salinity across zones relative to salinities during experiment A1 (Appendix S2; Fig. 2C). We also observed decreased drill abundance, including 100% reductions in the zones close and mid-distance from the river, and a 93% reduction at zones far from the river (Appendix S2; Fig. 2D). In A2, oyster survival again depended on the interaction between east–west region and treatment ($P = 0.04$; Appendix S6); survival was significantly lower in controls than in cages in the west, but not in the east (Tukey's HSD, $P = 0.002$, $P = 0.94$, respectively; Fig. 2E), where survivorship was high in both controls and cages. In general, oyster survival in cages was higher (88–97%) in A2 than in A1 (55–75%). Oyster survival in A2 was also affected by an interaction between treatment and distance from the river ($P = 0.03$, Appendix S6; Fig. 2F). Close to the river, oyster survival in the cage treatments was no different than that in the control treatments. But with increased distance from the river, survival decreased more in the control treatments (Fig. 2F). This difference between the cages and controls represented predation strength, which was lower at nearly all sites relative to experiment A1 and strengthened with increasing water salinity ($F_{1,4} = 21.1$, $P = 0.01$; $R^2 = 0.84$; $y = 0.06x - 0.26$; Appendix S5), with all predation attributed to oyster drills. Over the course of both experiments, spatial variation in predation strength was correlated with increasing salinity ($F_{1,10} = 14.5$, $P = 0.003$; $R^2 = 0.59$; $y = 0.04x - 0.19$; Fig. 3A).

In experiments A3–A7, we detected predation effects that increased with distance from the river and correlated positively with increasing water salinity, except for experiment A6 (Appendix S7). In addition, 99%, 99%, 100%, 92%, and 100% of the predation in experiments A3–A7 (respectively) were attributed to oyster drills. Because experiments A3–A7 were conducted during a wider range of water temperatures, we also detected a seasonal temperature effect, with less predation in cooler water. Across all seven experiments, the relationship between predation strength and salinity depended on temperature ($F_{3,38} = 4.78$, $P = 0.0001$, $R^2 = 0.42$; salinity × temp coefficient, $P = 0.03$; Fig. 3B). During these experiments, the mean ± length of drills was 44.78 ± 12.75.

Hypothesis 2

There was no linear trend over time in precipitation in Apalachicola Bay ($F_{1,45} = 0.203$, $P = 0.65$, $R^2 = 0.004$) or Ochlockonee Bay ($F_{1,26} = 0.072$,

