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Population dynamics of the eastern oyster in the northern Gulf of Mexico

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POPULATION DYNAMICS OF THE EASTERN OYSTER IN THE NORTHERN GULF OF
MEXICO

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The School of Natural Resources

by
Benjamin S. Eberline
B.S., Virginia Polytechnic Institute and State University, 2009
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Abstract

This project examined the economically and ecologically valuable eastern oyster (*Crassostrea virginica*) in the Northern Gulf of Mexico using field and laboratory experiments. Specifically, this project focused on natural rates of settlement, growth, and mortality in a variety of temperature and salinity regimes within Breton Sound, LA. Seed and market sized oysters in cages resting on the bottom, as well as settlement tiles, were monitored at four sites in Breton Sound, LA, along what is typically a salinity gradient ranging from ~5 to ~20. In April 2010, the Caernarvon Freshwater Diversion was fully opened with the goal of minimizing the impacts of the Deepwater Horizon oil spill on wetlands, resulting in extreme low salinity (< 2) at all sites through August 2010. High seed and market-sized mortality and reduced condition were observed in oysters at all sites. *Perkinsus marinus* infection prevalence in surviving market oysters was low at all sites and all infection intensities were light. Settlement only occurred at the highest salinity site. In May 2011, the Mississippi River flooded to record levels, resulting in low salinity (< 10) at all sites through June 2011. This short period of low salinity minimized disease infection intensity and settlement at all sites. Oysters at the lowest salinity site experienced high mortality and low growth. Oysters at higher salinity sites experienced limited mortality, mostly from predation, along with higher growth and condition. While low salinity may be beneficial to oyster populations by reducing *P. marinus* infection levels, prolonged extreme low salinity through spring and summer appears to cause heavy mortality and negatively impact recruitment in the short term. While not only is it clear that the timing and duration of freshwater inputs will significantly affect the impacts on oyster resources, it is likely that large scale global climate patterns (including El Niño and La Niña events) will also modify how and to what extent freshwater events may affect Breton Sound. This project highlights the importance of understanding the timing and duration of low salinity events and their impacts on oyster life history stages.

Chapter 1: Introduction

Oyster reefs around the world are quickly becoming the most jeopardized marine habitats, with a greater than 90% decline from historic levels and 85% permanently lost (Beck et al. 2009; Kirby 2004; Mackenzie 2007). In the northern Gulf of Mexico, the native eastern oyster (*Crassostrea virginica*) has proven to be an extremely important commercial and ecological resource (ASMFC 2007; Coen et al. 2007; Kennedy 1996; Lellis-Dibble et al. 2008; Plunket and La Peyre 2005). The commercial fishery surrounding harvest of *C. virginica* provides nearly \$296 million in total economic effect to the state of Louisiana annually (LDWF 2005). Not only this, but eastern oyster reefs are focal points for ecological importance due to the bioengineering nature of the species. Reefs provide habitat for a multitude of aquatic species, including refuge for prey species, feeding grounds for predators, and spawning areas for both (Grabowski and Powers 2004; Harding and Mann 2001; Lenihan et al. 2001; Peterson et al. 2003; Soniat et al. 2004). Additionally, oyster reefs can dramatically improve water quality and stabilize shorelines (Dame and Libes 1993; Dame et al. 1984; Meyer et al. 1997; Piazza et al. 2005; Smith et al. 2009). However, oysters may not provide these eco-services for much longer because they are in danger due to decades of over-exploitation, shifting abiotic factors, and prolonged exposure to predation and disease (Beck et al. 2011; Harvell et al. 1999).

Fortunately, Louisiana estuaries along the northern Gulf of Mexico coast have one of the most productive oyster industries in the world, accounting for 34% of the United States' landings and over 50% of Gulf of Mexico landings (LDWF 2009). This highly productive commercial fishery can be attributed partly to the Louisiana Department of Wildlife and Fisheries' (LDWF) management system. LDWF manages public grounds for the production of sub-market oysters for transplant to private leases where they are cultivated and subsequently harvested. Louisiana's management combination of public seed grounds and private leases is an essential facet to its relatively successful marriage between government regulation and commercial harvest. The largest of several public seed grounds is located in Breton Sound, LA. However, like many Louisiana estuaries, Breton Sound has been subjected to altered flow regimes and even isolation from Mississippi River input. In order to address this isolation, structures were developed to divert river flow directly back into coastal wetlands. One such freshwater diversion of particular importance is the Caernarvon Freshwater Diversion (CFD). This large-scale structure restores

freshwater to the Breton Sound estuary directly from the Mississippi River. While CFD was originally developed to benefit oyster resources, there is still considerable controversy over the effects of its freshwater flows on Breton Sound (DeLaune et al. 2003; Hyfield et al. 2008; La Peyre et al. 2009; Lane et al. 2004; Snedden et al. 2007; US Army Corps of Engineers 1984).

The productivity of highly variable large coastal river ecosystems is greatly influenced by freshwater flows, especially when anthropogenic activities have altered the freshwater quality, quantity, and timing (Poff et al. 2007). With downstream estuaries like Breton Sound dependent upon nutrient-rich riverine waters for high productivity, altered flow regimes directly impact physicochemical characteristics including salinity, temperature, and organic matter concentrations. The shift of these attributes can then affect key ecosystem processes such as biological productivity (Fry 2002; Kimmerer 2002; Sklar and Browder 1998). Therefore, CFD's impacts are of the utmost importance, especially since Breton Sound is home to the largest public oyster seed grounds and high amounts of both public and private oyster activity.

Furthermore, dramatically increased oyster harvest levels in Breton Sound, in addition to factors like environmental disturbances (e.g. hurricanes) over the last 15 years have caused not only a net loss of shell, which is essential for future seed availability and thus oyster production, but also declining statewide oyster stock size since 1989 (Figure 1.1). While the state cannot manage natural disturbances such as hurricanes, they do control oyster harvest levels on the public seed grounds. Therefore, determining the quantity of seed oysters that can be harvested from public grounds in any given year is of primary importance because management of oyster harvest for long term fishery sustainability is the ultimate goal.

With the complex nature of oyster production, a management tool based on natural rates of recruitment, growth, and mortality is necessary to determine (1) how many new oysters are being created annually, (2) how fast they are reaching harvestable size, and (3) how many are lost before being harvested. Currently, scientific models based on these three factors and more exist in areas like the Chesapeake and Delaware Bays and can be used by management agencies to predict maximum sustainable harvest from commercially-fished oyster grounds (Klinck et al. 2001; Powell et al. 2008; Powell et al. 1994). Such a management tool based on data and field tests from the eastern oyster fishery in the Gulf of Mexico does not exist.

Given that managers in coastal Louisiana work in a highly variable and ecologically unique environment compared to other oyster producing states, especially in terms of abiotic

factors (e.g. temperature and salinity) that affect oyster production, the need for a region-specific management model is critical. In order to develop a predictive management model, natural recruitment, growth, and mortality rates of Louisiana oysters need to be known to better understand the driving factors behind optimal oyster production conditions. The primary factors that control these conditions, and thus drive recruitment, growth, and mortality, are temperature and salinity (Butler 1949; Galstoff 1964; Gunter 1953; Bataller et al. 1999). These abiotic factors vary greatly between regions, e.g. Delaware Bay, Chesapeake Bay, and Gulf of Mexico, and can even vary between sites within regions. The result is highly region-specific, and sometimes site-specific, water temperature and salinity level requirements that contribute to optimal oyster production conditions.

Temperature and salinity directly control recruitment, with the majority of spawning events only occurring at water temperatures greater than 25°C and a salinity range of 10 to 30 (Cake 1983; Dekshenieks et al. 1993; Hayes and Menzel 1981; Ingle 1951). In the Chesapeake Bay, these conditions may only exist from approximately June to October, while the Gulf of Mexico may provide suitable conditions from April to November. Additionally, a salinity range of 18 to 22 is optimal for oyster larvae setting in the northern Gulf of Mexico (Chatry et al. 1983; Pollack et al. 2011). While other factors contribute directly to the success of recruitment, like proper substrate and/or light conditions, temperature and salinity remain the major driving factors, and show region-specificity (Butler 1949; Ingle 1951; Loosanoff and Nomejko 1951; Obeirn et al. 1995; Ortega and Sutherland 1992; Turner et al. 1994).

Temperature and salinity also play a major role in the growth and mortality of *C. virginica*. While these oysters can survive sustained salinities from 5 to 40, growth (along with most physiological processes) is greatly increased at levels of 10 to 20 (Butler 1949; Gunter 1955; Galstoff 1964; Gullian and Aguirre-Macedo 2009; Heilmayer et al. 2008; Encomio et al. 2005). In fact, oysters use anaerobic respiration for survival if salinity levels become extremely low. This can lead to mass mortality if exposure remains under 2 for several weeks (Galstoff 1964; Gunter 1953; Heilmayer et al. 2008; Loosanoff 1953; Shumway 1996). *C. virginica* can also become dormant at water temperatures below 8°C, or be killed with long exposure to temperatures above 32° to 34°C (Galstoff 1964; Austin et al. 1993). However, within the extremes, oyster growth increases as water temperature increases assuming adequate food

availability. For example, individual oysters in the Gulf of St. Lawrence (northern-most populations) can take four years to reach spawning size, when in the Gulf of Mexico oysters can reach the same size within 4 weeks of settlement (Cake 1983; Dekshenieks et al. 1993; Ortega and Sutherland 1992; Powell et al. 2002; Singh and Zouros 1978).

Predation and disease are the main contributors to oyster mortality in the Gulf of Mexico, and these factors are in turn also largely controlled by water temperature and salinity levels. Predation, mainly from oyster drills (*Stramonita haemastoma* - a predatory snail), fish like the black drum (*Pogonias cromis*), and crabs like stone crabs (*Menippe adina*), is much more prevalent with higher salinities and water temperatures (Cake 1983). Disease, mainly from the pathogen Dermo (*Perkinsus marinus*), is also more lethal at increased salinity levels and water temperatures (Chu and La Peyre 1993; Chu et al. 1993; Hofmann et al. 1995; La Peyre et al. 2009; La Peyre et al. 2003; Ragone and Bureson 1993; Volety et al. 2000). Disease is another factor of oyster population dynamics that is highly region-specific. For example, the Chesapeake Bay has problems with MSX (disease caused by parasite *Haplosporidium nelson*), which poses no real threat to Gulf of Mexico oysters (Volety et al. 2000). This region-specificity can be attributed to either abiotic differences or perhaps genetic stock diversity (Encomio et al. 2005; Hare et al. 2006).

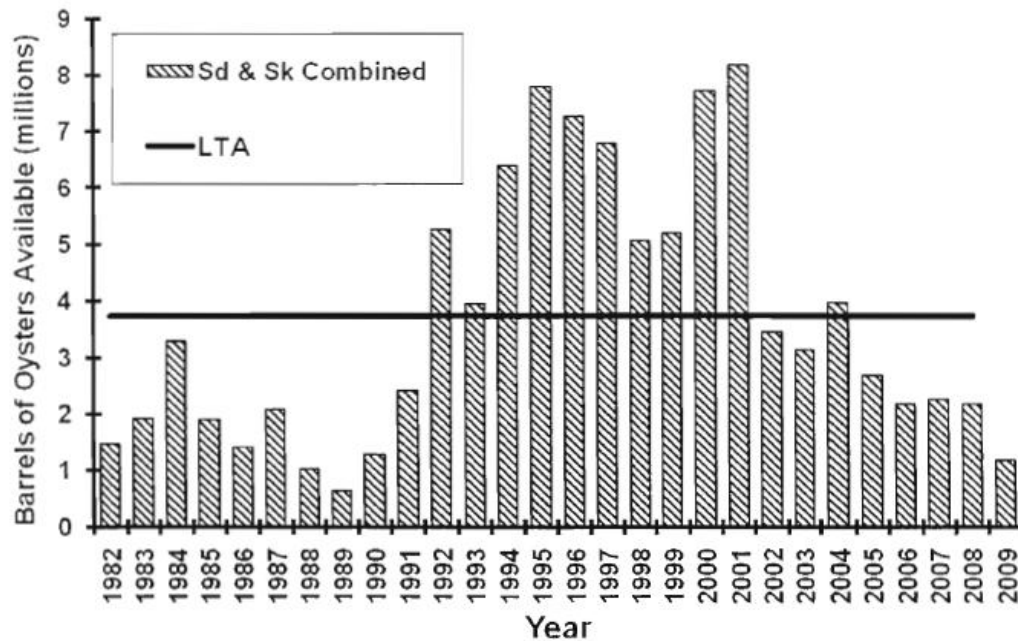


Figure 1.1 Historical estimated oyster stock size (Sd = seed oysters; Sk = market oysters) on the public oyster areas of Louisiana. LTA denotes long-term average. (LDWF 2009)

The objectives of this project were to quantify natural oyster recruitment, growth, and mortality along a salinity gradient in Breton Sound, LA, in order to support the development of a region specific population model for the eastern oyster. This project also monitored oyster plasma osmolality, condition index, and dermo infection intensities to paint a more complete picture of the complex interactions that drive recruitment, growth, and mortality. The information collected from this project is being used to inform a management model being developed for the Breton Sound oyster seed ground.

During the course of this study, two events occurred that provided the opportunity to collect unique data. In 2010, as a response to the BP oil spill in the Gulf of Mexico, the CFD structure was opened to near capacity flow of $225 \text{ m}^3 \text{ s}^{-1}$ for several months. Chapter 2 reports on the Breton Sound water quality and oyster response during 2010 to this large flux of Mississippi river water from the prolonged freshwater diversion. In 2011, the Mississippi River experienced a 100-year flood, reaching record levels across the South. At Tarbert Landing, MS, the river's discharge maxed out at 45,845 cubic meters per second. Chapter 3 reports on the Breton Sound water quality and oyster response during this event.

Chapter 4 synthesizes the information from both 2010 and 2011 to provide a complete picture of oyster population dynamics, and the effects of salinity and temperature in the Breton Sound estuary. Additionally, it places these potentially different water events in a 20 year context of freshwater inputs.

Chapter 2: Prolonged Freshwater Exposure and Its Effects on Eastern Oysters in Breton Sound, Louisiana

2.1 Introduction

On April 20, 2010 the explosion of the *Deepwater Horizon* oil rig drilling on the BP prospect Macondo resulted in the largest oil spill (DHOS) in history. Nearly 5 million barrels of oil ($\sim 800,000 \text{ m}^3$) were released into the Gulf of Mexico before the well was capped almost three months later on July 15. By August 4, half of the spilled oil had been directly recovered from the wellhead, burned, skimmed, evaporated, or dissolved. An additional 24% was chemically or naturally dispersed, and was being degraded within marine waters. The final 26% included light oil sheen around the surface, weathered tar balls, or oil washed ashore. More than 650 miles of Louisiana, Mississippi, Alabama, and Florida Gulf coast were oiled (Graham et al. 2011). The DHOS has the potential to impact all aspects of marine life from hydrothermal vent communities in the deep ocean to massive planktonic populations and subsequently reliant fish food webs at the surface to sensitive wetlands and seabirds onshore. However, the impacts are still not clear, and possible long term effects will not be realized for years to come (Fodrie and Heck 2011; Graham et al. 2011; Graham et al. 2010; Ober 2010).

Louisiana's fragile coastal habitats were hit hardest, with over 100 miles considered moderately to heavily oiled. A multitude of marine and coastal species were exposed to oil, and of particular economic importance were those species that represent the Louisiana seafood industry (Graham et al. 2011; Ober 2010; Gohlke et al. 2011). The eastern oyster (*Crassostrea virginica*) is one species that has a major impact on Louisiana seafood economics (LDWF 2005). Oil in estuarine waters can significantly affect oyster populations through filtration, accumulation, and fouling (Roberts et al. 2008; Hulathduwa and Brown 2006; Banks and Brown 2002; Michel and Henry 1997). However, while oil did hit Louisiana shores and may have affected oyster populations, it is still not clear that oil entered all Louisiana estuaries and the full array of effects on oysters is unknown.

Several freshwater diversion structures along the estuary were opened to maximum capacity in order to push Mississippi River water into the bays and keep potentially oiled marine waters offshore. The result was an estuary exposed to prolonged high freshwater input during times of rising water temperature. This consequently affected the typical salinity gradient of Breton Sound, a key parameter in oyster population dynamics.

The objectives of this project were to quantify the effects of prolonged freshwater exposure from diversions on natural oyster population dynamics along what is normally a salinity gradient ranging from 5 to 20 in Breton Sound, LA. These data will also be used in the development of a region specific population model for the Gulf of Mexico eastern oyster.

2.2 Methods

Study Area

This study was conducted in Breton Sound, LA, a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana. Breton Sound consists of microtidal bays, lakes, bayous, and canals and contains fresh, intermediate, brackish and salt marsh types. The Breton Sound estuary is subject to flooding from the Caernarvon Freshwater Diversion structure (Caernarvon). Caernarvon became operational in 1991 and was designed to moderate salinities and reintroduce controlled river inflows to Breton Sound. Caernarvon is located at the head of Breton Sound and pulses are capable of delivering substantial amounts of fresh water (up to $249 \text{ m}^3 \text{ s}^{-1}$) to the basin (Snedden et al. 2007). Yearly winter/spring experimental high-flow releases began in spring 2001 to simulate seasonal flood-pulse events. Pulses release periodic large fluxes of river water into the basin and are capable of inundating upper basin marshes for several days. In response to the Deep Horizon oil spill occurring April 20, 2010, Caernarvon was opened April 24, 2010 to near capacity flow of $225 \text{ m}^3 \text{ s}^{-1}$ until August 10 in an attempt to prevent oil from entering into Breton Sound (Figure 2.1).

Oysters

All oysters (eastern oyster; *Crassostrea virginica*) used for the field study were collected by dredge from public and private oyster leases located within Breton Sound in February 2010. Experiments used 2,400 total oysters, half of which were seed size oysters ($< 75 \text{ mm}$), and half were market size oysters ($> 76 \text{ mm}$). Collected oysters were stored at Louisiana Sea Grant Bivalve Hatchery located on Grand Isle, LA and maintained in cages until deployment. Average salinity and temperature in Grand Isle during this period were 21.4 and 18.3°C , respectively.

