Role of Flood Disturbance in Natural Oyster (*Crassostrea virginica*) Population Maintenance in an Estuary in South Texas, USA

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Abstract A 2-year period with flood versus drought conditions provided the opportunity to examine the effects of flood disturbance on subtidal eastern oyster *Crassostrea virginica* biology and population dynamics in a south Texas estuary. Oysters were sampled monthly in 2007 and 2008 to examine the impacts of changing environmental conditions on oyster populations. Oysters were also examined quarterly for the presence of *Perkinsus marinus*. Filtration rates were calculated as a function of oyster size, temperature, salinity, and total suspended solids. Flood events in 2007 caused temporary reductions in salinity and were associated with reductions in oyster abundance, spat settlement, disease levels (weighted prevalence and percent infection), and filtration rates. Oyster populations had generally recovered within 1 year's time—the oysters were younger and smaller but were just as abundant as pre-flood levels. The rapid return of oysters to pre-flood abundance levels is attributed in part to the ability of oysters in Gulf coast estuaries to spawn multiple times in a single season and in part to their relatively high growth rates. Although flood disturbance may temporarily reduce or destroy oyster populations, the ability of the Mission–Aransas Estuary to retain freshwater pulses within the system and maintain low salinities that are unfavorable for predators and disease can facilitate oyster population recovery. Episodic flood events appear to play a critical role in promoting long-term oyster population maintenance in the Mission–Aransas Estuary. The response of oysters to changing environmental conditions over the short term provides some insights into the potential long-term effects of changing climate.

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Introduction

Eastern oysters, *Crassostrea virginica*, provide important ecological and economic benefits to coastal ecosystems and humans. As filter feeders, oysters remove phytoplankton and other particles from bay waters (Newell and Jordan 1983), and as reef-builders, oysters create biogenic habitat for fish and invertebrates (Zimmerman et al. 1989; Lenihan et al. 2001). Oyster reefs also protect shorelines from erosion, which benefits multiple natural resources by reducing erosion rates and protecting valuable habitats such as marsh and wetlands and the associated organisms (Meyer et al. 1997; Piazza et al. 2005). Within the USA, Texas produces the second-largest oyster harvest, with an estimated $17 million generated from oyster harvests in 2006 (e.g., Culbertson et al. 2004).

Environmental factors, such as salinity and temperature, control oyster reproduction, survival, and growth in estuarine ecosystems (Prytherch 1928; Butler 1949). In particular, the combination of high salinity and temperature increases oyster mortality due to disease (e.g., *Perkinsus marinus*) and predation (e.g., crabs, oyster drills) (Gunter 1955; Garton and Stickle 1980; Andrews and Ray 1988; Chu et al. 1993). The Mission–Aransas Estuary, located in the semi-arid south Texas Coastal Bend, is the southern-most in Texas to support a commercial oyster fishery. Water temperatures are generally warm, with a 32-year mean (±SE) temperature (1976–2007) of 23.1°C (± 0.04). Seasonality dominates the long-term monthly temperature means, ranging from 29.5°C (± 0.03) in the summer to 15.0°C (± 0.05) in winter. In south Texas, high temperatures limit oyster growth

most of the year (Copeland and Hoese 1966). Freshwater influence is minimal; precipitation patterns are highly variable and influenced by the El Niño Southern Oscillation (ENSO) (Ropelewski and Halpert 1986; Gershunov and Barnett 1998; Tolan 2007). Thus, the salinity structure is driven by episodic freshwater pulses (Orlando et al. 1993; Tolan 2007). On a year-to-year basis, evaporation far exceeds precipitation (Orlando et al. 1993). The 32-year mean (±SE) salinity is 19.3 (±0.06), with the long-term monthly means ranging from 23.1 (±0.25) in August to 17.9 (±0.18) in March. Long-term monthly salinity means were highly variable with no clear seasonality. Hypersaline conditions (>34) have been measured in 4% of all measurements. Oysters grow in comparably hypersaline conditions in many areas of the Atlantic and Gulf coasts, but only intertidally (Copeland and Hoese 1966).

A monthly oyster field monitoring program was initiated in the Mission–Aransas Estuary in 2007 to study the effects of changes in freshwater inflow on oyster biology and population dynamics. ENSO signals are linked to the salinity structure in Texas estuaries within a 4- to 6-month time frame (Tolan 2007). Globally, 2007 began with weak El Niño conditions which transitioned into near-average conditions by the end of March and then into moderate La Niña conditions for the remainder of the year (NCDC 2009). In 2008, the year began with La Niña conditions which returned to near-average conditions mid-year. El Niño/La Niña cycles occur irregularly, approximately every 2 to 7 years, with short-term climate changes that last approximately 1 year (NOAA 2009). Thus, in the Mission–Aransas Estuary, wet conditions and declining salinities prevailed during the first two thirds of 2007, and dry conditions with continuously increasing salinities prevailed in the last third of 2007 and throughout 2008. This 2-year period of drastically different environmental conditions provided the opportunity to examine the effects of flood events on oyster biology and population dynamics in the Mission–Aransas Estuary. The larger rationale for this investigation is that understanding the response of oysters to changing environmental conditions over the short term can help to predict long-term effects of climatic variability, particularly in light of a predicted future hotter, drier climate for the Gulf coast (Twilley et al. 2001; IPCC 2007; Nielsen-Gammon 2009).

