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Jeffrey D. Plumlee
LSU Agricultural Center

Sean P. Powers
University of South Alabama

David L. Kimbro
Northeastern University

John C. Lehrter
University of South Alabama

Jason Herrmann
Marine Resources Division

See next page for additional authors

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Authors
Jeffrey D. Plumlee, Sean P. Powers, David L. Kimbro, John C. Lehrter, Jason Herrmann, and John Mareska

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Original Articles

Increasing duration of heatwaves poses a threat to oyster sustainability in the Gulf of Mexico

Jeffrey D. Plumlee [a,*], Sean P. Powers [b], David L. Kimbro [c], John C. Lehrter [b], Jason Herrmann [d], John Mareska [d]

[a] School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803 USA
[b] Stokes School of Marine and Environmental Sciences, University of South Alabama and the Dauphin Island Sea Lab, Dauphin Island, Alabama 36528 USA
[c] Department of Marine and Environmental Sciences, Marine Science Center, Northeastern University, Nahant, MA 01908, USA
[d] Alabama Department of Conservation and Natural Resources, Marine Resources Division, Dauphin Island, Alabama 36528, USA

ABSTRACT

The future of the wild oyster fishery in the northern Gulf of Mexico is largely uncertain due to changing environmental conditions and declining abundance of harvestable oysters. Specifically, rising temperatures can directly impact the physiological thresholds of the eastern oyster (Crassostrea virginica) at all life history stages and alter the narrow ecological niche this oyster occupies. The impact of rising temperatures is likely most pronounced during atmospheric heatwaves, defined as three or more days above the 90th percentile of daily maximum air temperatures, which have been shown to be increasing in frequency. Increasing exposure to high temperature extremes may contribute to and exacerbate an already declining oyster fishery. Critical to fishery health is recruitment i.e., the addition of new harvestable biomass, which is a dynamic process strongly driven by temperature. Here, we examine the relationship between heatwave characteristics and the prediction of poor oyster recruitment, measured as the abundance of post-larval oysters (e.g. spat) below the site-specific median density observed in historically productive oyster fisheries over 46-years (1976 – 2020) in Mobile Bay, Alabama and 21-years (1993 – 2014) in Apalachicola Bay, Florida. We acquired daily maximum air temperature measurements measured over 50 years (1970 – 2020) at weather monitoring stations adjacent to the bays to identify site specific annual heatwave events (maximum yearly air temperature, yearly and consecutive heatwave days, and number of annual heatwaves). Then, years with extreme heatwaves that exceeded the 75th percentile for the 50-year measurements were compared to years with non-extreme heatwave events. Years with extreme total heatwave days and extreme consecutive heatwave days were correlated with low post-larval oyster density. Across both bay systems, if consecutive heatwave days exceeded 11 days, then poor recruitment of oysters occurred 83 % of the time. Extreme heatwave duration as an indicator for poor recruitment has the potential to be a powerful tool for fishery managers to forecast recruitment and inform sustainable oyster harvest based on year-to-year variability in heatwave duration and long-term warming trends. Our findings illustrate how extreme temperatures can exacerbate multiple physiological and ecological stressors resulting in the loss of a keystone species for healthy and resilient coastal ecosystems.

1. Introduction

Prolonged periods of extreme heat (e.g. heatwaves) have increased in frequency and duration globally over the past 50 years (Perkins-Kirkpatrick and Lewis, 2020). Extreme heatwave events result in an array of economic (Lobell and Field, 2007, Thornton et al., 2009, Kjellstrom, 2016), ecological (Westerling et al., 2006), and cultural (King and Harrington, 2018) consequences that in some cases may be considered as irreversible. The widespread ecological change resulting from heatwaves can be especially impactful for ectothermic sessile invertebrates that are disproportionately associated with coastal marine environments. Marine heatwaves have been widely observed to be increasing in both frequency and duration concurrently with atmospheric heatwaves (Oliver et al., 2018). Widespread loss of marine invertebrate populations (Garrabou et al., 2009, Oliver et al., 2017), alterations to the faunal community due to changes in the native range of individual species (Cavole et al., 2016, Wernberg et al., 2016), food web responses resulting in poor early life history survival (Correia-Martins et al., 2022), and changes to the fishery take and quotas for marine invertebrate fisheries (Caputi et al., 2016) have occurred in response to this increase in extreme heatwaves. The breadth of ecological and economic impact resulting from heatwaves in marine environments provides pressing need for understanding and attempting to forecast their prevalence and preemptively alter management strategies as extreme heatwaves become increasingly more common.

Heatwaves can manifest as a pulse, an acute period of stressful conditions coinciding with an equally acute period of recovery, or as a press disturbance, where stress is extended over a longer period of time

* Corresponding author.
E-mail address: jplumlee@agcenter.lsu.edu (J.D. Plumlee).

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resulting in permanent change or long recovery times (Glasby and Underwood, 1996). Heatwave events may also have both pulse and press components, where periodic survivable pulses of stress can culminate in press-level mortality events due to increases in frequency and/or duration (i.e. protracted pulses) (Sutherland, 1981). While the pulse and press dynamics of a heatwave are defined by duration and magnitude, the underlying temporal dynamics depend on the focal organism due to the vast differences in physiology, motility, and metabolism across taxa. Heatwaves, defined as periods of three or more days of above the 90th percentile maximum daily temperature (Perkins and Alexander, 2013), include both pulse (number of heatwaves and maximum temperature) and press characteristics (sum of days and continuous period of days exceeding heatwave temperatures). For many sessile marine invertebrates, it widely varies among taxa and across life history (i.e. larval vs. adult) how heatwaves act as pulse or press stressors. However, there is clear evidence that for some species, including oysters, increasing heatwave intensity and duration can have substantial negative population-level consequences (Lagarde et al., 2017, Green et al., 2019, Scanes et al., 2020, Raymond et al., 2022). One population-level process that is especially vulnerable to the effects of high heat is recruitment, which for marine invertebrates, is entirely dependent on larval dispersal and survival (Becker et al., 2007). As such, understanding the temporal scale for defining pulse and press stressors for individual organisms is necessary for forecasting population-level consequences of environmental disturbance.

Good recruitment years are inherently difficult to predict because they result when many complex biotic and abiotic processes coincide; however, poor recruitment years can be more easily predicted as they can be caused by a single unfavorable process. The "poor recruitment paradigm" is predicated on the principles that exceptional recruitment is inherently difficult to predict, but it is possible to predict poor recruitment given a specific environmental condition (e.g. extreme conditions) (Gross et al., 2022). Selection of which environmental variables are included for investigation into their value as forecasters of recruitment are often made *a priori* as many of them covary in nature. In estuarine systems heatwaves often covary with drought, freshwater input, and low dissolved oxygen concentrations (Colombano et al., 2022, Tassone et al., 2022). For coastal and estuarine fisheries, managers can benefit from the simplicity of accurate forecastable environmental conditions when setting yearly quotas or attempting to restore low-density fisheries. Complex stock assessment models often used in fishery recruitment forecasting hinge on detailed, and often contextual, understanding of environmental conditions. However, if one environmental condition is known to be unequivocally lethal to fishery recruits, identifying and accurately predicting the lethal threshold would be especially useful to managers looking to make adaptive management decisions.

