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RANGIA CUNEATA CLAM DECLINE IN LAKE PONTCHARTRAIN FROM 2001 TO 2014 DUE TO AN EL NIÑO SOUTHERN OSCILLATION SHIFT COUPLED WITH A PERIOD OF HIGH HURRICANE INTENSITY AND FREQUENCY

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ABSTRACT: The clam, *Rangia cuneata*, occurs in low salinity zones of Atlantic and Gulf of Mexico estuaries. Prior to 2001, it was abundant in Lake Pontchartrain, a large and shallow oligohaline estuary, located north of New Orleans. However, density abruptly decreased by 96% after an extreme drought from an El Niño Southern Oscillation (ENSO) shift (1998–2000). Stable higher salinities resulted in the establishment of higher salinity communities. The hooked mussel, *Ischadium recurvum*, increased abruptly and colonized live *R. cuneata*. Competition from *I. recurvum* and the *R. cuneata* decline occurred at the end of the drought, despite a decrease in salinity. After the drought, there was a period of high hurricane intensity and frequency which stifled clam recovery. Their densities remained relatively low due to declines from hurricane disturbances in 2005, 2008 and 2012. In 2014, after two years without severe hurricane effects, density and biomass recovered to baseline years (1954 and 1997). Barrier island erosion caused by Hurricane Georges in 1998 and adverse effects of the ENSO drought on wetlands may have set the stage for increased effects of subsequent hurricanes. High relative sea level rise, wetland loss and erosion of barrier islands, which occurred with each successive storm, potentially increased the size of surges. Surges resuspended sediments which buried clams and abruptly increased salinity and lowered dissolved oxygen. Salinity stratification persisted after storms and caused hypoxia in bottom waters. Storm surge interactions with discharges from the Bonnet Carré Spillway, a Mississippi River flood diversion structure, and the MRGO, a ship channel, also exacerbated hurricane effects.

KEY WORDS: drought, storm surges, sea level rise, climate change, *Ischadium*

INTRODUCTION

Rangia cuneata (Sowerby I, 1832) is indigenous to low salinity areas of Atlantic and Gulf of Mexico estuaries, and has recently been reported from Europe (Verween et al. 2006). It is an important component of estuarine ecosystems because it provides food for fishes, crabs, shrimp, waterfowl, and humans (LaSalle and de la Cruz 1985), and performs important environmental services, including water filtration and shell production, which stabilizes soft bottoms. It generally occurs at salinities < 18, but is more abundant in oligohaline (0.5–5) waters where it experiences less competition and predation due to low species diversity (LaSalle and de la Cruz 1985). Fairbanks (1963) studied the growth rate of *R. cuneata* in 2 areas of eastern Lake Pontchartrain during 1957 and 1958. His estimated annual growth in length for 3 years were 15–20 mm (year 1), 20–29 mm (year 2) and 24–34 mm (year 3). LaSalle and de la Cruz (1985) estimated the average life span to be 4–5 years and, based on several studies reported in Louisiana, spawning may be continuous with most spawning from March to May and late summer to November. Spawning, however, has been reported by Cain (1975) to be dependent upon a salinity shift of ± 5 at temperatures above 15°C. *Rangia cuneata* has been considered an indicator species in Lake Pontchartrain, Louisiana, where its density (N/m²) has been proposed as a measure of recovery from shell dredging, saltwater intrusion (Abadie and Poirrier 2000), and general anthropogenic disturbances (Houck 1989).

The earliest baseline data for *R. cuneata* from Lake Pontchartrain were obtained by Suttkus et al. (1954). They only studied clams > 20 mm and reported a mean density of 95/m². Studies conducted in 1969–1972 (Tarver and Dugas 1973), 1978–1980 (Sikora and Sikora 1982) and 1982–1983 (Poirrier et al. 1984) indicated declines in large clams (> 20 mm) from 1954 baseline densities, which were mainly attributed to commercial shell dredging (USACE 1987). Densities increased to 1954 levels after dredging was stopped in 1990, but large clams were still absent from a 250 km² area subject to saltwater intrusion from the MRGO (Abadie and Poirrier 2000). The post-dredging increase in large clam density from 1996 through 2000 was regarded as a return to normal conditions. However, there was an unexpected, abrupt 96% density decrease between 2000 and 2001 (Figure 1) after a severe drought (Visser et al. 2002), linked to an El Niño Southern Oscillation (ENSO) shift from the strongest El Niño in the last century (Zheng et al. 2003) to a La Niña from 1997 to 2001 (Cho and Poirrier 2005, Poirrier et al. 2009). We were uncertain about the cause of the 2001 clam density crash after the drought and whether or not recovery to pre-drought density levels would eventually occur. Densities have remained substantially lower than pre-drought levels (1998–2000) even after the closure of the MRGO (Poirrier 2013). Poirrier et al. (2013) proposed that clam density recovery from the 2001 density crash did not occur because of storm surges from a period of high

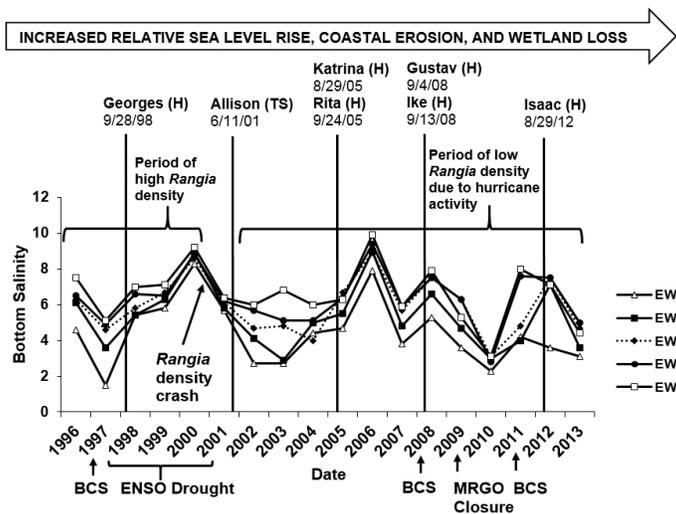


Figure 1. Pre-drought period of high clam density, the post-drought 2001 density crash, and period of low density associated with hurricane activity. Years sampled during 1996–2013 and events including: hurricanes and tropical storms, Bonnet Carré Spillway openings (BCS), El Niño Southern Oscillation (ENSO) drought years, Mississippi River Gulf Outlet (MRGO) closure, spatial and temporal bottom salinity changes across the width of the Lake on 5 E–W transects (EW1 – EW5). H = hurricanes and TS = tropical storms.

hurricane intensity and frequency (Figure 1). These surges were enhanced by relative sea-level rise (Burkett 2008, Roth 2010), associated accelerated wetland and barrier island loss (Penland et al. 2001), and a possible increase in the cross-sectional area of the tidal passes (Li et al. 2009) during and after severe hurricanes. Anthropogenic climate change may have also directly increased hurricane intensity (Burkett 2008). Severe hurricane surges can have a direct lethal effect on benthic invertebrates (Poirrier et al. 2008): they disturb sediments, which bury clams, abruptly increase salinity, and produce water column stratification with anoxic and hypoxic bottom water (Poirrier et al. 2013).