Methods

The Mission–Aransas Estuary is a shallow, bar-built estuary on the south Texas coast. The estuary has an area of ~540 km^2 with an average depth of 2 m at mid-tide level (Fig. 1, NOAA 1990). The estuary comprises several bays; the two largest are Aransas Bay, the primary bay, located

closest to the Gulf inlets, and Copano Bay, the secondary bay, located closest to the Mission and Aransas Rivers. The estuary experiences a typical salinity gradient from the river mouths to the Gulf of Mexico. Only 15% of the annual freshwater inflow to the estuary is through gaged inflow; 49% of this comes from the Mission River and 15% from the Aransas River (Orlando et al. 1993). The estuary has low mixing efficiency ($e<0.05$) and long residence times (~360 days, Solis and Powell 1999). The salinity structure is driven by episodic freshwater pulses that depress salinities and then maintain low salinities for a prolonged period (Orlando et al. 1993).

Oysters in the Mission–Aransas Estuary primarily occur on large subtidal reefs in the low- to moderate-salinity regions of the estuary. Navigational maps indicate that the vertical relief (height of oyster reefs off the bottom) of these reefs ranges from ~0.3 to 1.8 m in height. In cooperation with the Texas Parks and Wildlife Department's (TPWD) Coastal Fisheries Division, oysters were sampled monthly in 2007 and 2008 by oyster dredge (0.5-m-wide, 5-cm-diameter mesh) at 20 randomly selected locations on known reefs in Copano Bay and Aransas Bay (442 sites over 2 years) to examine the impacts of changing environmental conditions on oyster populations (Fig. 1). Dredges were towed for 30 s in duration at a speed of 1.3 ms^{-1} for approximately 40 m in distance. Because oysters were collected by oyster dredge, a relatively inefficient gear, these data represent a relative index of abundance and oyster size (Powell et al. 2007). At each location, 19–20 live oysters (approximately 95% of all oysters collected) were randomly selected (removed from the total sample by trained TPWD personnel), measured for shell length and biomass parameters (wet weight, dry weight, ash-free dry weight). A subset of five live oysters was examined for quantification of spat (shell length ≤25 mm) settlement. The amount of dead shell (shell length >25 mm) in each sample was enumerated, and a subset of five shells was also examined for spat settlement. Although oyster reefs also occur in Mission, St. Charles, and Mesquite Bays (Fig. 1), these areas had no sampling effort and were thus excluded from this analysis.

Oysters were also examined for the presence of *P. marinus*, a protozoan parasite that causes severe mortalities in Gulf of Mexico oyster populations (Ray 1996). On a quarterly basis, 10 submarket (26–75 mm) and 10 market-size (≥76 mm) oysters were collected from eight fixed sampling locations on reefs in Copano Bay and Aransas Bay (Fig. 1). A section of mantle tissue was removed and incubated in Ray's fluid thioglycollate medium for 2 weeks following the culture method of Ray (1966). Tissue cultures were then stained with Lugol's solution and examined under the microscope. The percentage of oysters infected by *P. marinus* was calculated by dividing the number of oysters infected by the number of oysters tested. Infection intensity was ranked

Fig. 1 Mission–Aransas Estuary, TX, USA showing *P. marinus* sampling stations (*gray triangles*) and oyster sampling sites (*dark circles*) on oyster reefs within each bay
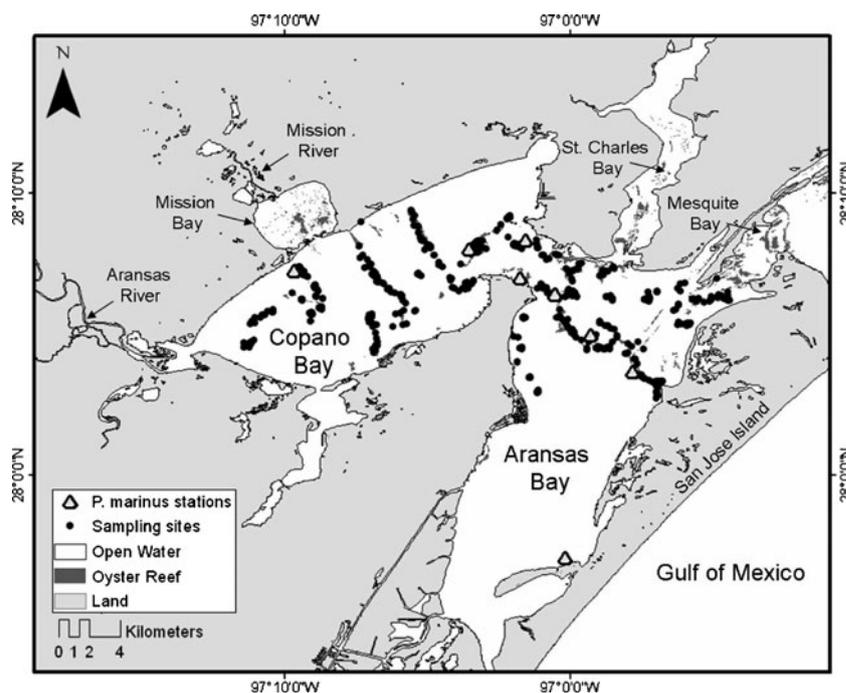
using a five-point scale (after Mackin 1962; modified by Craig et al. 1989) from uninfected (0) to heavily infected (5). Weighted prevalence was calculated by ranking the infections on the Mackin Scale and then calculating the average.

Hydrographic characteristics (salinity, temperature, dissolved oxygen, pH, and turbidity) were measured approximately 0.2 m above the top of the oyster reef at each station during each sampling period using a YSI series 6 data sonde. Daily river discharge values of the Aransas and Mission Rivers to the Mission–Aransas Estuary were measured from USGS upstream gages no. 08189700 (Aransas River near Skidmore, Texas) and no. 08189500 (Mission River at Refugio, Texas).

