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VARIATION IN BIVALVE LARVAL DENSITY AND SETTLEMENT OF THE EASTERN OYSTER (*CRASSOSTREA VIRGINICA*, GMELIN 1791) IN A MODIFIED ESTUARY

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ABSTRACT Estuaries globally are changing due to rapid land use transformation, degrading water quality, human activity, and climate change. Oyster reefs are common and important habitats in estuarine systems across North America, providing numerous services that contribute to the health of these ecosystems. Yet, a paucity of oyster reef habitat data exists, particularly in estuaries with limited or no commercial harvest. Even less information is available on oyster larval supply, patterns of recruitment, and their impact on oyster population resilience. Bivalve larval distributions and patterns of oyster settlement were monitored at sites across the lower Charlotte Harbor Estuary, FL, from 2020 to 2023 to better understand drivers of oyster reef decline, as well as the implications of early life stage distributions on future restoration efforts. In this study, both bivalve larval density and oyster settlement varied by year and across regions within the estuary. Densities of bivalve larvae and spat increased with distance from the mouth of the Caloosahatchee River, where high densities of living oyster habitat are found. Bivalve larval abundance was strongly correlated with temperature and food availability, but surprisingly not salinity. Oyster settlement showed a positive correlation with temperature and a slight negative correlation with salinity. For both metrics, no clear patterns emerged to explain temporal and spatial variation, even following major disturbances (e.g., Hurricane Ian, FL red tide, heat wave event). These results suggest that bivalve larvae and oyster spat in Southwest Florida are resilient to environmental stressors and that both are abundant throughout the Charlotte Harbor Estuary over the duration of the oyster spawning season. Furthermore, substrate may be limiting population recovery in the region and restoration efforts to place shell would likely be successful.

KEY WORDS: bivalve, spat, hurricane, food availability, Charlotte Harbor Estuary

INTRODUCTION

The eastern oyster, *Crassostrea virginica* (Gmelin 1791), is a common inhabitant of estuaries along the Gulf and Atlantic coasts of North America. Oysters provide numerous ecosystem services (Cerco & Noel 2007, Grabowski et al. 2012), including habitat (Wells 1961, Coen et al. 1999, Gutiérrez et al. 2003) and high filtration capacity (Newell 2004, Pomeroy et al. 2006). Although once abundant in shallow areas, globally oyster populations are in decline because of habitat destruction, overharvesting, and increased disease prevalence (Coen 1995, Jackson et al. 2001, Beck et al. 2011, Seavey et al. 2011, Powell et al. 2012). Reduction of oyster habitat has had drastic impacts on ecosystem function, notably in Chesapeake Bay and along the central Louisiana coast (Newell 1988, Rothschild et al. 1994, Kirby 2004, zu Ermgassen et al. 2013). Thus, oyster restoration has been a priority in impaired waters across the United States as a natural means of remediation (see Smith & Pruett 2025 for a review). Oyster population recovery has also been used as a bioindicator for the success of the Comprehensive Everglades Restoration Plan (Volety et al. 2009), which aims to improve degraded water quality in estuaries along the Southern Gulf Coast of Florida. As a result, efforts have focused on identifying drivers of oyster decline and strategies to enhance restoration success in Southwest Florida.

Early life stages play a critical role in understanding population declines and promoting recovery. Oysters have a multiphasic life cycle, spending 2 to 3 wk in the water column before settling back into adult oyster reefs (Kennedy 1996). Oysters are gregarious settlers, preferring to settle in established oyster habitat that offers crevices and refuge, thereby enhancing survival (Nesterode et al. 2007). Although necessary for population persistence, recruitment of benthic marine invertebrates can be variable across spatial and temporal scales (Underwood & Fairweather 1989). Numerous factors influence successful recruitment, including egg quality, the environmental conditions and food availability experienced by larvae, larval mortality, dispersal, and availability of suitable substrate (Abbe 1986, Mann 1988, Kennedy 1996). Once settled, oyster spat also face various stressors, including predation and disease, that can limit postsettlement survival (Roegner 1991).

Within estuaries where oysters are common, a suite of abiotic and biotic stressors can lead to both larval and postset mortality (Carriker 1951, Prichard 1953, Loosanoff 1974, Osman et al. 1989). In Charlotte Harbor Estuary (CHE), local oyster populations have declined, partly due to estuarine modifications, such as increased freshwater flows for flood control and human use (Sklar & Browder 1998, Childers et al. 2006). Research in CHE has focused on managing water discharges, citing low salinity, disease, and altered flow as drivers of oyster decline (Barnes et al. 2007, Volety et al. 2009, McFarland et al. 2022a). Although these previous studies have examined recruitment, the relationship between larval distributions, recruitment hot spots, resident oyster reefs, and environmental conditions remain unknown.

In other systems, larval supply is a limiting factor for oyster population recovery and persistence (Lipcius et al. 2021, Morgan & Rakocinski 2022), yet larval distributions remain grossly understudied (Lindeque et al. 2015). To adequately understand population dynamics, the larval pool and environment under which larvae develop must be considered (Grosberg & Levitan 1992), as conditions that favor a shorter larval duration increase survival and settlement success (Dekshenieks et al. 1993,

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Meyer et al. 2018). As larval distributions are difficult to study, modeling efforts have attempted to fill this knowledge gap for CHE (e.g., Dye et al. 2022), but require site-specific data to validate models across the oyster life cycle (La Peyre et al. 2014). To improve the understanding of larval supply in the lower CHE and evaluate model effectiveness in predicting distributions, patterns of bivalve larval density and oyster settlement across environmental gradients were investigated.

MATERIALS AND METHODS

Study Site

Charlotte Harbor Estuary is the second largest estuary in Florida, covering approximately 700 km^2 of the Southwest Florida coastline (Fig. 1, Taylor 1974). The estuary is dominated by freshwater flows from three rivers—the Peace, Myakka, and Caloosahatchee—with tidal mixing resulting in a net estuarine circulation. According to the modeling study by Zheng and Weisberg (2004), outflow currents are stronger and associated with lower salinity in the northern CHE (e.g., Peace and Myakka Rivers) whereas the shallow passes in San Carlos Bay (e.g., Caloosahatchee River) act independently. Alterations in flow regimes and salinity gradients in the southern CHE are, in part, due to the artificial connection of the Caloosahatchee River to the greater Everglades system and Lake Okeechobee beginning in 1884 (Doering & Chamberlain 1999, Barnes 2005). Favorable winds for upwelling and downwelling (northwesterly or southeasterly) push water from San Carlos Bay into Charlotte Harbor, bypassing the shallow depth constraints of Matlacha Pass and Pine Island Sound. Even relatively weak winds can have a dominating effect on the tide-averaged flow and subsequent exchange of nutrients and other materials (Hewageegana et al. 2023). Overall, the estuary is well-mixed through tidal flushing from the Gulf of Mexico.