Unlike most estuaries, Lake Pontchartrain has a slow flushing rate due to narrow tidal passes and weak lunar tides. This makes it more sensitive to variation in rainfall and stratification from storm surges. High sediment re-suspension from wind occurs due to its shallow depth and large fetch. Re-suspended sediments are not flushed, but rather are re-deposited on the bottom (Flowers and Ispording 1990). Earlier studies based only on large clams (Poirrier et al. 2009, Poirrier et al. 2013) documented the significant, potentially drought-driven 2000–2001 population crash, but did not find recovery. They did not have the statistical power to determine significant annual differences due to hurricanes because large clam densities were low and there was high variance due to only 5 sampling sites being used.

This study was divided into two components, the La Niña drought and hurricane effects. The overall goal of the drought study was to investigate the specific causes of the 2001 crash by examining 1) changes in the density of 5 mm

size classes and total biomass, 2) the relationship between density and salinity changes, 3) competition from substantial increases in the hooked mussel, *Ischadium recurvum*, and other related changes in community structure of *R. cuneata* from 1998 through 2005. Goals of the hurricane effects and recovery study were 1) to determine if there were significant reductions in clam density and biomass of major size classes (15 mm) in years after major hurricanes compared to non-hurricane years, and 2) to determine if recovery of *R. cuneata* to 1954 and 1997 baseline levels occurred after 2013 and 2014, two years without hurricanes or high-salinity related stress. This study was part of a general, long-term study of benthic invertebrate community structure, which supported our results, but was too complex to include with this *R. cuneata* study.

MATERIALS AND METHODS

Area of Study

Lake Pontchartrain is a large, shallow, oligohaline estuary located north of New Orleans, Louisiana, USA (Figure 2). Its two relatively narrow tidal passes open into Lake Borgne, the Biloxi Marsh and the Chandeleur Islands, which are part of a deteriorating Mississippi River deltaic system abandoned by the Mississippi River (Saucier 1963). Lake Pontchartrain has a mean salinity of 3.9 (Francis et al. 1994), a surface area of 1,630 km², and a mean depth of 3.7 m (Sikora and Kjerfve 1985). Higher salinity waters enter from the east through these tidal passes. It receives fresh water from rivers and bayous to the west and north, urban outfall canals on the south shore, and from periodic openings and leakage of the Bonnet Carré Spillway, a Mississippi River flood diversion structure (Brammer et al. 2007). Therefore, salinity generally decreases from east to west (Swenson 1980). It is adversely affected by urban and agricultural runoff, shoreline modification (Penland et al. 2001), Bonnet Carré Spillway openings, and was affected by saltwater intrusion from a former ship channel, the Mississippi River Gulf Outlet (MRGO), that produced salinity stratification and periodic bottom water anoxia/hypoxia from 1968 to 2009 (Poirrier 2013).

Field and Laboratory

In the field, 3 replicate infaunal samples were taken at sites sampled throughout Lake Pontchartrain (Figure 2) using a 15 cm² petite Ponar dredge. Samples were separated from fine sediment using a Wildco 12 L, 0.6 mm sieve bucket, and then preserved in 10% Borax-buffered formalin with Rose Bengal stain. Salinity and dissolved oxygen were measured at 30 cm below the surface and above the bottom with a YSI-85 S–C–T meter. In the laboratory, samples were rinsed in a 0.5 mm sieve and preserved in 70% isopropanol. Clams were removed from rinsed dredge samples, placed in 5 mm size classes and counted. Clams < 5 mm were excluded from the data set due to their low numbers

when large clams were present, their rapid and high recruitment after various stressful events, and difficulty in separating small *R. cuneata* from small dwarf surf clams, *Mulinia lateralis*. Number (N) of individuals sampled by the dredge was converted to N/m^2 . *Rangia cuneata* dry weight biomass was determined by drying soft tissue at 60°C for 48 hours (Edmondson 1971). Soft tissue dry weight was regressed against shell length to obtain the predictive equation used in this study (Spalding et al. 2007). *Ischadium recurvum*, whose population exploded during the drought, was also counted and placed in 5 mm size classes.

In the analysis of samples, possible effects of the La Niña drought during 1998–spring 2005, and hurricanes during 2004–2014 were treated separately because only samples from the E–W and N–S transects with 7 sites and 3 replicates per site (Figure 2) were taken during the drought study period. April 2005 was used in the drought analysis instead of fall 2005 samples, because fall samples were severely affected by Hurricane Katrina. Samples from all of Lake Pontchartrain during the period of high hurricane frequency were from 30 sites (Figure 2) with 3 replicates per site. Lake Pontchartrain fall 1997 data were obtained during a strong El Niño year, which was not affected by droughts or damaging hurricanes; these data were used in the hurricane effects analysis as a baseline year to determine recovery.

During the drought study, 7 sites on the E–W and N–S transects were sometimes sampled several times. Only 2 northern sites on the N–S transect (Figure 2, NS 1 and 2) were used because others were affected by saltwater intrusion and hypoxia from a navigation canal. Year and month sampled and total number of samples (N) are as follows: 1998 November (21); 1999 April, August, and October (63); 2000 January, May, and July (63); 2001 April (21); 2002 August (21); 2003 November (21); 2004

April, October, and November (62); and 2005 April (21). We combined monthly within–year data because an early analysis using uncombined monthly data excluding < 5 mm clams indicated no significant differences from monthly within–year data, and past analyses using separate monthly samples gave similar results (Poirrier et al. 2013). This was due to spawning in the sub–tropical waters of Lake Pontchartrain being almost continuous and dependent upon random salinity shifts rather than seasonal changes. The only seasonal sample that could have affected recruitment was January 2000, which was included in the year before the 2001 crash. Also, the crash was so severe that decline and recovery of size classes was easy to detect.