The northern Gulf of Mexico is the last area of large-scale commercial oyster harvest in the United States (Kirby, 2004, Beck et al., 2011). The Apalachicola Bay oyster fishery alone once represented 10 % of all US oyster landings, with harvests peaking in the early-mid 1980 s (Pine III et al., 2015). Recently, due to declining stocks, the fishery was closed in 2020 through at least 2025. The Mobile Bay oyster fishery has measured harvest records since the late 1800′s (May, 1971) with peaks in the 1950′s at 900 thousand kilograms landed and a peak value in 2021 at 5.2 million dollars. In 2008 through 2010 and 2014 through 2018 the fishery recorded its lowest harvest rates with less than 32 thousand kilograms. The all-time lowest harvest occurring in 2009 at 10 thousand kilograms of oyster meat landed (NOAA Fisheries Marine Landings Statistics, 2022). Fishery-independent surveys have also tracked a similar decline in adult oyster densities in the northern Gulf of Mexico. In Mobile Bay oyster densities declined of 60 % from mean reef densities of 29 oysters per m^2 to 11 oysters per m^2 over a ~ 100 year period (Zu Ermgassen et al., 2012, zu Ermgassen et al., 2016a).

There are many working hypotheses for why the wild oyster harvest in the northern Gulf of Mexico shows such considerable interannual variability leading to near collapse, including hurricanes, drought, and disease (Gregalis et al., 2008, Pine III et al., 2015). Oysters have broad physiological tolerances and can survive in a wide range of environmental conditions (Lowe et al., 2017). However, extreme environmental conditions, e.g. freshets, can be metabolically taxing while remaining within the physiological ranges for adult oyster survival (Pruett et al., 2021). Adapting to these extreme conditions for adult oysters can result in altered growth and reproduction which may have wide-spread population effects such as reduced spawning and fecundity.

Oyster life histories are intrinsically linked to temperature, and thus susceptible to extreme heat. Oysters in the northern Gulf of Mexico grow rapidly compared to other regions throughout their range due to higher temperatures, reaching marketable size (7.62 cm) in 9 to 18 months. Additionally, northern Gulf of Mexico oysters spawn multiple times in a year respective of temperature cues which sets a high ceiling for population productivity (Stanley and Sellers, 1986). In the northern Gulf of Mexico oysters predictably spawn during > 2 °C decreases in water temperature within 24 h (Kim et al., 2010). Not only can temperature alter larval supply through spawning, larval oysters have high rates of mortality and are vulnerable before they settle, often requiring a suite of optimal conditions to settle as recruits (Keough and Downes, 1982, Kingsford et al., 2002, Levin, 2006). Oyster larval recruitment is driven in part by abiotic environmental stressors as well as biotic conditions that covary with temperature such as increased predation and decreased settlement area due to competing colonizing invertebrates (Osman et al., 1989, Lagarde et al., 2018, Lagarde et al., 2019). Yet, extreme heat remains the most logical environmental variable to affect recruitment as larval and juvenile oysters are physiologically vulnerable to water temperatures greater than 30 °C (Roegner and Mann, 1995). As such, prolonged heatwaves may alter oyster early-life mortality and recruitment in several ways including spawning and fecundity as well as post-larval survival and settlement.

The goal of this study was to identify poor recruitment years for oysters in Apalachicola Bay, Florida and Mobile Bay, Alabama and to assess if these years were related to temperature extremes. We investigate this relationship using the "poor recruitment paradigm" postulated in Gross et al., 2022, using extreme heatwave conditions (i.e. greater than the 75th percentile of observations) and fishery-independent measurements of oyster post-larval spat density among six independently managed naturally occurring oyster reefs. In our examination we deconstruct heatwaves into multiple components that represent their pulse and press mechanics, including magnitude, duration, and frequency. We hypothesized that at least one of these heatwave covariates would serve as a reliable predictor of the poor recruitment of oysters.

2. Materials and methods

To investigate the influence of high air temperature on oyster recruitment we examined oyster recruitment that occurred on three naturally occurring oyster reefs in Mobile Bay, Alabama (Buoy Reef, Cedar Point, and Kings Bayou) and Apalachicola Bay, Florida (Dry Bar, Cat Point, and East Hole) (Fig. 1). Reefs were monitored annually by divers from the Alabama Marine Resources Division (AMRD) in Mobile Bay and the Florida Department of Agricultural & Consumer Services (FDACS) in Apalachicola Bay. AMRD collects quadrat samples after deploying a 100-m dive transect on the survey site. Along the transect, divers place a 0.836 m^2 quadrat and collect oysters and reef material down to 2.5 cm. In Apalachicola Bay, samplers place 10 (earlier than 2007) or 15 (2008 and later) 0.25 m^2 quadrats randomly throughout the estimated reef footprint and excavate oysters and reef material to a depth of 17 – 19 cm (Radabaugh et al., 2019). In both systems live oysters are counted and measured (to the nearest mm), including visual identification and counting of post-larval juvenile oysters, hereafter "spat".

For oyster reefs in Mobile Bay monitoring began in 1976 and was conducted annually at randomly selected sites across the three reefs primarily in August and September. In our analysis, we used samples for

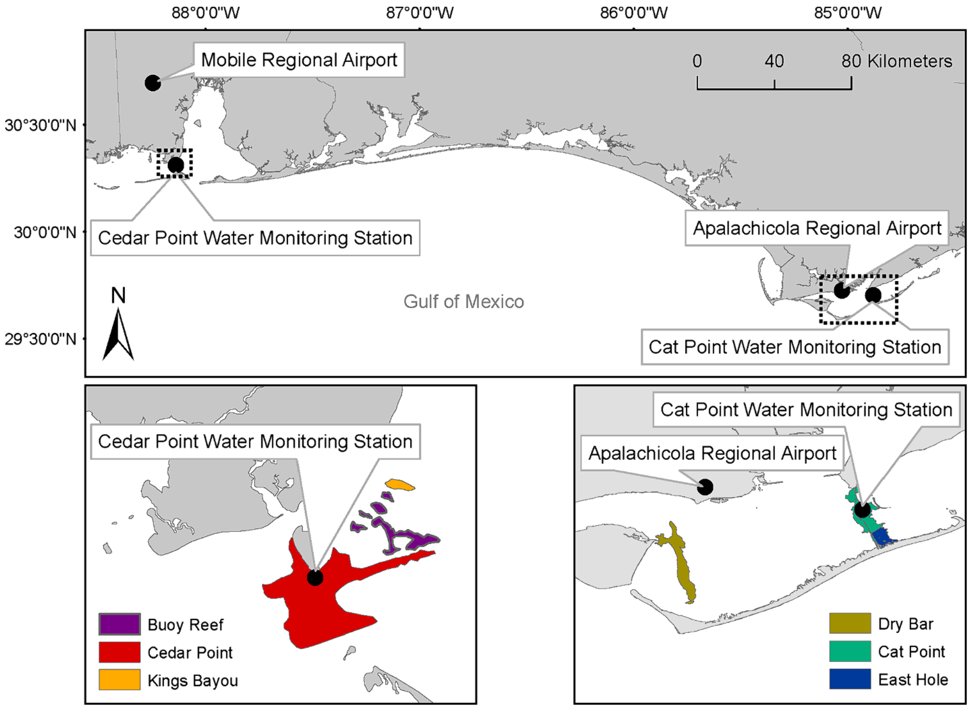

Fig. 1. Map of oyster reef extent in northern Gulf of Mexico, insets are maps of reef extent in Apalachicola Bay, Florida and Mobile Bay, Alabama. Apalachicola Bay has three independently-monitored oyster reefs (Cat Point, Dry Bar, and East Hole). Mobile Bay also has three independently-monitored oyster reefs (Buoy Reef, Cedar Point, and Kings Bayou). Black circle indicates location of the meteorological monitoring areas (Apalachicola Regional Airport and Mobile Regional Airport) where air temperature was measured over the 50 years (1970 – 2020) as well as the hydrographic monitoring stations (Cat Point Monitoring Station and Cedar Point Monitoring Station) where a subset of water temperatures were measured.