The connection of the Caloosahatchee River to the lower CHE has been problematic, particularly during periods of managed discharge for flood protection. The heavy inflow of freshwater leads to stratification (Doering & Chamberlain 1999) and modification of tidal and subtidal flows (Shi et al. 2023). Oyster populations have been negatively impacted by lowered salinity, increased sedimentation rates, and outward

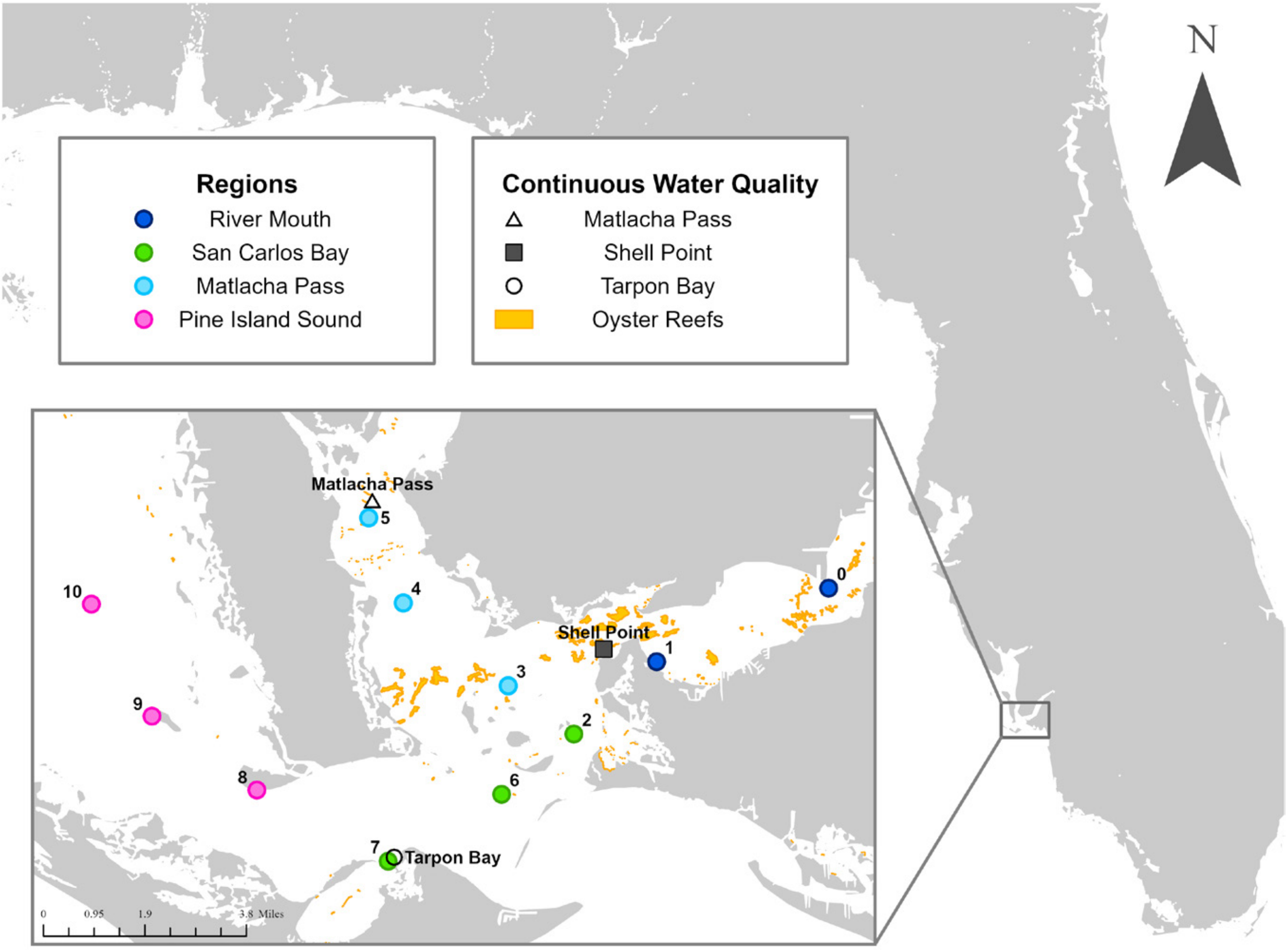


Figure 1. Site map of the lower Charlotte Harbor Estuary with sampling locations within each of the four regions targeted in this study: the River Mouth, (dark blue), San Carlos Bay (green), Matlacha Pass (light blue), and Pine Island Sound (pink). The locations of living oyster reefs are shown in dark grey whereas the locations of the sensors used for continuous water quality data sites are represented by symbols: Matlacha Pass (open triangle), Shell Point (closed square), and Tarpon Bay (open circle).

flow (Volety 2008, Volety et al. 2014), which can alter growth, reproduction, or advect oyster larvae from the system (Wilson et al. 2005, McFarland et al. 2022a). To investigate the spatial and temporal variation in bivalve larval density and settlement of the eastern oyster (*Crassostrea virginica,* Gmelin 1791) in the lower CHE, a field-based survey of sites across the region was used during the spawning seasons of 2020–2023.

Eleven sites spanned four regions of the lower CHE (Fig. 1), to assess oyster connectivity throughout the lower estuary under different flow regimes. The river mouth (0,1) and San Carlos Bay (2, 6–7) contain the highest density of living oyster reefs in this region and previous studies have focused on the influences of discharge on these local oyster populations (e.g., Volety 2008, Volety et al. 2014, McFarland et al. 2022a). Matlacha Pass (3–5) and Pine Island Sound (8–10), conversely, have low densities of living oysters but may serve as a sink and/or refuge for oyster larvae during periods of high freshwater flow (Dye et al. 2020, McFarland et al. 2022a). Sites were sampled biweekly from June through November (the oyster spawning season) following the methods outlined below, with the exceptions of Site 8 only being sampled in 2020 and Site 0 added in 2021. Biweekly sampling was intended to capture spring and neap tidal cycles and corresponds to the minimum larval duration at the temperatures and salinity for this region (Davis & Calabrese 1964).