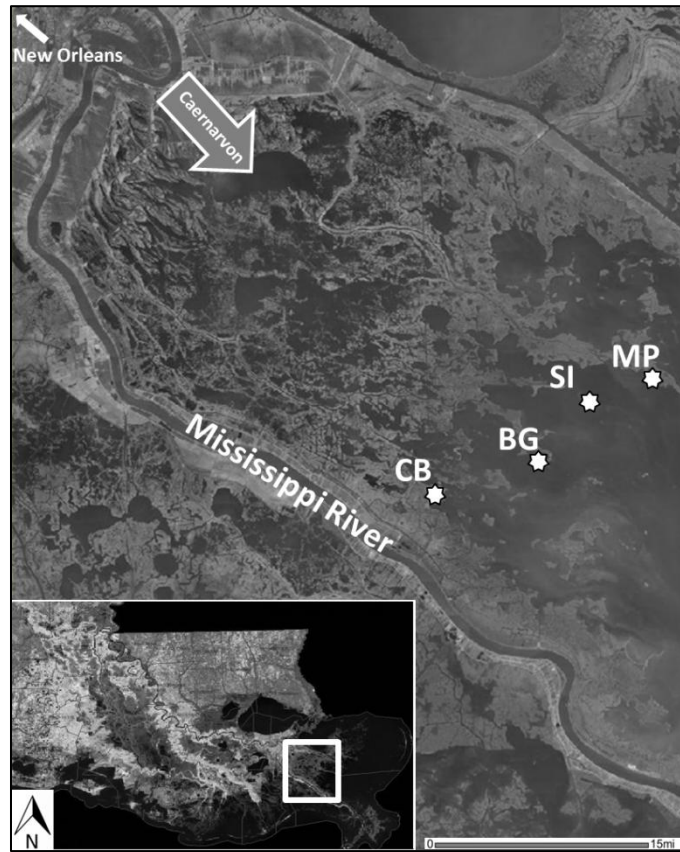


Figure 2.1 Study area map of Breton Sound, LA with study sites located along a salinity gradient (Cow Bayou (CB: salinity ~ 5), Bay Gardene (BG: salinity ~ 10), Snake Island (SI: salinity ~ 15) and Mozambique Point (MP: salinity ~ 20)).

Experimental Design

Four study sites were established within the estuary across what is normally a salinity gradient ranging from a mean of 5 to a mean of 20: Cow Bayou (CB: salinity ~ 5), Bay Gardene (BG: salinity ~ 10), Snake Island (SI: salinity ~ 15) and Mozambique Point (MP: salinity ~ 20) (Figure 2.2). At each of the four study sites, four modified aquaculture cages (60 cm x 90 cm x 30 cm) were rested on the sediment and attached to permanent structures. Two cages were used for market oysters, and two cages were used for seed oysters. Each cage was divided into three 30 cm sections for a total of 6 sections of cage per oyster size, with 3 of the sections per oyster size open to predation by removing the top section of the cage, and three sections enclosed to prevent mortality from predation. Each section held 20 individually identifiable oysters, for a total of 960 oysters (20 oysters x 6 sections x 4 sites x 2 oyster size classes = 960 oysters).

Oysters were ziptied on a rope, and their order allowed tracking of individual oyster growth rates. These cages were used for growth and mortality sampling (Figure 2.2). Two cages (one for each size class) per site were deployed on March 30 with the remaining two deployed to all sites on April 21, 2010. A loss of equipment at the high salinity site (MP) required deployment of new cages on June 10, 2010.

Additionally, six modified aquaculture bags (30 cm x 60 cm x 30 cm) designed for predator exclusion were placed at the four study sites on 30 cm legs and attached to permanent structures. Four bags contained 40 market oysters each and two bags contained 100 seed oysters each, for a total of 1,440 oysters $[(40 \text{ oysters} \times 4 \text{ bags} \times 4 \text{ sites}) + (100 \text{ oysters} \times 2 \text{ bags} \times 4 \text{ sites}) = 1,440 \text{ oysters}]$. These bags were used for growth, mortality, disease, plasma osmolality, and condition index sampling (Figure 2.3). All bags were deployed on April 21, 2010. A loss of equipment at the high salinity site (MP) required deployment of new bags on June 10, 2010.

Finally, three spat plates (0.09 m² non-treated raw Mexican clay tile) and two additional oyster bags filled with loose shell were placed at each site for a total of 12 tiles (3 tiles x 4 sites = 12 tiles) and 8 bags (2 bags x 4 sites = 8 bags). These tiles and bags were used for settlement sampling. Tiles were established at all sites on May 18, 2010. A loss of equipment at the high salinity site (MP) required deployment of new tiles on June 10, 2010. Bags of loose shell were deployed at all sites on June 24, 2010.

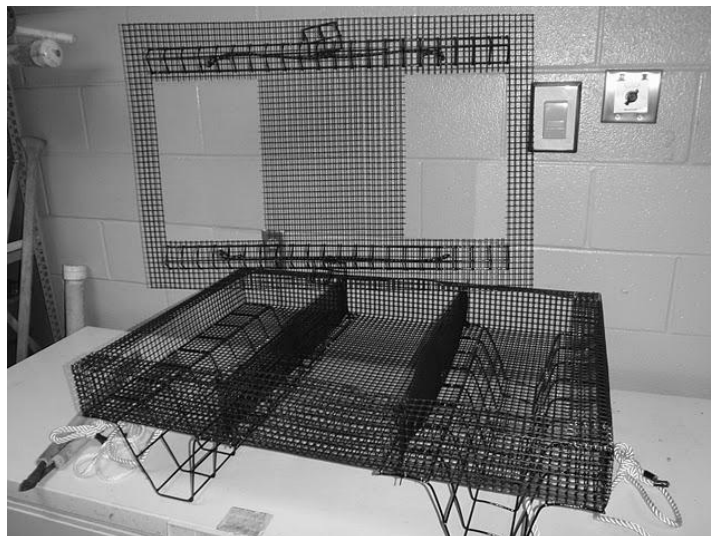


Figure 2.2 Oyster research cages for growth and mortality data.



Figure 2.3 Oyster research bags for growth, mortality, and lab analysis.

Water Quality

All sites but MP were located adjacent to USGS continuous data recorders which provide hourly temperature and salinity readings (USGS Recorders: CB - 073745258; BG - 07374527; SI - 07374526). No data recorders are located in our highest salinity zone (MP), but Louisiana Department of Wildlife and Fisheries collects weekly isohaline data providing a record of salinity at this site. Salinity, temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}) were all recorded monthly during field site visits using a YSI 85 handheld multimeter. Additionally, water samples were collected in duplicate at each site for turbidity (total particulate matter in mg L^{-1}) and chlorophyll a ($\mu\text{g L}^{-1}$) measurements. Samples were placed on ice and taken back to the lab where they were processed following standard methods for the examination of water and wastewater (Taras 1971).

To better understand the salinity dynamics at our sites, daily salinity and temperature records were taken from the site specific data recorders. Long-term records on potential freshwater inputs into the system were also collected. These freshwater inputs include daily rates of Caernarvon discharge data (m^3s^{-1} ; USGS Recorder # 295124089542100), Mississippi River Flow at Tarbert Landing, MS (m^3s^{-1} ; US Army Corps of Engineers Recorder # 01100), and rainfall (cm; Southern Regional Climate Center's monitoring station # 166295 at Louis Armstrong New Orleans International Airport).

Settlement

Settlement of spat was monitored monthly at all four sites in Breton Sound by sampling the clay tiles with replacement (Banks and Brown 2002). Spat per shell were counted on ten randomly sampled shells from each bag of loose shell in November for a total of 80 shells (10 shells x 2 bags x 4 sites = 80 shells).

Mortality and Growth

Oyster mortality and height (mm) kept in cages and bags were measured bi-monthly (April, June, August, November) at all sites. Interval percent mortality was measured by dividing the number of dead oysters by the total number of oysters in each cage at each sampling. Cumulative mortality was then calculated by multiplying interval percent mortality by the proportion of surviving oysters from the previous sampling period and adding to the cumulative mortality from the previous sampling period.

$$\text{Cumulative Mortality} = \text{CM}_{t-1} + \text{IM}_t \times (1 - \text{CM}_{t-1})$$

Where CM_{t-1} is last month's cumulative mortality and IM_t is interval mortality (Ford et al. 2006). Monthly growth rates (mm mo^{-1}) were calculated by dividing the change in average oyster height (mm) for each time period by the number of elapsed days, then multiplying by 30.

$$\text{Monthly Growth} = [(H_t - H_{t-1}) / t - (t-1)] \times 30$$

Where H is average oyster height (mm), t is the current sampling date, and t-1 is the last sampling date.

Disease, Condition Index and Plasma Osmolality

Ten oysters of each size class were collected bi-monthly from April to November at each site and brought back to the lab to determine dermo infection intensities, condition index, and plasma osmolality using standard techniques. Oysters were kept cool and dry once sampled in the field and then maintained in a cold room (3°C) until processing at lab.

Sampled oysters were notched near the adductor muscle using an electric grinder, and then hemolymph (0.2 ml) was withdrawn from the pericardial cavity using a 27 gauge needle. The sampled hemolymph was immediately transferred into vials and centrifuged at $600 \times g$ for 15 min at 4°C to obtain cell-free hemolymph. After being stored in a freezer, plasma osmolality in mOsm kg^{-1} was determined using a vapor pressure osmometer (Wescor).

Disease infection intensities were measured as parasites per gram of oyster tissue. The whole-oyster procedure was used to determine the number of parasites per gram of oyster tissue (Fisher and Oliver 1996; La Peyre et al. 2003). All chemicals were from Sigma Chemical unless otherwise indicated. Each oyster was homogenized in alternate fluid thioglycollate medium (ARFTM) supplemented with 16 g marine salts (Hawaiian Marine Imports) and 5% of commercial lipid concentrate 100 \times at a ratio of 1 ml oyster tissue per 9 ml of ARFTM. After one week of incubation in ARFTM, samples were centrifuged at $1500 \times g$ for 10 minutes and the ARFTM was discarded. The resulting pellets were incubated in 2 N NaOH at 60°C to digest oyster tissues, leaving the parasites intact. The samples were rinsed twice with 0.1 M phosphate buffer saline containing 0.5 mg ml^{-1} of bovine serum albumin to prevent parasite clumping. Samples were then serially diluted in 96-well plates and stained with Lugol's solution. The number of parasites was counted from wells containing 100 to 300 parasites (i.e. hyphospores) with an inverted microscope at a magnification of 200 \times .

Condition index (condition) was calculated as the ratio of dry tissue weight to dry shell weight multiplied by 100. For each oyster, a 10 ml aliquot of oyster tissue homogenate was dispensed into an aluminum pan and dried for 48 hours at 65°C . Dry weight of the sample was then determined by subtracting the weight of the pan. The dry weight for the whole oyster was calculated based on the total volume of homogenized tissue. Dry shell weight was determined by weighing shells dried for 48 hours at 65°C .

Statistical Analysis

Cumulative mortality, growth, plasma osmolality, disease infection intensity, condition index, and all water quality parameters (daily salinity, temperature, monthly dissolved oxygen, TPM, chlorophyll a) were analyzed separately using generalized linear mixed models (GLMMs) using several different distributions and logit link function. A GLMM is a statistical tool for

analyzing nonnormal data that involve random effects (Bolker et al. 2009). We tested all possible statistically and biologically relevant models with different combinations of the following fixed factors: site, size, open or closed cages, date, and site by date interaction. All GLMMs were followed by LSMeans with a Tukey adjustment when significant differences were found ($p < 0.05$), and all data are presented as mean \pm standard deviation unless otherwise stated.

2.3 Results

Water Quality

In 2010, water temperature, dissolved oxygen (DO), chlorophyll a concentrations, and total particulate matter (TPM) did not vary between sites throughout the year (Table 2.1). Salinity differed between sites throughout the year except from April to August. During the rest of the year, average site salinities followed the normal gradient from low to high: CB, BG, SI, MP. Mississippi River flow ranged from 6,600 to 28,800 m^3s^{-1} and Caernarvon discharge ranged from 0 to 235 m^3s^{-1} (Figure 2.4).

Settlement

No settlement was recorded on spat tiles from April to November. Settlement only occurred on loose shell at BG, SI, and MP between August and November, with an average of 0.05 ± 0.2 , 0.7 ± 1.2 , and 33.4 ± 12.3 spat per shell, respectively. The average height of attached spat was 27.5 ± 12.5 mm.

Table 2.1 Breton Sound water temperature ($^{\circ}\text{C}$), dissolved oxygen concentration (mg L^{-1}), chlorophyll a concentration ($\mu\text{g L}^{-1}$), and total particulate matter (mg L^{-1}) ranges, means, and standard deviations for all sites in 2010. No differences between sites were detected during the course of this study.

Parameter	Range	Mean \pm S.D.
Water Temperature ($^{\circ}\text{C}$)	26.4 – 31.6	29.7 ± 2.1
DO (mg L^{-1})	4.9 – 10.5	7.5 ± 1.5
Chlorophyll a ($\mu\text{g L}^{-1}$)	9.8 – 79.3	26.5 ± 19.8
TPM (mg L^{-1})	0.9 – 1.9	1.4 ± 0.2

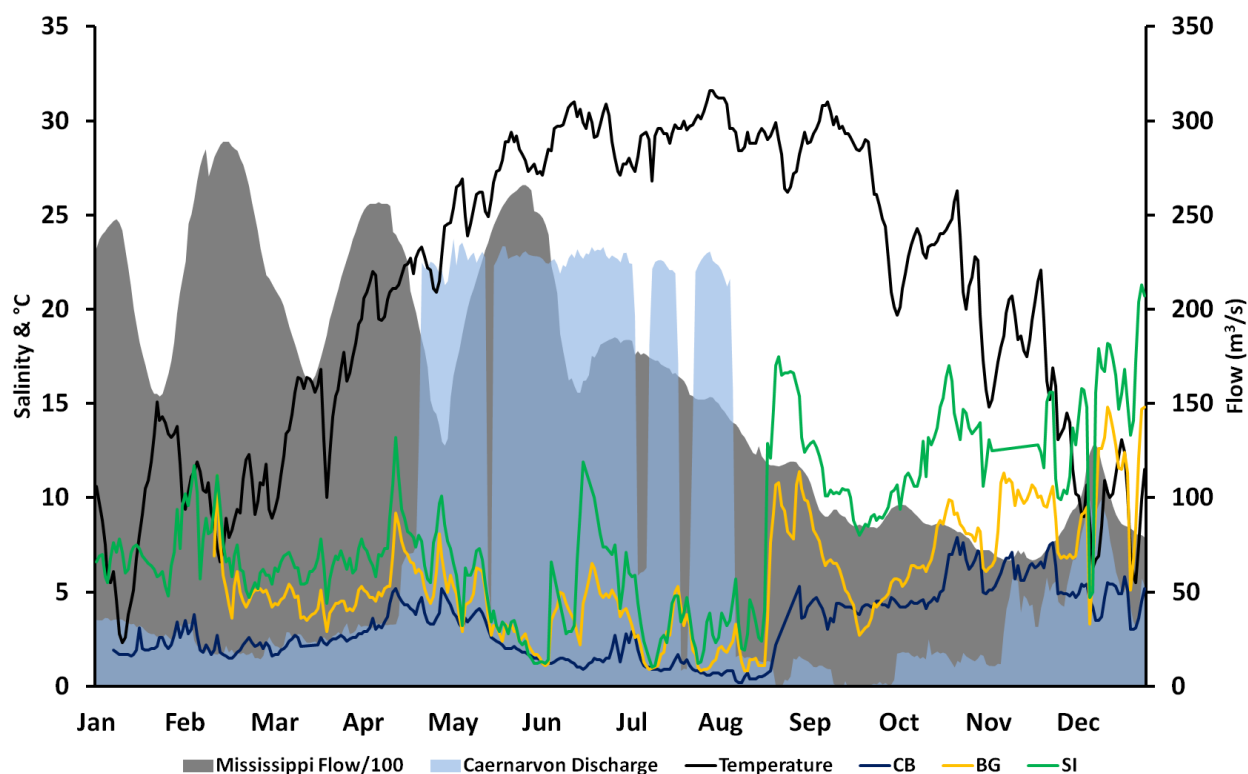


Figure 2.4 Miss. River flow ($\text{m}^3 \text{s}^{-1} 100^{-1}$), Caernarvon discharge ($\text{m}^3 \text{s}^{-1}$), water temperature ($^{\circ}\text{C}$), and site salinities for Breton Sound, LA in 2010. Miss. River flow data are taken from US Army Corps of Engineers Recorder # 01100. All other data are from USGS continuous water quality recorders: CB - 073745258, BG - 07374527, SI - 07374526, Caernarvon - 295124089542100.

Mortality and Growth

There was high mortality of both market and seed-sized oysters in experimental bags at all sites, and no significant differences in mortality rates by size class. CB sustained 100% cumulative mortality of both market and seed-sized oysters by July 2010, which was significantly higher than cumulative oyster mortality at the other three sites ($p=0.04$; Figure 2.5a). Interval mortalities were significantly different at all sites from June to July except between SI and MP (Figure 2.5b). CB sustained 100% mortality between June and July, while other sites had much less mortality during this time period with 4% at BG, 30% at SI, and 25% at MP (Figure 2.5b, 2.6).

There was also high mortality of oysters in experimental cages in 2010, with no significant differences in mortality by size class, or between open and closed predator exclusion cages. CB had 100% cumulative mortality by August while BG and SI both had greater than 60% by November. MP, on the other hand, had significantly less mortality than all sites with only 30% cumulative oyster mortality (Figure 2.7). While BG and SI had similar cumulative mortality from April through November, MP had lower mortality from August through November (Figure 2.8).