In the hurricane study, sites from the all of Lake Pontchartrain were sampled, and all were obtained during the fall (October and November) with a total of 90 per year (Figure 2). Figure 1 presents time sequences for the drought, hurricane events, and other disturbances.

Statistical Analyses

One–way analysis of variance (ANOVA) was used to test for differences among annual clam densities. Clam densities were \log_{10} transformed to produce a data distribution acceptable for parametric analyses. Although most data exhibited mild departures from normality, this was considered acceptable because the ANOVA is considered robust with regard to minor departures from normality (Gotelli and Ellison 2004, Neter et al. 1990). *Post-hoc* Tukey pairwise comparisons were used to test for differences among means. Analyses were performed with SPSS (IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY) using a 0.05 significance level.

For the drought analysis, ANOVA was used to determine significant annual changes in *R. cuneata* density, size classes and biomass, coupled with significant differences in salinity, and *I. recurvum* density. For the hurricane disturbance effects (the combination of clam burial, abrupt salinity change with anoxia and hypoxia) and recovery analysis, ANOVA was used to determine annual changes in *R. cuneata* density, biomass, and salinity. An ANOVA was also run on clams > 20 mm with data from 1954, 1997, 2004, 2005, 2006, 2008, 2012, 2013, and 2014 to see if recovery had occurred based on the earliest 1954 > 20 mm clam densities. A one–way between–groups multivariate analysis of variance (MANOVA) was performed to investigate differences in *R. cuneata* size classes during the drought period. Necessary Bonferroni alpha level adjustments were made in the MANOVA. Dependent variables were the clam densities of 5 mm size classes (6–10, 11–15, 16–20, 21–25, 26–30, 31–35, and 36–40). The independent variable was year.

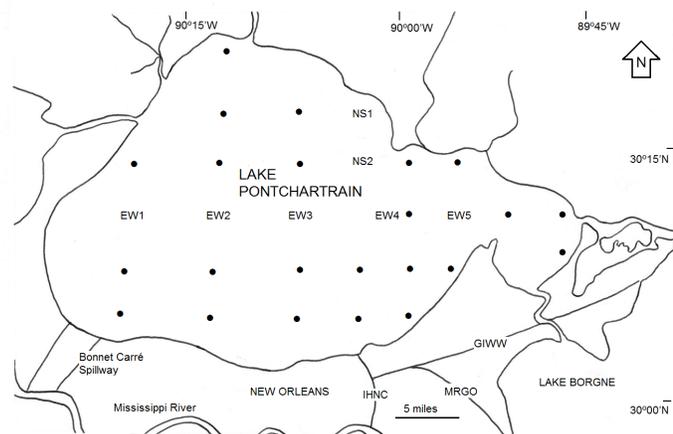


Figure 2. *Rangia cuneata* sampling sites in Lake Pontchartrain, indicating sites on the E–W and N–S transects and other Lake Pontchartrain sites (solid circles ●). IHNC = Inner Harbor Navigational Canal, MRGO = Mississippi River Gulf Outlet, and GIWW = Gulf Intracoastal Waterway.

RESULTS

La Niña Drought

There were significant differences in clam densities (all

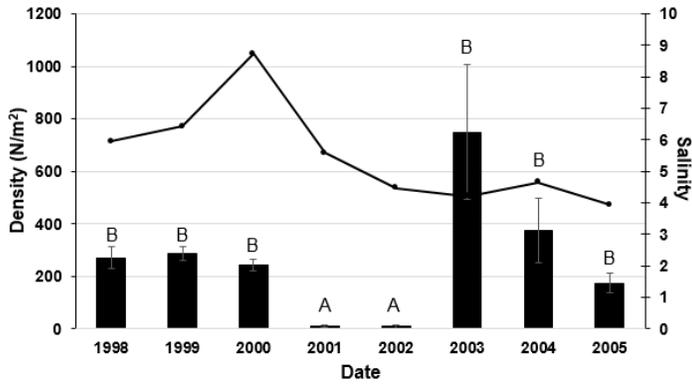
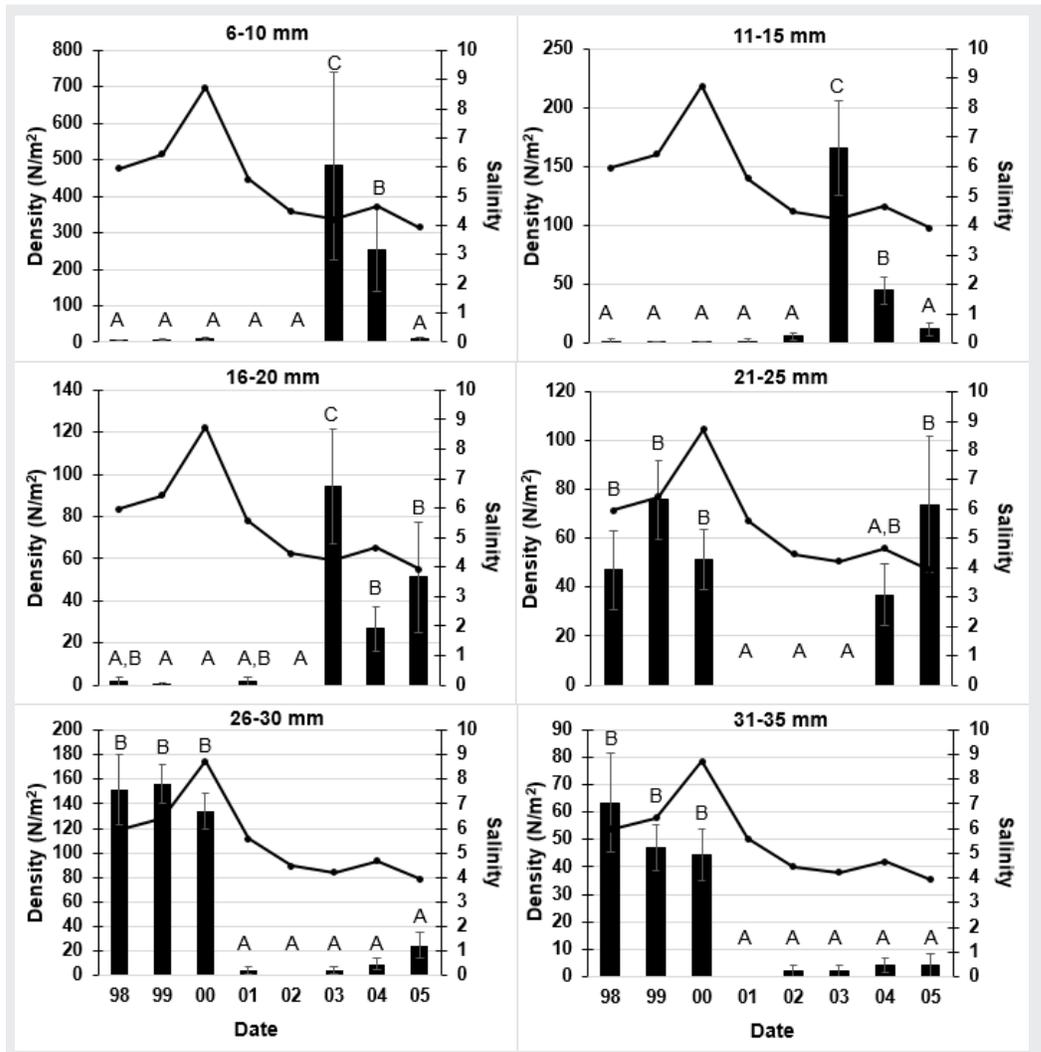