Bivalve Larval Density

At each site and on every sampling trip, 10 L of water was pumped from approximately 0.5 m below the surface to sample a well-mixed water column. The total depth at all sites was less than 1.5 m, so the sampling depth was at the approximate elevation of natural, intertidal reefs in the region. Water samples were filtered through 75 um mesh to retain larvae, fixed with 70% ethanol in seawater, and stored at room temperature until further analysis. Fixed samples were stained with Rose Bengal and sorted in water using a dissecting scope at 40× magnification to identify and quantify bivalve larvae. There was no attempt to distinguish among species of bivalve larvae, given the high diversity of species in this region with veliger stages and overlapping spawning periods.

Oyster Settlement

At each site, a PVC "T" was deployed with 3 strings, each containing 10 oyster shells (~7–10 cm long) strung on stainless steel wire (Southworth & Mann 2004). Each shell string was hung with the interior of each shell oriented downward from a PVC frame at -0.5 m MLW to approximate the depth of intertidal reefs in the region. Strings were deployed for 2-wk intervals throughout the sampling period. Oyster spat were counted on both sides of the shell in the field to determine the total number of *Crassostrea virginica* per string, and the three replicate strings used to calculate mean spat per string. Spat density was estimated based on the average number of oyster shells that fill a 1-m^2 quadrat. Briefly, a subset of shells used for the strings were arranged to cover the area within a 1-m^2 quadrat and counted; this was repeated multiple times to determine that roughly 180 shells (7–10 cm long) fit per m^2. This number was used to approximate shell area for each string. Finally, average spat density was divided by the number of days; the strings were deployed to represent spat settlement rate in spat per m^{-2}·d^{-1}.

Environmental Parameters

A YSI EXO2 sonde was deployed to profile water quality parameters from 0 to 0.5 m depth during each sampling trip. Measurements of salinity, temperature, depth, dissolved oxygen, turbidity, and *in situ* chlorophyll were recorded at each site. The YSI was calibrated monthly according to the manufacture specifications and checked using a 50 mS salinity standard and 100% air saturated seawater solution within 24 h of use. The YSI profiles at each site were used to capture spatial and temporal variation in water quality across the 11 sites within CHE.

Continuous water quality data were used from four sources across the lower CHE to obtain a more accurate understanding of drivers of settlement and postsettlement survival. Hourly observations of water temperature, salinity, dissolved oxygen, turbidity, and *in situ* chlorophyll-*a* were downloaded from the River, Estuary and Coastal Observing Network (RECON) website (http://recon.sccf.org) for Shell Point and Tarpon Bay during the study period, as proxies for water quality in San Carlos Bay and Pine Island Sound, respectively. Continuous data from Matlacha Pass were downloaded from Florida Department of Environmental Protection Office of Resilience and Coastal Protection site (https://floridaapdata.org) for the YSI sonde at MP2B, which collects measurements of water temperature, salinity, dissolved oxygen, and turbidity at 15-min intervals. Data from this site were only available from May 2020 to September 2022, as the sonde was damaged during Hurricane Ian. No representative continuous data exists near the sampling locations within the river mouth used in this study. Additionally, flow data (in ft^3·s^{-1}) collected at 15-min intervals from Franklin Lock (S-79, Fig. 1) in the Caloosahatchee River during the study period were downloaded from the United States Geological Survey (https://waterdata.usgs.gov).

Statistical Analyses

All analyses were conducted using JMP Pro 18 (SAS Institute). To test variation of bivalve larval density and oyster settlement by region, two one-way ANOVAs were run. For each model, all pairwise comparisons were tested using Tukey's HSD *post hoc* analysis. To investigate the relationships between bivalve larval density and measurements of water temperature, salinity, and chlorophyll-*a* concentrations recorded using the YSI handheld sonde, Gaussian Process regression (Rasmussen 2003) was used. To normalize the data, larval density and chlorophyll-*a* concentrations were log transformed. The discrete measurements were selected for this analysis as they would represent the conditions that matched the larval density for a given water mass.

To investigate drivers of spat density, continuous water quality data for each parameter were averaged to match the duration that spat collectors were deployed (e.g., 2-wk intervals) for San Carlos Bay, Pine Island Sound, and Matlacha Pass. The minimum, maximum, and mean spat settlement rates, water temperature, salinity, dissolved oxygen, and turbidity were calculated for each deployment interval. Principal components analysis and restricted maximum likelihood estimates were used to investigate relationships among mean spat density and water temperature, dissolved oxygen, turbidity, and salinity. Because there was no representative continuous water quality data for the river mouth, the settlement data for this region were excluded from these analyses.

RESULTS

Environmental Trends

Water quality data were similar for measurements taken during each sampling trip using a YSI EXO2 and those continuously recorded at three sites across the lower CHE. Salinity was the most variable of the parameters recorded (0.9–35.8), particularly in sites closer to the river mouth (Fig. 2C). The highest and most stable salinity was recorded near Pine Island Sound (e.g., Tarpon Bay), whereas greater fluctuations in salinity occurred in San Carlos Bay and Matlacha Pass (Fig. 3B). Interannual variation in salinity was apparent, as there was