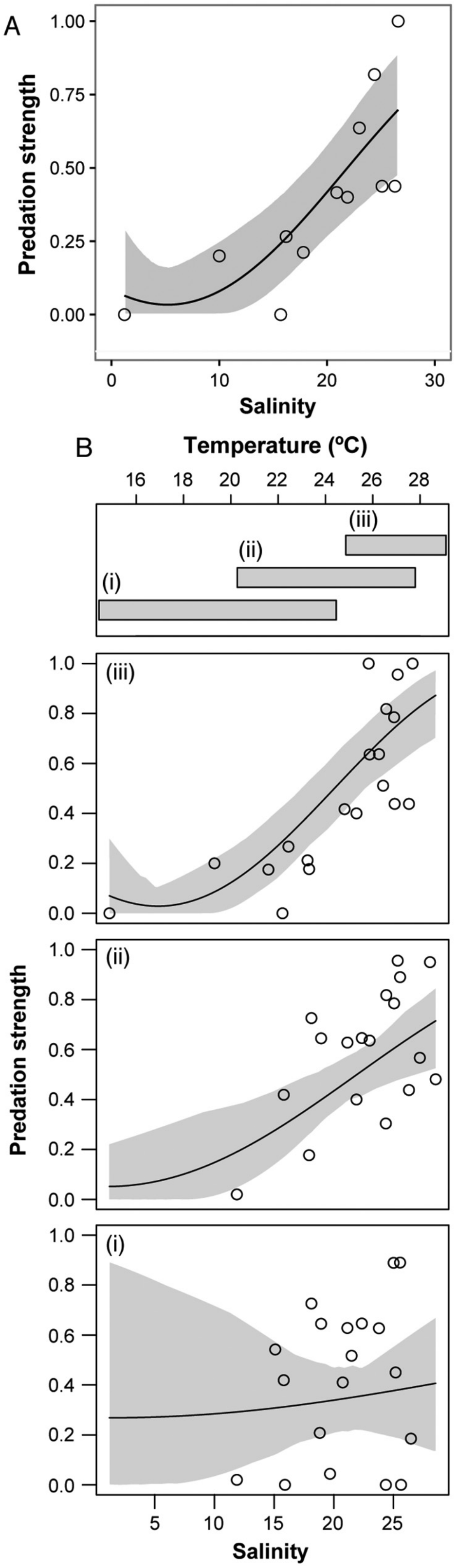

Fig. 3. (A) The relationship between the strength of predation (back-transformed) and salinity during experiments A1–A2. (B) Coplot of the relationship between predation strength (back-transformed) and salinity at three different ranges of temperature during experiments A1–A7.

$P = 0.79$, $R^2 = 0.003$). However, precipitation at the two bays in 1970–2015 was correlated (Pearson's correlation; $R = 0.65$, df = 26, $P = 0.0002$). The seasonal flow anomaly (log transformed) declined over time in Apalachicola Bay ($F_{1,45} = 9.83$, $P = 0.003$, $R^2 = 0.18$), but not in Ochlockonee Bay ($F_{1,45} = 2.18$, $P = 0.15$, $R^2 = 0.04$).

In experiments O1 and O3, 81% of oyster predation was attributed to the drill. Because our analysis of both data sets demonstrated no significant interaction between treatment and round (Appendix S8), we pooled the results of experiments A3, A6, O1, and O3 and detected a significant three-way interaction among treatment, estuary, and proportional distance from the river (Appendix S8). Oyster survival was lower in controls than in cages, and this difference (which reflected predation) increased with proportional distance from the river (Fig. 4A). In Apalachicola Bay, predation was statistically detectable throughout the entire estuary, while in Ochlockonee Bay, predation was not detectable in the upper half of the estuary. Across both experiments, predation increased significantly with increasing salinity (with outlier, $F_{1,16} = 14.93$, $P = 0.001$, $R^2 = 0.48$, $y = 0.05x - 0.58$; without outlier $F_{1,15} = 21.51$, $P = 0.0003$, $R^2 = 0.59$, $y = 0.06x - 0.66$; Fig. 4B). (One site in the high-salinity zone lacked drills during one experimental round, possibly in response to a temporary lack of ambient oysters.)

DISCUSSION

Our results are consistent with the hypothesis that the oyster fishery collapse in Apalachicola Bay, Florida, was caused by an interaction between local- and regional-scale processes that facilitated a salinization-induced outbreak of predatory drills. In May 2013, we demonstrated that water salinity, drill abundance, and drill predation on oysters were high throughout the entire bay and increased with distance from the primary