Mobile Bay taken during in August and September, coinciding with peak spawning season in Alabama (Yao, 2013), to facilitate comparisons between years and sample locations and reduce confounding seasonal variation resulting in 100 samples of yearly median spat abundance taken across reefs in Mobile Bay (Buoy Reef, n = 33, Cedar Point = 40, Kings Bayou = 27). For reefs in Apalachicola Bay, monitoring began in 1990 and spat were included in the survey starting in 1993 with sampling conducted throughout the year with two samples taken after peak spawning in August and November, which were averaged. Similarly, we constrained the analysis to samples taken in August and November to remove seasonal bias from our interannual comparisons of spat abundance, which resulted in 62 samples of yearly median spat abundance taken across reefs in Apalachicola Bay (Cat Point = 22, Dry Bar = 22, and East Hole = 18). Recruitment (spat per m^2) was calculated independently for each reef and kept independent for analysis within in each bay (Mobile Bay and Apalachicola Bay).

Historic air temperature measurements were taken at the Mobile Regional Airport, in Mobile, Alabama and the Apalachicola Regional Airport in Apalachicola, Florida (Fig. 1). We used air temperature measurements from both locations over the last 50 years from 1970 to 2020 to estimate heatwave characteristics and prevalence across the study period. For this study, heatwaves were defined as three continuous days of air temperatures greater than or equal to 90th percentile of the daily maximum air temperature measured in July and August over the 50 years, which varied between Mobile (33.6 °C) and Apalachicola (33.3 °C). Air temperatures in July and August were selected as benchmarks for the heatwave analysis because they typically contained the highest mean maximum daily temperature in both Mobile (July, 32.8 ± 2.2 °C standard deviation; August 32.6 ± 2.2 °C) and Apalachicola (July, 32.3 ± 2.0 °C standard deviation; August 32.2 ± 2.0 °C). Consequently, heatwaves were defined differently between the two regions. For each bay system we estimated four parameters of heatwaves calculated across the entire year: 1) the maximum observed yearly air temperature (°C), 2) the number of days when maximum air temperature was above the heatwave threshold, 3) the maximum consecutive days where the maximum air temperature was above the heatwave threshold, and 4) the number of heatwaves in a single year.

Concurrent water temperature was also measured at both reefs. In Mobile Bay, water temperature was measured from 2008 to 2020 at an adjacent hydrographic and meteorological monitoring station at Cedar Point belonging to the Alabama Real-Time Coastal Observing System (ARCOS) maintained by Dauphin Island Sea Lab in Dauphin Island, Alabama (Fig. 1). In Apalachicola Bay, water temperature was measured from 2002–2020 at a hydrographic monitoring station at Cat Point maintained by the Apalachicola National Ecological Research Reserve (ANERR) system. Each station monitors air and water temperature (°C), salinity (PSU), and dissolved oxygen (mg/L) along with multiple other environmental parameters in regular 30-minute intervals, with only intermittent downtime over the observation period. Air temperature at each regional airport was correlated to water temperature at each hydrographic monitoring station using a Pearson's Correlation Test in R Version 4.3.0 (R Core Team, 2014).

We also calculated heatwave characteristics (maximum yearly air temperature, days above the heatwave threshold, continuous heatwave days, and annual number of heatwaves) on an annual scale and determined years with "extreme" heatwaves to be at or exceeding the 75th percentile threshold across the 50 years of meteorological weather observations made at each airport respectively. The 75th percentile was selected as a conservative estimate of extremeness, reflecting relative historical rarity of extreme heatwave events in the 50-year dataset but also retaining adequate sample sizes to make inference in the effect of extreme vs. normal heatwaves. We elected to adopt this analytical framework relative to more complex statistical techniques which allow the data to determine extreme thresholds for two reasons – simplicity of use among non-specialist fisheries managers, and avoidance of overfitting the data resulting in statistical type I or type II error. The cut-off for extreme heatwaves varied between Apalachicola Bay and Mobile Bay.

In Apalachicola Bay, the 75th percentile cutoff for the 50-year observations of maximum yearly air temperature was 36.7 °C. The 75th percentile cutoff for days above mean daily maximum for July and August (33.3 °C) in Apalachicola Bay was 43 days and the cutoff for consecutive days was 11 days. Lastly, the 75th percentile cutoff for the number of heatwaves in Apalachicola Bay was five. For Mobile Bay using the same criteria, the 75th percentile cutoff for maximum yearly air temperature was 37.2 °C, days above 33.6 °C was 45, consecutive days were 11, and the number of heatwaves in a year was six.

Patterns of poor oyster recruitment were calculated across two metrics, median spat per m^2 and the proportion of years with poor vs. good recruitment. The proportion of years with poor vs. good recruitment were compared for years with extreme and normal conditions using a Pearson's Chi-squared test for count data. Significance was determined if $p < 0.05$, and all analysis were conducted in R 4.3.1 (R Core Team, 2014). Each of these two oyster recruitment metrics were then compared to annual heatwave metrics maximum annual air temperature, annual days above the heatwave threshold, maximum consecutive days above the heatwave threshold, and the number of heatwaves categorically separated into normal and extreme years.

To estimate the sensitivity of using 75th percentile cutoff for extreme conditions, we also conducted concurrent analysis using cutoffs at 66th percentile and 85th percentile recalculated for each heatwave component (maximum temperature, days above heatwave threshold, consecutive days above the heatwave threshold, and annual number of heatwaves). The 66th percentile cutoffs for extreme heatwave conditions in Apalachicola were 36.7 °C maximum yearly air temperature, 35 days above 33.3 °C, 9 consecutive days above 33.3 °C, and four heatwaves in a year. The 85th percentile cutoffs for extreme heatwave conditions in Apalachicola were 37.2 °C maximum yearly air temperature, 65 days above 33.3 °C, 20 consecutive days above 33.3 °C, and eight heatwaves in a year. For Mobile Bay, the 66th percentile cutoffs were 37.2 °C maximum yearly air temperature, 38 days above 33.6 °C, 9 consecutive days above 33.6 °C, and five heatwaves in a year. The 85th percentile cutoffs for extreme heatwave conditions in Mobile Bay were 38.3 °C maximum yearly air temperature, 55 days above 33.6 °C, 18 consecutive days above 33.6 °C, and eight heatwaves a year.

3. Results

In both bay systems, air temperatures measured at the airports were strongly correlated with water temperature measured in the bays adjacent to the oyster reefs over the subset of years the data were available (Apalachicola 2002 – 2020; Mobile Bay 2008 – 2020). Meteorological maximum daily air temperature measured at the Mobile Regional Airport (MRA) and the Apalachicola Regional Airport (ARA) were strongly correlated with water temperature measured at the Cat Point (Apalachicola Bay, $r^2 = 0.86$; $t_{2,6064} = 197.7$, $p < 0.001$) and Cedar Point (Mobile Bay, $r^2 = 0.82$; $t_{2,4495} = 144.0$, $p < 0.001$) hydrographic stations, respectively. A majority (88 %) of the time that the daily maximum air temperature at ARA was ≥ 33.3 °C from 2002 to 2020, the water temperature at Cedar Point was ≥ 30 °C. Similarly, at MRA, 91 % of the time the daily maximum air temperature was > 33.6 °C from 2008 to 2020, the daily maximum water temperature was ≥ 30 °C (Fig. 2). While these statistical correlations show a very close relationship between air and water temperature, they are not perfect and should be monitored in tandem prior to making management decisions. Heatwave components showed similarities between the two regions. In Apalachicola Bay, years with extreme days above the heatwave threshold (43 days or more above 33.3 °C) were the same years that there were extreme long-duration heatwaves (11 consecutive days or more above 33.3 °C). All other combinations of variables showed lower correlations between extreme and normal years ($r^2 \leq 0.41$). Similarly, in Mobile Bay 2/3rd of the extreme years with days above the heatwave threshold (57 days or more above 33.6 °C) also had extreme consecutive days above the heatwave threshold (11 consecutive days or more above 33.6 °C),