Figure 3. Annual mean (\pm se) *Rangia cuneata* clam densities (6–55 mm/m²) before (1998), during (1999, 2000 and early 2001), and after (late 2001–2005) the La Niña drought years. Dots on the black line indicate annual mean bottom salinity from samples at the time of collection. Groups with the same letters indicate no significant difference (Tukey post-hoc test, $p < 0.05$).

clams 6–55 mm) among years (1998–2005; $F_{(7,265)} = 16.98$; $p < 0.001$) (Figure 3). The Tukey comparisons, with $p < 0.001$ for all results, indicated a significant decline in total clam density in 2001 and 2002, and density returned to 1998–2000 levels in 2003–2005 (Figure 3). Between July 2000 and April 2001, density was reduced to only 10 clams/m², a 96% reduction. MANOVA found a statistically significant difference in density among years on the combined size classes ($F_{(49,1319)} = 8.69$; $p < 0.001$) (Figure 4). When the results of the dependent variables were considered separately, using a Bonferroni adjusted alpha level of 0.01, only the 36–40 mm size class did not show significant annual differences because of their low density.

Figure 4. Plots of annual mean (\pm se) *Rangia cuneata* densities (N/m²) in size classes: 6–10, 11–15, 16–20, 21–25, 26–30 and 31–35 mm, set against years before (1998), during (1999, 2000 and early 2001), and after (late 2001–2005) the La Niña drought. Dots on the black line indicate annual mean bottom salinity from samples at the time of collection. Groups with the same letters indicate no significant difference (Tukey post-hoc test, $p < 0.05$).



Changes in density occurred in all size classes (Figure 4). When annual densities within individual size classes were compared, smaller clams (6–20 mm) were not very dense prior to the 2001 population crash, when large clams were dense (Figure 4). However, they rapidly increased in 2003 and then declined as larger size classes became established. In contrast, larger clams (21–35 mm) were more dense prior to the crash and, depending on size, slowly recovered. By 2005 there was a general trend toward return to pre-crash density levels for the 21–25 mm clams, but not the largest clam class (26–35 mm; Figure 4).

The ANOVA analysis of total biomass of 6–55 mm clams from 1998–2005 found significant differences among years ($F_{(7,265)} = 19.9$; $p < 0.001$) (Figure 5). The Tukey comparisons support a significant decrease in biomass from 2000 to 2001 (95%), and an increase in 2003–2005, but no recovery to 1998–2000 levels. Density and biomass results differed across years because the few but large clams that occurred from 1998 through 2000 had a high total biomass, whereas the few clams of any size had relatively low biomass during 2001 and 2002; in 2003 dense small clams with low biomass became established while in 2004 and 2005 there was

Figure 5. Annual mean (\pm se) dry weight biomass (g/m^2) of *Rangia cuneata* before (1998), during (1999, 2000 and early 2001), and after (late 2001–2005) the La Niña drought years. Dots on the black line indicate annual mean bottom salinity from samples at the time of collection. Groups with the same letters indicate no significant difference (Tukey post-hoc test, $p < 0.05$).

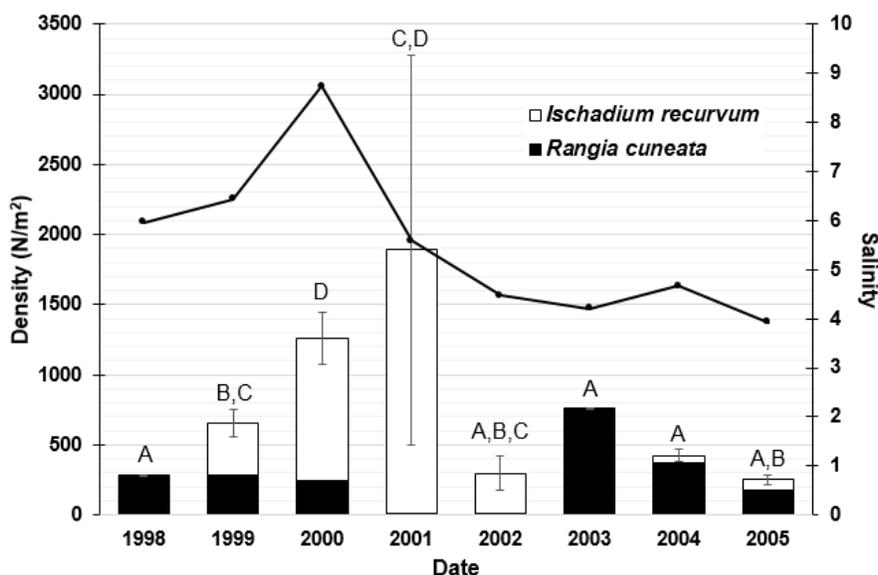
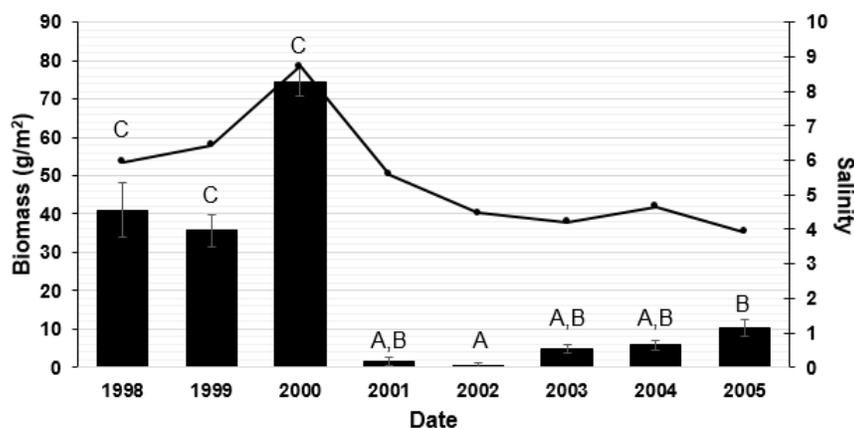