Allometric relationships between shell length and biomass are often used as an index of oyster growth. The relationship between mean shell length and mean weight can be expressed as a power function (Dame 1972):

$$L = aW^b \qquad (1)$$

where L is shell length (mm), W is wet, dry, or ash-free meat weight (g), and a and b are empirically derived coefficients. In this study, allometric parameters, a and b, were derived by fitting field data with Eq. 1. Allometric relationships were calculated for oyster populations in both bays and were compared with previously reported relationships (Table 1).

Bivalve filtration rate is a function of environmental variables such as temperature, salinity, and total suspended solids (TSS) (Dame 1972; Schulte 1975). Bivalve size also has important influences on filtration rate; in general, filtration rate increases with body size (Gerdes 1983; Riisgard 1988; Dame 1996). Concurrently measured hy-

drographic data (temperature, salinity, and TSS) and bivalve data (shell length) were used to model filtration rates. Missing TSS values were estimated from turbidity measurements using known TSS/turbidity ratios ($r=0.76$; $P<0.0001$). In this study, authors followed equations from Powell et al. (1992) which presented parameterized filtration rates of *C. virginica* as a function of temperature, salinity, and total particulate content. The filtration rate was empirically derived and modified previously (Doering and Oviatt 1986; Powell et al. 1992) in order to limit the number of size classes for modeling.

All statistical analyses were conducted using SAS version 9.2. Hydrographic and biological variables were log-transformed, and *P. marinus* variables were arcsine-transformed prior to statistical analysis. These transformations were performed to improve the distribution of the residual values for each measurement to approximate a normal distribution and to improve performance of multivariate tests that do not require this assumption. Pearson's correlation coefficients were calculated to determine the strength and direction of linear relationships between oyster and environmental variables and sampling date. A three-way analysis of variance (ANOVA) with bay, year, and oyster size class (submarket-size [26–75 mm] or market-size [≥76 mm]) as independent variables was used to test for differences between *P. marinus* weighted prevalence and percent infection in Copano and Aransas Bays in 2007 versus 2008. A two-way ANOVA with bay and year as independent variables was used to test for differences between filtration rates in Copano and Aransas Bays in 2007 versus 2008. A significant interaction effect was detected using the two-way ANOVA, and thus a

Table 1 Allometric relationships between shell length (L) and biomass of bivalves

W_{ww}, W_{dw}, and W_{afdw} are wet, dry, and ash-free dry weight, respectively. A and B are coefficients varying with different locations of the reefs in Galveston Bay, TX, USA. Overall, A ranges from 27.229 to 60.170, and B ranges from 29.408 to 46.390, respectively (see Hofmann et al. (1994) for more detail)

a	Bivalve species	Sites	Sources
$L=10^{1.582}W_{ww}^{0.330}$ $L=10^{1.846}W_{dw}^{0.258}$ $L=10^{1.957}W_{afdw}^{0.266}$	*Crassostrea virginica* (Eastern oyster)	Mission–Aransas Bay, Texas, USA	This study
$L=A\log W_{ww}+B$		Galveston Bay, Texas, USA	Hofmann et al. (1994)
$L=10^{1.645}W_{ww}^{0.340}$ $L=10^{1.892}W_{dw}^{0.291}$	*Crassostrea gigas* (Pacific oyster)	Seto Inland Sea, Japan	Kobayashi et al. (1997)
$L=10^{1.598}W_{ww}^{0.231}$ $L=10^{1.753}W_{dw}^{0.161}$		Kamakman Bay, South Korea	Hyun et al. (2001)
$L=19.97\ln W_{ww}+29.21$			Lee (1993)

simple main effects analysis was used for analysis of filtration rates.

Results

River discharge to the Mission–Aransas Estuary was an order of magnitude higher in 2007 than 2008 (Fig. 2a). This difference was due to more storm events (defined by river discharges 10 times greater than median discharge value) in 2007 than 2008 (Mooney 2009). In 2007, there were 12 storm events in the Mission River and 10 in the Aransas River. In 2008, there was only one storm event in the Mission River and two in the Aransas River. In 2007, the average discharge of water to the estuary (calculated from daily values) was 2.95×10^{8} m^{3}year^{-1} from the Mission River and 7.94×10^{7} m^{3}year^{-1} from the Aransas River. In 2008, the average discharge was 6.22×10^{6} m^{3}year^{-1} from the Mission River and 1.02×10^{7} m^{3}year^{-1} from the Aransas River.

The increased amounts of freshwater inflow to the Mission–Aransas Estuary in 2007 depressed salinities in Aransas Bay and Copano Bay and maintained them at low levels for several months (Fig. 2b). The largest rain event, in July 2007, caused the most rapid drop and lowest salinities in Copano Bay and Aransas Bay. Salinities remained <10 in Copano Bay for 7 months and in Aransas Bay for 5 months. For comparison, 20-year average salinities for Copano Bay and Aransas Bay are ~17 and 20, respectively. Beginning in late 2007 and continuing through 2008, salinities steadily increased as the south Texas coast experienced drought conditions. Salinities at the end of the study period were well above average, with salinities of 28 in Copano Bay and 30 in Aransas Bay.