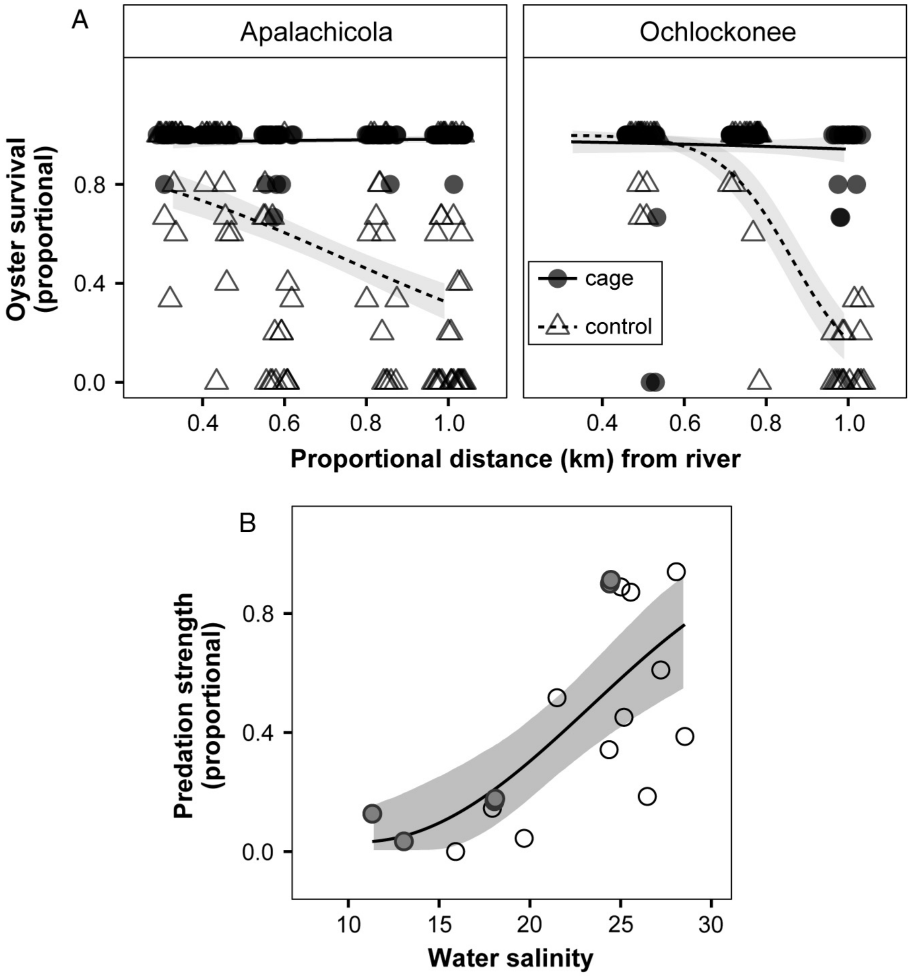

Fig. 4. (A) Results of experiments simultaneously conducted in Apalachicola Bay (left panel) and Ochlockonee Bay (right panel). In both panels, data represent oyster survival as a function of proportional distance from the river as well as cage (closed circles) and control (open triangles) treatments. (B) The relationship between the strength of predation (back-transformed) and salinity during the experiments in Apalachicola Bay (open circles) and Ochlockonee Bay (gray circles). Removal of outlier increased R^2 from 0.48 to 0.59.

source of freshwater, the Apalachicola River. By August 2013, intense precipitation had lowered salinity, and we detected baywide reductions in drill abundance and predation on oysters. These experiments suggested causal links among water salinity, predator abundance, foraging activity, and oyster mortality. By repeating this experiment over four years, we confirmed that predation on oysters consistently intensified with increasing salinity during non-winter months. Given that a regional-scale drought promoted unusually high salinity in Apalachicola Bay leading up to the 2013 oyster fishery collapse (Fig. 1D), it is reasonable to surmise that the fishery collapse could have been precipitated by a localized outbreak of predatory drills. Furthermore, results from a set of parallel observations and experiments in nearby Ochlockonee Bay revealed a lower intensity and extent of salinity-dependent predation. Therefore, a predator outbreak in Apalachicola Bay was driven by factors local to that bay, such as declining freshwater inflow due to upstream water withdrawal, in addition to regional factors affecting both bays, such as rainfall.

There was a similar positive relationship between salinity and drill predation in Ochlockonee

Bay and Apalachicola Bay. Further, predation on oysters intensified with increasing distance from the river (corresponding with increasing salinity) in both bays. These patterns support the general paradigm that stenohaline predators restrict oysters to lower-salinity areas of estuaries (Galtsoff 1964, Pollard 1973; Breithaupt and Dugas 1979, Wilber 1992, Kirby 2000). However, our experimental results also showed a key difference between the two bays: While drill predation occurred throughout all of Apalachicola Bay during warm summer months, 66% of the oyster reefs in Ochlockonee Bay (those nearest the Ochlockonee River) did not experience significant predation. Thus, river input and low salinity near the river mouth protected oysters from predation in Ochlockonee Bay, but not in Apalachicola Bay.

The presence of a predator refuge for oysters in Ochlockonee Bay—but not Apalachicola Bay—cannot be explained by differences in precipitation between the bays, because they experienced similar rainfall patterns over the past 45 yr. In contrast, there were differences in river flow into the two bays over the same period. The seasonal average of river flow during the driest portion of each year has declined since 1970 for the Apalachicola River, but not for the Ochlockonee River. Given similar precipitation conditions for the two bays, this difference in river flow stands out as a factor unique to Apalachicola Bay that would have increased salinity, particularly near the river mouth and in turn facilitated higher drill predation in the upper bay than that observed in Ochlockonee Bay. Because upstream water withdrawals in the ACF watershed have increased dramatically since 1970 (Marella and Fanning 2011), it is possible that water withdrawals interacted with the regional-scale drought to promote a salinization-induced outbreak of predatory drills in Apalachicola Bay and in turn the oyster fishery collapse.