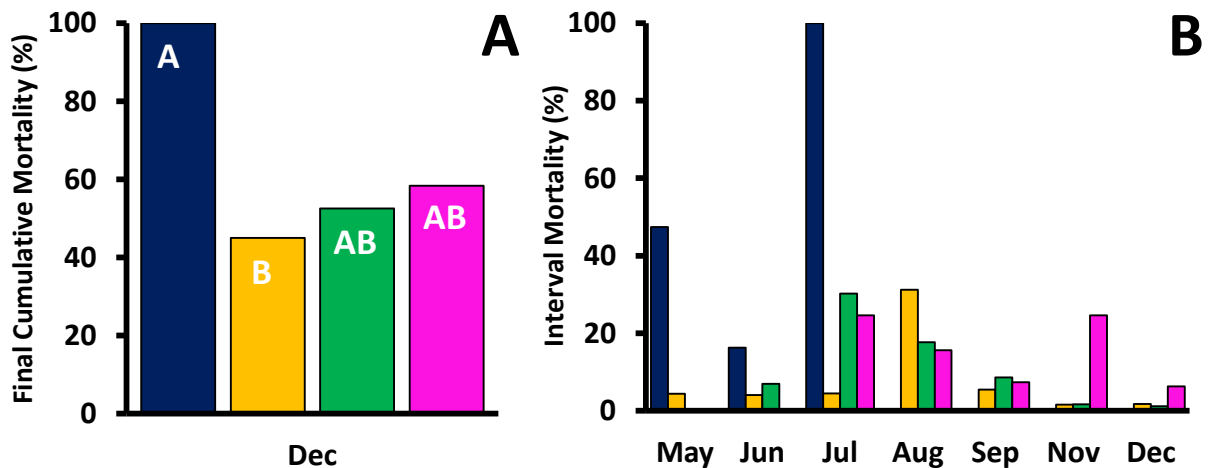


Figure 2.5 Cumulative and interval mortalities of market and seed oysters in bags from 2010 in Breton Sound. There were no differences in mortality between market and seed size oysters. Letters denote significance groupings. (CB - blue, BG - yellow, SI - green, and MP - pink)

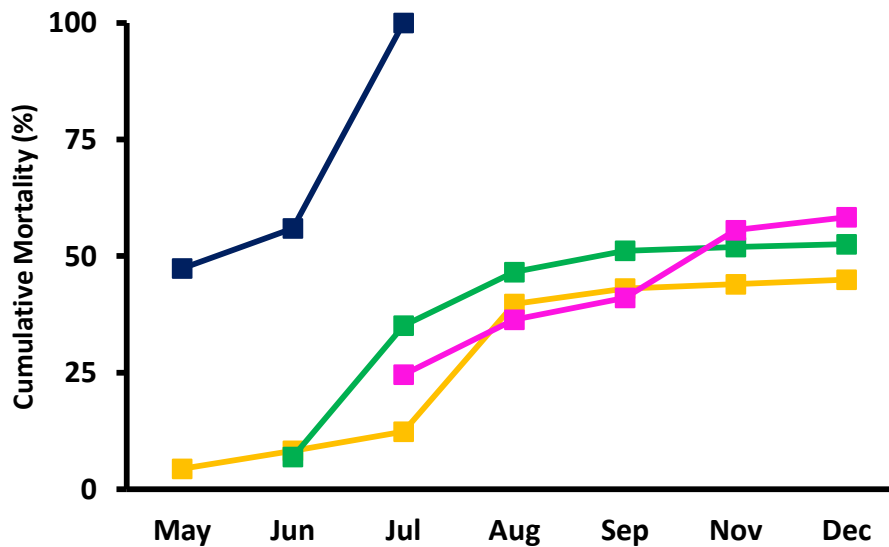


Figure 2.6 Cumulative mortalities of market and seed oysters in bags from 2010 in Breton Sound. There were no differences in mortality between market and seed size oysters. (CB - blue, BG - yellow, SI - green, and MP - pink)

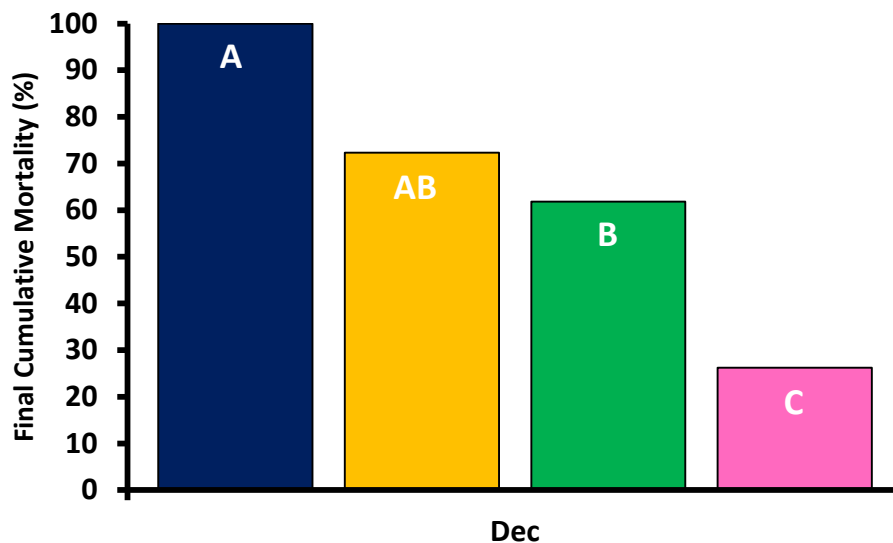


Figure 2.7 Cumulative mortalities of market and seed oysters in cages from 2010 in Breton Sound. There were no differences in mortality between market and seed size oysters. Letters denote significance groupings. (CB - blue, BG - yellow, SI - green, and MP - pink)

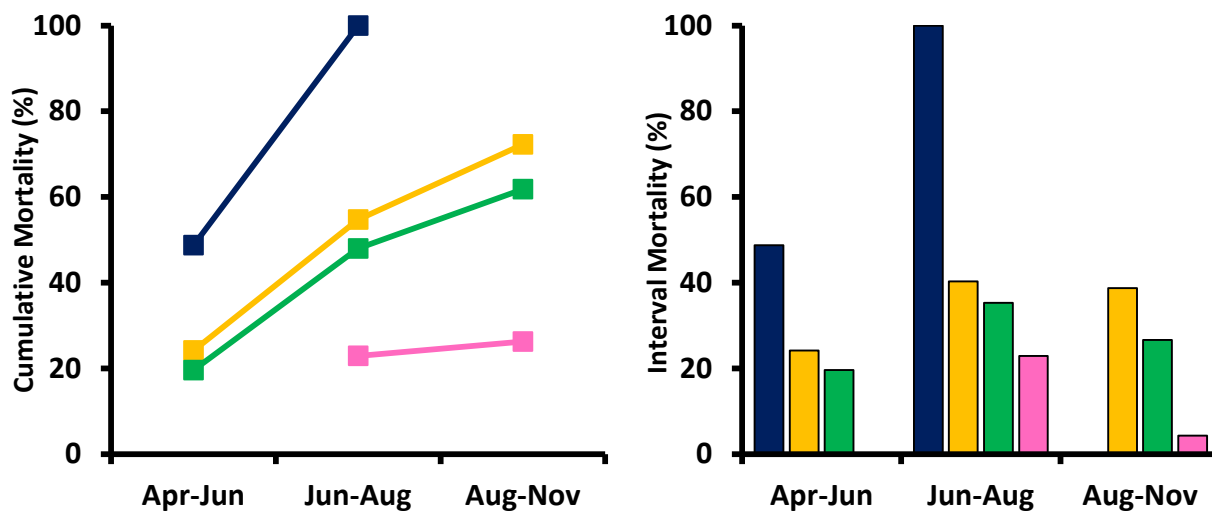


Figure 2.8 Cumulative and interval oyster mortalities in experimental cages from 2010 in Breton Sound. There were no differences in mortality between market and seed size oysters. (CB - blue, BG - yellow, SI - green, and MP - pink)

Growth was very limited among oysters in 2010. In experimental bags, there were no significant differences in growth between months, sites, or the interactions of sites and months. In experimental cages, there was a significant oyster size effect, and a significant month effect.

Seed oyster growth ($2.1 \text{ mm mo}^{-1} \pm 2.4$) was significantly greater than market ($0.8 \text{ mm mo}^{-1} \pm 1.3$; $p=0.02$). Furthermore, growth from August to November at all sites was significantly higher than any other time period. There were no significant differences in growth between sites and no significant interactions (Figure 2.9).

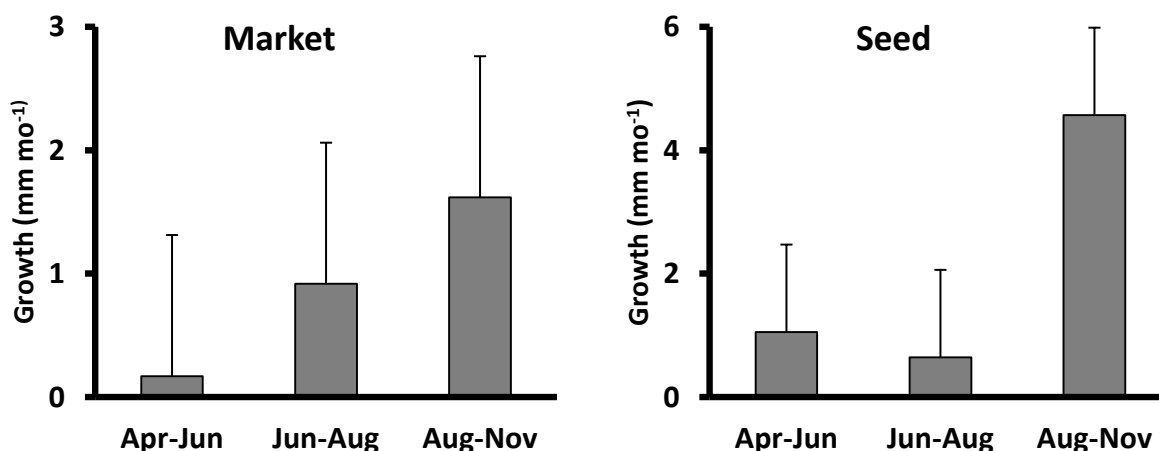


Figure 2.9 Mean monthly market and seed-sized oyster growth and standard deviation in cages from 2010 in Breton Sound. (CB - blue, BG - yellow, SI - green, and MP - pink)

Plasma Osmolality, Condition Index, and Disease

Mean oyster plasma osmolalities varied from 148 to 570 mOsm kg⁻¹. While there was no significant difference between size classes, there was a significant interaction between site and month. BG osmolalities were significantly higher in August ($561 \text{ mOsm kg}^{-1} \pm 89$) than any other month (June: $393 \text{ mOsm kg}^{-1} \pm 144$, $p<0.0001$; October: $355 \text{ mOsm kg}^{-1} \pm 92$, $p<0.0001$), while SI osmolalities were significantly lower in October ($333 \text{ mOsm kg}^{-1} \pm 80$) than any other month (June: $447 \text{ mOsm kg}^{-1} \pm 148$, $p=0.0015$; August: $571 \text{ mOsm kg}^{-1} \pm 90$, $p<0.0001$). MP osmolalities were significantly lower in August ($148 \text{ mOsm kg}^{-1} \pm 22$) and significantly higher in June ($494 \text{ mOsm kg}^{-1} \pm 109$) than any other month. MP was significantly higher than BG in June ($p=0.0362$), but significantly lower than BG and SI in August ($p<0.0001$; Figure 2.10).

Mean condition of both market and seed-sized oysters decreased over time in 2010. Condition of oysters in April (3.5 ± 1.1) was significantly higher than October (1.2 ± 0.4 ; $p=0.0437$). There were no significant differences between the two size classes or four sites (Figure 2.11).

All dermo infection intensities were less than 500,000 parasites per gram with most being less than 10,000 parasites per gram, and never affected more than 60% of the population. There were no significant differences between size classes or sites, but mean dermo infection was significantly higher in April (210 parasites $g^{-1} \pm 806$) than in both June (6 parasites $g^{-1} \pm 20$; $p < 0.0001$) and August (8 parasites $g^{-1} \pm 30$; $p = 0.0001$). Furthermore, mean infection was significantly higher in October (32617 parasites $g^{-1} \pm 95118$) than any other month (Figure 2.12).

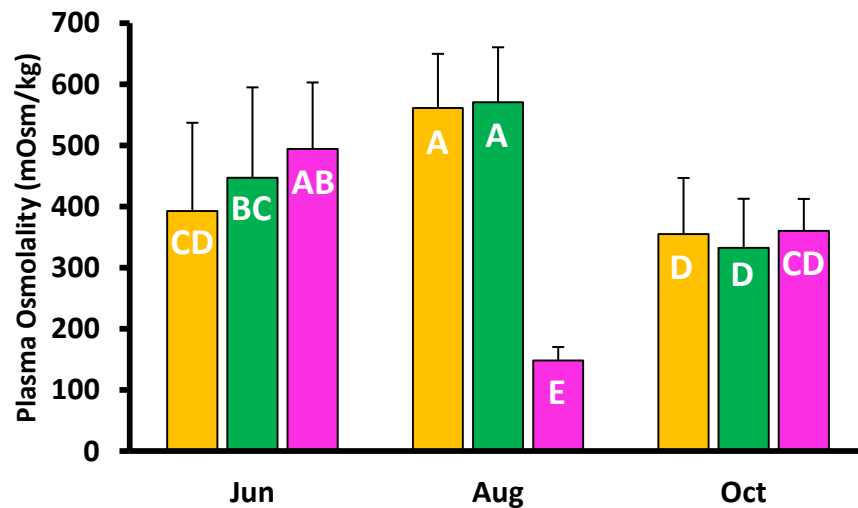


Figure 2.10 Mean oyster plasma osmolality and standard deviation from 2010 in Breton Sound. There were no differences between market and seed size oysters; CB not included due to early mortality. Letters denote significance groupings. (BG - yellow, SI - green, and MP - pink)

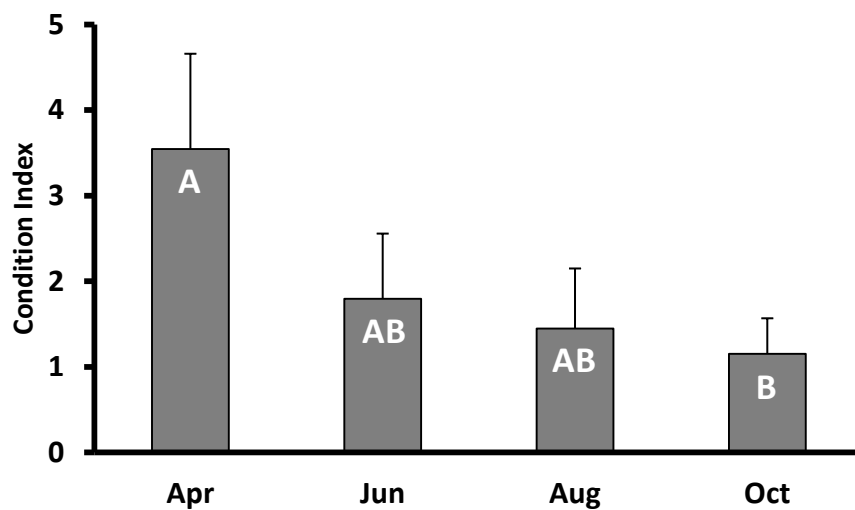


Figure 2.11 Mean oyster condition index and standard deviation from 2010 in Breton Sound. There were no differences by site or oyster size. Letters denote significance groupings.

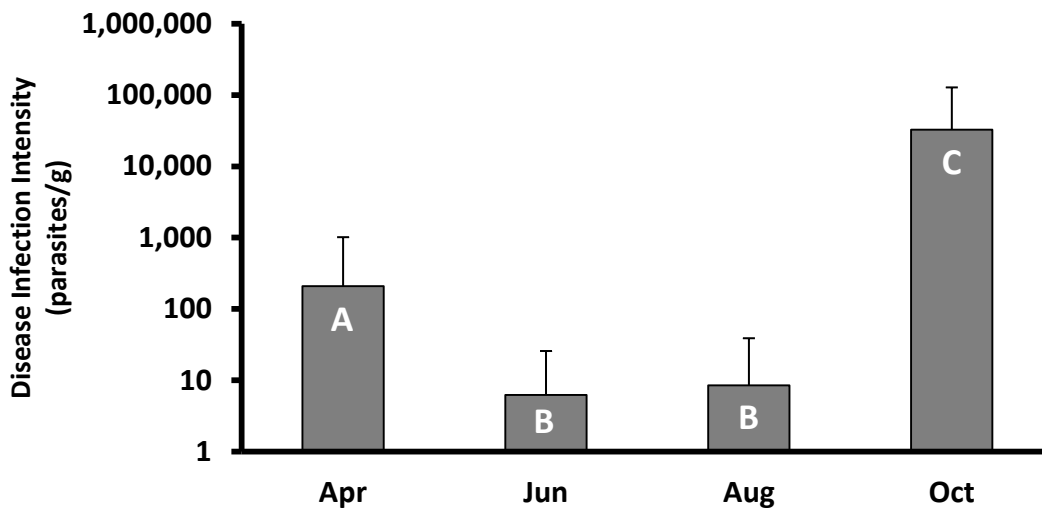


Figure 2.12 Mean dermo infection intensities of oysters and standard deviation from 2010 in Breton Sound. There were no differences by site or oyster size. Letters denote significance groupings.

2.4 Discussion

Breton Sound estuary experienced unique conditions in 2010, with prolonged high freshwater input from the Caernarvon Freshwater Diversion during the hot summer months in an effort to minimize oil intrusion into the estuary. As a result, salinity was lowered throughout the estuary, during the time of year when water temperatures were highest. Oyster populations in Breton Sound were thus exposed to the synergistic effects of low salinity and high temperatures, resulting in high mortality, minimal growth and settlement, and decreased oyster condition. On the other hand, oysters were unaffected by disease and predation. These data indicate that prolonged freshwater exposure (< 2) by oysters combined with high water temperature ($> 26^{\circ}\text{C}$) for more than 2 months is detrimental to oyster populations as it negatively impacts all the critical stages of the oyster life history from recruitment, to growth, to mortality.