In both Copano and Aransas Bay, monthly mean water temperatures varied seasonally, ranging from ~11°C in winter to ~31°C in summer (Fig. 2c). Dissolved oxygen levels ranged from ~4 mg l^{-1} in summer to 12 mg l^{-1} in winter, and levels declined over the study period. Turbidity levels were fairly constant over the study period, with peaks
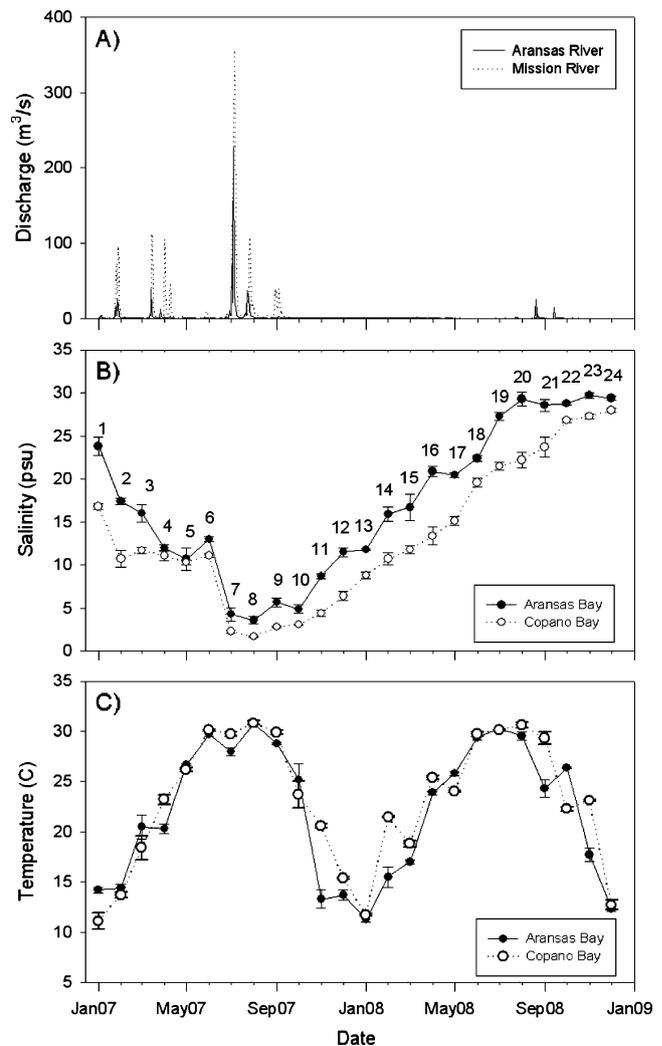
Fig. 2 Estuary hydrology. **a** Daily river discharge (m^{3}s^{-1}) from Aransas River (*solid line*) and Mission River (*dotted line*), measured from USGS upstream gages no. 08189700 (Aransas River near Skidmore, TX) and no. 08189500 (Mission River at Refugio, TX) (USGS data). **b** Monthly mean (±SE) salinities in Copano Bay and Aransas Bay 2007–2008; *numbers* indicate consecutively numbered months of sampling, **c** monthly mean (±SE) temperatures in Copano Bay and Aransas Bay 2007–2008

observed in May and August 2007, likely due to the concurrent high river discharge and the presence of resuspended particles.

Oyster abundances declined from 2007 to May 2008 in Copano Bay ($r=0.62$; $P=0.007$) and Aransas Bay ($r=0.41$; $P=0.10$) (Fig. 3a). Live oyster abundance was significantly positively correlated with salinity in Copano Bay ($r=0.17$; $P=0.010$); there was no relationship for Aransas Bay. Live oyster abundance in Copano Bay was also significantly negatively correlated with dissolved oxygen ($r=-0.20$; $P=0.003$) and turbidity ($r=-0.27$; $P<0.0001$). Dead shell abundance in Copano Bay was also significantly positively correlated with salinity ($r=0.21$; $P=0.002$).

Oyster shell lengths in Copano Bay ($r=-0.16$; $P<0.0001$) and Aransas Bay ($r=-0.17$; $P<0.0001$) declined significantly during the study period (Fig. 3b). The sharpest

decline was observed for oysters in both bays during the summer of 2008. Oyster shell lengths in both Copano Bay ($r=-0.26$; $P<0.0001$) and Aransas Bay ($r=-0.13$; $P<0.0001$) were negatively correlated with salinity and positively correlated with dissolved oxygen ($r=0.17$) and turbidity ($r=0.05$) during the study ($P<0.02$). Shell lengths were significantly greater in Aransas Bay than in Copano Bay ($P=0.0008$). In both bays, there was a trend of increasing abundance of submarket-size oysters and decreasing abundance of market-size oysters. The ratio of market- to submarket-size oysters declined significantly ($r=-0.55$; $P=0.006$) in Copano Bay and did not change in Aransas Bay over the 2-year study.

The differences in settlement patterns of oyster spat on live oysters between 2007 and 2008 for Copano Bay and Aransas Bay were obvious and dramatic (Fig. 3c). Spat abundance significantly increased from 2007 to 2008 ($P<0.0001$). In 2007, during the period of low salinities, there was very little spat settlement. In 2008, with higher salinities present in the estuary, spat settlement increased throughout the summer and fall (coincident with increases in oyster abundance). Spat settlement was significantly positively correlated with salinity ($r=0.45$, $P<0.0001$). The same trend was observed for spat settlement on dead shell. Spat settlement was also significantly positively correlated with temperature and significantly negatively correlated with dissolved oxygen and turbidity ($P<0.05$).