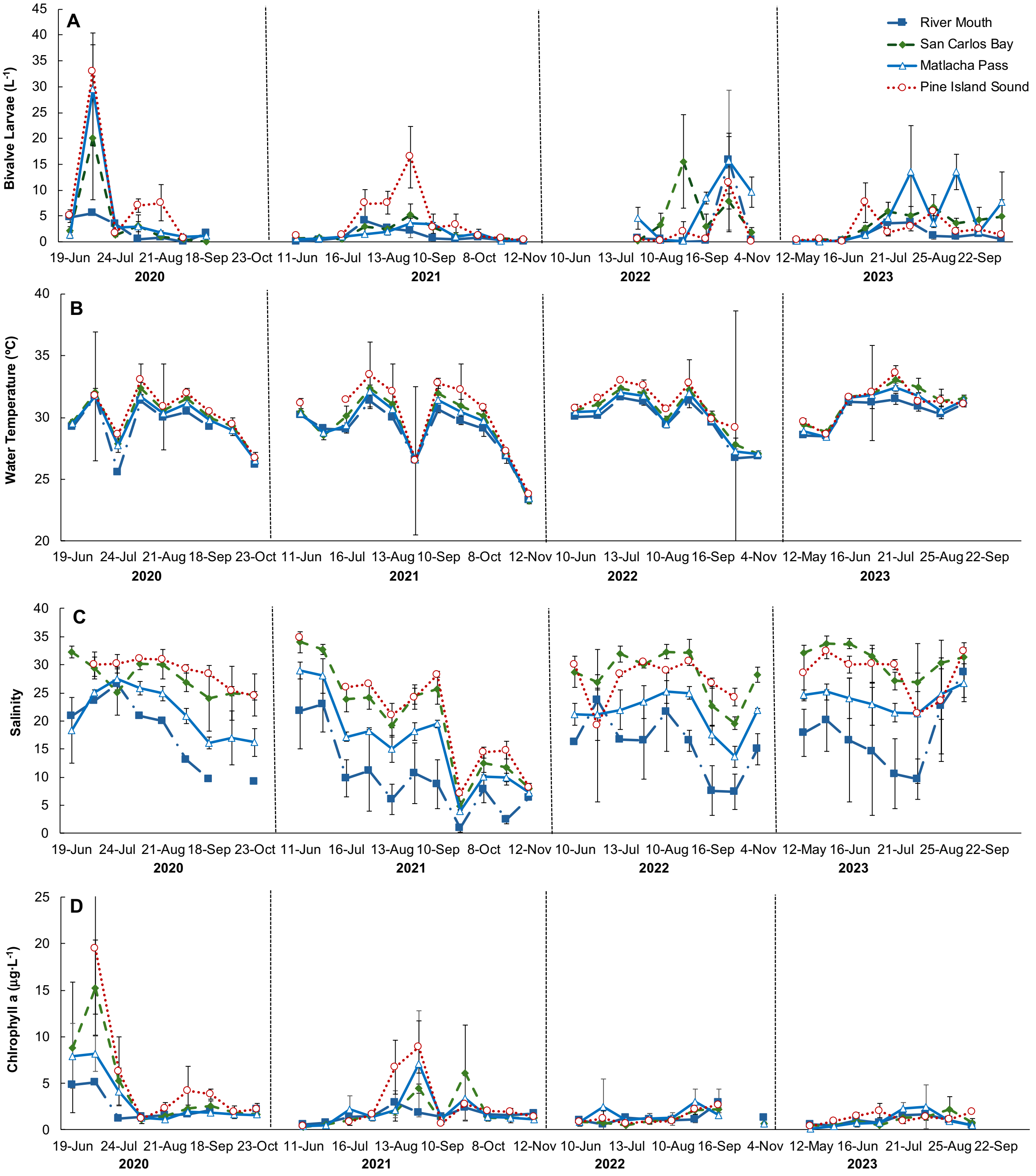


Figure 2. Time series of regional means (±SE) for (A) bivalve larval density, L^{-1}, (B) water temperature, °C, (C) salinity, and (D) chlorophyll-*a* concentration, μg·L^{-1} during the spawning seasons of 2020–2023 . Seawater parameters were measured using a YSI multiparameter sonde at the time larvae were sampled.