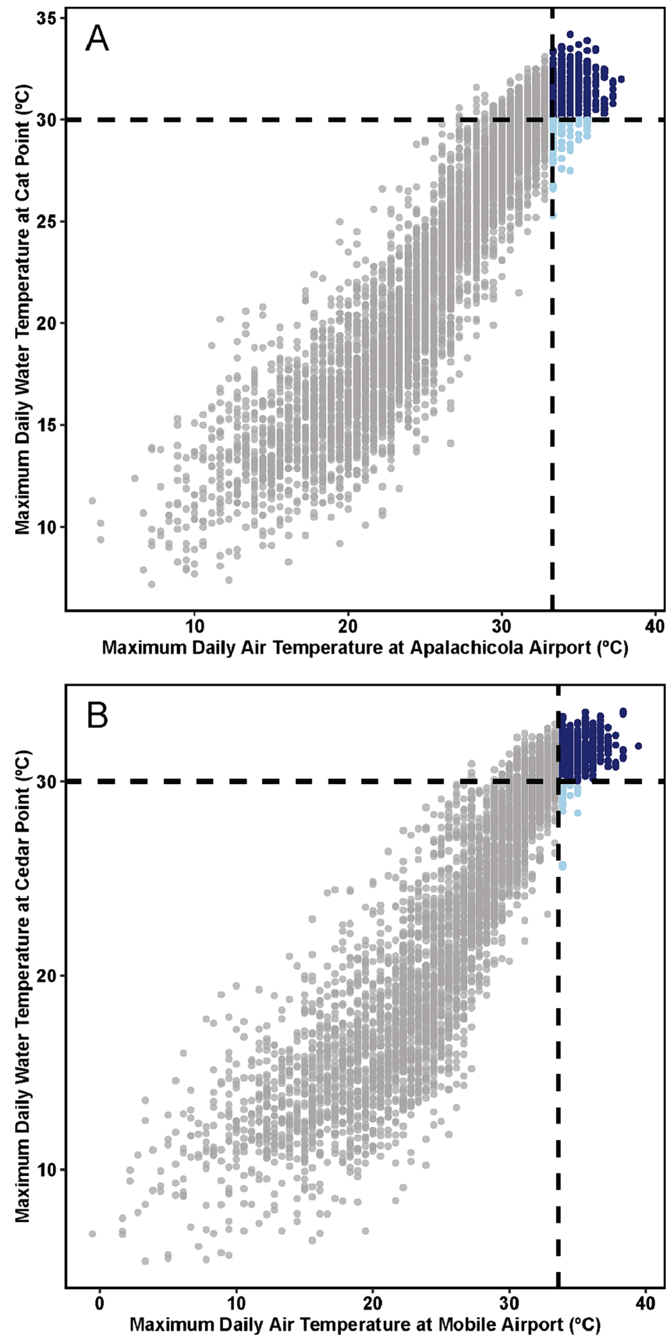

Fig. 2. Scatterplot of daily maximum air temperature (C°) measured at the Apalachicola Regional Airport (A) and the Mobile Regional Airport (B) and the daily maximum water temperature measured at the Cat Point Monitoring Station (A) from 2002 – 2020 and the Cedar Point Monitoring station (B) from 2008 to 202. Grey points indicate daily maximum air temperature (Apalachicola Bay < 33.3C° and Mobile Bay < 33.6C°) and daily maximum water temperature < 30.0C°, respectively. Light blue points indicate daily maximum air temperatures measured at the Apalachicola Regional Airport ≥ 33.3C° and Mobile Regional Airport ≥ 33.6C° and daily maximum water temperatures measured < 30.0C°. Dark blue points indicate the same conditions only where daily maximum water temperature was ≥ 30.0C°.

with all other variables having lower correlations between extreme and normal years ($r^2 \leq 0.49$).

Annual measurement of the density of spat (per m^2) differed among sites and among bay systems. In Apalachicola Bay the highest spat density was at East Hole (117.3 median spat per m^2 ± 103.8 standard deviation), followed by Dry Bar (98.0 ± 256.4), and lastly Cat Point

(85.4 ± 81.5). In Mobile Bay, the highest spat density was on Cedar Point (7.8 ± 17.6), followed by Buoy Reef (6.9 ± 35.9), and the lowest spat density at Kings Bayou (5.1 ± 10.6) (Table 1).

Across the two bay systems, maximum yearly air temperature, and number of individual heatwaves had little forecasting power for the below-median recruitment of oysters. The proportion of poor-recruitment years with annual maximum air temperature exceeding extreme thresholds (Apalachicola, 36.7 °C; Mobile, 37.2 °C) was statistically indistinguishable from proportion of poor-recruitment years with annual maximum air temperature less than or equal to the 75th percentile for all reefs (All Reefs; $p > 0.05$). Poor recruitment in the months of August and September in Mobile Bay was not correlated with 57 or more annual heatwave days above 33.6 °C at any of the three reefs, Buoy Reef (p-value = 0.89, $\chi^2 = 0.02$), Cedar Point (p-value = 0.66, $\chi^2 = 0.20$), Kings Bayou (p-value = 0.35, $\chi^2 = 0.89$), or all reefs combined (p-value = 0.49 $\chi^2 = 0.43$). The number of designated heatwaves was not a good predictor of oyster recruitment across either bay system aside for two reefs in Mobile Bay, Buoy Reef, and Kings Bayou. For Buoy Reef (normal median, 3.5 ± 10.9 spat/m^2; extreme median, 8.8 ± 8.1 spat/m^2; p-value = 0.24, $\chi^2 = 1.35$), 20 % of years with greater than 6 heatwaves had poor oyster recruitment, and for Kings Bayou (normal median, 6.0 ± 41.6 spat/m^2; extreme median, 15.9 ± 7 spat/m^2; p-value = 0.12, $\chi^2 = 2.34$), 25 % of years with greater than 6 heatwaves had poor oyster recruitment. For Cedar Point (normal median, 11.6 ± 16.2 spat/m2; extreme median, 13.7 ± 30.0 spat/m^2; p-value = 0.68, χ2 = 0.17), 42 % of years with years with greater than 6 heatwaves also had poor recruitment of oysters. Across all Mobile Bay reefs combined (normal median, 11.6 ± 16.2 spat/m2; extreme median, 13.7 ± 30.0 spat/m^2; p-value = 0.68, χ2 = 0.17), it appears that the greater than 6 heatwaves in a given year is a predictor of above median recruitment (Table 3). For all reefs in Apalachicola, years with greater than 5 heatwaves was a non-significant predictor ($p > 0.05$).

In Apalachicola Bay the number of days above the heatwave threshold was a significant predictor of poor recruitment; however, this relationship was not shared with any of the Mobile Bay oyster reefs. At Cat Point (normal median, 96.0 ± 80.8 spat/m^2; extreme median, 22.4 ± 13.2 spat/m^2; p-value = 0.06, $\chi^2 = 3.47$) and at East Hole (normal median, 144.8 ± 270.6 spat/m^2; extreme median, 19.2 ± 16.5 spat/m^2; p-value = 0.06, $\chi^2 = 3.60$) 100 % of the years with 43 days above 33.3 °C had poor oyster recruitment. For the remaining oyster reef in Apalachicola Bay, Dry Bar (normal median, 129.6 ± 101.1 spat/m^2; extreme median, 38.8 ± 142.1 spat/m^2; p-value = 0.53, $\chi^2 = 0.39$) had poor recruitment of oysters 66 % of years with 43 or more days above 33.3 °C. For all reefs combined in Apalachicola Bay (normal median, 123.2 ± 165.9 spat/m^2; extreme median, 22.4 ± 83.6 spat/m^2; p-value = 0.01, $\chi^2 = 6.37$), 89 % of observations of spat density in extreme years were below the median spat density (Table 2, Fig. 3).