Mortality rates are typically higher during summer months when temperature and salinity are high, because of increased disease and predation (Davis and Barber 1994; Ford et al. 2006; Ragone and Burreson 1993). While mortality was high during summer months in Breton Sound, it was certainly not from disease and predation. Disease never affected more than 60% of oyster populations, and of those affected infection intensities were very low. Most oyster mortality from dermo infections does not occur until populations experience heavy infection intensities

(>500,000 parasites g⁻¹ wet tissue weight) (Quick and Mackin 1971). Furthermore, in this study, predation did not appear to be a factor, as there was no significant difference in mortality between oysters protected from predators (closed cage sections) and those exposed (open cage sections).

Aside from disease and predation, the combined effects of temperature and salinity are held to be the two dominant abiotic controls on *C. virginica*, and can affect virtually every aspect of oyster biology, and ultimately, their survival, and may explain the high mortality and low growth rates found in this study (Butler 1949; Galstoff 1964; Gunter 1953; Bataller et al. 1999; Shumway 1996). A past lab study found significantly higher cumulative mortality of oysters exposed to a 3 week freshet (salinity < 1) event in the summer (July; 28°C) as compared to in the spring (April; 18°C) or winter (December; 16°C) suggesting that mortality was higher under the combined effects of low salinity conditions and higher temperatures (La Peyre et al. 2003). Furthermore, numerous field observations have documented oyster survival in low salinity for extended periods of time, but only at low temperatures (Lossanoff 1953, Wells 1961, Kennedy 1991, Austin et al. 1993, Winstead 1995). For example, Gunter (1953) documented eastern oysters surviving salinities as low as 2 for a month, but only in winter/spring water conditions. When salinities drop below 3 to 5, oysters stop feeding, close their valves, and increase anaerobic metabolism to a point that results in high mortality (Galstoff 1964; Gunter 1953; Heilmayer et al. 2008; Loosanoff 1953; Shumway 1996). Higher temperatures increase metabolic activities, which would increase the rate of mortality (Heilmayer et al. 2008; Michaelidis et al. 2005; Shumway 1996). In this study, all sites experienced prolonged periods of low salinity (< 3) while temperatures remained high, and consequently suffered high mortality.

Spawning is directly correlated with water temperature, and for the Gulf of Mexico coast there is a bi-modal pattern of gametogenesis and spawning, with most events occurring when water temperatures are greater than 25°C (Hayes and Menzel 1981; Ingle 1951; Shumway 1996; Supan and Wilson 2001). However, many factors directly affect spawning and settlement independently of temperature such as currents, substrate composition, light conditions, dissolved oxygen concentrations, or even lunar phases (Ingle 1951; Johnson et al. 2009; Knights and Walters 2010; Loosanoff and Nomejko 1951; Obeirn et al. 1995; Ortega and Sutherland 1992; Turner et al. 1994). All have the ability to detrimentally affect spawning and settlement in the

Gulf, even when temperatures are ideal; however, salinity is the most important of these secondary factors.

Salinity is well known to affect spawning, although to a lesser degree than temperature. Gametogenesis, spawning, and settlement have been shown to be significantly reduced or stopped at low salinity, regardless of temperature (Butler 1949; Chatry et al. 1983; Pollack et al. 2011). Typically salinities within the Breton Sound estuary are ideal for spawning/settlement and temperature is the limiting factor. However, in 2010, rather than the typical bimodal distribution of oyster spat attachment when water temperatures rise in early summer and fall in late summer (Pollard 1973), Breton Sound experienced very low settlement only once late in the season. In late May and early June, when optimal rising temperatures should allow for the first spat set, site salinities were all below 5. A similar study in the Copano and Aransas bays in Texas also found very little spat settlement during periods of low salinity and ideal temperatures (Pollack et al. 2011). Chatry et al. (1983) analyzed 11 years of Breton Sound settlement and found virtually none when mean salinity was less than 10 during summer when water temperatures are high. The effects of the low salinity on spawning and settlement have the potential to have the greatest lasting impact on oyster production because it affects future populations. With minimal settlement in just one year, following years will have fewer oysters that reach reproductive and harvestable size, i.e. reduced recruitment (Powell et al. 2009; Southworth and Mann 2004). Additionally, valuable oyster reef structure will suffer without large numbers of oysters settling as spat and adding hard substrate.

Typically, growth rates increase with increasing temperature as well as with increasing salinity (Dekshenieks et al. 1993; Harding 2007; Hofmann et al. 2004). As a result, growth rates are typically higher in warmer months, and in higher salinity sites. In 2010, despite typical summer temperature patterns, all sites experienced abnormally low salinity (< 2) for an extended period of time. Despite the high temperatures, growth was extremely low at all sites during reduced salinities; and in fact, monthly growth rates from this study at all sites were lower than one of the lowest salinity sites (mean 8.6 ± 3.3) in a previous winter/spring study in Breton Sound ($1.14 \text{ mm mo}^{-1} \pm 2.3$; La Peyre et al. 2009). Growth is thought to be reduced in low salinity waters because of valve closure resulting in reduced feeding. Loosanoff (1953, 1965) reported no feeding in oysters in salinity lower than 3. Of the 124 days from May to September

2010 (time period of greatest Caernarvon flow and lowest salinities) CB, BG, and SI experienced 110, 123, and 114 recorded days of mean salinity under 3, respectively. These results emphasize the critical importance of maintaining both appropriate temperatures and salinity to ensure the high growth rates which allow for the good productivity and high harvest rates along the LA coast. Clearly, prolonged freshwater flow which reduces the mean salinity at sites, particularly during the normal growing season, will significantly affect the productivity and harvest availability of oysters beyond a single year.

It is interesting to note the interaction between site salinities and oyster plasma osmolalities. Oysters are commonly known to be osmo-conformers (Hand 1977; McFarland et al. 2011). However, in 2010, Breton Sound oysters sustained high internal osmolalities through periods of low salinity, with the exception of MP oysters. It seems that rather than heavily filter-feeding and conforming to external salinities, Breton Sound oysters were closed and essentially starving themselves, and thus their osmolalities remained higher than the surrounding waters. This is a similar finding compared to previous studies of oyster plasma osmolality, in which eastern oysters in the northern Gulf of Mexico failed to decrease osmolalities below 200 mOsm kg⁻¹ during low salinity events (La Peyre et al. 2003, 2009). These results highlight the limitations of eastern oysters ability to osmo-conform.

The condition index and disease infection intensities among Breton Sound oysters followed predictable patterns in 2010: both decreased over time with decreasing salinity, and remained low while salinity was low. This pattern follows findings from numerous field and lab studies which have shown that condition index and *P. marinus* viability are significantly reduced in low salinity and low temperatures (Burreson and Ragone-Calvo 1996; Hofmann et al. 1995; La Peyre et al. 2003, 2009, 2010; Ragone and Burreson 1993; Soniat 1996; Volety et al. 2000). Specifically, some in vitro research examining *P. marinus* viability found reduced viability at salinity of less than 7 (La Peyre et al. 2006). This current field study, however, had low salinity combined with high temperatures. Field and lab studies have observed a decrease in infection intensities in late winter and early spring as temperatures increase, and it has been suggested that the high temperature reduction in infection intensities may be due to the active process of elimination of oyster host defenses (Ray 1954; Mackin 1962; Soniat 1985; La Peyre et al. 2008; Goedken et al. 2005). However, as host health (condition) decreased throughout the year, it is

unlikely that active elimination was occurring, and both the low disease infection level and condition are most likely from extreme and prolonged low salinity.

The Breton Sound estuary is a highly variable coastal system, with large variations in biotic, abiotic, and anthropogenic factors through time. As anthropogenic influence increases in large river environments, variability is exacerbated, and Breton Sound is no exception. The management of Mississippi River freshwater diversions, especially Caernarvon, is a clear example of this concept. Over the last twenty years, freshwater diversions are being used more often, nearer to maximum capacity, and for longer periods of sustained discharge.

Keeping in mind that temperature and salinity tend to drive oyster productivity in estuarine areas, the long term influence of the several freshwater sources on Breton Sound are very important. As these freshwater inputs vary greatly, the resulting site characteristics (especially salinities) of Louisiana's most productive oyster grounds are affected, and may affect oyster population dynamics for multiple years. Clearly, increasing freshwater input during high temperature periods are likely to be highly detrimental to oyster production and long-term population sustainability by affecting all aspects of the oyster life history from spawning, to settlement, to growth and mortality. Furthermore, regardless of long-term trends, the role of freshwater in Breton Sound in 2010 was extremely influential. The combined freshwater inputs drove site salinities well below their typical levels for an extended period of time during warmer spring and summer months. The combination of sustained low salinities during warmer water temperatures is an uncommon event, as low salinities usually occur during cooler winters and springs when precipitation and flooding is higher. Breton Sound in 2010 was unique during this particularly important transitional time of year for oysters and their resulting population dynamics.

Chapter 3: The 2011 Mississippi River Flood and Its Effects on Eastern Oysters in Breton Sound, Louisiana

3.1 Introduction

In May 2011 the Mississippi River flooded to record levels across seven southern states. On May 9, 2011, the US Army Corps of Engineers' Mississippi River Commission opened the Bonnet Carré Spillway, which is located north of New Orleans, LA. This spillway diverts Mississippi River waters into Lake Pontchartrain and subsequently into the Gulf of Mexico. The spillway passed nearly $9,000 \text{ m}^3 \text{ s}^{-1}$ until June 11, 2011. On May 14, 2011, for the first time since 1973, the Morganza Spillway in Louisiana was opened, flooding the Atchafalaya Basin in order to prevent major flooding in Baton Rouge and New Orleans. By May 20, 2011 the river peaked at Tarbert Landing, MS at $45,845 \text{ m}^3 \text{ s}^{-1}$ (US Army Corps of Engineers 2011). The Mississippi River flood of 2011 not only impacted a large portion of inland communities in Louisiana, but it could have potentially lasting effects on Louisiana wetlands and coastal resources. While all of the impacts on coastal resources are still unknown, eastern oysters (*Crassostrea virginica*) have a considerable affect on Louisiana economics (LDWF 2005), and are known to be sensitive to flood events (Gunter 1953; La Peyre et al. 2003, 2009; Pollack et al. 2011; Turner 2006).

The Breton Sound estuary is home to several of the largest public oyster seed grounds and private leases. Breton Sound oyster populations are also directly impacted by Mississippi River input through several freshwater diversion structures. Fortunately, however, the largest of these structures was operated at minimal flow during the Mississippi River flood of 2011, potentially preventing mass oyster mortality in Breton Sound for the second consecutive year after the Deepwater Horizon Oil Spill in 2010. However, freshwater flow through upper-estuary wetlands, into Lake Pontchartrain and the Mississippi River Gulf Outlet via the Bonnet Carré Spillway, and from the mouth of the Mississippi River still considerably altered Breton Sound salinity regimes in the spring and early summer of 2011 (Figure 3.1).

The objectives of this project were to quantify the effects of the 2011 Mississippi River flood on natural oyster population dynamics along what is normally a salinity gradient ranging from 5 to 20 in Breton Sound, LA. These data will also be used in the development of a region specific population model for the Gulf of Mexico eastern oyster.



Figure 3.1 Flood waters from the 2011 Mississippi River flood surrounding Breton Sound. Imagery courtesy of LSU Earth Scan Laboratory and University of Wisconsin Space Science and Engineering Center.

3.2 Methods

Study Area

This study was conducted in Breton Sound, LA, a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana. Breton Sound consists of microtidal bays, lakes, bayous, and canals and contains fresh, intermediate, brackish and salt marsh types. Upper Breton Sound estuary, where this study took place, is subject to flooding from the Caernarvon Freshwater Diversion structure (Caernarvon). Caernarvon became operational in 1991 and was designed to moderate salinities and reintroduce controlled river inflows to Breton Sound. Caernarvon is located at the head of Breton Sound and pulses are capable of delivering substantial amounts of fresh water (up to $249 \text{ m}^3 \text{ s}^{-1}$) to the basin (Snedden et al. 2007). Yearly

winter/spring experimental high-flow releases began in spring 2001 to simulate seasonal flood-pulse events. Pulses release periodic large fluxes of river water into the basin and are capable of inundating upper basin marshes for several days. In response to the Deep Horizon oil spill occurring April 20, 2010, Caernarvon was opened April 24, 2010 to near capacity flow of $225 \text{ m}^3 \text{ s}^{-1}$ in an attempt to prevent oil from entering into Breton Sound. This study was designed in 2009, prior to the 2010 oil spill with the goal of assessing oyster population dynamics at four study sites across a gradient of salinity: Cow Bayou (CB: salinity ~ 5), Bay Gardene (BG: salinity ~ 10), Snake Island (SI: salinity ~ 15) and Mozambique Point (MP: salinity ~ 20) (Figure 3.1).

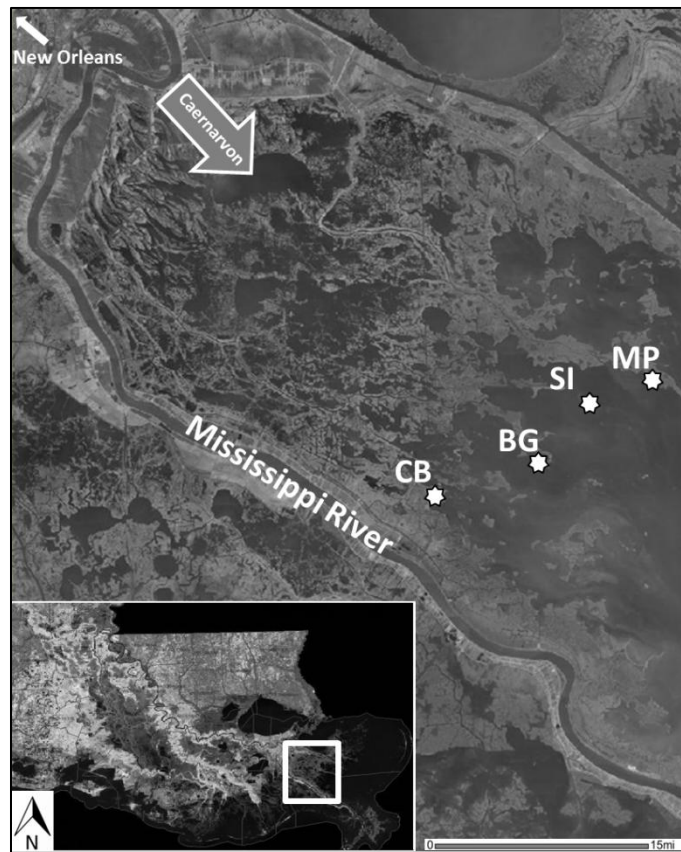


Figure 3.1 Study area map of Breton Sound, LA with study sites located along a salinity gradient (Cow Bayou (CB: salinity ~ 5), Bay Gardene (BG: salinity ~ 10), Snake Island (SI: salinity ~ 15) and Mozambique Point (MP: salinity ~ 20)).

Oysters

All oysters (eastern oyster; *Crassostrea virginica*) used for the field study were collected by dredge from public oyster seed grounds located within Breton Sound during the winter of 2010/2011. Experiments used 2,160 total oysters, 200 of which were spat size (< 45 mm), 1,000 of which were seed size oysters (< 75 mm), and 960 were market size oysters (> 76 mm). Collected oysters were stored at Louisiana Sea Grant Bivalve Hatchery located on Grand Isle, LA and maintained in cages until deployment. Average salinity and temperature in Grand Isle were 24.9 and 12.7°C, respectively.

Experimental Design

At each of the four study sites, 22 modified aquaculture bags (1' x 2' x 1') were placed on PVC legs, and attached to permanent structures. Nine bags were used for market oysters, eight bags were used for seed oysters, one bag was used for spat, and four bags were used for loose shell and spat plates.

Six market oyster bags, five seed oyster bags, and one spat oyster bag were enclosed and lifted off of the sediment to prevent mortality from predation. Three of these bags contained 25 market oysters, three contained 25 seed oysters, and one contained 50 spat for a total of 800 oysters [(25 oysters x 3 bags x 4 sites x 2 size classes) + (50 oysters x 1 bag x 4 sites)]. These bags were used for growth and mortality sampling. Three bags contained 30 market oysters and three bags contained 50 seed oysters for a total of 760 oysters [(30 oysters x 3 bags x 4 sites) + (50 oysters x 2 bags x 4 sites)]. These bags were used for mortality, disease, plasma osmolality, and condition index sampling. (Figure 3.2)

Additionally, six further modified bags were placed at the four study sites on PVC stakes. The tops of these bags were cut to expose oysters to predators and the PVC legs were shortened to allow each bag to rest on the sediment (to allow crawling predators access). Three bags contained 25 market oysters each and three bags contained 25 seed oysters each, for a total of 600 oysters (25 oysters x 3 bags x 4 sites x 2 size classes). These bags were used for mortality sampling. (Figure 3.3A)

Finally, four bags filled with loose shell were placed at each site containing 2 spat tiles (non-treated raw Mexican clay tile) for a total of 32 tiles (2 tiles x 4 bags x 4 sites). These tiles and bags were used for settlement sampling. (Figure 3.3B)

Breton Sound oysters were dredged and moved to Grand Isle for storage and prepping in January 2011. All oyster bags were deployed in February. Bags of loose shell and tiles were deployed in March. Due to the loss of oysters in open bags, those bags were modified, re-filled with oysters, and re-deployed in May.



Figure 3.2 Oyster research bags for growth, mortality, and lab analysis.



Figure 3.3 (A) Open research bags for mortality sampling; (B) recruitment bag and spat tile.