Figure 6. Annual *Rangia cuneata* and *Ischadium recurvum* mean (\pm se) densities of *Ischadium recurvum* before (1998), during (1999, 2000, and early 2001), and after (late 2001–2005) the La Niña drought years. Dots on the black line indicate annual mean bottom salinity from samples at the time of collection. Groups with the same letters indicate no significant difference in *Ischadium recurvum* densities (Tukey post-hoc test, $p < 0.05$).

a shift to fewer larger clams with higher biomass (Figure 5). A MANOVA analysis of annual changes among 5 mm size classes found significant results ($F_{(49, 1319)} = 6.73$; $p < 0.001$) and the Tukey comparisons agreed with groupings found in the size class density analysis.

The *R. cuneata* decline occurred within a 10 month period between July 2000 and April 2001 after the drought-driven peak in salinity values (Figures 3 and 5). Salinity increased prior to the decline, but the decline occurred after the drought when the salinity decreased. This indicates that salinity was not the direct cause of the density crash. Salinity increased to 8.8 in 2000 and decreased to 6.0 in April 2001, and was further reduced to 4.6 by Tropical Storm Allison in June 2001. Based on an ANOVA, the 2000 increase in salinity was significantly different ($F_{(7,265)} = 70.1$; $p < 0.001$) compared to other years from 1998 through 2005.

ANOVA and Tukey comparisons found significant changes in *I. recurvum* density from 1998–2005 (Figure 6). *Rangia cuneata* decreased in 2001 after the 1999 and 2000 *I. recurvum* increase. Prior to 1999, few ($< 20/\text{m}^2$) small (< 5 mm) *I. recurvum* occurred mainly at site E–W 5 at higher salinities in the eastern end of Lake Pontchartrain (Figure 2). As salin-

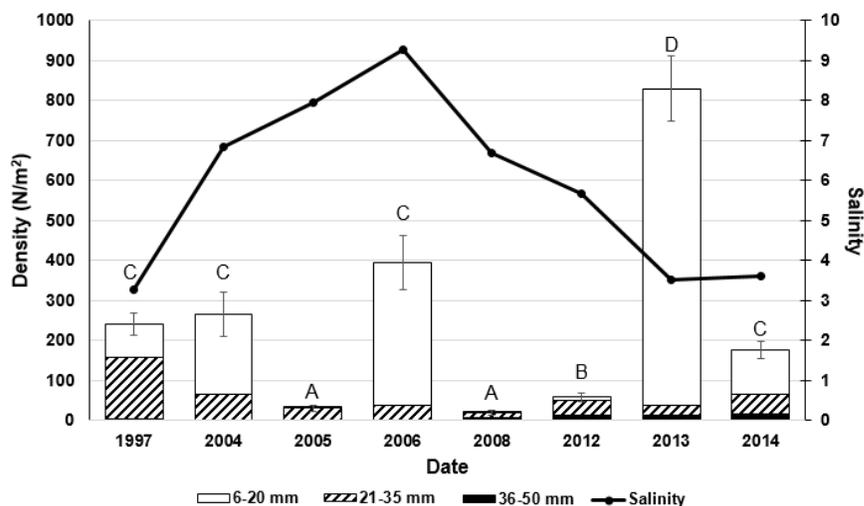
ity increased at all sites from 1999 through 2000, *I. recurvum* colonized all E–W sites (Figure 2) and mussels up to 35 mm became abundant (Figure 6). This rapid increase in larger mussels on live *R. cuneata* shells often formed small spherical reefs about 30 cm in diameter. Other filter feeders including the barnacles, *Balanus improvisus*, and *B. eburneus*, Conrad's false mussel, *Mytilopsis leucophaeta*, and the bryozoan, *Conopium* sp., became abundant on *I. recurvum* in these reefs. These specialized filter feeders, in addition to *I. recurvum*, probably removed a broad range of particles that were normally available to *R. cuneata*. After 2002, *I. recurvum* abruptly decreased and *R. cuneata* increased (Figure 6).

Hurricane Effects

The ANOVA analysis comparing annual mean densities of 6–50 mm clams for years 1997, 2004, 2005, 2006, 2008, 2012, 2013, and 2014 found significant ($F_{(7,712)} = 50.56$; $p < 0.001$) differences among years (Figure 7). Tukey comparisons (Figure 7) revealed that hurricane years 2005 (Katrina and Rita), 2008 (Ike and Gustav), and 2012 (Isaac) differed from all other years ($p < 0.001$).

A MANOVA of annual differences among 15 mm size

FIGURE 7. Annual mean density of 6–50 mm *Rangia cuneata* clams/m² from fall samples of 30 representative sites throughout Lake Pontchartrain during 1997, 2004, 2005 (Katrina), 2006, 2008 (Ike & Gustav), 2012 (Isaac), 2013 and 2014. Representation of 15 mm size classes in stacked columns is presented with standard errors for total density. Dots on the black line indicate annual mean bottom salinity from samples at the time of collection. Groups with the same letters indicate no significant difference (Tukey post-hoc test, $p < 0.05$).



classes found significant differences ($F_{(21, 2246)} = 29.54$; $p < 0.001$). Tukey comparisons among years for 6–20 mm clams clearly separated the hurricane years from all others and separated 2013 from all years. There were abrupt decreases of 6–20 mm clams in hurricane years and rapid increases when followed by years without hurricanes or salinity stress, such as 2013. 2014 was different from all other years in the 21–35 mm comparison with poor separation of other years. In the 36–50 mm comparison, years 2005 through 2014 grouped together, but 2005 and 2014 also grouped with 1997 and 2004 (Figure 7).