Oyster shell lengths were normally distributed in 2007, ranging in size from 26 to 155 mm with a mean shell length ($\pm$SE) of 72.3 ($\pm$0.45) mm (Fig. 4). Oysters in the 40–120-mm-size classes were collected in 11–12 months of the year. In 2008, oyster distribution became bimodal. A large increase in the abundance of oysters in the smallest-size classes was observed in August through November as recently settled spat ($\leq$25 mm) grew into the smallest-juvenile-size classes. Shell lengths in 2008 ranged from 26 to 136 mm with a mean shell length ($\pm$SE) of 65.6 ($\pm$0.46) mm. Oysters in the 40–110-mm-size classes were collected in all months.

Based on quarterly measurements of oyster disease, the highest mean *P. marinus* weighted prevalence and percent infection occurred in early 2007 (Fig. 5). Weighted prevalence and percent infection decreased coincident with reduced salinities and temperatures in fall 2007 and increased steadily throughout 2008. *P. marinus* weighted prevalence ($r=0.46$; $P=0.0004$) and percent infection ($r=0.40$; $P=0.003$) in market-sized oysters (>75 mm) were significantly positively correlated with salinity. There were no significant correlations between disease parameters and temperature. *P. marinus* percent infection and weighted prevalence data were lagged by one and two quarters and also examined for relationships with temperature and salinity, but no consistent patterns emerged. Percent infection of oysters by *P. marinus* ($P=0.04$) and *P. marinus* weighted prevalence ($P=0.02$) were both
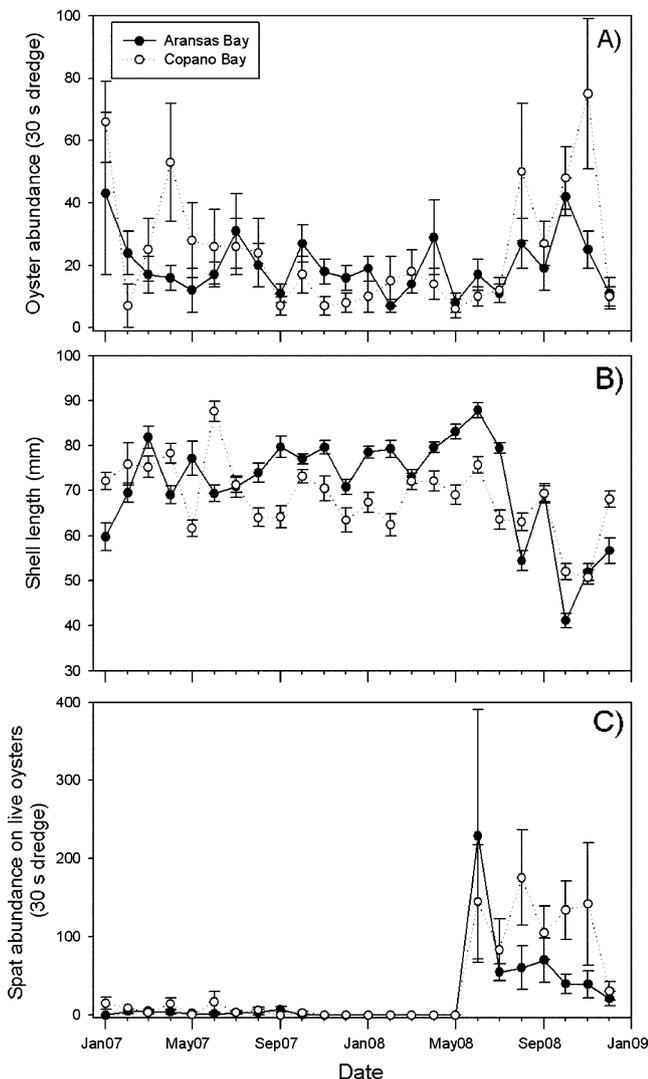
Fig. 3 Monthly mean ($\pm$SE) oyster metrics. **a** Abundance (number per 30-s dredge). **b** Shell length (mm). **c** Number of spat on live oysters in Copano Bay and Aransas Bay
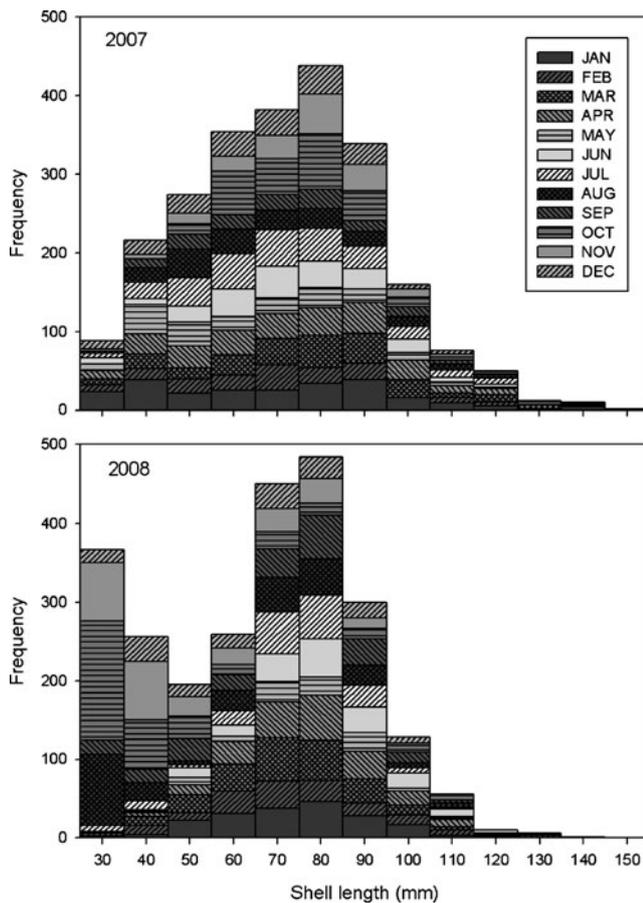
Fig. 4 Monthly size distribution of oyster shell lengths (mm) in 2007 and 2008

significantly higher in market-sized oysters (≥76 mm) than in submarket-sized oysters (26–75 mm). Weighted prevalence and percent infection did not differ between bays or between years, and there were no significant interaction effects (all $P>0.05$).