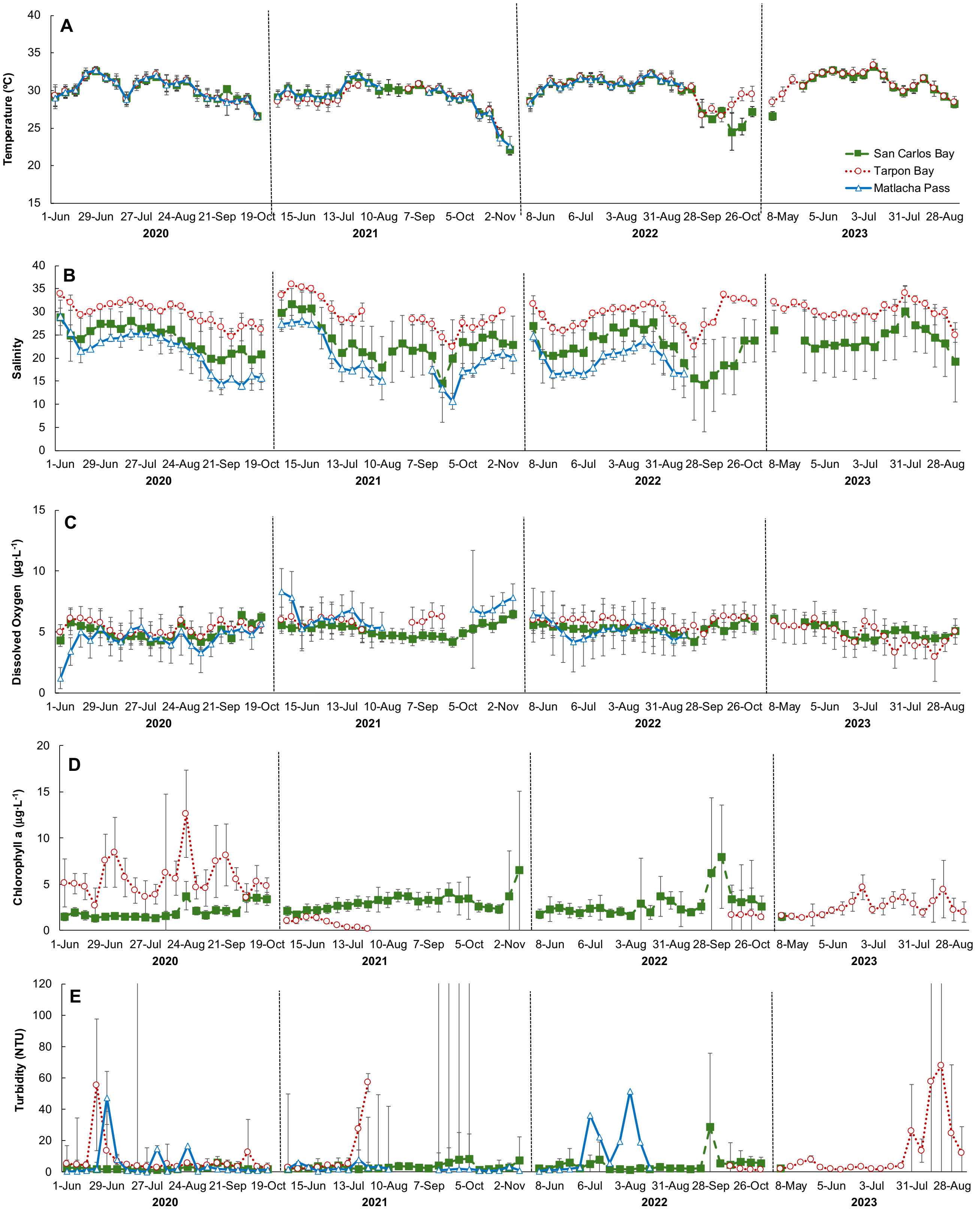


Figure 3. Time series of (A) water temperature, °C, (B) salinity, (C) chlorophyll-*a* concentration, µg·L^{-1}, (D) dissolved oxygen, µg·L^{-1}, and turbidity (NTU) during the spawning seasons of 2020–2023. The data plotted for San Carlos Bay (filled box) and Tarpon Bay (open circle) are weekly means ± SE from the SCCF RECON sensors (https://recon.sccf.org). The data from Matlacha Pass (open triangles) are weakly means ± SD from Florida DEP (https://floridaapdata.org) from 2020 to 2022; chlorophyll-*a* was not collected at this site.

an observed freshening of the system throughout the wet season (e.g., June–October) in 2020 and 2021 that did not persist in 2022 and 2023. Discharge events from S-79 lock typically occur in September of each year to lower water levels in Lake Okeechobee and prevent flooding during the wet season, likely contributing to decreased salinity in the estuary during these times. In 2022, Hurricane Ian made landfall on one of the barrier islands of CHE on 28 September and brought storm surge that increased salinities for the remaining of the 2022 sampling period. In 2023, salinities were higher throughout the season due to low rainfall.

Water temperature showed seasonal, but less interannual, variation during the spawning seasons of 2020–2023 (22.1°C–33.6°C) and was comparable across sites (Fig. 2B). Chlorophyll-*a* concentrations were also similar across regions (Fig. 2D), with seasonal blooms occurring infrequently. Chlorophyll was generally low (<4 $\mu g \cdot L^{-1}$), with maximum concentrations reaching 19.5 $\mu g \cdot L^{-1}$. A large Florida red tide event formed in the region following Hurricane Ian in October 2022, but was not recorded in these chlorophyll data, as field sampling was not feasible and the continuous sondes were offline. Dissolved oxygen showed little variation with mean concentrations around 5 $\mu g \cdot L^{-1}$ (Fig. 3C), and one possibly hypoxic event (1.2 $\mu g \cdot L^{-1}$) in Matlacha Pass during June 2020. Finally, several times throughout the study period, turbidity increased above 30 NTU, although localized to one region, usually away from the mouth of the river (Fig. 3E).

Bivalve Larval Density

Bivalve larval density varied across sites and seasons (Fig. 2A). Peak densities were observed at different sites over the 4-y sampling period, but with no distinct pattern when bivalve larvae were most abundant in the lower CHE. As a general trend, larval density was lowest at sites in the river mouth and significantly higher in Pine Island Sound (Tukey's HSD, $P = 0.05$, Fig. 4). The Gaussian correlation function showed that bivalve larval distributions were best explained by variation in temperature (76.4%) and chlorophyll (49.9%), but surprisingly not salinity (Table 1). The Gaussian model indicated that bivalve larval density was maximized at 30.0°C and 2.19 $\mu g \cdot L^{-1}$ chlorophyll, but was also in high abundance at lower temperatures if food was readily available. Finally, bivalve larval density appeared to increase during peak flow events from S-79 lock, although this relationship was not explicitly tested.

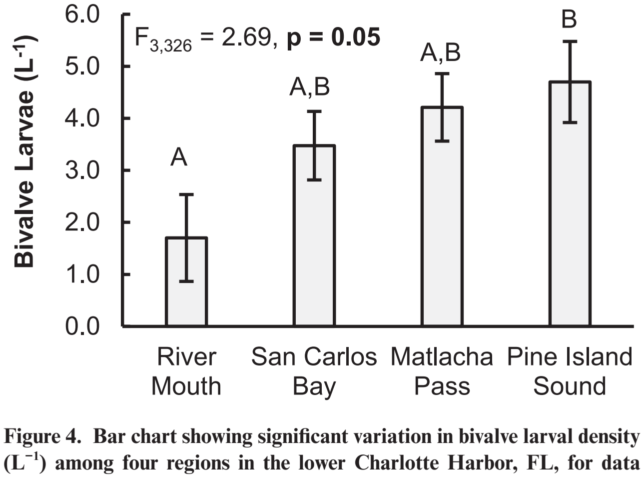


Figure 4. Bar chart showing significant variation in bivalve larval density (L^{-1}) among four regions in the lower Charlotte Harbor, FL, for data pooled from 2020 to 2023 (±SE). The river mouth consistently had lower larval densities than Pine Island Sound.

TABLE 1.

Gaussian Process Model Report for the impacts of environmental parameters on bivalve larval distributions.

	Theta	Total sensitivity	Main effect
Chlorophyll-*a*	0.67	**0.50**	0.24
Temperature	0.27	**0.76**	0.50
Salinity	5.9 × 10–10	0.00	0.0
$\mu = 0.64$	$\sigma^2 = 1.21$	−2*Loglikelihood = 830.93	

Variables in bold are significant at $\alpha = 0.05$.

Oyster Settlement

Oyster settlement varied by region, seasonally, and across years, with one to two settlement peaks during each spawning season (Fig. 5). As with bivalve larval density, settlement was lowest near the river mouth and increased with distance from the mouth (Fig. 6). Spat densities were significantly higher across years in Matlacha Pass compared with the River Mouth (Tukey's HSD, $P < 0.001$) and San Carlos Bay (Tukey's HSD, $P = 0.004$), where established reefs are found. Pine Island Sound also had significantly higher settlement than the river mouth (Tukey's HSD, $P = 0.01$), but not San Carlos Bay (Fig. 6). According to the principal components analysis, component 1 explained only 33% of the variation and was strongly influenced by chlorophyll-*a* and turbidity, whereas component 2 (21%) was strongly influenced by salinity and dissolved oxygen, which were negatively correlated. Spat density had a higher partial contribution in component 3, where it positively correlated with temperature (not shown). The relationships of environmental parameters and settlement were more clearly demonstrated using multivariate correlations (Table 2), which show significant relationships of spat density with temperature and salinity. More specifically, mean weekly water temperature and spat density showed a strong positive relationship ($F_{1,93 = 32.98}$; $P < 0.001$; Fig. 7A) and a negative relationship with mean weekly salinity ($F_{1,93 = 5.90}$; $P = 0.02$; Fig. 7B).