Biomass results differed from density results due to biomass increasing exponentially with clam size. The ANOVA of annual mean biomass of 6–50 mm clams for years 1997, 2004, 2005, 2006, 2008, 2012, 2013, and 2014 found significant differences ($F_{(7,712)} = 9.43$; $p < 0.001$) (Figure 8). Tukey comparisons showed 2004, 2005, 2006, 2008 and 2012 were grouped into a common subset (Figure 8). This group contains three hurricane years, 2005, 2008 and 2012, but also contains 2004, a year that was still recovering from the La Niña drought, and 2006, a year after the acute disturbances caused by Katrina and Rita in 2005. Within this group, 2004, 2006 and 2012 also group with 2013 and 2014, two years with relatively low salinity and without severe damaging hurricanes. However, 2013 and 2014 also grouped with 1997, indicating overall biomass recovery to 1997 levels in 2013 and 2014. Tukey comparisons of the three 15 mm size classes based on biomass did not give distinct groups except for 2013 differing from all other years for the 6–20 mm clams, and 1997 differing from all other years for 21–35 mm clams. The 36–50 mm comparisons did not give clear separations of groups among years. However, groups supported differences between 2012 through 2014 compared to 2004, 2005 and 2006, which supports the increase in biomass due to the increase in large clams during and after 2012.

Large Clam (> 20 mm) changes over time

An ANOVA of samples of large clams (> 20 mm) from years with a minimum of 30 sites from 1954 data (the earliest baseline data from Suttikus et al. (1954)) through 2014 showed significant differences among years ($F_{(8,744)} = 15.72$; $p < 0.001$). The Tukey comparisons grouped 2004 and 2014 with 1954 indicating recovery to 1954 levels, but not 1997 levels, based on > 20 mm clams.

DISCUSSION

General Overview

Study results using more sites and size classes than Poirrier et al. (2013) appear to confirm that the La Niña drought: (1) contributed to the abrupt 2001 population crash of *R. cuneata*, (2) appeared to affect all size classes and biomass, (3) resulted in a shift to a higher salinity community that caused *I. recurvum* overgrowth, and (4) decreased large clam density and biomass which did not completely recover prior to Hurricane Katrina. Links between the 1997–2001 ENSO shift and low precipitation with increased salinity were not included in this study because they were established in earlier studies of submersed aquatic vegetation in Lake Pontchartrain (Cho and Poirrier 2005). Based on comparisons of hurricane and non-hurricane years, we found that hurricanes Katrina, Ike, Gustav and Isaac reduced clam densities and total biomass, and recovery occurred by 2014, during relatively low salinities and after 2 years without hurricanes.

La Niña Drought

Rangia cuneata is an estuarine endemic (Carriker 1967). Although adults are physiologically capable of tolerating limnetic to polyhaline waters, it is more abundant in the oligohaline zone where it is protected from predation and competition due to low species richness (Remane and Schlieper 1971). In nature, *R. cuneata* occurs at salinities up to 18 (LaSalle and de la Cruz 1985) and it is known to survive at

a salinity of 32 in the laboratory (Bedford and Anderson 1972). An important aspect of the drought was a change in the salinity regime that resulted in persistent, relatively high salinity throughout the estuary with no episodes of low salinity from runoff (Poirrier et al. 2009). Periodic low salinity, characteristic of poikilohaline estuaries, keep higher salinity species, including competitors and predators, from becoming established (Boesch 1977). During the drought, stable salinity allowed the establishment of higher salinity communities, which potentially increased biotic stress on the *R. cuneata* population due to increased competition and predation. We obtained reasonable results in the drought analysis, despite the time of sampling varying among years, because *R. cuneata* spawning is almost continuous in Lake Pontchartrain and stimulated by salinity shifts rather than seasonal changes. The lack of salinity shifts required for *R. cuneata* spawning and recruitment (Cain 1975) during the drought may have directly contributed to the decline, but was probably not the primary cause because density levels of 6–10 and 11–15 mm clams remained the same from 1998 through 2002.

The *I. recurvum* increase characterized the community shift and also appeared to be another important causal factor for the *R. cuneata* decline. *Ischadium recurvum* is more characteristic of a euryhaline marine species, does not survive episodes of fresh water, and is more abundant in the mesohaline zone. It can be invasive and rapidly colonizes the Eastern oyster, *Crassostrea virginica*, and the fouling that results interferes with commercial oyster production (Coleman 2003). Although some oysters colonized artificial fishing reefs in the southwestern part of Lake Pontchartrain, we did not find any oyster spat on *R. cuneata*. However, without the *I. recurvum* invasions, we speculate that oyster

colonization on *R. cuneata* may have occurred.

Rangia cuneata densities did not change from 1998 through 2000. Although clams were subjected to increasing stress from competition in 1999 and 2000, the crash did not occur until 2001. It occurred under conditions of decreased salinity, but while a higher salinity community was still present. This time lag supports *I. recurvum* overgrowth rather than the singular effect of salinity as the cause of the crash. A similar explosion in *I. recurvum* abundance occurred on the New Orleans seawall during the same time period (Poirrier, unpublished data). *Ischadium recurvum* was absent in 1998, dominated the epifaunal community, reached a maximum size of 60 mm in 2001, and was absent in 2003. Lasting effects of low recruitment of *R. cuneata* during the drought and subsequent low-levels of reproduction and future recruitment appeared to interact synergistically with *I. recurvum* overgrowth in causing the decline.

Increased competition and predation from numerous specialized species in the higher salinity communities could have also negatively affected most aspects of *R. cuneata*'s life cycle (e.g., larval predation by jellyfish, competition from other specialized filter feeders). However, increased predation on *R. cuneata* clams by bivalve fish predators does not appear to be the major cause of the decline because the *I. recurvum* population, which should have also been subjected to predation, exploded while the *R. cuneata* population crashed.