The most accurate predictor for the poor recruitment of oysters was the maximum number of consecutive days in a year above the heatwave threshold (Apalachicola = 33.3 °C; Mobile = 33.6 °C). For Apalachicola reefs, Cat Point (normal median, 96.0 ± 80.8 spat/m^2; extreme median, 22.4 ± 13.2 spat/m^2; p-value = 0.06, $\chi^2 = 3.47$) and East Hole (normal median, 144.8 ± 270.6 spat/m^2; extreme median, 19.2 ± 16.5 spat/m^2; p-value = 0.06, $\chi^2 = 3.60$), there was 100 % poor recruitment for years when the maximum consecutive days at or above 33.3 °C exceeded 11 days. The remaining reef in Apalachicola, Dry Bar (normal median, 129.6 ± 101.13 spat/m^2; extreme median, 38.8 ± 142.1 spat/m^2; p-value = 0.53, $\chi^2 = 0.39$), had 66 % of years with poor recruitment when the maximum consecutive days at or above 33.3 °C exceeded 11 days. Apalachicola Bay with all reefs included in the same model (normal median, 123.2 ± 165.9 spat/m^2; extreme median, 22.4 ± 83.6 spat/m^2; p-value = 0.01, $\chi^2 = 6.37$) had poor recruitment in 88.9 % of observations during extreme conditions (Table 2, Fig. 4).

In Mobile Bay, Buoy Reef (normal median, 17.3 ± 42.0 spat/m^2; extreme median, 0.7 ± 2.9 spat/m^2; p-value < 0.01, $\chi^2 = 8.36$) and Kings Bayou (normal median, 5.8 ± 10.8 spat/m^2; extreme median, 0.7 ± 2.0 spat/m^2; p-value = 0.04, $\chi^2 = 4.36$), 100 % of the years with greater than 11 consecutive days above 33.6 °C had below-median recruitment of spat. For Cedar Point (normal median, 18.2 ± 19.6 spat/m^2; extreme median, 6.9 ± 18.7 spat/m^2; p-value = 0.26, $\chi^2 = 1.29$), 66 % of years where there was greater than 11 consecutive days above 33.6 °C had below-median recruitment of spat. For all reefs in Mobile Bay combined (normal median, 11.4 ± 27.9 spat/m^2; extreme median, 3.8 ± 13.5 spat/m^2; p-value < 0.01, $\chi^2 = 9.00$), there was an 80 % likelihood that if there were 11 consecutive days above 33.6 °C, there would also be below median recruitment of oysters (Table 3, Fig. 5).

Combining all oyster reefs into one analysis resulted in only one predictor being a significant indicator of poor recruitment, and that was consecutive days above the heatwave threshold. Combining all reefs and using regional specific definitions of consecutive heatwave days (Apalachicola, greater than 11 consecutive days above 33.3 °C; Mobile, greater than 11 consecutive days above 33.6 °C) and reef specific definitions of poor recruitment (median spat/m^2), we noted that 24 of 29 (83 %) observations made in the years where extreme consecutive day heatwaves occurred poor recruitment was observed in both bays, while 43 % of observations made in years with normal heatwave conditions were poor by our definition.

A sensitivity analysis of the sensitivity of the extreme condition cutoff set at the 66th percentile threshold had overall lower rates of prediction than analysis set at the 75th percentile threshold (average change in prediction −2 ± 17 % standard deviation). The greatest change in prediction of oyster recruitment in extreme versus normal conditions at the 66th percentile threshold in Mobile Bay occurred using the number of heatwaves each year where prediction changed 21 % (Mobile Bay average prediction [75th percentile] = 29 %; Mobile Bay average prediction [66th percentile] = 50 %). In Apalachicola Bay the greatest change in prediction moving the threshold from the 75th percentile to the 66th percentile occurred for the number of days above 33 °C where prediction changed on average across all three reefs by –23.9 % (Apalachicola Bay average prediction [75th percentile] = 65 %; Apalachicola Bay average prediction [66th percentile] = 89 %) (Table A1). Increasing the threshold from the 75th percentile to the 85th percentile improved prediction (average change in prediction 11 ± 18 %). The greatest change in prediction moving from a 75th percentile to an 85th percentile threshold in Mobile Bay occurred for maximum

Table 1
Number of quadrats measured during yearly dive surveys conducted by Apalachicola National Estuarine Research Reserve in Apalachicola Bay, Florida from 1993 to 2014 and Alabama Marine Resources Division from 1976 to 2021 in Mobile Bay. Dive sampling occurred in August and September for three reefs in Mobile Bay (Buoy Reef, Cedar Point, and Kings Bayou) and from August and November in Apalachicola Bay (Cat Point, Dry Bar, and East Hole) for each year of sampling.

Area Name	n	Years	Yearly mean 0.9 m quadrat samples (±SD)	Total 0.9 m quadrat samples	Median yearly spat per m^2 (±SD)
Apalachicola Bay	**62**	1993 – 2014	58.9 ± 16.3	1295	133.4 ± 158.6
Cat Point	22	1993 – 2014	28.0 ± 9.1	615	96.6 ± 81.5
Dry Bar	22	1993 – 2014	20.0 ± 7.7	440	128.4 ± 103.8
East Hole	18	1993 – 2014	13.3 ± 4.4	240	184.5 ± 256.4
Mobile Bay	**100**	1976 – 2020	128.9 ± 57.9	5544	6.9 ± 22.2
Buoy Reef	33	1977 – 2017	29.7 ± 10.5	1216	6.9 ± 35.9
Cedar Point	40	1976 – 2020	29.3 ± 13.6	3689	7.8 ± 17.6
Kings Bayou	27	1979 – 2017	22.0 ± 8.6	639	5.1 ± 10.6

Table 2
Results from the poor recruitment analysis indicating the predictive power of each component of heatwaves in extreme (>75th percentile) conditions and their proportional correlation to poor recruitment for Apalachicola Bay. **Bolded** percentages indicate significant (χ^2 p-value > 0.05) predictors of poor recruitment.

Reef Name	Maximum Yearly Air Temperature (°C)		Days above 33.3 °C		Maximum consecutive days above 33.3 °C		Heatwaves (≥5 Days above 33.3 °C)	
	Below 36.7 °C	Above 36.7 °C	Below 43 Days	Above 43 Days	Below 11 Days	Above 11 Days	Below 5 Heatwaves	Above 5 Heatwaves
Cat Point	63.6	36.4	42.1	100	42.1	100	47.4	66.7
Dry Bar	63.6	36.4	40.0	66.7	47.3	66.6	52.6	33.3
East Hole	55.6	44.4	40.0	100	40.0	100	53.3	33.3
All Reefs	61.3	38.7	43.4	**88.9**	43.4	**88.9**	44.4	50.9