DISCUSSION

Distributions of Bivalve Larvae and Juvenile Oysters

This is the first multiyear study to evaluate patterns of bivalve larval distributions within the CHE. As in other regions, bivalve larval densities in the lower CHE showed high interannual variability, with peak abundance shifting from late June in 2020 to August in 2022 and 2023 (Fig. 2A). Numerous factors influence larval distributions (Carriker 1951, Prichard 1953, Loosanoff 1974), including flow regimes within the estuary and other physical and biological characteristics of the water column. In the present study, bivalve larval density was highest further from the river mouth (Fig. 4). Previous studies have suggested that high flow rates in the CHE negatively influence oyster larvae, either from prolonged exposure to reduced salinity from freshwater input or advection from the system (Volety et al. 2009, Dye et al. 2022, McFarland et al. 2022a). Evidence

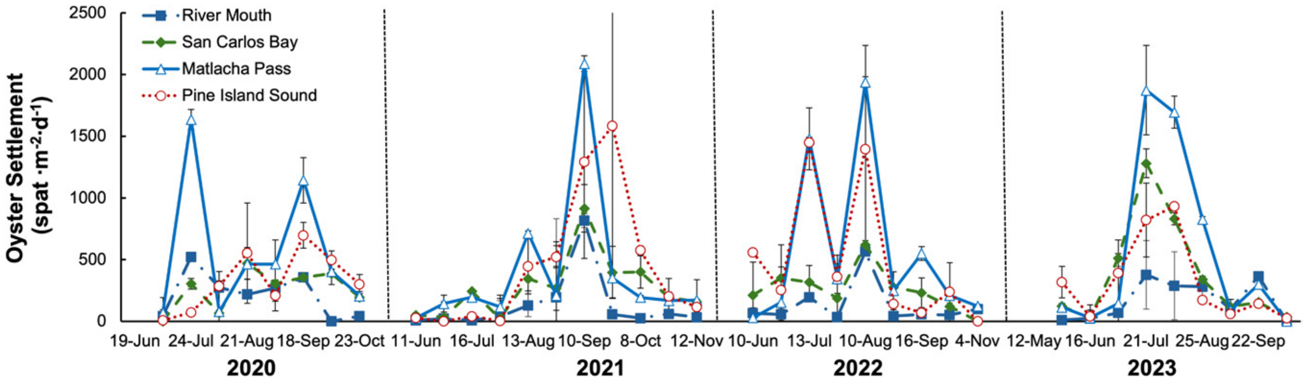


Figure 5. Concentrations of oyster spat, measured as mean spat $m^{-2}\cdot d^{-1}$ (±SE), at four regions in the Charlotte Harbor Estuary, over the spawning periods of 2020–2023.

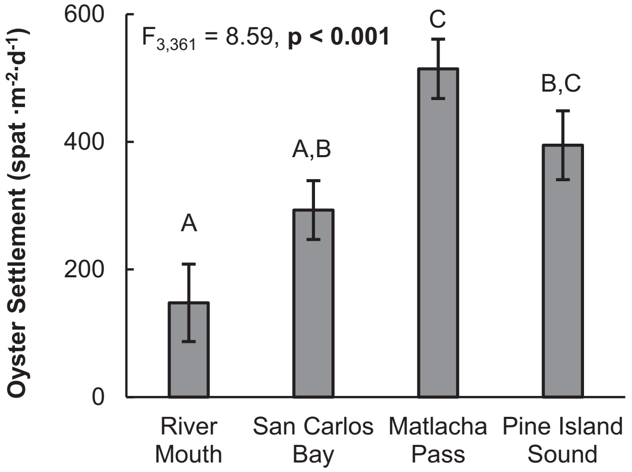


Figure 6. Bar chart showing significant variation in mean oyster settlement ($m^{-2}\cdot d^{-1}$) among four regions in the lower Charlotte Harbor, FL, for data pooled from 2020 to 2023 (±SE). The river mouth consistently had lower settlement than Matlacha Pass and Pine Island Sound.

from the present study similarly suggests that bivalve larvae may be concentrated away from the river mouth during periods of increased river discharge, but only in some years (e.g., 2022 and 2023). The age of larvae collected during sampling may also influence patterns of high abundance in some regions. Early larvae tend to be aggregated, with dispersal and advection from one another increasing with larval duration (Kennedy 1996). Although D-stage, veligers, and pediveligers were only distinguished during the 2022 season (data not shown), most larvae sampled were not yet in the pediveliger stage. Thus, it is possible that high concentrations of bivalve larvae in Matlacha Pass and Pine Island Sound were the result of limited dispersal over the short distance traveled within the first few days postfertilization. This hypothesis would need to be tested with much higher temporal resolution but would be integral to understanding the interpretation of whether bivalve larvae are truly more abundant in these regions because of flow regimes or just more concentrated during early development.

In this study, it was assumed that a large portion of the bivalve larval pool measured was comprised of oyster larvae. Yet, given regular tidal flushing and varied rates of freshwater flow throughout the study, it is difficult to directly correlate patterns of high abundance of bivalve larvae to oyster settlement. Oyster settlement in the CHE (Fig. 5) was variable in terms of the timing and distribution of setting events, which did not always follow patterns of high bivalve larval density. Observed variation in recruitment is likely the result of postsettlement mortality (Roegner 1991), resulting from predation (Osman et al. 1989, Barnes et al. 2010, Hanke et al. 2017, Baillie & Grabowski 2019), infection from the protist *Perkinsus marinus* (Volety et al. 2014), and even recreational boating activity (Wall et al. 2005). As there was no attempt to distinguish between species of bivalve larvae, it is probable that some periods of high bivalve larval abundance were from different species, and thus, would not correspond to a spike in oyster settlement. Despite this limitation, bivalve larvae were present in the water throughout the spawning season, and two pronounced peaks in oyster settlement were observed between July and October each year (Fig. 5).