ENSO shifts to La Niña that occurred at other times (1973–1976; 1988–1989) may have affected clam abundance. However, no La Niña events occurred during periods of low *R. cuneata* densities attributed to shell dredging (Tarver and Dugas 1973, Sikora and Sikora 1982, Poirrier et al. 1984), suggesting that these low density periods should

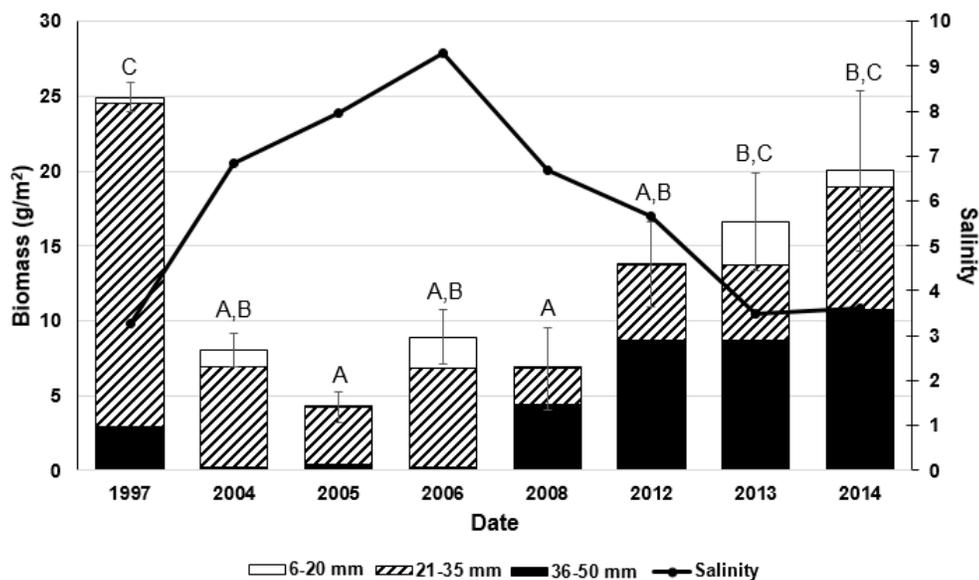


Figure 8. Annual mean dry weight biomass (g/m^2) of *Rangia cuneata* clams from fall samples of 30 representative sites throughout Lake Pontchartrain during 1997, 2004, 2005 (Katrina), 2006, 2008 (Ike & Gustav), 2012 (Isaac), 2013 and 2014. Representation of 15 mm size classes in stacked columns is presented with standard errors for total biomass. Dots on the black line indicate annual mean bottom salinity from samples at the time of collection. Groups with the same letters indicate no significant difference (Tukey post-hoc test, $p < 0.05$).

not be attributed to ENSO shifts.

Hurricane Effects and Recovery

The lack of complete recovery of large size class clams and overall biomass after the drought appears to have contributed to the later damage to *R. cuneata* populations caused by hurricanes. The decrease in clam density during the hurricane years, 2005, 2008 and 2012 indicated distinct hurricane effects. These effects are supported by previous studies of benthic invertebrate impacts from Katrina and Rita (Poirrier et al. 2008, Engle et al. 2009) and Ike and Gustav (Ray 2009). We found that density changes in 6–20 mm clams accounted for most of the differences. There were significant decreases of *R. cuneata* in hurricane years and significant increases in years without hurricanes. The density reduction in hurricane years was probably due to small clams being more sensitive to direct physical hurricane damage, while their rapid recovery is due to recruitment and growth to 20 mm within a year. Possible effects of Hurricanes Isidore and Lili were not detected because they occurred in 2002 when *R. cuneata* populations were already very low due to the drought.

Annual biomass changes agreed with the density changes when the exponential relationship between biomass and size was considered. Many small clams made minor contributions to total biomass; whereas, fewer large clams made major contributions. There was a time lag in the recovery of large clams. Clams from 6 to 20 mm recovered within a year, but recovery of large clams took several years. This resulted in biomass recovery being a slow process compared to density recovery. Our 1997 baseline year had a high proportion of 21–35 mm clams when compared to later years. Large clams were almost eliminated during the 2001 crash from the drought and were slow to recover, presumably due to hurricanes in 2005 and 2008. This contributed to the low biomass prior to 2012. The steady increase in biomass from 2012 to 2014, despite the effects of Isaac, may have been due to large clams being more resistant to hurricanes, Isaac having less of an impact than earlier storms, and the closure of the MRGO in 2009 which reduced storm surges and stopped episodes of detrimental dissolved oxygen. Prior to the MRGO closure, these episodes were frequent in the area north of the Inner Harbor Navigational Canal (IHNC), but also spread to other areas of Lake Pontchartrain during late summer (Poirrier 1978, 2013). Biomass reached 1997 baseline recovery levels by 2014, following 2 years without salinity or hurricane stress. Recovery based on density occurred in 2013 and 2014, but densities statistically equal to 1997 also occurred in 2004 and 2006. Because of the rapid change in small clams less than a year old, biomass is a better indicator of recovery in a given year. However, loss of the 6–20 mm size class results in the lack of production of larger size classes in subsequent years.

Hurricane effects differ based on their track and the

landfall coastal morphology (Chen et al. 2008). Lake Pontchartrain has a higher risk of surges due to the extension of the Mississippi River delta into the Gulf which can intensify surges that form and enter from the east. A severe disturbance should be expected when a 3.7–4.9 m storm surge, such as the one that occurred during Katrina, enters a soft-bottomed estuary with a mean depth of 3.7 m. Damage and burial from storm surges were important factors in *R. cuneata* clam decline. Poirrier et al. (2008) found recently dead and dying *R. cuneata* after Katrina. After Isaac, articulated shells with non-weathered periostraca from dead *R. cuneata* clams were common in sediment samples (Poirrier et al. 2013). Shells did not show any signs of damage from predation and were apparently produced by clams dying in the sediment. Flocks et al. (2009) found that the top 1 m of sediments are constantly being reworked by major storms and circulation gyres. Because of slow flushing rates, sediments suspended by storms are not transported out of Lake Pontchartrain, but rapidly settle to the bottom across broad areas (Flowers and Isphording 1990).