Water Quality

All sites but MP were located adjacent to USGS continuous data recorders which provide hourly temperature and salinity readings (USGS Recorders: CB - 073745258; BG - 07374527; SI - 07374526). No data recorders are located in our highest salinity zone, but Louisiana Department of Wildlife and Fisheries collects weekly isohaline data providing a record of salinity at this site. Salinity, temperature, dissolved oxygen were all recorded monthly during field site visits using a YSI 85 handheld multimeter. Additionally, water samples were collected in duplicate at each site for turbidity (total particulate matter in mg/L) and chlorophyll a ($\mu\text{g/L}$) measurements. Samples were placed on ice and taken back at the lab where they were processed following standard methods for the examination of water and wastewater (Taras 1971).

To better understand the salinity dynamics at our sites, daily salinity and temperature records were taken from the site specific data recorders. Long-term records on potential freshwater inputs into the system were also collected. These freshwater inputs include daily rates of Caernarvon discharge data (USGS Recorder # 295124089542100) and Mississippi River Flow at Tarbert Landing, MS (US Army Corps of Engineers Recorder # 01100).

Settlement

Settlement of spat was monitored monthly from March 2011 to November 2011 at all four sites in Breton Sound by sampling clay tiles with replacement (Banks and Brown 2002).

Mortality and Growth

Oyster mortality and height (mm) in bags were measured bi-monthly from February through December. Mortality was measured by counting dead oysters and the proportion of dead to total oysters within each bag was calculated to determine natural monthly mortality rates.

$$\text{Cumulative Mortality} = \text{CM}_{t-1} + \text{IM}_t \times (1 - \text{CM}_{t-1})$$

Where CM_{t-1} is last month's cumulative mortality and IM_t is this month's interval mortality. (Ford et al. 2006).

Monthly growth rates (mm mo^{-1}) were calculated by dividing the change in average oyster height (mm) for each time period by the number of elapsed days, then multiplying by 30.

$$\text{Monthly Growth} = [(H_t - H_{t-1}) / t - (t-1)] \times 30$$

Where H is average oyster height (mm), t is the current sampling date, and t-1 is the last sampling date.

Disease, Condition Index and Plasma Osmolality

Ten oysters of each size class were collected every three months from February to December at each site and brought back to the lab to determine disease infection intensities, condition index, and plasma osmolality using standard techniques. Oysters were kept cool and dry once sampled in the field and then maintained in a cold room (3°C) until processing at lab.

Oyster plasma osmolality was measured in mOsm/kg. Sampled oysters were notched near the adductor muscle using an electric grinder, and then hemolymph (0.2 ml) was withdrawn from the pericardial cavity using a 27 gauge needle. The sampled hemolymph was immediately transferred into vials and centrifuged at $600 \times g$ for 15 min at 4°C to obtain cell-free hemolymph. After being stored in a freezer, plasma osmolality was determined using a vapor pressure osmometer (Wescor).

Disease infection intensities were measured as parasites per gram of oyster tissue. The whole-oyster procedure was used to determine the number of parasites per gram of oyster tissue. (Fisher and Oliver 1996; La Peyre et al. 2003) All chemicals were from Sigma Chemical unless otherwise indicated. Each oyster was homogenized in alternate fluid thioglycollate medium (ARFTM) supplemented with 16 g marine salts (Hawaiian Marine Imports) and 5% of commercial lipid concentrate 100 \times at a ratio of 1 ml oyster tissue per 9 ml of ARFTM. After one week of incubation in ARFTM, samples were centrifuged at $1500 \times g$ for 10 minutes and the ARFTM was discarded. The resulting pellets were incubated in 2 N NaOH at 60°C to digest oyster tissues, leaving the parasites intact. The samples were rinsed twice with 0.1 M phosphate buffer saline containing 0.5 mg ml^{-1} of bovine serum albumin to prevent parasite clumping. Samples were then serially diluted in 96-well plates and stained with Lugol's solution. The

number of parasites was counted from wells containing 100 to 300 parasites (i.e. hyphospores) with an inverted microscope at a magnification of 200 \times .

Condition index (condition) was calculated as the ratio of dry tissue weight to dry shell weight multiplied by 100. For each oyster, a 10 ml aliquot of oyster tissue homogenate was dispensed into an aluminum pan and dried for 48 hours at 65°C. Dry weight of the sample was then determined by subtracting the weight of the pan. The dry weight for the whole oyster was calculated based on the total volume of homogenized tissue. Dry shell weight was determined by weighing shells dried for 48 hours at 65°C.

Statistical Analysis

Cumulative mortality, growth, plasma osmolality, disease infection intensity, condition index, and all water quality parameters (daily salinity, temperature, monthly dissolved oxygen, TPM, chlorophyll a) were analyzed separately using generalized linear mixed models (GLMMs) using several different distributions and logit link function. A GLMM is a statistical tool for analyzing nonnormal data that involve random effects (Bolker et al. 2009). We tested all possible statistically and biologically relevant models with different combinations of the following fixed factors: site, size, open or closed cages, date, and site by date interaction. All GLMMs were followed by LSMeans with a Tukey adjustment when significant differences were found ($p < 0.05$), and all data are presented as mean \pm standard deviation unless otherwise stated.

3.3 Results

Water Quality

In 2011, water temperature, dissolved oxygen (DO), chlorophyll a concentrations, and total particulate matter (TPM) did not vary between sites throughout the year (Table 2.1). Mean annual salinity at CB (5.1 ± 2.8) was significantly lower than all other sites (BG: 9.7 ± 3.7 ; SI: 11.7 ± 4.6 ; MP: 11.1 ± 3.8). Furthermore, there was a significant interaction of site and month with CB salinity being significantly lower than BG and SI salinity throughout the whole year except from March to April where all sites had similar salinity. Mississippi River flow ranged from 7,362 to 45,845 $\text{m}^3 \text{s}^{-1}$ and Caernarvon discharge ranged from 6 to 136 $\text{m}^3 \text{s}^{-1}$ (Figure 2.8).

Settlement

Spat tiles showed minimal recruitment from April to November. One spat occurred on a single tile at SI in June and single tiles at BG and MP in August. This is the equivalent to 5.4 spat m^{-2} per month only in June and August.

Table 2.1 Breton Sound water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), chlorophyll a concentration ($\mu\text{g L}^{-1}$), and total particulate matter (mg L^{-1}) ranges, means, and standard deviations for all sites in 2011.

Parameter	Range	Mean \pm S.D.
Water Temperature ($^{\circ}\text{C}$)	22.6 – 33.5	28.3 ± 2.9
DO (mg L^{-1})	3.3 – 11.2	7.0 ± 1.8
Chlorophyll a ($\mu\text{g L}^{-1}$)	7.8 – 57.0	29.8 ± 16.0
TPM (mg L^{-1})	1.0 – 2.0	1.5 ± 0.3

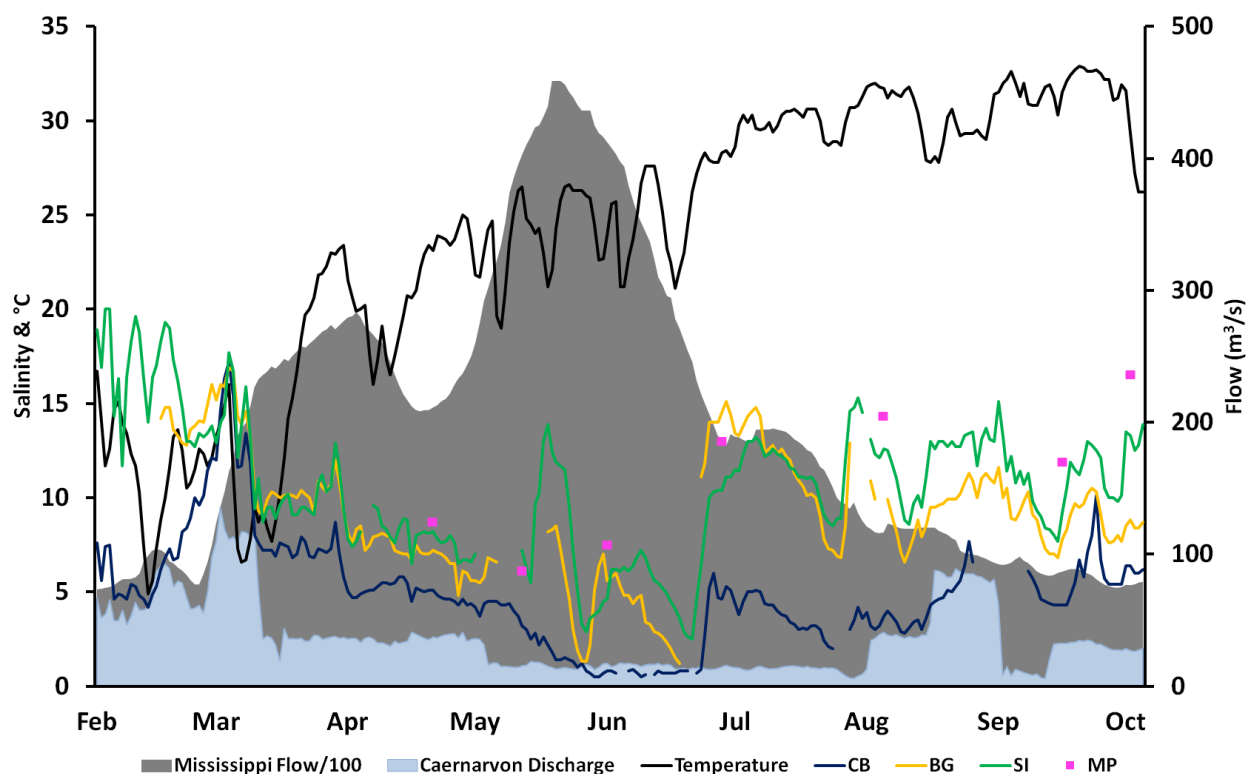


Figure 2.8 Miss. River flow ($\text{m}^3 \text{s}^{-1} 100^{-1}$), Caernarvon discharge ($\text{m}^3 \text{s}^{-1}$), water temperature ($^{\circ}\text{C}$), and site salinities for Breton Sound, LA in 2011. Miss. River flow data are taken from US Army Corps of Engineers Recorder # 01100. All other data are from USGS continuous water quality recorders: CB - 073745258, BG - 07374527, SI - 07374526, Caernarvon - 295124089542100.

Mortality and Growth

There was low mortality of both market and seed-sized oysters in experimental bags at all sites except CB, where 100% mortality of both market and seed-sized oysters occurred by August 2011. There was no significant difference in cumulative mortality between market and seed-sized oysters so results are from all size classes grouped together. There was a significant interaction in cumulative mortality of oysters among sites and type of bag (open or closed to predation). Cumulative mortality of closed bags at MP ($3\% \pm 4$) was significantly lower than all other bags except closed bags at SI ($6\% \pm 12$). Furthermore, cumulative mortality of oysters in closed bags at SI was significantly lower than all other bags except closed bags at MP (as stated above) and open bags at BG ($25\% \pm 9$) and SI ($25\% \pm 9$; Figure 2.9).

Significant differences in interval mortality occurred between April and October. From April to June, seed oyster mortality ($12\% \pm 20$) was significantly higher than market oyster mortality ($2\% \pm 4$; $p=0.0149$), and mortality within open bags ($15\% \pm 22$) was significantly higher than in closed bags ($2\% \pm 6$; $p=0.0056$). Not until August was there a significant interaction of site and type of bag in interval oyster mortality. From June to August, oysters in both closed and open bags at CB sustained 100% interval mortality. Interval mortality during this period within closed bags at CB was significantly higher than all other bags except open bags at CB, and vice versa. Aside from CB, open bags at SI ($10\% \pm 10$) and MP ($12\% \pm 9$) suffered higher interval oyster mortality than all other closed bags from June to August (Figure 2.10a). Finally, from August to October, interval oyster mortality within closed bags at MP ($0.4\% \pm 1$) was significantly lower than in closed bags at BG ($18\% \pm 17$; $p=0.0531$), and in open bags at BG ($18\% \pm 12$; $p=0.0231$) and MP ($13\% \pm 16$; $p=0.0450$; Figure 2.10b).

There were significant differences in growth rates of oysters by size class in 2011. Growth of spat sized oysters ($4.7 \text{ mm mo}^{-1} \pm 2.0$) was significantly higher than growth of seed sized oysters ($2.8 \text{ mm mo}^{-1} \pm 1.4$) and both had significantly greater growth than market sized oysters ($1.9 \text{ mm mo}^{-1} \pm 1.2$). Therefore, each size class was analyzed individually.

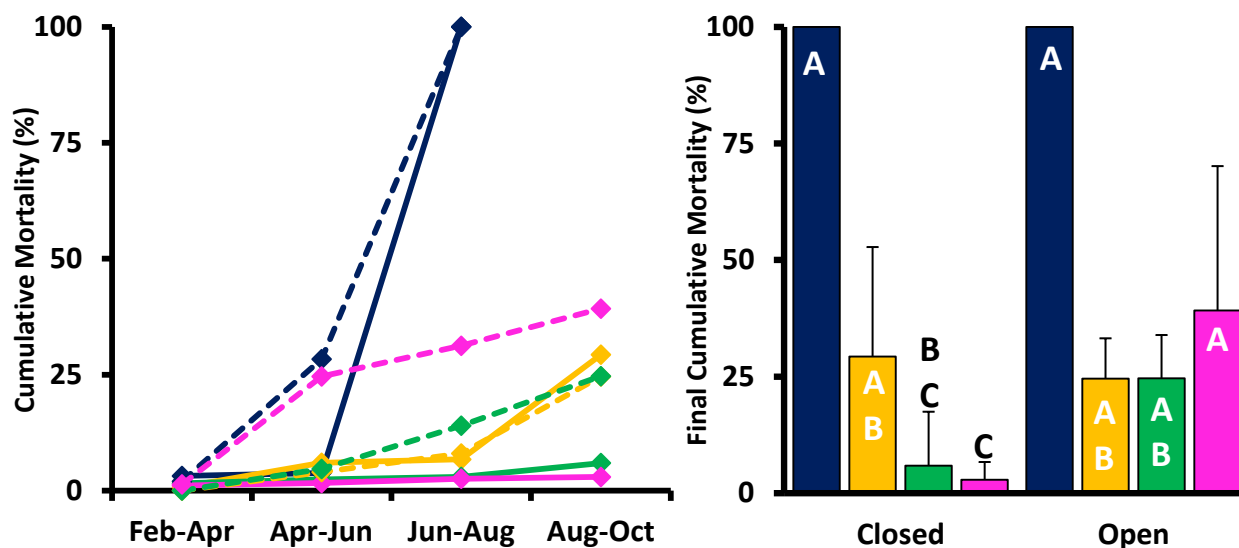


Figure 2.9 Cumulative mortalities of market and seed oysters in bags from 2011 in Breton Sound. There were no differences in mortality between market and seed size oysters so all size class data are grouped together. Letters denote significance groupings. (CB - blue, BG - yellow, SI - green, MP - pink; closed bags - solid lines, open bags - dotted lines)

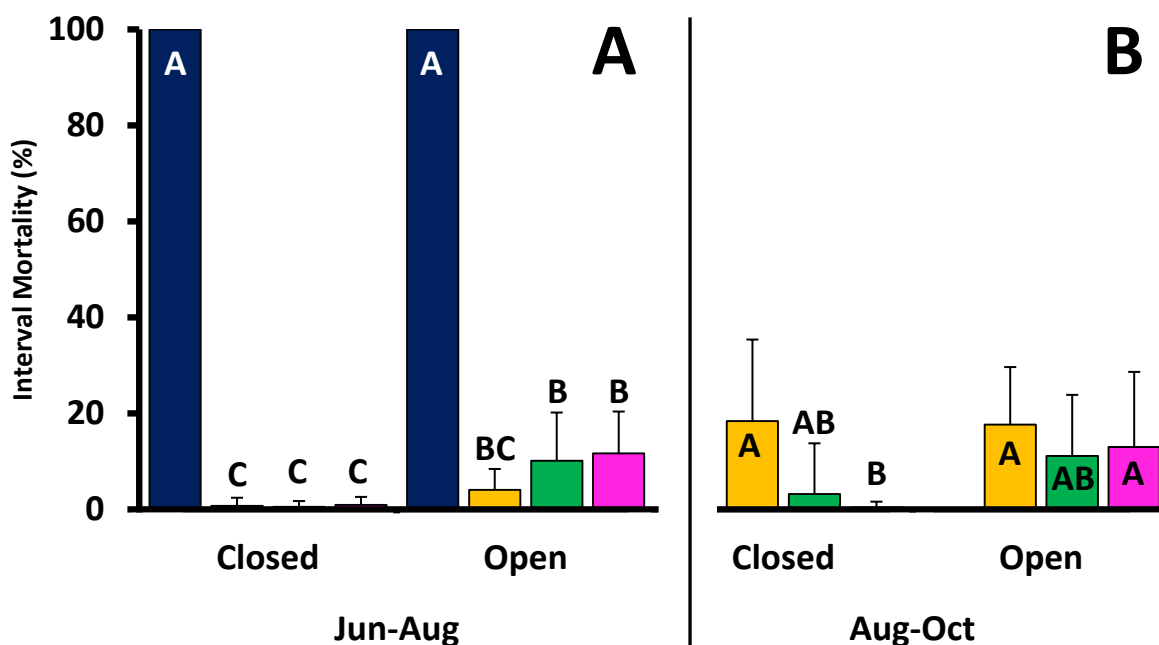


Figure 2.10 Interval oyster mortalities in experimental bags from 2011 in Breton Sound. There were no significant differences in mortality between market and seed size oysters. Small letters denote significance groupings. (CB - blue, BG - yellow, SI - green, MP - pink)