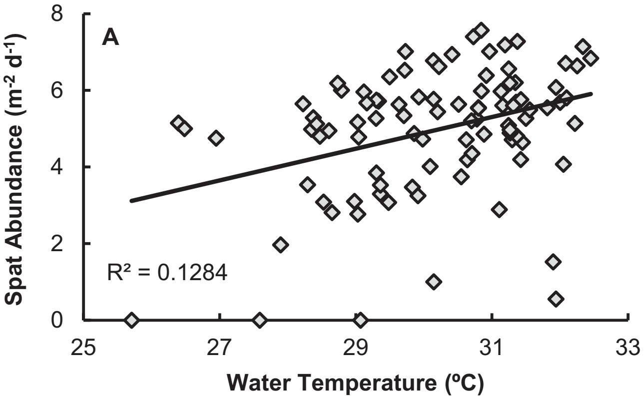
With respect to the timing of peak oyster set, settlement appears to be occurring earlier in the season than was reported

TABLE 2.

Correlation coefficient matrix from multivariate analysis of drivers of spat density using discrete measurements.

	Spat density	Temperature	Salinity	Chlorophyll-*a*	Turbidity	DO
Spat density	1.00	**0.38**	**−0.26**	0.23	0.09	−0.02
Temperature		1.00	0.10	0.15	0.13	−0.14
Salinity			1.00	−0.13	−0.11	−0.17
Chlorophyll-*a*				1.00	0.75	−0.14
Turbidity					1.00	−0.06
DO						1.00

Variables in bold are significant at α = 0.01.



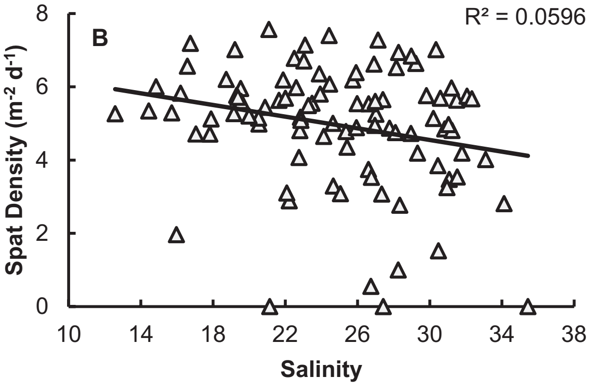


Figure 7. Regression plots of oyster settlement and temperature (A) and salinity (B). Both parameters were significantly correlated with spat density, where settlement increased linearly with temperature but decreased with increasing salinity.

over a 10-y study in CHE (Volety et al. 2009, McFarland et al. 2022a). Previously, settlement did not occur until late July or August, whereas the present study found settlement peaks beginning as early as June. The spatial patterns of settlement in the lower CHE also seem to have shifted, moving from areas of highest living oyster densities (e.g., River Mouth and San Carlos Bay) toward Pine Island Sound and Matlacha Pass (Fig. 6) over the past 20 y (see McFarland et al. 2022a). Variation in peak density of settlement is common in other estuaries (Andrews 1951, Ingle 1951, Loosanoff & Nomejko 1956, Ortega & Sotherland 1992, Austin et al. 1996, Kennedy 1996, Atwood & Grizzle 2020, Raabe & Gilg 2020), but continued research should explore these shifts are due to changes in water management (Julian & Reidenbach 2024) and what the implications of this for the persistence of established communities.

Environmental Drivers of Bivalve Larvae and Juvenile Oysters

To better understand bivalve larval distributions and oyster settlement in CHE, the environmental conditions in each region were evaluated. Not surprisingly, temperature was a significant driver of both. Throughout this study, temperatures were within the optimal ranges reported by Davis and Calabrese (1964) and MacInnes and Calabrese (1979), remaining above 26°C, apart from a cold spell in November 2021 (Fig. 2B). Somewhat surprisingly, increasing temperature corresponded to higher settlement, even approaching 33°C (Fig. 7A). Oysters in southwest Florida live near the upper end of their thermal optima and laboratory studies have shown decreased survival of juveniles as temperature increased from 25°C to 30°C (McFarland et al. 2022b). High temperatures, particularly in southwest Florida, have been associated with high prevalence of *Perkinsus marinus* infection and predation pressure (Garton & Stickle 1980, Osman et al. 1989, Chu & La Peyre 1993), which are significant sources of mortality for juvenile oysters. Regardless, warm temperatures did not negatively impact spat in this study, consistent with other research that has shown broad thermal tolerances of spat, particularly in the Gulf of Mexico (Rybovich et al. 2016, Lowe et al. 2017).

Chlorophyll concentration was also a significant predictor of bivalve larval density and oyster settlement. Bivalve larvae are planktotrophic, feeding primarily on phytoplankton (Davis 1953), but are also capable of consuming protists and bacteria (Baldwin & Newell 1991). Meroplankton often peak during algal bloom events (Lindeque et al. 2015), as observed in 2020–2022 (Fig. 2D) and may aggregate near fronts where food concentrations are high. Thus, consistent with other studies in bivalves, temperature and food availability are the largest drivers of bivalve larval density (Thompson et al. 2012, Daigle et al. 2014, Chícharo & Chícharo 2000, Chapman et al. 2021). Although temperature and chlorophyll-*a* variation were low across regions within the CHE, these parameters explain the timing of peak bivalve larval density. This is intuitive, as optimal conditions facilitate a shorter larval duration, thereby increasing chances of survival (Davis and Calabrese 1964, Dekshenieks et al. 1993). Postsettlement success is also improved by the quantity and quality of food, which increases growth and survival of oyster juveniles (Lenihan et al. 1996) and stress tolerance in many bivalve species (e.g., Fitzgerald-Dehoog et al. 2012, Schwaner et al. 2023, and others).