While this conclusion is supported by our circumstantial evidence from monitoring and experiments, the conclusion would be more strongly supported if our results were based on a BACI experimental approach (Underwood 1993). Such an approach would have required research in both bays to have begun before the observed increase in upstream water withdrawal, maintained into the present, thus providing a consistent time series of when predator outbreaks developed relative to temporal changes in upstream water withdrawals, water salinity, and the oyster fishery. Then, if results demonstrated that a salinization-induced outbreak of predatory drills intensified more in Apalachicola Bay than in Ochlockonee Bay in 2012, we could more directly attribute the fishery collapse to upstream water withdrawals. Because our research began during the collapse, we adopted a space-for-time substitution approach, which assumes that the causes of spatial differences in predation between the two bays also reflect the causes of changes in predation within Apalachicola Bay over time. This can be a powerful approach, particularly when "before" data are unavailable. For example, in a recent test, a space-for-time approach was 70% as accurate as a before–after approach in predicting how the taxonomic composition of plant communities will be altered by climate change (Blois et al. 2013). A similar approach could be used to investigate multi-scale causes of sudden ecological shifts (e.g., predator outbreak) in other systems that also lack the requisite data to support a BACI approach.

Even if upstream withdrawals caused a predator outbreak by intensifying salinization, it remains unclear whether predation was the primary cause of the oyster fishery collapse. For instance, less freshwater input and higher salinity could also have increased the prevalence of the Dermo pathogen (Hoffmann et al. 1995, Powell et al. 2003). In fact, low oyster survival in protective cages during our first experiment suggests that disease may have also been a major contributor to mortality during the fishery collapse. However, all subsequent experiments failed to show a strong influence of disease. Less freshwater may have also decreased the nutrient supply needed by phytoplankton, which are ultimately consumed by oysters, thereby essentially starving oysters. Commercial fishing is another potential cause of oyster decline. Despite the management of the Apalachicola Bay oyster fishery being commended for facilitating one of the most productive and sustainable oyster fisheries worldwide (Zu Ermgassen et al. 2012), fishing has historically been a driver of oyster losses in north and mid-Atlantic estuaries (Kirby 2004). Thus, while pairing observations with field experiments—as we have done—is a powerful approach, there are limitations to the numbers and types of factors that can be manipulated. Furthermore, if predation, recruitment, growth, and harvesting fluctuate over time, then short-term experiments may not accurately reveal factors that shaped population-scale patterns of oysters. As Hastings and Boettiger (2013) argued, mechanistic models are required to reveal how causal factors interact and to predict the conditions under which large-scale systems or populations are likely to cross a dynamic threshold into a state of degradation. Consequently, our next research step will involve the integration of our empirical data (monitoring and experiments) with a mathematical model to produce the most reliable inference for the cause of the oyster fishery collapse.

If the combination of empirical data and modeling determines that salinity-induced predation was the primary cause of the oyster fishery collapse, then it behooves us to understand the mechanism by which salinity affects drills. Salinity could control drill abundance by inhibiting snail reproduction, if like *Melongena corona*, larvae of *Stramonita haemastoma* fail to metamorphose at reduced salinities (Garland and Kimbro 2015). Salinity could also exert population-scale control if sudden salinity reductions—such as the intense precipitation event of July 2013—overwhelm the osmoregulatory capacity of the drill and cause death or non-lethal effects that reduce their local populations (e.g., egress from oyster reefs). The ability of oysters to tolerate such conditions more than drills would align with the environmental stress model (Menge and Sutherland 1976) as well as the long-held (but previously untested) suggestion that oysters use inner portions of estuaries as refuge from stenohaline predators (Galtsoff 1964, Pollard 1973, Breithaupt and Dugas 1979, Wilber 1992, Kirby 2000). Less severe reductions in salinity could also operate at the individual level by causing non-lethal stress that impairs drill foraging. A combination of laboratory and field experiments is also needed to evaluate how realistic variation in water salinity influences drill populations and drill behavior.