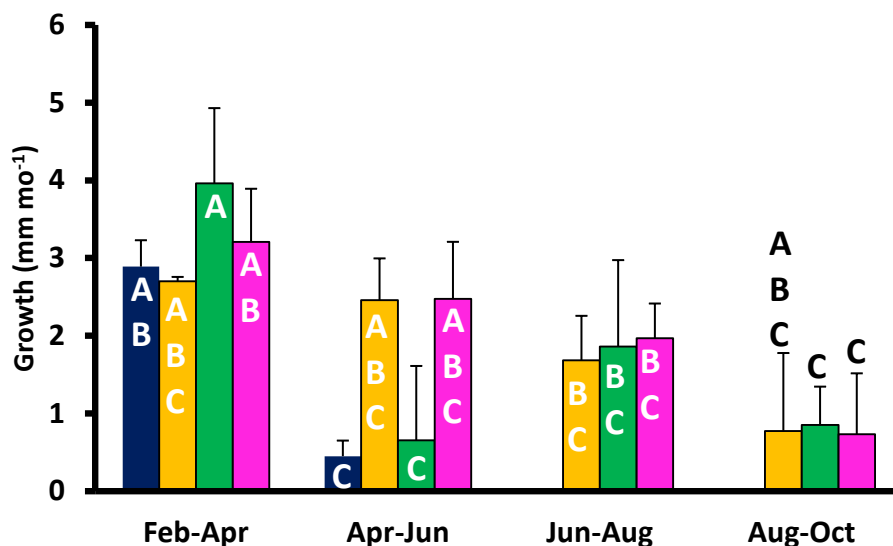


Figure 2.11 Mean market oyster growth and standard deviation in experimental bags from 2011 in Breton Sound. Letters denote significance groupings. (CB - blue, BG - yellow, SI - green, MP - pink)

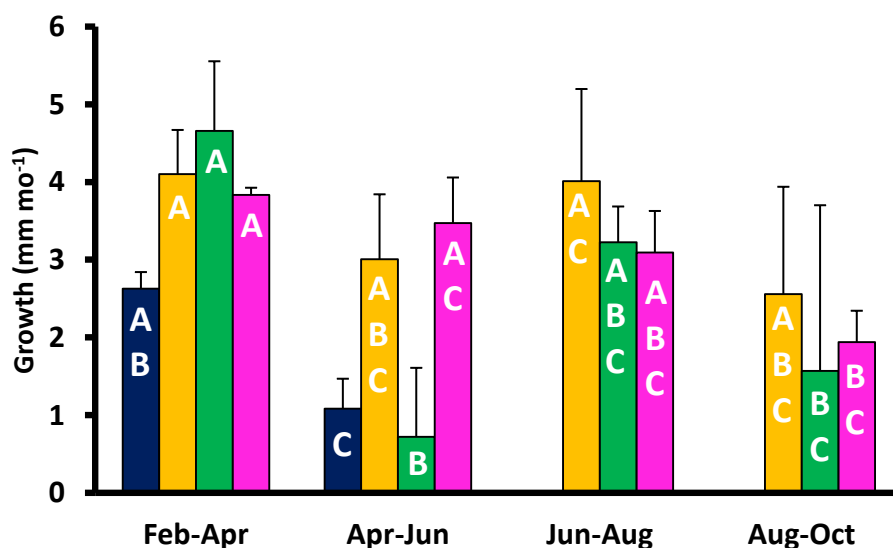


Figure 2.12 Mean seed oyster growth and standard deviation in bags from 2011 in Breton Sound. Letters denote significance groupings. (CB - blue, BG - yellow, SI - green, MP - pink)

There was a significant interaction of site and month within market oyster growth with a general trend of decreasing growth rates from February through October. Specifically, growth of oysters at CB ($0.4 \text{ mm mo}^{-1} \pm 0.2$) and SI ($0.6 \text{ mm mo}^{-1} \pm 1.0$) from April to June was significantly lower than at all sites ($3.2 \text{ mm mo}^{-1} \pm 0.7$) from February to April. Growth of oysters at SI from February to April ($4.0 \text{ mm mo}^{-1} \pm 1.0$) was significantly higher than growth at SI during any other time period, and growth at all sites from June to August. Furthermore, oyster

growth at MP from August to October ($0.7 \text{ mm mo}^{-1} \pm 0.8$) was significantly lower than at all sites from February to April except BG ($2.5 \text{ mm mo}^{-1} \pm 0.5$). Finally, growth at SI from August to October was significantly lower than oyster growth from February to April at CB ($2.9 \text{ mm mo}^{-1} \pm 0.3$) and MP ($3.2 \text{ mm mo}^{-1} \pm 0.7$; Figure 2.11).

There was also a significant interaction of site and month within seed oyster growth with a similar general trend of decreasing growth from February through October. Growth of oysters at CB from April to June ($1.1 \text{ mm mo}^{-1} \pm 0.4$) was significantly lower than at all sites ($3.8 \text{ mm mo}^{-1} \pm 0.9$) from February to April. Growth of oysters at SI from April to June ($0.7 \text{ mm mo}^{-1} \pm 0.9$) was significantly lower than growth at all sites from February to April except CB, growth at MP from April to June ($3.5 \text{ mm mo}^{-1} \pm 0.6$), and growth at BG from June to August ($4.0 \text{ mm mo}^{-1} \pm 1.2$). Finally, oyster growth at SI from February to April ($4.7 \text{ mm mo}^{-1} \pm 0.9$) was significantly higher than growth at MP ($1.9 \text{ mm mo}^{-1} \pm 0.4$) and SI ($1.6 \text{ mm mo}^{-1} \pm 2.1$) from August to October (Figure 2.12)

Spat oysters followed a similar pattern of growth, with growth at SI from February to April (7.9 mm mo^{-1}) being the highest, and growth at CB from April to June (1.2 mm mo^{-1}) being the lowest. There was only a single bag of spat oysters at each site, so no statistical analyses or standard deviation calculations could be conducted.

Plasma Osmolality, Condition Index and Disease

Mean oyster plasma osmolalities varied from 133 to 890 mOsm kg^{-1} . While there was no significant difference between size classes, there was a significant interaction between site and month. First, initial oyster plasma osmolality in February ($890 \text{ mOsm kg}^{-1} \pm 25$) was significantly higher than all sites at any date. CB osmolality in June ($133 \text{ mOsm kg}^{-1} \pm 3$) was significantly lower than all sites at any date. Osmolalities in September at SI ($364 \text{ mOsm kg}^{-1} \pm 8$) and MP ($400 \text{ mOsm kg}^{-1} \pm 8$) were significantly higher than any sites in June and BG in September ($279 \text{ mOsm kg}^{-1} \pm 6$). Finally, oyster plasma osmolality in June was significantly higher at BG ($286 \text{ mOsm kg}^{-1} \pm 6$) than SI ($240 \text{ mOsm kg}^{-1} \pm 3$; Figure 2.13).

All dermo infection intensities were less than 500,000 parasites per gram with most being less than 10,000 parasites per gram, and never affected more than 60% of the population other than the initial sampling in February. There were no significant differences between size classes

but there was as significant site and month effect. While not significantly different from each other, initial infection intensity ($1464 \text{ parasites g}^{-1} \pm 7991$), SI infection intensity in June ($828 \text{ parasites g}^{-1} \pm 1968$), and intensity at BG in September ($6403 \text{ parasites g}^{-1} \pm 22992$) were all significantly higher than intensity at SI in September ($1 \text{ parasites g}^{-1} \pm 3$) and all other sites in June. Furthermore, oyster infection intensity was higher at MP in September ($165 \text{ parasites g}^{-1} \pm 508$) than at SI in September ($p=0.0009$; Figure 2.15).

Mean condition of both market and seed-sized oysters decreased over time in 2011 and there was a significant site and date interaction. Condition of oysters at BG in September (1.1 ± 0.1) was significantly lower than the condition of oysters at all sites in June and the initial sampling in February (2.7 ± 0.2 ; Figure 2.14). There were no significant differences between the two size classes.

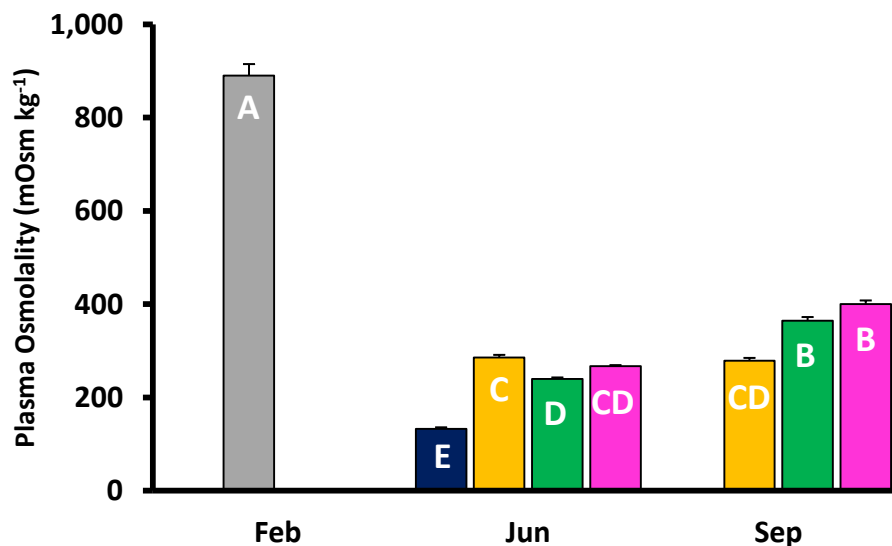


Figure 2.13 Mean oyster plasma osmolality and standard deviation from 2011 in Breton Sound. There were no significant differences between market and seed size oysters. Letters denote significance groupings. (Initial – gray, CB – blue, BG - yellow, SI - green, MP - pink)

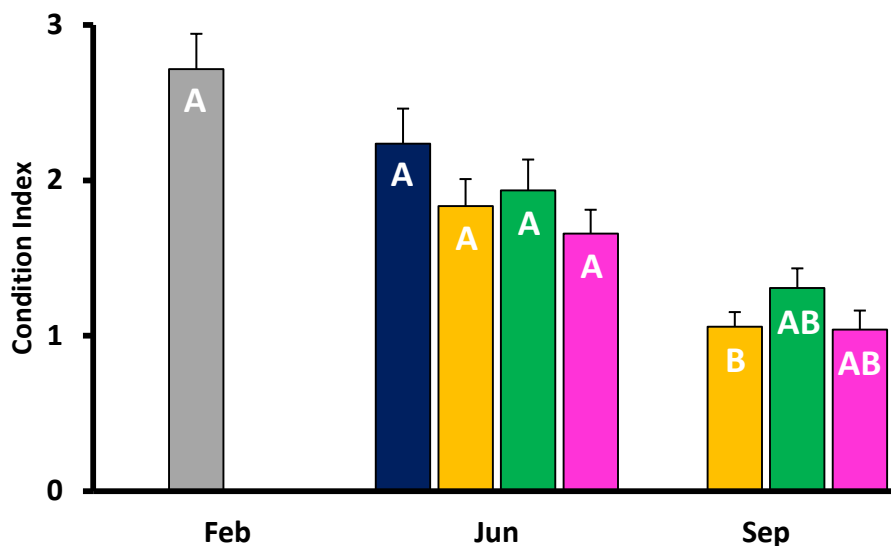


Figure 2.14 Mean oyster condition index and standard deviation from 2011 in Breton Sound. There were no significant differences between market and seed size oysters. Letters denote significance groupings. (Initial – gray, CB – blue, BG - yellow, SI - green, MP - pink)

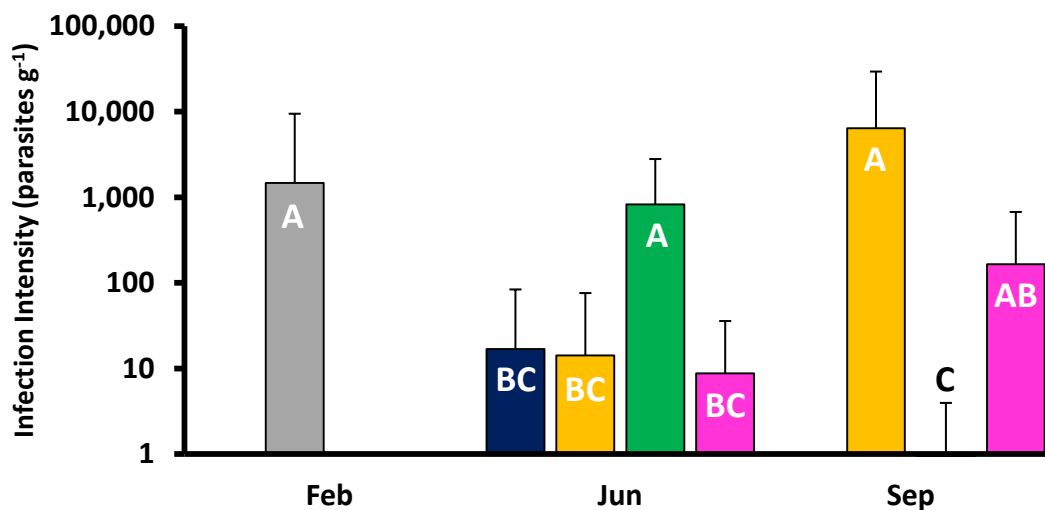


Figure 2.15 Mean dermo infection intensities of oysters and standard deviation from 2011 in Breton Sound. There were no significant differences between market and seed size oysters. Letters denote significance groupings. (Initial – gray, CB – blue, BG - yellow, SI - green, MP - pink)

3.4 Discussion

The Breton Sound estuary experienced unique conditions in 2011, with record flooding of the Mississippi River in late spring and early summer. Despite limited freshwater diversion flow, this 100-year flood event lowered salinity throughout the estuary from April to June, with

particularly extreme lows in late May and late June. Breton Sound oyster populations were exposed to a short period of low salinity that limited disease infection intensity, but also resulted in minimal spawning and/or spat settlement. Oysters where salinity was lowest experienced high mortality and low growth, while the rest of Breton Sound oysters experienced limited mortality mostly from predation along with higher growth and condition. These data show that the timing and duration of low salinity events (<10), are integral pieces in understanding the potential impacts on oyster life history stages.

The greatest potential impact of low salinity on oyster populations is reduced spawning and settlement. Minimal settlement affects future production because it means fewer oysters reach reproductive and harvestable size, i.e. reduced recruitment (Powell et al. 2009; Southworth and Mann 2004). Furthermore, without a large number of oysters settling as spat, oyster reefs will be depleted of valuable hard substrate. Spawning is directly correlated with water temperature, and for the Gulf of Mexico coast there is a bi-modal pattern of gametogenesis and spawning, with most events occurring when water temperatures are greater than 25°C (Hayes and Menzel 1981; Ingle 1951; Shumway 1996; Supan and Wilson 2001). However, many factors directly affect spawning and settlement independently of temperature such as currents, substrate composition, light conditions, dissolved oxygen concentrations, or even lunar phases (Ingle 1951; Johnson et al. 2009; Knights and Walters 2010; Loosanoff and Nomejko 1951; Obeirn et al. 1995; Ortega and Sutherland 1992; Turner et al. 1994). While all have the ability to detrimentally affect spawning and settlement in the Gulf, even when temperatures are ideal; salinity is the most important of these secondary factors. Gametogenesis, spawning, and settlement have been shown to be significantly reduced or stopped at low salinity, regardless of temperature (Butler 1949; Chatry et al. 1983; Pollack et al. 2011). Typically salinities within the Breton Sound estuary are ideal for spawning/settlement and temperature is the limiting factor. However, in 2011, rather than the typical bimodal distribution of massive amounts of oyster spat attachment when water temperatures rise in early summer and fall in late summer (Pollard 1973), Breton Sound experienced no large settlement event. A similar study in the Copano and Aransas bays in Texas also found very little spat settlement during periods of low salinity and ideal temperatures (Pollack et al. 2011). Chatry et al. (1983) analyzed 11 years of Breton Sound settlement and found virtually none when mean salinity was less than 10 during summer when

water temperatures are high. Only mean salinity at MP (11.6 ± 4.0) was greater than 10 from May to September in 2011, when water temperatures averaged 29°C.

Mortality rates are typically higher during summer months when temperature and salinity are high, because of increased disease and predation (Davis and Barber 1994; Ford et al. 2006; Ragone and Burreson 1993). While mortality was higher during summer months in Breton Sound in 2011, disease appeared to have minimal impacts. Dermo never infected more than 60% of oyster populations, and of those affected infection intensities were very low. Most oyster mortality from dermo infections does not occur until populations experience heavy infection intensities (Quick and Mackin 1971). Predation, on the other hand, did appear to be a factor, as there were significant differences in mortality between oysters protected from predators (closed bag sections) and those exposed (open bag sections) at the two higher salinity sites. A similar study by Aronhime (2010) in Barataria Bay found higher oyster mortality from predation in higher salinity which they attributed to blue crab and black drum, although had no direct evidence.

Predation at the higher salinity sites in Breton Sound in 2011 was most likely from blue crabs (*Callinectes sapidus*), stone crabs (*Menippe alidina*), and black drum (*Pogonias cromis*). While oyster drills (*Stramonita haemastoma*) are typically a main predator of eastern oysters in the Gulf (Brown and Richardson 1987; Galtsoff 1964; St. Amant 1938), they require sustained salinities greater than 15 (Garton and Stickle 1980; St. Amant 1938), and they were only observed at MP in August. Furthermore, at sites with high mortalities in open bags, shell fragments and/or whole shells were observed, which would be indicative of black drum (Brown et al. 2003, 2008) and blue and/or stone crabs (Aronhime and Brown 2009; Powell and Gunter 1968).