Extensive research suggests that low salinity is the primary driver of decline in Florida estuaries (e.g., Wilson et al. 2005, Bergquist et al. 2006, Volety et al. 2009, Parker et al. 2013, McFarland et al. 2022a). Although mass mortality events for bivalve larvae are common (Loosanoff 1974), within CHE, it is suspected that larval mortality occurs during high discharge events, in part from extended exposure to low salinity conditions (McFarland et al. 2022a). Prolonged exposure to salinities below 12.5 decreases survival of oyster larvae (Davis 1958, Davis & Calabrese 1964, MacInnes & Calabrese 1979, Scharping et al. 2019, McFarland et al. 2022b, McDonald et al. 2023). Throughout the study period, salinity dropped below 12 once in 2021 (Figs. 2C and 3B), and bivalve larval density often peaked before the wet season freshening occurred. The optimal salinity for oyster larvae in the CHE is 15–27 (Barnes et al. 2007), so it was not surprising that no relationship between salinity and bivalve larval abundance was observed (Table 1). These findings suggest that increased flow rates are a primary driver of bivalve larval distributions within CHE, as has been suggested by model efforts (Dye et al. 2022). Usually, high flow transports larvae further downstream, and therefore, higher spat density is further from freshwater sources (Gancel et al. 2021), as was observed in the present study (Fig. 6). Thus, oyster settlement will be influenced by the timing and duration of freshwater input (Barnes et al. 2007, Jones et al. 2019, Pruett et al. 2021, McFarland et al. 2022a), particularly if larvae are being advected out of the system.

Of note, for high salinity sites (e.g., not including the river mouth), spat abundance was negatively correlated with salinity (Fig. 7B). Low salinity may act as a temporary refuge from parasite infection for adults or may shift predator density (Loosanoff 1974, Livingston et al. 2000), thereby increasing survival during sublethal exposures. Although data were not available to include the low salinity sites in this analysis, spat seem to perform well salinities of 15–25, as observed in Matlacha Pass (Fig. 3B).

Implications for Restoration

Oyster reefs in the CHE have suffered significant declines over the past 100 y (Geselbracht et al. 2013), resulting in efforts to restore reefs and the associated ecological services (Beck et al. 2011). One limitation to restoration efforts can be larval supply, which is necessary for the growth and resilience of oyster populations (Lipcius et al. 2021). Only two studies have documented *Crassostrea virginica* larval densities (Carriker 1951, Sasse et al. 2021) in natural systems. Carriker (1951) reported similar oyster larval concentrations to the present study (mean: 3.38 and max: 32.9 bivalve larvae L^{-1}) and other mixed bivalve studies (Chícharo & Chícharo 2000, Daigle et al. 2014), but noted that oyster larval densities were tidally influenced rather than from resident populations. Sasse et al. (2021), on the other hand, documented low veliger densities attributed to widespread declines of oyster reefs in Great Bay Estuary, NH. Although the proportion of oyster larvae observed in this study is unknown, rates of settlement at some sites compared with other studies (Bartol & Mann 1997, Poirier et al. 2019, McFarland et al. 2022a) suggest that oyster larval supply in CHE is not limiting (Southworth & Mann 2004, Knights & Walters 2010). Thus, restoration efforts in CHE would likely benefit from additional substrate in areas of high larval abundance.

In this study, settlement was higher in areas where native oyster reefs do not exist (Fig. 6), even though spat and bivalve densities were within expected ranges. Dye et al. (2022) estimated that larvae are transported in high numbers to downstream sites (e.g., Pine Island Sound and Matlacha Pass) and, effectively lost from the system during high flow events. This advection from source reefs may limit self-seeding of the reefs in the river mouth and San Carlos Bay, possibly contributing to their decline. When high flows were mitigated and limited in an oyster carbon model, oyster densities increased (Buzzelli et al. 2013). Compared with data from a 15-y study of the CHE, settlement throughout the estuary appears to have increased, despite having extremely high flow events in multiple years of this study (McFarland et al. 2022a). This may, in part, be due to shifts in the timing of peak settlement that occur earlier or later than periods of peak flow or flow from the natural watershed rather than from managed discharges (Montefiore et al. 2024), which may contribute to shifts and increases in bivalve larval supply across the estuary. In addition to increased substrate, passive means of restoration (Barrett et al. 2024) that minimize discharges from Lake Okeechobee and other anthropogenic stressors will be highly beneficial in this system.

Impacts of Disturbance

During the study, Southwest Florida experienced numerous disturbances. Hurricane Ian made landfall toward the northern end of CHE as a Category 4 storm on September 28, 2022, initially inundating the area with storm surge, followed by prolonged, heavy riverine discharge and high turbidity. Although settlement dropped following the storm (Fig. 5), it appeared to follow patterns of natural variation seen in previous years rather than an isolated event driven by the storm. Interestingly, bivalve larval supply increased after the Hurricane passed (Fig. 2), indicating that the storm may have induced a spawning event. Under normal flow conditions, it is estimated that >50% of larvae are advected to the Gulf of Mexico (Dye et al. 2022), so it is likely heavy flow increased the proportion of bivalve larvae transported out of CHE, as flow rates exceeded the recommendations to promote recruitment (e.g., <2,000 cfs; McFarland et al. 2022a). High turbidity, along with low salinity, is detrimental to larvae and settlers (Carriker 1986), which may have also increased postsettlement mortality. Alternatively, high larval abundance following Hurricane Ian may have been a different bivalve species. Regardless, other studies show oyster larvae and spat are resilient after hurricanes (Livingston et al. 1999, Patrick et al. 2020) and suggest such disturbances may increase habitat availability for recruits (Underwood & Fairweather 1989) by causing storm-related mortality of adults and predators.

Shortly after Hurricane Ian, a large Florida red tide event (*Karenia brevis*) moved into the region. Red tides cause extensive fish die offs and can lead to widespread hypoxia (Milbrandt et al. 2021), causing unfavorable conditions for oyster larvae and juveniles. Although adult oysters show brevetoxin resistance (Plakas et al. 2002, Leverone et al. 2007), early life stages (e.g., embryos and larvae) are susceptible to these toxins, which leads to mortality (Rolton et al. 2015). Because the continuous sondes were offline following the hurricane, the spatial extent of the bloom within the lower CHE was difficult to capture. Although the direct impacts of this event are difficult to discern, bivalve larval concentrations in Matlacha Pass were high in early November 2022 (Fig. 2A), indicating either a spatial refuge or limited impact of the toxin in the region. As sampling did not extend past November 4, settlement following the bloom was not recorded (Fig. 5).

The following year, FL experienced a heat wave, with hottest temperatures on record in July 2023 and water temperatures reaching 38°C (Shi et al. 2024). During this event, the maximum water temperature recorded at study sites in CHE was 34°C, yet settlement was unaffected, with the high densities of spat observed throughout July (Fig. 5). Bivalve larval densities were beginning to increase during this time (Fig. 2A), so it is possible that the warm water stimulated a small spawning event. Although not the focus of this study, the three different disturbances occurring in Southwest Florida during the study period had no detectable impact on bivalve larvae and juvenile oyster populations.

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