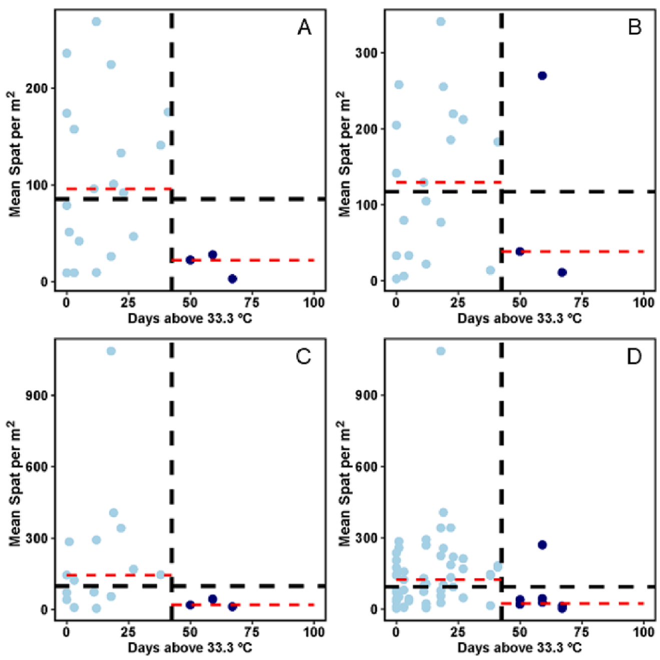

Fig. 3. Recruitment scatterplots comparing spat density (median spat per m^2) in Apalachicola Bay to the annual number of heatwave (daily maximum ≥ 33.3C°) days for Cat Point (A), Dry Bar (B), East Hole (C), and all reefs combined (D). Dashed horizontal black line indicates the median of the mean spat densities, dashed vertical black lines indicate the extreme cutoff (≥43 annual heatwave days). The red dashed line to the left of the vertical black line is median of the mean spat densities in "normal" conditions, and the red dashed line to the right of the vertical black line are median of the mean spat densities in "extreme" conditions.

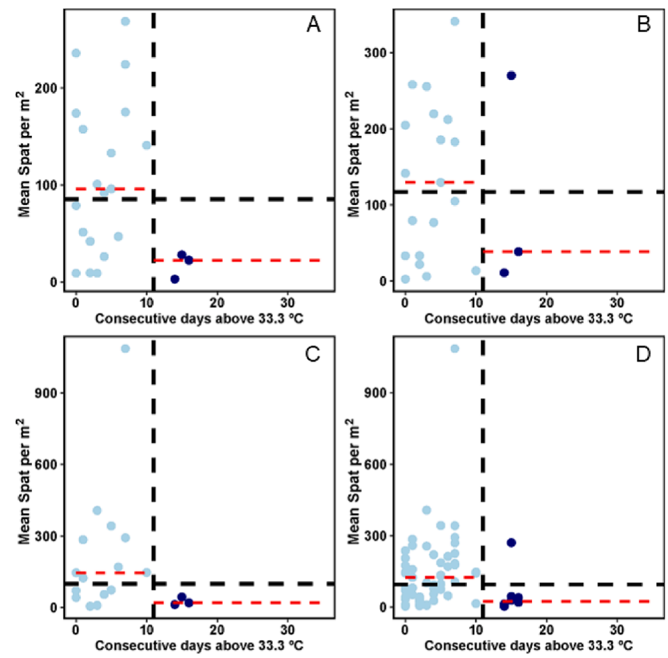

Fig. 4. Recruitment scatterplots comparing spat density (median spat per m^2) in Apalachicola Bay to the annual maximum consecutive heatwave (daily maximum ≥ 33.3C°) days at Cat Point (A), Dry Bar (B), East Hole (C), and all reefs combined (D). Dashed horizontal black line indicates the median of the mean spat densities, dashed vertical black lines indicate the extreme cutoff (>11 consecutive heatwave days). Red dashed lines to the left of the vertical black line is the median of the mean spat densities in "normal" conditions, and red dashed lines to the right of the vertical black line are median of the mean spat densities in "extreme" conditions.

yearly air temperature, where prediction of poor spat recruitment in extreme years increased by 42 % (Mobile Bay average prediction [75th percentile] = 45 %; Mobile Bay average prediction [85th percentile] = 87 %). However, there was little change using a different threshold for Apalachicola, with the largest change being again for maximum yearly air temperature moving from a 75th percentile to an 85th percentile threshold, changing on average 9 % (Apalachicola Bay average prediction [75th percentile] = 39 %; Mobile Bay average prediction [85th percentile] = 48 %) (Table A2). At a cost from improving prediction across the two bays, increasing the threshold to the 85th percentile from the 75th percentile decreased the overall sample size of years where extreme conditions were observed in the 50-year dataset by ~ 40 % across all heatwave characteristics (Apalachicola Bay, Δ N = -38 % ± 7 %; Mobile Bay, Δ N = -47 % ± 8), which makes the predictive power using these thresholds substantially lower.

4. Discussion

There is a clear and apparent link between anomalous warm temperature and the poor recruitment of oysters in the northern Gulf of Mexico. According to our analysis across six independently managed naturally-occurring oyster reefs in two bay systems, if the maximum continuous duration of a heatwave exceeds 11 days in a given year, then the poor recruitment of oysters is predicted 83 % of the time (80 % of the time in Mobile Bay and 88.9 % of the time in Apalachicola Bay). Alternatively, annual days above the heatwave threshold was also a reliable predictor for poor recruitment; however, only at reefs in Apalachicola Bay (42.5 days above 33.3 °C, 88.9 % poor recruitment). According to the "poor recruitment" analysis, no other component of heatwave was a reliable indicator of recruitment. Heatwaves are a natural phenomenon, and coastal organisms (including oysters) have developed refuge strategies to mitigate their effects. However, as the components of heatwaves increase to a threshold of high magnitude and long duration, these refuge strategies become less and less effective resulting in unmanageable stress, and in some cases, mortality (Buckley and Huey, 2016). These results suggest that heatwave duration may have a strong correlative link to spat settlement and oyster recruitment when approaching an extreme threshold, and that heatwave duration may serve as a reliable recruitment indicator allowing for adaptive management strategies.

Table 3
Results from the poor recruitment analysis indicating the predictive power of each component of heatwaves in extreme (>75th percentile) conditions and their proportional correlation to poor recruitment for Mobile Bay. **Bolded** percentages indicate significant (χ^2 p-value > 0.05) predictors of poor recruitment.

Reef Name	Maximum Yearly Air Temperature (°C)		Days above 33.6 °C		Maximum consecutive days above 33.6 °C		Heatwaves (≥5 Days above 33.6 °C)	
	Below 37.2 °C	Above 37.2 °C	Below 45 Days	Above 45 Days	Below 11 Days	Above 11 Days	Below 6 Heatwaves	Above 6 Heatwaves
Buoy Reef	47.6	58.3	48.0	62.5	38.5	**100**	57.1	20.0
Cedar Point	56.0	40.0	50.0	50.0	45.2	66.6	51.5	42.8
Kings Bayou	62.5	36.4	50.0	57.1	43.5	**100**	56.5	25.0
All Reefs	51.6	47.3	52	49.3	42.5	**80.0**	54.8	25.0