Allometric relationships between shell length and biomass (Eq. 1) were derived from oyster data collected from both bays in 2007 and 2008. Oyster shell lengths were significantly correlated with various meat weights (wet, dry, and ash-free dry weight) measured in the two bays (Fig. 6). The rate of increase in shell length was higher per unit weight for smaller oysters and lower for larger oysters. Empirically derived allometric relationships between shell length (mm) and biomass (g) of bivalves are listed in Table 1. The coefficients (a and b) for the allometry in this study ($a = 10^{1.582}$; $b=0.33$) were similar to those reported in previous studies of *Crassostrea gigas* (Kobayashi et al. 1997; Hyun et al. 2001) and *C. virginica* (Hofmann et al. 1994).

Filtration rates (milliliter per individual per minute) of oysters collected from both bays for 2007 and 2008 were modeled using the equations of Powell et al. (1992) (Fig. 7) to examine the effects of temperature, salinity, and total

suspended solids. Oyster filtration rates in 2007 were significantly lower than in 2008 for both Copano Bay and Aransas Bay ($P<0.05$). Within years, oyster filtration rates in 2007 were significantly higher in Aransas Bay than in Copano Bay ($P<0.05$), and in 2008 oyster filtration rates were similar between bays. Mean filtration rates (±SD) in 2007 were 16.6 (±11.2) ml per individual per minute in Aransas Bay and 12.9 (±13.3) ml per individual per minute in Copano Bay. Mean filtration rates in 2008 were 22.8 (±11.0) ml per individual per minute in Aransas Bay and 23.8 (±10.5) ml per individual per minute in Copano Bay.

Discussion

Resilient systems are able to return to pre-disturbance or near-pre-disturbance conditions within a reasonable time frame following a disturbance (Holling 1973). Floods can be classified as disturbance events in estuaries because rapid changes in salinity can affect benthic communities (Montagna et al. 2002). The timing, magnitude, and duration
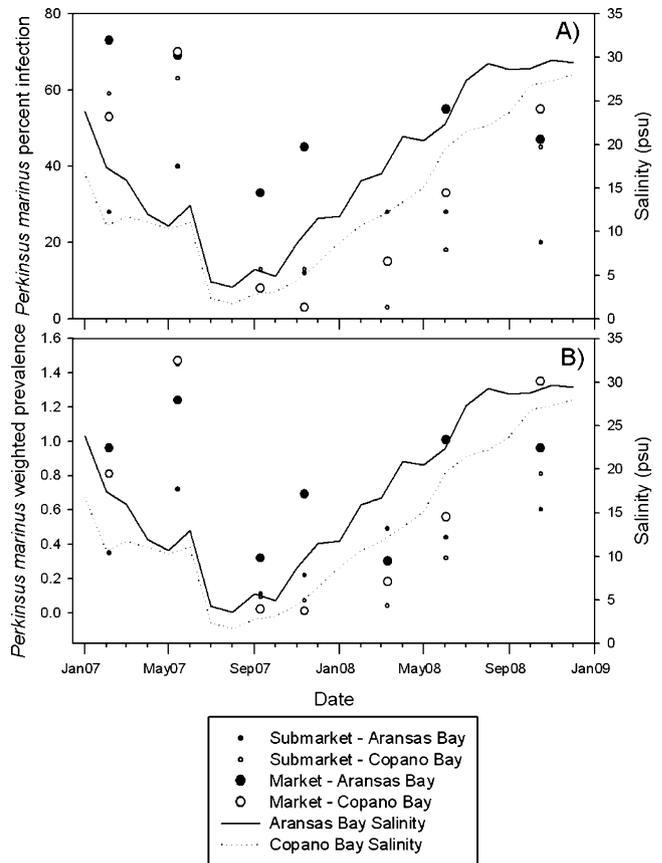
Fig. 5 Quarterly mean *P. marinus* **a** percent infection and **b** weighted prevalence in submarket- and market-sized oysters in Copano Bay and Aransas Bay 2007–2008. *Solid* and *dashed lines* are monthly mean salinities in Aransas Bay and Copano Bay, respectively