It is clear that natural systems are hierarchically organized by forces operating at local and regional scales (Gouhier et al. 2010, Menge et al. 2015). Indeed, our study demonstrated that the development of a predator outbreak associated with the decline of an oyster fishery required both regional-scale and localized stressors in Apalachicola Bay. Furthermore, our study highlights how experiments and observations can be combined to disentangle the relative influence of regional- and local-scale forces even in the absence of a traditional BACI approach. Although predator outbreaks are a natural phenomenon observed in a diversity of systems (Silliman et al. 2013), their frequency and duration are predicted to increase with global climate change and the intensification of environmental stress. Accordingly, predicting and mitigating outbreaks fundamentally depends on the development of theoretical and empirical research approaches that account for the effects of multiple processes operating at local and regional scales.

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LITERATURE CITED

Beck, M. W., et al. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61:107–116.

Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the National Academy of Sciences 110:9374–9379.

Breithaupt, R. L., and R. J. Dugas. 1979. A study of the southern oyster drill (*Thais haemastoma*) distribution and density on the oyster seed grounds. Technical Bulletin 30:1–20.

Cook, B. I., R. L. Miller, and R. Seager. 2009. Amplification of the North American “Dust Bowl” drought through human-induced land degradation. Proceedings of the National Academy of Sciences USA 106:4997–5001.

Fabricius, K. E., K. Okaji, and G. De’ath. 2010. Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. Coral Reefs 29:593–605.

Florida Department of Agriculture and Consumer Services. 2012*a*. Oyster Assessment Report. http://www.floridaaquaculture.com/publications/Oyster_Res_Assessment_Report_August_2012.pdf

Florida Department of Agriculture and Consumer Services (FDACS). 2012*b*. Shellfish Harvesting Area Maps. http://www.freshfromflorida.com/Business-Services/Aquaculture/Shellfish-Harvesting-Area-Classification/Shellfish-Harvesting-Area-Maps

Florida Fish and Wildlife Conservation Commission (FFWCC). 2013. 2012–2013 Florida Gulf coast oyster disaster report. http://www.floridajobs.org/docs/default-source/2015-community-development/2015-cmty-plan-acsc/20122013floridagulfcoastoysterdisasterreport.pdf?sfvrsn=2

Florida Department of Environmental Protection's (FDEP) Office of Coastal and Aquatic Managed Areas (CAMA). 2013. Apalachicola national estuarine research reserve management plan. https://www.doi.gov/sites/doi.gov/files/migrated/deepwaterhorizon/adminrecord/upload/Apalachicola-National-Estuarine-Research-Reserve-Management-Plan-undated.pdf

Florida v. Georgia. 2014. Complaint – Florida v. Georgia, No. 142, Original. http://www.pierceatwood.com/floridavgeorgia142original

Galtsoff, P. S. 1964. The American oyster *Crassostrea virginica* Gmelin. Bulletin 64. U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries, United States Government Printing Office, Washington, D.C., USA.

Garland, H. G., and D. L. Kimbro. 2015. Drought increases consumer pressure on oyster reefs in Florida, USA. PLoS ONE 10:e0125095. https://doi.org/10.1371/journal.pone.0125095

Gouhier, T. C., F. Guichard, and A. Gonzalez. 2010. Synchrony and stability of food webs in metacommunities. American Naturalist 175:E16–E34.

Grabowski, J. H., R. D. Brumbaugh, R. F. Conrad, A. G. Keeler, J. J. Opaluch, C. H. Peterson, M. F. Piehler, S. P. Powers, and A. R. Smyth. 2012. Economic valuation of ecosystem services provided by oyster reefs. BioScience 62:900–909.

Hastings, A., and C. Boettiger. 2013. From patterns to predictions. Nature 493:157–158.

Heinze, G., and M. Ploner. 2002. SAS and SPLUS programs to perform Cox regression without convergence problems. Computer Methods and Programs in Biomedicine 67:217–223.

Hoffman, E. E., E. N. Powell, J. M. Klinck, and G. Saunders. 1995. Modeling *Perkinsus marinus* infections in oysters. Journal of Shellfish Research 14:121–151.

Kaul, L. W., and P. N. Froelich Jr. 1984. Modeling estuarine nutrient geochemistry in a simple system. Geochimica et Cosmochimica Acta 48:1417–1433.

Kirby, M. X. 2000. Paleoecological differences between Tertiary and Quaternary *Crassostrea* oysters, as revealed by stable isotope sclerochronology. Palaios 15: 132–141.