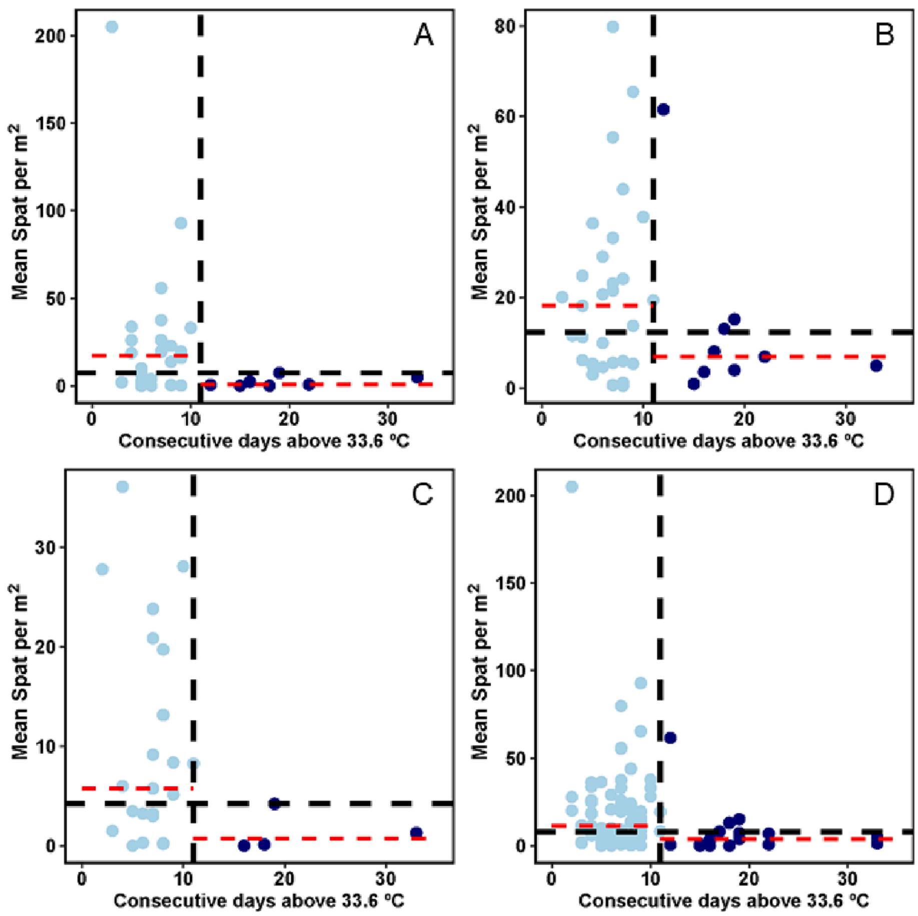

Fig. 5. Recruitment scatterplots comparing spat density (median spat per m^2) to the annual maximum consecutive heatwave (daily maximum ≥ 33.6C°) days at Buoy Reef (A), Cedar Point (B), Kings Bayou (C), and all reefs combined (D). Dashed horizontal black line indicates the median of the mean spat densities, dashed vertical black lines indicate the extreme cutoff (>11 consecutive heatwave days). Red dashed lines to the left of the vertical black line is the median of the mean spat densities in "normal" conditions, and red dashed lines to the right of the vertical black line are median of the mean spat densities in "extreme" conditions.

Key to adaptive fisheries management is understanding the primary uncertainties involved with managing a stochastic ecological system (Bakun et al., 2010). The population dynamics of oysters are largely recognized as being non-linear with rapid population-level regime shifts attributable to recruitment substrate, variable natural mortality, and harvest (Powell et al., 2009). These highly variable year to year changes in population size can result in over-exploitation if constant harvest is maintained, especially in years of low abundance. Proactive management to reduce harvest based on informed relationships between biological production and observable (and predictable) environmental covariates, may be a suitable alternative to reactive closures and loss of harvest. This is especially true considering post-larval early life history settlement (i.e. spat abundance) has been shown to be a key indicator in determining harvestable oyster density (Hemeon et al., 2020) Adopting adaptive management practices for oysters based on estimating and predicting spat density may be as beneficial for wild oyster fisheries than measuring spawning stock biomass, as it is the current standing management protocol. Given the high correlation between spat abundance and long duration heatwaves, adaptively monitoring spat abundance following heatwave events may optimize management strategies to protect affected oyster reefs vulnerable to poor recruitment. Even with the increased risk of poor recruitment following extreme long-duration heatwaves, a chance still exists for non-heatwave associated recruitment failure to occur – requiring proactive fishery monitoring.

Mechanistically, there are many potential co-occurring stressors with long duration heatwaves that could be the underlying cause of below median recruitment; however, heatwaves appear to be a common link. For organisms with short lifespans, or vulnerable developmental phases, stressors that are short pulses in duration may result in long term press population dynamic shifts if concurrent physiological stress is high

(Lake, 2000). Adult oysters are physiologically adaptable to short pulse dynamics e.g. desiccation, low salinity waves, and hypoxic events (Levinton et al., 2011, Patterson et al., 2014, Baillie and Grabowski, 2019). However, persistent stressful environmental conditions may act as unmanageable stressors resulting in increased mortality (Lenihan et al., 1999), which could have lingering population-level effects resembling the consequences of press stressors (Richard et al., 2022). This is especially true for pre-settlement oyster larvae, which is a vulnerable life history stage, and where large-scale mortality events due to unfavorable environmental conditions can determine year-class success and fishery yield.

Increased water temperature resulting from atmospheric heatwaves is often not a stand-alone condition and is correlated with other detrimental changes to the local environment, such as drought and changing salinity (Russo et al., 2019) and increasing prevalence of hypoxia which results in physio-metabolic changes (Ivanina et al., 2013, Matoo et al., 2013, Tassone et al., 2022). For oyster larvae, increased metabolism and growth rates during heatwave conditions increases oxygen demand resulting in a vulnerability to low levels of dissolved oxygen (Davis and Calabrese, 1964, Widdows et al., 1989). However, if these conditions occur over a short period of time, relative to the larval duration of oysters, oyster larvae can be resilient and this resiliency persists throughout their ontogeny (McFarland et al., 2022). Oyster larvae in the northern Gulf of Mexico have a larval duration during the summer months of approximately 10 – 12 days; observed during spawning events from late May to early September in Mobile Bay (Kim et al., 2010). If oysters were spawned at the beginning of an extreme continuous heatwave (>11 continuous days) the heatwave would encompass their entire larval duration, shifting from a manageable pulse event to a high-mortality press event. For ectothermic, sessile young oysters, the pulse aspects of heatwaves within their physiological range can be potentially mitigated through changes in their metabolism (Ivanina et al., 2013), but long-term press exposure carry a high level of lethality.

Wild oyster populations are in decline, with some estimates up to 85 % declines for wild oyster reefs globally (Beck et al., 2011). In the northern Gulf of Mexico, considered to be one of the last bastions of wild oyster harvest, oyster reefs have undergone relative abundance declines of up to 60 % (zu Ermgassen et al., 2016a). The persistence of wild oyster populations does not exclusively benefit the oyster fishery itself; oysters serve as critical estuarine habitat for enhancing juvenile fish and macroinvertebrate populations in estuaries (Zu Ermgassen et al., 2016b). In response to historic loss of oyster reef, fishery production, and ecosystem services; ecosystem managers use restoration to recover and limit loss of natural habitat (Zu Ermgassen et al., 2020). Reproductive success through larval supply and recruitment is essential to sustained wild oyster populations, and theoretically, to restoration of degraded oyster reef habitat. Examination of the Olympia oyster (*Ostrea lurida*) in Coos Bay, Oregon showed that both high larval supply and high oyster recruitment were correlated with abundant adult oyster populations, and conversely low larval supply or low recruitment were correlated with fewer adult oysters (Pritchard et al., 2016). Oyster larvae are the only mechanism linking small subpopulations to a networked metapopulation as oysters are sessile and dispersal only happens prior to settlement (Theuerkauf et al., 2021). As oyster populations shrink, and the capacity for outsourced larval supply diminishes within a greater network of oyster reefs, the inherent resiliency of the metapopulation degrades. Predicting recruitment along with managing and monitoring larval supply (Kim et al., 2013) may also be an effective mechanism to facilitating restoration and promoting sustained wild harvest. If continuous heatwave duration indeed is a reliable predictor of recruitment success for oysters due to its effect on early life history viability, monitoring heatwaves may be a powerful tool in determining the time or place restoration occurs to maximize success and maintain the larger interconnected metapopulation.