Fig. 6 Oyster allometry. Relationships between **a** shell length (mm) and wet weight (g), **b** shell length (mm) and dry weight (g), **c** shell length (mm) and ash-free dry weight (g), and **d** dry weight (g) and wet weight (g). Equations are allometric relationships and values of r^2 are correlation coefficients for fitted curves
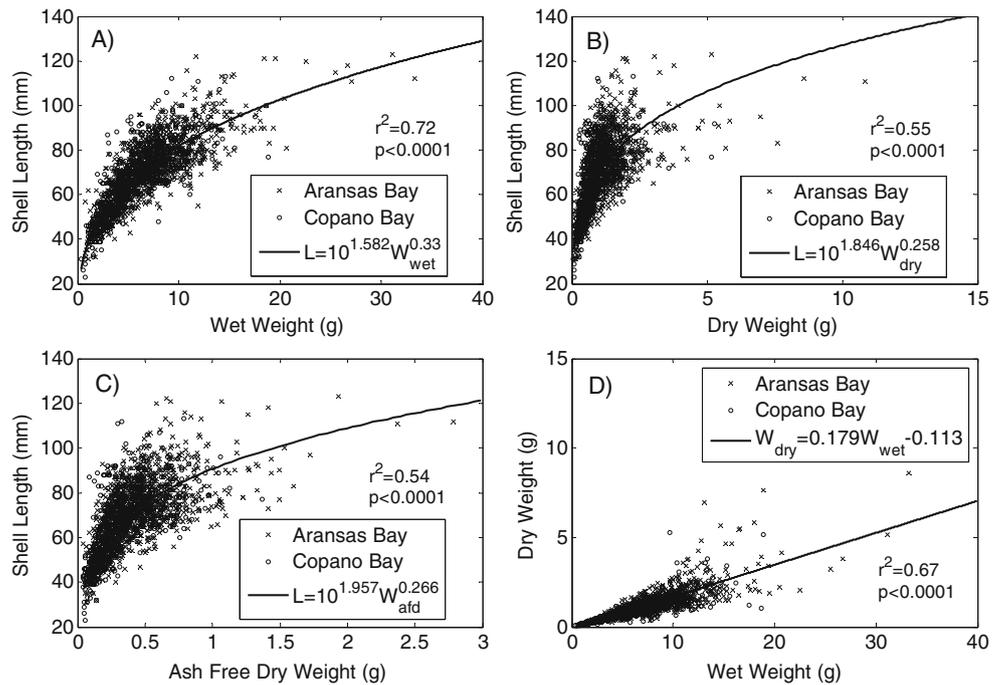
of flood events and the rate of salinity change can have varying effects on oyster population dynamics (La Peyre et al. 2009). In general, the flood events in 2007 were associated with temporary reductions in oyster abundance, spat settlement, disease levels (weighted prevalence and percent infection), and filtration rates. In Copano Bay, oyster abundance and the ratio of submarket- to market-sized oysters declined significantly during the study period, and live oyster and dead shell abundance were significantly correlated with salinity. These responses were not observed in Aransas Bay and may have been modulated by the generally higher salinities during the study period. Reductions

Fig. 7 Calculated oyster filtration rates (all size classes) for 2007 and 2008 in Aransas Bay and Copano Bay. *Boxes* represent the upper and lower quartiles and median value. *Error bars* are one standard deviation above and below the mean and *dots* represent outlier values

in disease levels should be interpreted with caution, as it is possible that mortality of oysters post-flood contributed to the decline in disease levels if oysters with higher weighted prevalence died at a faster rate than those with lower weighted prevalence (La Peyre et al. 2003). Salinities during the normal spawning period remained below 10 in Copano Bay for 7 months and in Aransas Bay for 5 months. Oysters that are exposed to sustained low salinities can experience depression or arrest of gametogenesis, disintegration of gonads, delayed spawning, and catastrophic post-settlement mortality (Loosanoff 1953; Allen and Turner 1989; Livingston et al 1997). Indeed, although fully developed gonads were observed in oysters from the Mission–Aransas Estuary, no major spat settlement was observed in 2007.

Oysters in Gulf coast estuaries have several unique characteristics that support resilience and rapid recovery following flood disturbance. Because of the long period of warm temperatures in Gulf coast estuaries, the spawning period is extended, often resulting in two major spawning events in the spring and the fall, with minor spawning throughout the summer (Hayes and Menzel 1981). The extended period of warm temperatures promotes faster growth of spat—oysters that set in the spring grow to sexual maturity and spawn before the end of their first year (Menzel 1951; Butler 1954). In contrast, in northern estuaries, the spawning period is compressed and oyster populations are often limited to a single spawning period during the summer months (Kennedy and Battle 1964). Once set, growth rates tend to be higher in warmer Gulf coast waters (Gunter 1951; Loosanoff 1965), with oysters reaching 90 mm SL in 2 years, whereas 4 to 5 years are

required to reach the same size in northern waters such as Long Island Sound (Churchill 1921). The role of tertiary bays as sources or sinks for oyster larvae is unknown, although intra-estuarine circulation is diminished due to spit accretion and shell berm formations, which partially isolate bays such as Mission Bay from Copano Bay (Brown et al. 1976). The relatively warm temperatures year-round in the Mission–Aransas Estuary may also be responsible for the lack of a relationship between *P. marinus* disease and temperature in the current study. This response is consistent with data collected in the Mission–Aransas Estuary from 2004 to 2009. Warm winter temperatures can result in a higher proportion of over-wintering parasite cells and is critical in the development of *P. marinus* epizootics (Ewart and Ford 1993; Powell et al. 1996; Cook et al. 1998).

The semi-arid Mission–Aransas Estuary has a unique combination of characteristics that helps to promote oyster growth and survival under harsh environmental conditions. The estuary has low mixing efficiency and long residence times (Solis and Powell 1999). Thus, despite relatively small volumes of freshwater inflow, the Mission–Aransas Estuary has a good memory of flood events—isolated freshwater pulses, once introduced, are retained within the system (Orlando et al. 1993). Indeed, following the July 2007 flood disturbance, salinities within Copano Bay and Aransas Bay remained less than pre-flood levels for 11–12 months.