Kirby, M. X. 2004. Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. Proceedings of the National Academy of Sciences of the USA 101:13096–13099.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Livingston, R. J., et al. 2000. Modelling oyster population response to variation in freshwater input. Estuarine, Coastal and Shelf Science 50:655–672.

Marella, R. L., and J. L. Fanning. 2011. Water withdrawals, wastewater discharge, and water consumption in the Apalachicola-Chattahoochee-Flint River Basin, 2005, and water-use trends, 1970–2005. U.S. Geological Survey Scientific Investigations Report 2011–5130:1–34.

Menge, B. A., T. C. Gouhier, S. D. Hacker, F. Chan, and K. J. Nielsen. 2015. Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. Ecological Monographs 85: 213–233.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351–369.

Menge, B. A., et al. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences 100:12229–12234.

Menzel, R. W., N. C. Hulings, and R. R. Hathaway. 1966. Oyster abundance in Apalachicola Bay, Florida in relation to biotic associations influenced by salinity and other factors. Gulf and Caribbean Research 2:73–96.

Morey, S. L., D. S. Dukhovskoy, and M. A. Bourassa. 2009. Connectivity of the Apalachicola River flow variability and the physical and bio-optical oceanic properties of the northern West Florida Shelf. Continental Shelf Research 29:1264–1275.

Mortazavi, B., R. L. Iverson, W. R. Huang, F. G. Lewis, and J. M. Caffrey. 2000. Nitrogen budget of Apalachicola Bay, a bar-built estuary in the northeastern Gulf of Mexico. Marine Ecology Progress Series 195:1–14.

Packer, C., R. D. Holt, P. J. Hudson, K. D. Lafferty, and A. P. Dobson. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. Ecology Letters 6:797–802.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Petes, L. E., A. J. Brown, and C. R. Knight. 2012. Impacts of upstream drought and water withdrawals on the health and survival of downstream estuarine oyster populations. Ecology and Evolution 2:1712–1724.

Pollard, J. F. 1973. Experiments to reestablish historical oyster seed grounds and to control the southern oyster drill. Technical Bulletin 6. Louisiana Wildlife and Fisheries Commission, Baton Rouge, Louisiana, USA.

Powell, E. N., J. M. Klinck, E. E. Hofmann, and M. A. McManus. 2003. Influence of water allocation and freshwater inflow on oyster production: a hydrodynamic–oyster population model for Galveston Bay, Texas, USA. Environmental Management 31:100–121.

Putland, J. N., B. Mortazavi, R. L. Iverson, and S. W. Wise. 2013. Phytoplankton biomass and composition in a river-dominated estuary during two summers of contrasting river discharge. Estuaries and Coasts 37:664–679.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18: 648–656.

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319:952–954.

Sheng, Y. P., B. Tutak, J. R. Davis, and V. Paramygin. 2008. Circulation and flushing in the lagoonal system of the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR), Florida. Journal of Coastal Research SI55:9–25.

Sih, A. 1984. Optimal behavior and density-dependent predation. American Naturalist 123:314–326.

Silliman, B. R., M. W. McCoy, C. Angelini, R. D. Holt, J. N. Griffin, and J. van de Koppel. 2013. Consumer fronts, global change, and runaway collapse in ecosystems. Annual Review of Ecology, Evolution, and Systematics 44:503–538.

Trussell, G. C., P. J. Ewanchuk, and C. Matassa. 2006. Habitat effects on the relative importance of trait- and density-mediated indirect interactions. Ecology Letters 9:1245–1252.

Twichell, D. C., B. D. Andrews, H. L. Edmiston, and W. R. Stevenson. 2007. Geophysical mapping of oyster habitats in a shallow estuary, Apalachicola Bay, Florida. Estuarine Coastal and Shelf Science 88:385–394.

Underwood, A. J. 1993. The mechanics of spatially replicated sampling programs to detect environmental impacts in a variable world. Australian Journal of Ecology 18:99–116.

Wilber, D. H. 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. Estuarine, Coastal and Shelf Science 35:179–190.

Zu Ermgassen, P. S. E., et al. 2012. Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. Proceedings of the Royal Society B 279:3393–3400.

Data Availability

Data are available online through Dryad: https://doi.org/10.5061/dryad.796t8