Aside from disease and predation, the combined effects of temperature and salinity are held to be the two dominant abiotic controls on *C. virginica*, and can affect virtually every aspect of oyster biology, and ultimately, their survival (Butler 1949; Galstoff 1964; Gunter 1953; Bataller et al. 1999; Shumway 1996). A past lab study found significantly higher cumulative mortality of oysters exposed to a 3 week freshet (salinity < 1) event in the summer (July; 28°C) as compared to in the spring (April; 18°C) or winter (December; 16°C) suggesting that mortality was higher under the combined effects of low salinity conditions and higher temperatures (La

Peyre et al. 2003). Furthermore, numerous field observations have documented oyster survival in low salinity for extended periods of time, but only at low temperatures (Lossanoff 1953, Wells 1961, Kennedy 1991, Austin et al. 1993, Winstead 1995). For example, Gunter (1953) documented eastern oysters surviving salinities as low as 2 for a month, but only in winter/spring water conditions. When salinities drop below 5, oysters stop feeding, close their valves, and increase anaerobic metabolism to a point that results in high mortality (Galstoff 1964; Gunter 1953; Heilmayer et al. 2008; Loosanoff 1953; Shumway 1996). Higher temperatures increase metabolic activities, which would increase the rate of mortality (Heilmayer et al. 2008; Michaelidis et al. 2005; Shumway 1996). From May through July of 2011, mean salinity and temperature (°C) at CB were 2.7 ± 1.6 and 28.6 ± 2.7 , respectively. By August 2011, CB oysters suffered 100% mortality. Additionally, while oyster mortality was much lower at BG (< 30%), there were no significant differences in mortality between open and closed bags, except at our highest salinity site (MP) where open bags had greater than 35 % mortality as compared to less than 5% mortality in the closed bags suggesting that predation may have been more of a factor at the highest salinity site only. At the three lower salinity sites, the data suggest that the synergistic effect of high temperatures and low salinity was the main impact of mortality on oyster populations, with minimal impact at the highest salinity site (salinity never less than 6), where predation was more of a factor.

Typically, growth rates decrease as size increases (Kraeuter et al. 2007), and this was the pattern in Breton Sound oysters in 2011 (Figure 2.16). Spat grew faster than seed and market sized oysters, and seed sized oysters grew faster than market oysters. Growth rates usually increase with increasing temperature as well as with increasing salinity (Dekshenieks et al. 1993; Harding 2007; Hofmann et al. 2004). As a result, growth rates are typically higher in warmer months, and in higher salinity sites. This was not the case in Breton Sound in 2011, with most oyster growth occurring from February to April before salinity was lowered throughout the estuary. Furthermore, growth of oysters at CB and SI appeared to be most affected by dramatically lowered salinities from April to June. However, despite the less than ideal salinity conditions, mean market and seed oyster growth for all sites over the entire study ($2.4 \text{ mm mo}^{-1} \pm 1.4$) were greater than the highest salinity site (12.0 ± 4.4) in a previous winter/spring study in Breton Sound ($1.6 \text{ mm mo}^{-1} \pm 2.2$; La Peyre et al. 2009). However, this mean growth is less than or equal to half of previously reported oyster growth in Louisiana (4.9 mm mo^{-1} , Moore 1899;

5.5 mm mo⁻¹, Moore 1899; 7.6 mm mo⁻¹, Gunter 1951 - adapted from Shumway 1996). Growth is thought to be reduced in low salinity waters because of valve closure resulting in reduced feeding. Loosanoff (1953, 1965) reported no feeding in oysters in salinity lower than 3 and stunted growth at 7.5. However, only CB experienced salinity less than 3 for more than seven days in 2011, so most of the Breton Sound oysters were feeding and growing even at salinities less than 10. These results emphasize the interactive nature of temperature and salinity on oyster growth rates in Breton Sound.

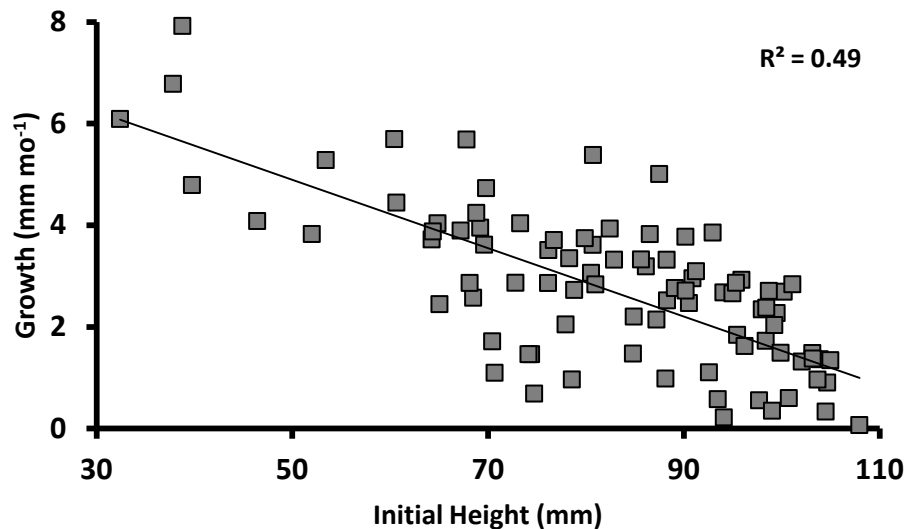


Figure 2.16 Relationship of oyster growth (mm mo⁻¹) to initial oyster height (mm) in Breton Sound oysters in 2011. R² value represents fit of the following equation: growth = -0.07(height) + 8.26.

Oyster plasma osmolalities, condition index, and disease infection intensities among Breton Sound oysters followed predictable patterns in 2011. Plasma osmolalities decreased over time with low salinity throughout the estuary, except for a slight increase in September when salinity was higher. Oysters are commonly known to be osmo-conformers (Hand 1977; McFarland et al. 2011) except in extremely low salinity (La Peyre et al. 2003, 2009). Salinity remained high enough in Breton Sound in 2011 in order for oysters to maintain their ability to osmo-conform.

The condition index and disease infection intensities among Breton Sound oysters followed predictable patterns in 2011: both decreased over time with decreasing salinity, and

remained low while salinity was low. This pattern follows findings from numerous field and lab studies which have shown that condition index and *P. marinus* viability are significantly reduced in low salinity and low temperatures (Burreson and Ragone-Calvo 1996; Hofmann et al. 1995; La Peyre et al. 2003, 2009, 2010; Ragone and Burreson 1993; Soniat 1996; Volety et al. 2000). Specifically, some in vitro research examining *P. marinus* viability found reduced viability at salinity of less than 7 (La Peyre et al. 2006). This current field study, however, had low salinity combined with high temperatures. Field and lab studies have observed a decrease in infection intensities in late winter and early spring as temperatures increase, and it has been suggested that the high temperature reduction in infection intensities may be due to the active process of elimination of oyster host defenses (Ray 1954; Mackin 1962; Soniat 1985; La Peyre et al. 2008; Goedken et al. 2005). However, as host health (condition) decreased throughout the year, it is unlikely that active elimination was occurring, and both the low disease infection level and condition are most likely from sustained low (< 10) salinity.

The Mississippi River flood of 2011 altered salinity regimes in the Breton Sound estuary during a time of rising water temperature. The synergistic impacts of temperature and salinity have the potential to drive oyster productivity, and low salinity combined with high water temperature can be a detrimental combination. There are several freshwater sources in Breton Sound, and as these inputs vary, oyster population dynamics respond. Increasing freshwater input during high temperature periods are likely to be harmful to oyster production and long-term population sustainability by affecting all aspects of the oyster life history from spawning, to settlement, to growth and mortality.

Chapter 4: Conclusion

There were two unique environmental disasters that impacted Breton Sound during the course of this study. The Deepwater Horizon Oil Spill in 2010 and the Mississippi River Flood in 2011 resulted in prolonged freshwater input during rising water temperatures in both years. Breton Sound was characterized by freshwater diversion discharge in an attempt to keep oil offshore in 2010, while in 2011 the estuary was exposed to minimal diversion flow but record Mississippi River flooding. The outcome was distinctive estuarine salinity regimes between the two years based upon the timing, duration, and source of freshwater resulting in different oyster population responses.

In 2010, Mississippi River water was diverted directly into Breton Sound by several freshwater diversion structures from late April until mid August. This drastically reduced salinity throughout the estuary to extremely low levels (< 2) for an extended period of time. In 2011, Mississippi River floodwaters lowered Breton Sound salinity to extreme levels only for a brief period, while lowering salinity below 10 for an extended period of time. The Caernarvon Freshwater Diversion structure in 2010 allowed much more freshwater directly into Breton Sound later in the summer and for a longer time period than the Mississippi flood in 2011 (Figure 4.1). The result was detrimental synergistic effects of extremely low salinity and high water temperature on oyster populations, especially in 2010.

There was a similar oyster response in both years in settlement, disease infection intensities, and condition; with an apparent lack of settlement and disease, along with decreasing condition over time. However, there were considerable differences in other oyster life history responses. The most striking difference would be in the ability of oysters to osmo-conform. Breton Sound oysters failed to lower plasma osmolality in extremely low salinity during 2010, but osmo-conformed in a more predictable way with slightly higher salinity in 2011. In June, when some of the lowest salinities occurred in both years (2010: 3.3 ± 2.6 , 2011: 5.2 ± 4.0), mean plasma osmolality was nearly twice as high in 2010 ($445 \text{ mOsm kg}^{-1} \pm 139$) than in 2011 ($230 \text{ mOsm kg}^{-1} \pm 61$). A possible explanation is a minimum salinity requirement for eastern oysters in the northern Gulf of Mexico to osmo-conform, which would be in agreement with findings of previous studies (La Peyre et al. 2003, 2009).

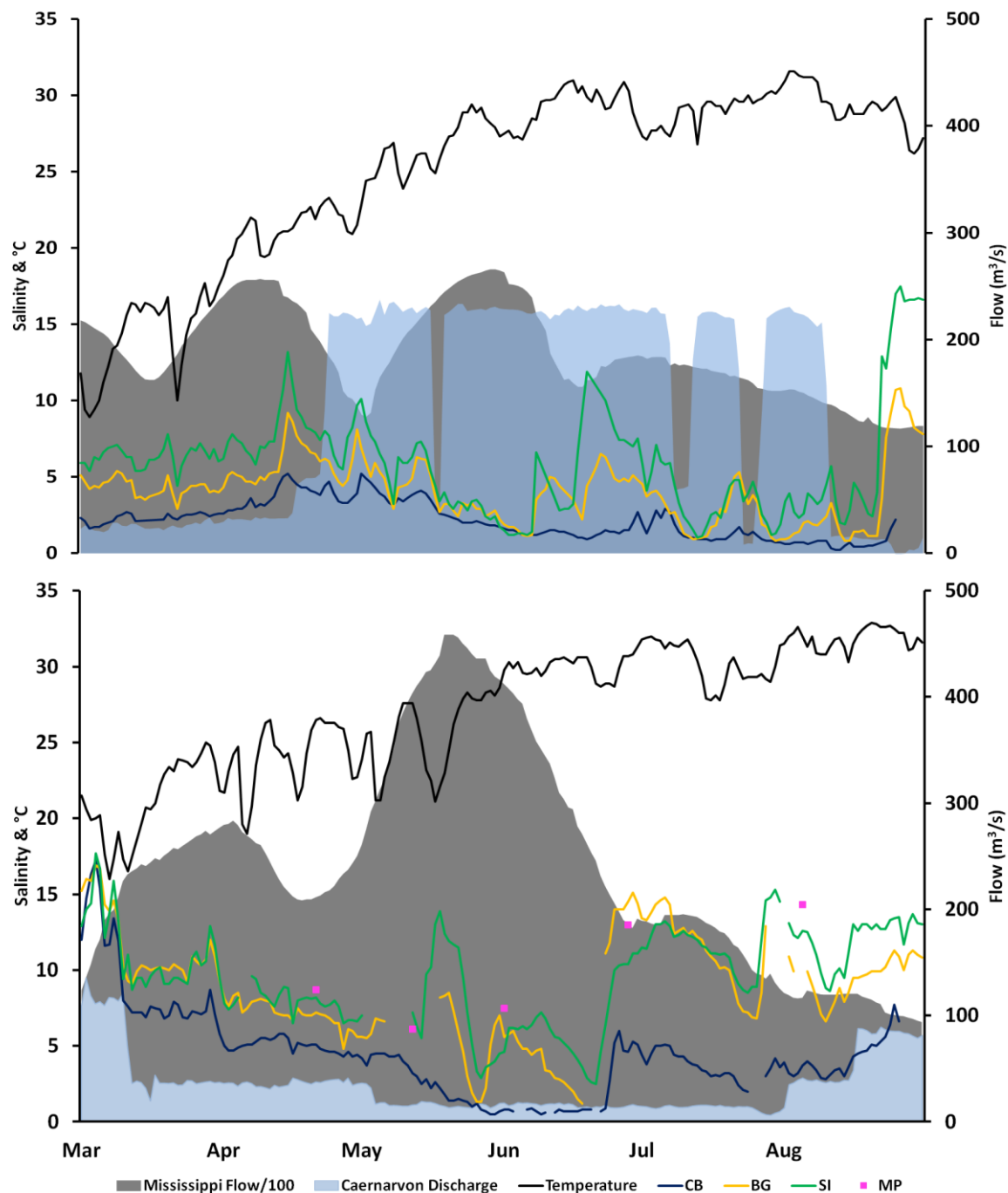


Figure 4.1 Timing and duration of extreme freshwater events and their impact on site salinities in Breton Sound from March to August in 2010 and 2011. Miss. River flow ($\text{m}^3 \text{s}^{-1} 100^{-1}$) data are taken from US Army Corps of Engineers Recorder # 01100. Caernarvon discharge ($\text{m}^3 \text{s}^{-1}$), water temperature ($^{\circ}\text{C}$), and site salinities taken from USGS continuous water quality recorders: Caernarvon - 295124089542100, CB - 073745258, BG - 07374527, SI - 07374526.

Similar disparities were found among oyster growth and mortality between 2010 and 2011 in Breton Sound. While growth was limited in both years, oysters grew more in 2011 than in 2010 because of slightly higher salinity. However, mean oyster growth in both years was much lower than previously reported growth rates in Louisiana (4.9 mm mo⁻¹, Moore 1899; 5.5 mm mo⁻¹, Moore 1899; 7.6 mm mo⁻¹, Gunter 1951 - adapted from Shumway 1996). Although there was similar cumulative oyster mortality in both years, mortality was higher in 2010 and the causes were much different. Oysters in 2010 were exposed to the lethal combination of high temperature and extremely low salinity, which was only the case at CB in 2011. The rest of oysters in 2011 were exposed to varying levels of predation, which accounted for most of the mortality.

Freshwater inputs were clearly different in Breton Sound between 2010 and 2011, especially when considering their impact on oyster response. However, it is also interesting to note the differences in freshwater influence on 2010 and 2011 in contrast to the last twenty years. Freshwater sources in Breton Sound were highly variable over the last twenty years. The Mississippi River varied from notably low flow, around 5,000 m³s⁻¹, in 2000 and 2006, to very high flow, over 40,000 m³s⁻¹, in 1997, 2008, and 2011 (Figure 4.2). Monthly rainfall was also highly variable, but follows the same pattern of wet and dry years as Mississippi River flow fairly well, with the exception of extremely high rainfall in December of 2009 (Figure 4.3). Flow from the largest freshwater diversion structure in Breton Sound (Caernarvon Freshwater Diversion) was also fairly variable, with flows ranging from 0 to 249 m³ s⁻¹ (which is maximum capacity for this structure) (Figure 4.4).

Water temperature and rainfall in 2010 and 2011 were not significantly different than in any other year in the past 20 years. However, Caernarvon discharge in 2010 was significantly higher than any year in the past 20 years except 2007 and the result were significantly lower site salinities in 2010 than in the past seven years. Furthermore, Mississippi River flow in 2010 and 2011 was significantly higher than all years except 1990, 1991, 1997, 1998, 2008, and 2009. All of these years were categorized as El Niño years, except 2008 (La Niña year), which supports the finding that Mississippi River flow is higher during El Niño years (Figure 4.5). This is interesting to note because neither 2010 nor 2011 were categorized as El Niño years but rather as a neutral (2010) and a La Nina (2011) year.

Clearly, the freshwater input of the Mississippi River into Breton Sound has a significant impact on oyster populations, and there is a steady increase of diversion discharge. This can be a dangerous trend when considering that diverted water has the greatest relative freshwater influence on the upper end of Breton Sound (Hyfield et al. 2008). While the relative influence of each freshwater source is still relatively unstudied, it is clear they are all greatly important and influential to the Breton Sound estuary. Additionally, there are several potentially positive impacts of freshwater inputs on oyster productivity, given correct timing and amounts, and these positive effects include possible increased nutrients and positive water quality effects that may also result in reduced predation or disease that have to be considered as well (La Peyre et al. 2009; Snedden et al. 2007; Lane et al. 2004; La Peyre et al. 2003).

While Breton Sound oyster population dynamics are a cause-effect driven system, with such a highly variable environmental setting and the complex interactive nature of all the influential factors, it is a complicated system. Above all, however, timing seems to be extremely important when considering any influential elements, and is especially significant on even a monthly scale with so many driving factors like in Breton Sound. In 2010 and 2011, water temperature and salinity controlled oyster population dynamics, but the differences in timing and duration of freshwater inputs resulted in considerably dissimilar salinity regimes between the two years.

While not only is it clear that the timing and duration of freshwater inputs will significantly affect the impacts on oyster resources, it is likely that large scale global climate patterns (including El Niño events) will also modify how and to what extent freshwater events may affect Breton Sound. This has been the case in Breton Sound for the last twenty years, with freshwater inputs like Mississippi River flow and rainfall being much higher during El Niño events than during La Niña or neutral years (Figure 4.5, 4.6). Furthermore, because of this freshwater, mean site salinities were lower during El Niño years over the last two decades (Figure 4.7). The only major freshwater source to Breton Sound that did not follow this pattern was the Caernarvon Freshwater Diversion, because it is a managed structure. Caernarvon discharge was considerably higher during neutral years (Figure 4.8). Soniat et al. (2009) suggested that Gulf of Mexico oyster populations are driven by large scale freshwater input cycles resulting from El Niño events. The result is a great need to understand the influence of

global climate patterns on northern Gulf of Mexico oyster response. This is particularly important to consider when implementing management actions. For example, the use of freshwater diversions should be greatly affected by global climate patterns, because the same timing and duration of freshwater input from diversions will have drastically different impacts in El Niño years versus La Niña years.