Floods appear to play an important ecological role in estuarine ecosystems. *P. marinus*, the most severe oyster disease in Gulf coast estuaries, is most prevalent in oyster populations in warm, high-salinity waters (Ogle and Flurry 1980). Freshwater inflow, depending on the volume, may dilute or even eliminate infective *P. marinus* stages in low-salinity areas (Mackin 1956; La Peyre et al. 2009). Oysters living in less saline water have the additional advantage of reduced predation pressure (Gunter 1955). Two important oyster predators in Gulf coast estuaries, the southern oyster drill *Thais haemastoma* and the stone crab *Menippe mercenaria*, are intolerant of sustained salinities of <15 (Menzel et al. 1958; MacKenzie 1977). High salinities during droughts allow these predators to become established outside their normal range, and flood conditions can eliminate these populations (Menzel et al. 1966; Breithaupt and Dugas 1979). Although flood disturbance may temporarily reduce or destroy oyster populations (Hofstetter 1977), floods also result in salinities unfavorable for predators and disease, and consequently facilitate oyster population recovery. The timing of storm events is also important and can have significant effects on *P. marinus* infection intensities and oyster mortality. Laboratory-based experiments suggest that oysters with moderate *P. marinus* infection intensities would be able to survive flood events in winter and spring but not in summer (La Peyre et al. 2003). The rate of salinity change or duration of lowered salinity may also be important.

Oysters exposed to a 24-h salinity reduction from 25 to 1 in the laboratory suffered higher cumulative mortalities than those exposed to a 1-week salinity reduction (La Peyre et al. 2009).

Flood disturbances followed by conditions that lower stress, both physiologically and due to reduced predation and disease, are important for the rapid reestablishment of oyster populations in the Mission–Aransas Estuary. From January to June 2007, flood disturbance reset the system— moderating salinities, predators, and disease. In the dry period that began in late 2007 and continued through 2008, salinities steadily increased to pre-flood levels, successful spat settlement occurred, oyster abundance increased, and disease levels increased. Multivariate analyses demonstrate that spat abundance is strongly positively correlated with salinity in the Mission–Aransas Estuary, which may ultimately drive the recovery of oyster populations following flood disturbance. From June to November 2008, the increases in oyster abundance were coincident with decreases in shell length, indicating that recently settled spat (5–25 mm) had survived and grown into the smallest-juvenile-size class. This is confirmed by the bimodal size distribution of oyster shell lengths in 2008. A post-settlement population dynamics model (Hofmann et al. 1992) is being calibrated for 2008– 2009 to better understand effects of changing environmental conditions on oyster population dynamics.

Dry and warm conditions are favorable for *P. marinus* infection (Soniat 1985; Andrews and Ray 1988), and those environmental conditions prevailed in 2008. *P. marinus* weighted prevalence, which was at its lowest levels post-flood, had steadily risen to pre-flood levels by the end of 2008. Percent infection still remained slightly below pre-flood levels, likely due to the predominance of small oysters not yet infected by the parasite. Simulations have demonstrated that oyster populations are able to expand more rapidly than *P. marinus*; thus, newly abundant populations of uninfected oysters are very unlikely to produce epizootics (Powell et al. 1996). Even at high salinity, an oyster population can resist a *P. marinus*-induced population crash as long as recruitment of uninfected individuals continues (Hofmann et al. 1995). Oysters with low infection levels may not have been successfully detected by the Ray's fluid thioglycollate medium technique (Bushek et al. 1994).

Estimated oyster filtration rates in 2007 were 27–46% lower than those in 2008, which was attributed to flood events and continuing low salinities. Oysters growing under sustained low-salinity conditions have been shown to cease or exhibit abnormal feeding activity (Loosanoff 1953; 1965). Bivalve filtration rate can be influenced by temperature (Dame 1972; Buxton et al. 1981) and turbidity or suspended solid concentrations (Schulte 1975; Hofmann et al. 1994), but there were no significant effects caused by these environmental conditions during the study period. Size also

affects bivalve filtration rates; in general, filtration rates increase with body size (Gerdes 1983; Doering and Oviatt 1986; Riisgard 1988). Further work is being conducted to determine the contribution of individual size classes to the filtration rates in the Mission–Aransas Estuary. Understanding the extent of changes in filtration rates as a result of episodic flood events is important because, as suspension feeders, oyster feeding activities may have strong effects on plankton and seston dynamics, nutrient cycling, and the overall functioning of shallow-estuarine systems (Dame et al. 1984; 2001; Grizzle et al. 2008). When populations are abundant, oysters can potentially regulate the availability of resources to other organisms by changing the quantity and quality of biotic and abiotic materials (Dame et al. 2001; Newell 2004). However, Dame et al. (2002) found that the presence or absence of oysters in ephemeral tidal creeks had minimal influence on organismal and population level characteristics.

Although estuaries are defined by salinity change over tidal cycles, floods of varying intensity, frequency, and duration can dramatically alter estuarine salinity regimes and affect benthic communities (Ritter et al. 2005). Episodic flood events appear to play a critical role in promoting long-term oyster population growth and survival in the semi-arid Mission–Aransas Estuary. In particular, freshwater pulses are retained within the system, which is important for moderating predation and disease and allowing for rapid reestablishment of oyster populations. The response of oysters to changing environmental conditions over the short term indicates long-term effects of climatic variability. In the future, for a given amount of precipitation, water demand and evaporation in Texas will increase and water supply will decrease (Nielsen-Gammon 2009). These changes could be devastating to oyster populations unless episodic floods occur.

Information on the mechanisms by which natural and anthropogenic disturbances, including management activities, affect individual species can help managers to identify ways to use disturbance to their advantage, or conversely, alert them to necessary post-disturbance mitigations (Falk et al. 2006). Likewise, understanding the ways in which episodic flooding promotes oyster growth and survival provides valuable guidance for ongoing research on the effects of long-term climatic variability in Gulf coast estuaries.

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