O'Connell et al. (2013) found minor compositional changes in post-Hurricane Katrina and Rita fish assemblages. Individually, there were increases in *Ariopsis felis* (Hardhead Catfish) and declines in *Gobiosoma bosc* (Naked Goby), *Syngnathus scovelli* (Gulf Pipefish), *Membras martinica* (Rough Silverside), *Micropogonias undulates* (Atlantic Croaker), *Scomberomorus maculatus* (Spanish Mackerel), and *Cynoscion arenarius* (Sand Seatrout), even though some of these species were not major components of assemblages. Although clam loss may appear to have a negative effect on consumers, physical damage from hurricanes and hypoxia may make large clams more susceptible to crab and fish predators after storm events. Also, loss of large clams is typically followed by rapid recruitment of small clams which are more easily consumed by shrimp, ducks, crabs and fishes, potentially increasing secondary productivity. However, reduction in clam biomass due to the loss of large clams may result in loss of filtration and other environmental services, likely contributing to poorer water quality in nearshore habitats where adults of *G. bosc*, *S. scovelli*, and *M. martinica* reside. Additionally, higher turbidity can result in loss of SAV and the services it provides (e.g., protection from predation for *S. scovelli*, egg habitat for *M. martinica*; Spalding et al. 2007, O'Connell et al. 2013).

Little information is available about bottom water quality in Lake Pontchartrain during and immediately after hurricanes. However, harmful dissolved oxygen concentrations have been reported in most other hurricane impact studies (Hagy et al. 2006, Tomasko et al. 2006, O'Connell et al. 2013). Salinity can increase or decrease depending on the track of the storm and associated wind and rainfall (Chen et al. 2008). Salinity increases from storm surges were found after most hurricanes we studied, but Tropical Storm AL-

lison decreased salinity in 2001. We used mean bottom salinity taken at the time of clam collection in this study because it was often higher than surface values. Increased salinity did not result in as much *R. cuneata* loss as it did during the La Niña drought, because after hurricanes, salinity increases and introduction of higher salinity species were temporary, compared to the multiple year effects of the prolonged drought, which produced a community shift that increased competition and resulted in *R. cuneata* decline. However, storm surges did increase bottom salinity which caused stratification in the water column and harmful hypoxic bottom waters. Poirrier et al. (2008) reported salinity stratification and low bottom dissolved oxygen after Hurricane Katrina. Poirrier et al. (2013) found salinity stratification and hypoxia at three sites south of Mandeville on 8 September 2012, 11 days after Hurricane Isaac's landfall.

Lack of complete recovery from the La Niña drought, Bonnet Carré Spillway openings, and saltwater intrusion from the MRGO also appears to have exacerbated hurricane effects. The spring 2008 Bonnet Carré Spillway opening, which filled Lake Pontchartrain with nutrient rich Mississippi River water, eliminated higher salinity species and introduced nutrients, which caused eutrophication in Mississippi and Chandeleur Sounds in the lower Basin. Storm surges from Ike and Gustav introduced higher salinity water that had become hypoxic from the Bonnet Carré Spillway opening, which affected the remaining lower salinity species. This synergistic effect likely produced stress which was greater than what would have been caused by either disturbance alone. Storm surges from Katrina, Rita, Ike and Gustav were severe because they also entered through the MRGO and the IHNC. Effects of Isaac were not as severe as these 2005 and 2008 storms because it was less intense and occurred after the closure of the MRGO (Shaffer et al. 2009, Poirrier 2013).

An obvious question is, have storm effects on *R. cuneata* clams recently increased? In 1998, Tropical Storms Frances and Hermine, and Hurricanes Earl and Georges affected southeastern Louisiana. No significant effects on clams from Georges were detected in 1998 and 1999 surveys. However, Hurricane Georges caused a 40% loss of land area in the Chandeleur Islands (Penland et al. 2001). We propose that coastal erosion caused by Hurricane Georges and other 1998 storms, adverse effects of the drought on wetlands (Visser et al. 2002), and increased sea level set the stage for increased effects of later storm surges on Lake Pontchartrain *R. cuneata* clams. From 1961–2000, the number and intensity of U.S. hurricanes decreased. After 2000, there was a period of increased hurricane frequency (Fearnley et al. 2009). Relative sea level rise in Louisiana is occurring 10 times faster than the global average and more than 5 times

faster than the Gulf of Mexico average (Penland and Ramsey 1990). Rates are high near the mouth of Lake Pontchartrain which is located in an abandoned, deteriorating Mississippi River Delta. Two sites in eastern Lake Pontchartrain have experienced relative sea level rise rates of 1 cm/yr (South Point 1949–1986; Little Woods 1931–1977; Penland and Ramsey 1990). This rate is comparable to that in Grand Isle, LA which has increased 0.93 cm/year (Burkett 2008). These factors should increase in the future as global climate changes.

At some point in time a tipping point for the loss of *R. cuneata* clams should occur due to increasing sea level (Burkett 2008), barrier island loss (Penland et al. 2001), wetland loss (463 km², 1932–2010; Couvillion et al. 2011), and possible enlargement of tidal passes (Li et al. 2009). We are currently, or will soon be, at this tipping point. We found clam recovery by 2014, but in the near future hurricanes may produce an irreversible decline due to direct surge damage, burial in sediment, anoxia and hypoxia from salinity stratification produced by the surge, and community changes from a long-term shift to higher salinity conditions.

CONCLUSIONS

Abrupt population changes in *R. cuneata* related to climate change occurred in Lake Pontchartrain, Louisiana. A 96% decrease occurred in 2001 after a drought from an ENSO shift (1998–2000). This decrease was caused by a salinity increase during the drought. More importantly, however, long periods without salinity decreases appeared to result in the establishment of higher salinity communities which, through competition, may have resulted in the *R. cuneata* decline. *Ischadium recurvum* colonized live *R. cuneata* and its overgrowth may have further influenced the *R. cuneata* decline. Rapid recovery following the drought did not occur due to a period of high hurricane frequency and intensity. After years of monitoring, we found density and biomass recovery in 2014. Recovery indicated that clam loss was not permanent, but caused by a series of climatic disturbances. Hurricane surges resuspended sediments which buried clams and abruptly increased salinity and lowered dissolved oxygen. Salinity stratification persisted after storms and caused hypoxia in bottom waters. Storm surge interactions with ENSO shifts, periodic operation of the Bonnet Carré Spillway, and the MRGO also intensified hurricane effects. Results of this study could be used to better understand the potential effects of global climate changes in the oligohaline zone of other Gulf of Mexico estuaries.

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