Only extreme heatwave duration appeared to be a significant predictor of poor recruitment years for oysters in our analysis, which indicates that long heatwaves may result in a negative physiological or ecological response for larval and newly recruited oysters. However, total number of heatwave days, was not a particularly powerful predictor while number of consecutive heatwave days were, potentially due to the typical conditions that result in an unbroken duration of extremely hot days. The mechanisms behind the relationship between years with oyster recruitment and long-duration heatwaves are not immediately clear and may be the result of direct effects (e.g., physio-metabolic responses to prolonged heat) or multiple indirect effects (i.e., lack of spawning activity for adults, vulnerability to predators, increased competition on recruitment habitat) (Fig. 6). Long-duration heatwaves as predictors of poor-recruitment years are especially valuable for oyster fishery managers as harvest is often set on annual estimates. Data for heatwave days and continuous heatwave duration are collected in real-time and can be used to guide management decisions when extreme thresholds are crossed within a given year and where quotas can be implemented. Considering the need for accessible and forecastable data to make fishery decisions, it is worth testing whether a similar temperature-threshold framework can be used to adaptively manage other fisheries.

Indirect effects are difficult to quantify as they are often the result of multiple interactions mediated through an intermediate species or abiotic components of an ecosystem (Bishop and Peterson, 2006). Oysters exposed to a gradient of increasing intertidal exposure indirectly resulted in less shell fouling, and fewer predators as oysters were exposed out of the water for longer periods of time (Bishop and Peterson, 2006). Conversely, in our study, as oysters may increase their exposure to extreme high temperatures, they may indirectly become more vulnerable to predation and competition. For example, a shift in post-marine heatwave algal communities resulted in fewer available trophic resources for post-larval Pacific oysters (*Crassostrea gigas*), and consequently lower oyster recruitment (Correia-Martins et al., 2022). Recruitment for oysters is also a direct effect of larval supply although the relationship between larval density and recruitment for shellfish is not exclusively limiting (Fraschetti et al., 2002). As temperatures reach extremes and remain high for prolonged periods, oyster spawning may decrease which reduces larval supply and recruitment (Kim et al., 2010). It is clear that these indirect stressors on post-larval oysters may compound when they are already physiologically or metabolically

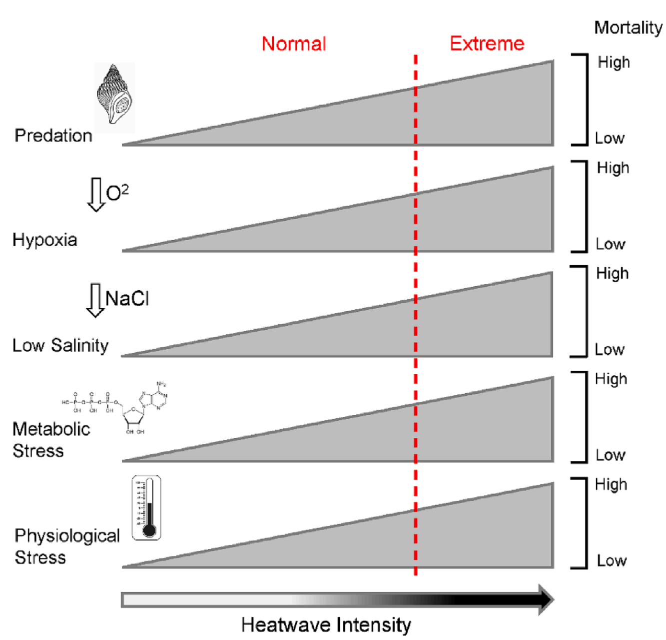

Fig. 6. Diagram illustrating the relationship between heatwaves and multiple sources of mortality (predation, hypoxia, salinity, metabolic and physiological stressors).

compromised (Donelan et al., 2021). The measurement of consecutive heatwave days serves as an indicator of poor recruitment, but does not fully describe the mechanisms therein, whether they are direct or indirect. In the context of this study, long-duration heatwaves may serve best as an indicator of poor recruitment; however, the root mechanisms driving oyster population health are complex and contextual requiring further investigation.

This work provides a potentially powerful tool for fishery managers of wild oyster harvest and oyster reef restoration in the northern Gulf of Mexico. Heatwaves in the northern hemisphere are forecast to become both more frequent and longer in duration than they have been since commercial oyster harvest has existed (Perkins-Kirkpatrick and Lewis, 2020). Studies on oyster restoration strategies call for the implementation of refugia from untenable environmental conditions as a part of reef building (Baillie and Grabowski, 2019); however, for wild oysters that are within their historic ranges and on unrestored native habitat, adaptive management may provide thermally stressed oyster populations reprieve from exploitation. Oysters have a wide physiological niche, but their ecological niche may be narrow as they are limited in distribution by a wide variety of factors that often co-occur (Powers et al., 2017). Future work still needs to be done elucidating the mechanisms that result in the poor recruitment of oysters during and post long-duration heatwaves. Reasonable hypotheses exist on how extreme heat may increase the mortality of spat caused by predation, stratified hypoxic water, metabolic and physiological stress that need to be tested. In the context of management tools, it appears that forecasting and observing long-duration heatwaves have a clear correlation to the poor recruitment of oysters and should be considered in adaptive management decisions.

CRediT authorship contribution statement

Jeffrey D. Plumlee: Writing – original draft, Visualization, Formal analysis, Conceptualization. **Sean P. Powers:** Writing – review & editing, Funding acquisition, Conceptualization. **David L. Kimbro:** Writing – review & editing, Data curation. **John C. Lehrter:** Writing – review & editing, Funding acquisition. **Jason Herrmann:** Writing – review & editing, Data curation. **John Mareska:** Writing – review & editing, Data curation.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix

Table A1
Change in results from poor recruitment prediction for reefs in Apalachicola and Mobile Bay by reducing threshold from the 75th percentile to the 66th percentile.

Bay	Reef	Maximum Yearly Air Temperature (°C)		Days Above Heatwave Threshold		Maximum Consecutive Days Above Heatwave Threshold		Yearly Heatwaves	
		66th	Δ%	66th	Δ%	66th	Δ%	66th	Δ%
Apalachicola Bay	Cat Point	36.7	1.6	35	−40	9	−25	4	8.3
	Dry Bar	36.7	1.6	35	−6.7	9	8.4	4	16.7
	East Hole	36.7	22.6	35	−25	9	−25	4	16.7
Mobile Bay	Buoy Reef	37.2	−0.3	38	−6.5	9	−12	5	30
	Cedar Point	37.2	0	38	0	9	−11.6	5	15.2
	Kings Bayou	37.2	−0.4	38	−0.1	9	−34	5	18

Table A2
Change in results from poor recruitment prediction for reefs in Apalachicola and Mobile Bay by increasing the threshold from the 75th percentile to the 85th percentile.

Bay	Reef	Maximum Yearly Air Temperature (°C)		Days Above Heatwave Threshold		Maximum Consecutive Days Above Heatwave Threshold		Yearly Heatwaves	
		85th	Δ%	85th	Δ%	85th	Δ%	85th	Δ%
Apalachicola Bay	Cat Point	37.2	1.6	53	0	14	0	6	−16.7
	Dry Bar	37.2	1.6	53	−16.7	14	−16.6	6	16.7
	East Hole	37.2	22.6	53	0	14	0	6	16.7
Mobile Bay	Buoy Reef	37.8	41.7	50	12.5	16	0	7	33
	Cedar Point	37.8	20	50	30	16	−0.6	7	17.2
	Kings Bayou	37.8	63.6	50	17.9	16	0	7	29

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