This project will provide valuable data for management agencies and scientists monitoring the Gulf of Mexico's eastern oyster fishery. It is also a large step in the collaborative development of a predictive management model for Gulf of Mexico oysters (Soniat et al. 2011). These results parameterize the range of growth, mortality, and recruitment under a variety of environmental conditions (i.e. temperature and salinity regimes) as well as predation and disease pressures. A successful management model could aid in the proper implementation of sustainable harvest limits as well as the most effective and efficient management of oysters during events of abnormality, e.g. extreme weather events, disease, etc. This project will also hopefully be the first of many that attempt to fine tune estimates of natural mortality and recruitment of Gulf of Mexico oysters. These factors of the fishery will quickly become valuable information when taking advantage of the full potential of a predictive management model.

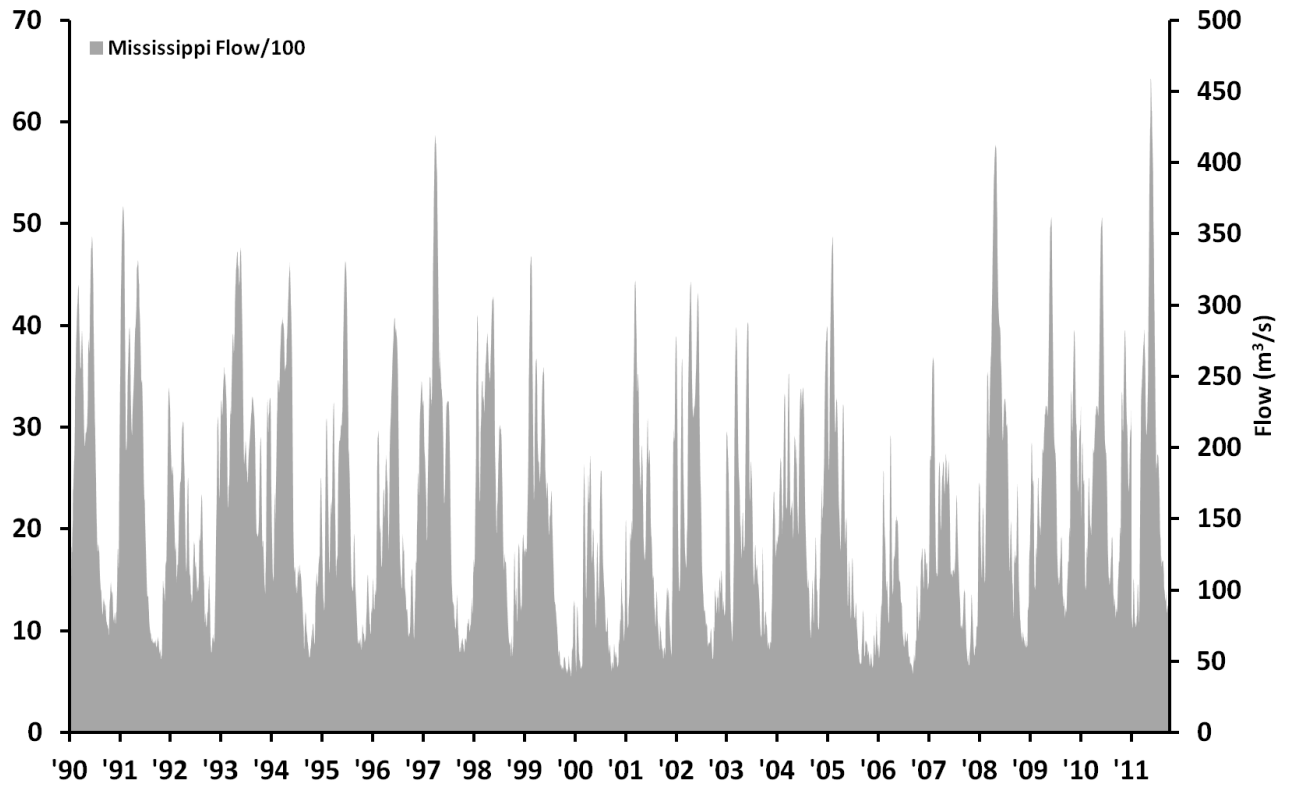


Figure 4.2 Daily Mississippi River flow at Tarbert Landing, MS from 1990 to 2011.

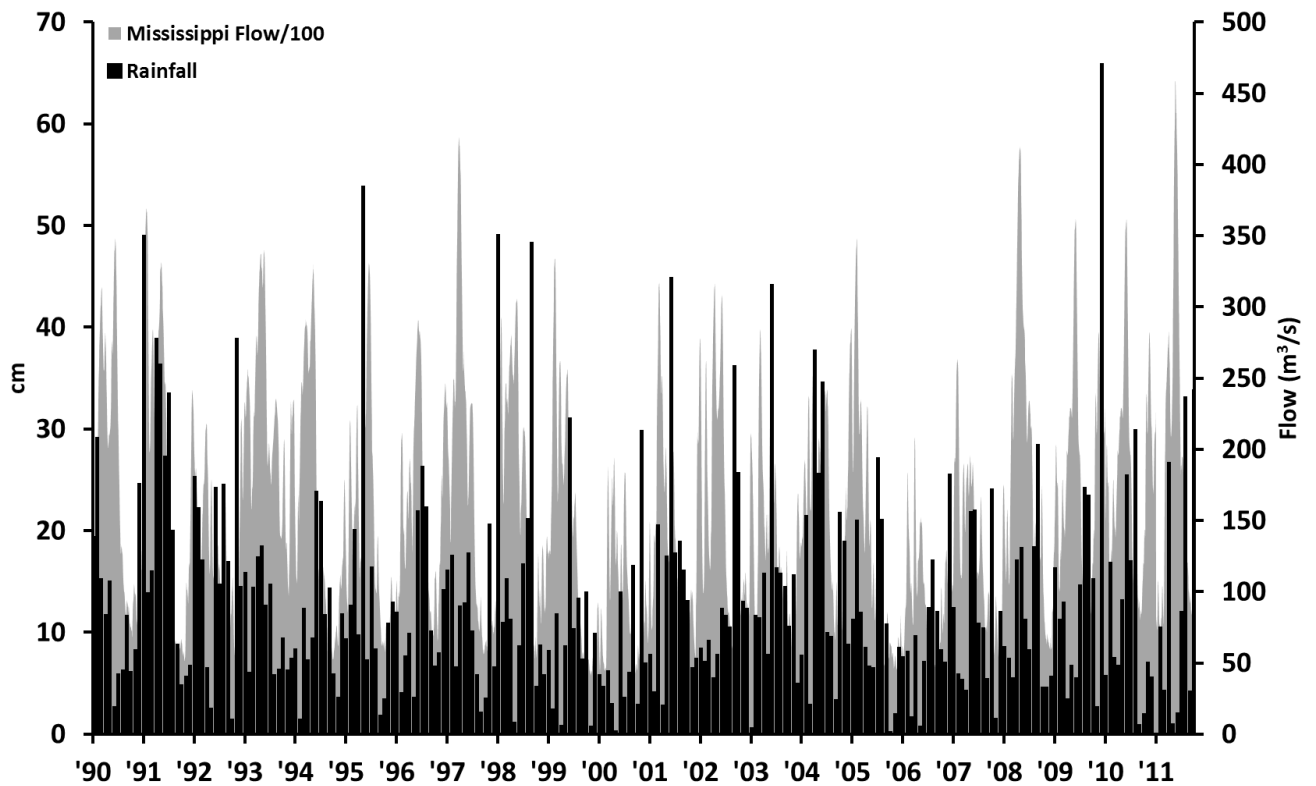


Figure 4.3 Monthly rainfall and Miss. River flow at Tarbert Landing, MS from 1990 to 2011.

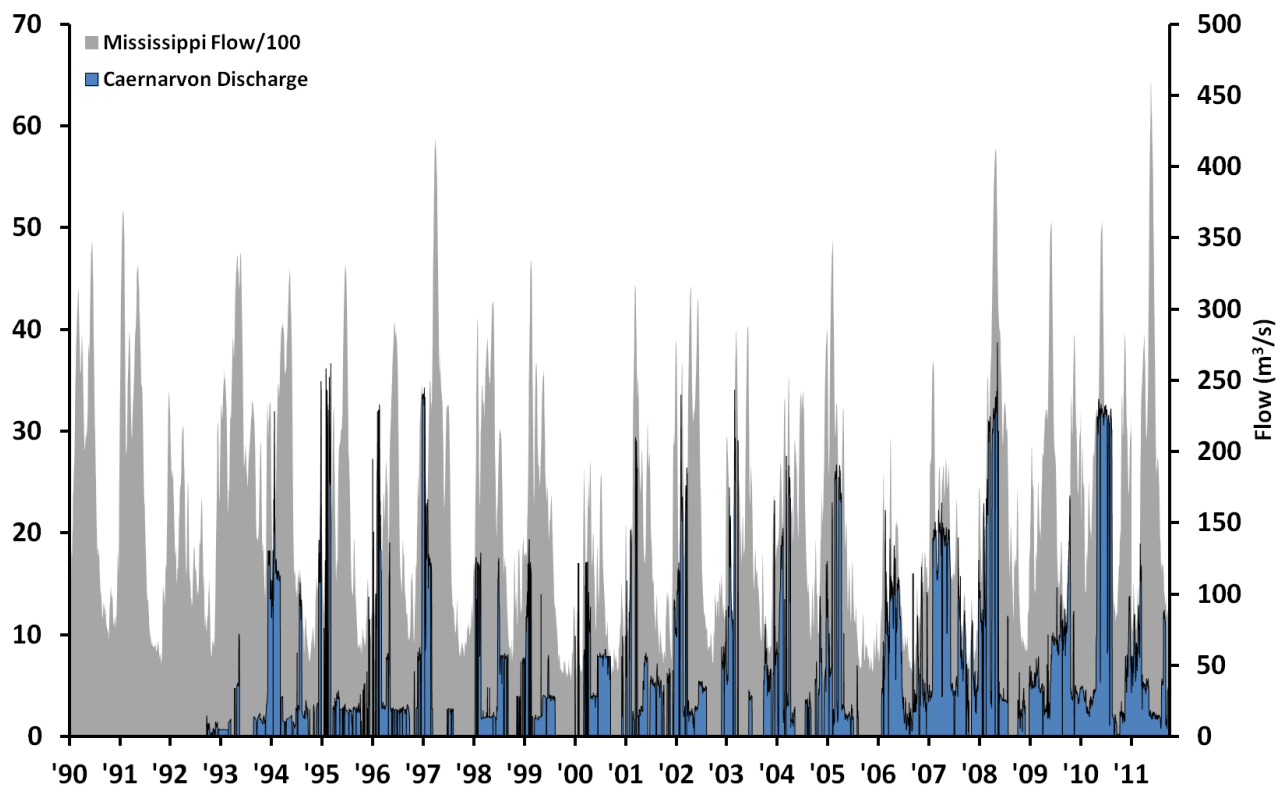


Figure 4.4 Caernarvon discharge and Miss. River flow at Tarbert Landing, MS from 1990 to 2011.

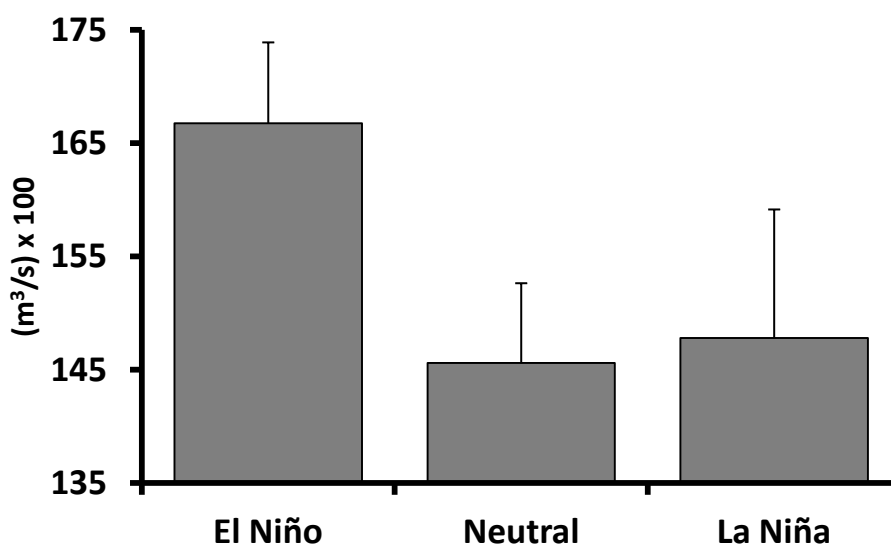


Figure 4.5 Mean monthly Mississippi River flow and standard error at Tarbert Landing, MS during El Niño, La Niña, and neutral years from 1990 to 2011.

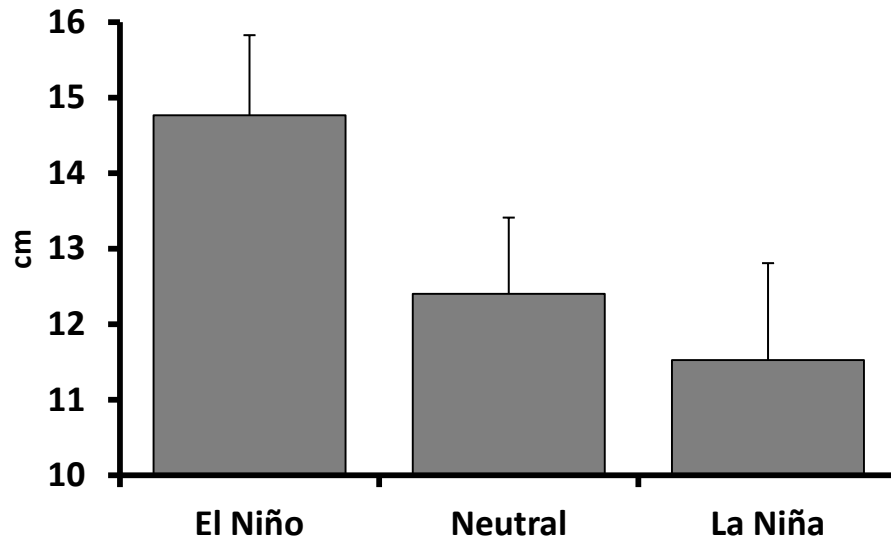


Figure 4.6 Mean monthly rainfall and standard error at Southern Regional Climate Center's monitoring station # 166295 at Louis Armstrong New Orleans International Airport during El Niño, La Niña, and neutral years from 1990 to 2011.

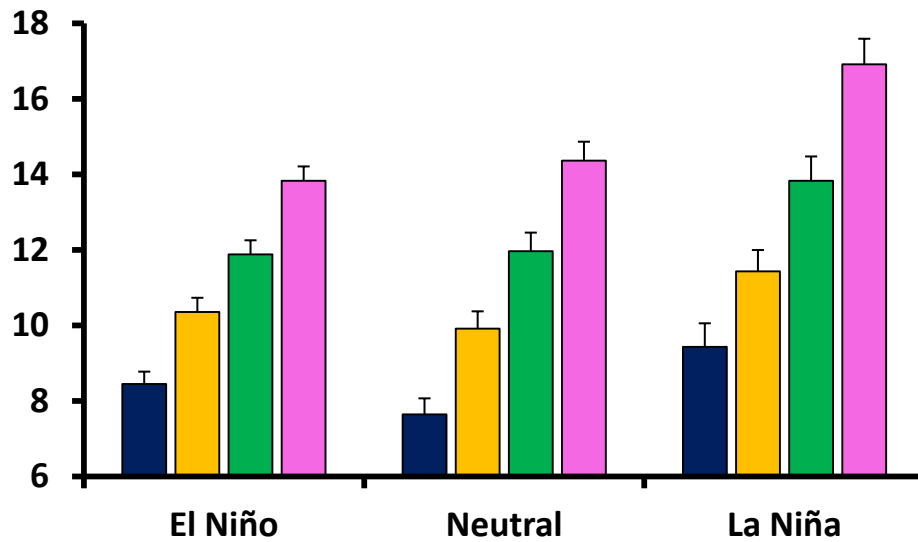


Figure 4.7 Mean monthly site salinities and standard error in Breton Sound during El Niño, La Niña, and neutral years from 1990 to 2011. (CB - blue, BG - yellow, SI - green, and MP - pink)

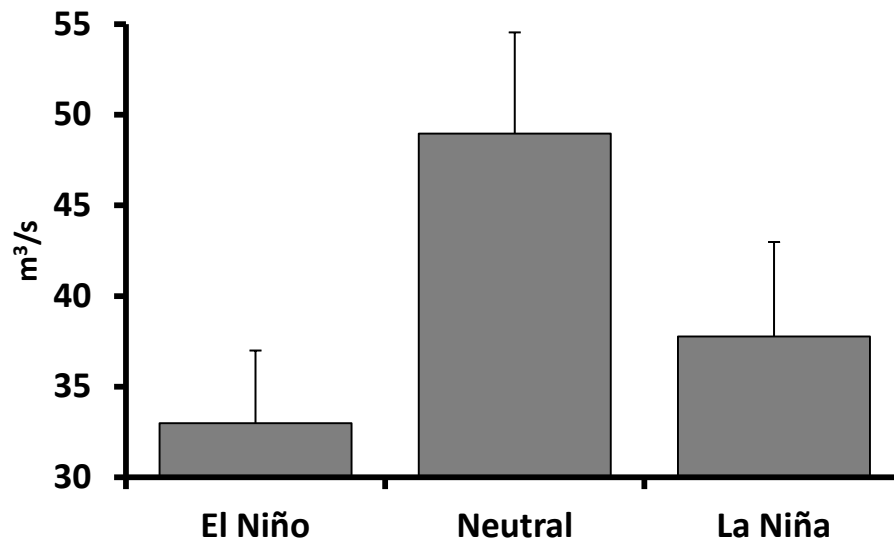


Figure 4.8 Mean monthly Caernarvon discharge and standard error into Breton Sound during El Niño, La Niña, and neutral years from 1990 to 2011.

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Vita

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