Decadal changes in oyster reefs in the Big Bend of Florida's Gulf Coast

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Abstract. Oyster reefs are among the world's most endangered marine habitats with an estimated 85% loss from historical levels worldwide. Oyster reefs offer diverse ecological and social services for people and natural environments; unfortunately, reefs are also highly sensitive to impairment from natural and human-induced disasters. Understanding the resilience of oyster reef communities to disturbance is key to developing effective conservation and restoration plans. Florida's Big Bend coastline (Gulf of Mexico coast from Crystal River to Apalachee Bay) supports large expanses of oyster reef habitat that have existed for thousands of years in a region that is one of the most pristine coastal zones in the continental US. We assessed trends in oyster habitat along the Big Bend region between 1982 and 2011 by examining changes in areal extent and distance of oyster reefs from shore. During our study period, we found a 66% net loss of oyster reef area (124.05 ha) with losses concentrated on offshore (88%), followed by nearshore (61%), and inshore reefs (50%). We also found that the spatial distribution of oyster reefs was moving inland. This rapid loss is likely a departure from historic geological succession. Multiple lines of evidence suggest that the primary mechanism for these observed losses in oyster reefs is reduced survival and recruitment, likely a result of decreased freshwater inputs which increases existing reef vulnerability to wave action and sea level rise. Once oyster reef substrate becomes unconsolidated and the nucleation site is lost, the regeneration of the oyster reef may not be reversible through natural processes. To test these predictions, we recommend restoration-based experiments to elicit the mechanisms of decline in order to foster long-term sustainability of estuarine habitat critical to oysters.

Key words: climate change; coastal conservation; *Crassostrea virginica*; Eastern Oyster; Florida; freshwater flow.

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INTRODUCTION

Oyster reefs are among the world's most endangered marine habitats with an estimated 85% decline worldwide (Beck et al. 2011). This loss is alarming as oyster habitat is a critical component of coastal estuaries (NOAA 2005), serving a wide range of important economic, cultural, and ecological roles (Coen et al. 2007).

Vital services attributed to oyster reefs include habitat creation for numerous species (Eggleston et al. 1999), including economically high value finfish (ASMFC 2007); coastal land protection (Borsje et al. 2011); water quality enhancement (Coen et al. 2007); carbon sequestration (Coen et al. 2007) and a multimillion dollar fishery (Coen et al. 2007, NMFS 2011). The world's largest wild oyster fishery, estimated to be larger than all

other global oyster harvests combined, is currently located in the U.S. portion of the Gulf of Mexico (Beck et al. 2011). As of 2010, the Gulf provides over 50% of the U.S. commercial oyster harvests (Beck et al. 2011), with Florida supporting about 10% of this total (Becnel 2010).

While oyster resources in the Gulf currently support large fisheries and critical ecosystem services, oysters in this region have declined from their historic levels (Kirby 2004, Beck et al. 2011). Documented threats to the Eastern oyster (*Crassostrea virginica*) throughout their range include overharvest (Berrigan et al. 1991, Jackson et al. 2001, EOBRT 2007, Carranza et al. 2009); development and pollution (Jackson et al. 2001, EOBRT 2007, Mearns et al. 2007); reductions in freshwater input to estuaries (Berrigan et al. 1991, Bergquist et al. 2006, EOBRT 2007, Buzan et al. 2009); erosion from boat wakes and storm events (Goodbred and Hine 1995, Wall et al. 2005); disease (Berrigan et al. 1991, Carranza et al. 2009); oil spills (Hulathduwa and Brown 2006, Mearns et al. 2007); and global change related trends (Wright et al. 2005, EOBRT 2007, Levinton et al. 2011). The Gulf is particularly vulnerable to anthropogenic oil spills due to a heavy concentration of oil production and refining in the region (Cappiello 2011) and this threat is only likely to increase with oil demand. The Gulf is also among the most vulnerable regions in the U.S. to severe storm events and sea level rise (Ning and Abdollahi 2003). Thus, the world's largest remaining natural oyster reefs are concentrated in a region particularly vulnerable to disturbance from anthropogenic activity and to global climate change. Understanding the resilience of oyster reef communities in the Gulf to these and other threats is thus important for developing effective conservation, management, and restoration plans for this species and this globally significant habitat.

The management of oyster habitat in the Gulf and the South Atlantic region has largely concentrated either on enhanced production through seeding and addition of settlement substrate (cultch), or the management and mitigation of anthropogenic threats such as boat wakes, water management and pollution (Coen et al. 2007). Emerging threats such as sea level rise, increasing storm intensity, and changes to ocean chemistry are less understood partly because these "treatments" occur at broad spatial scales and partly because oyster community response to these stressors may be locally confounded with other stressors such as dredging or overharvest. Detection of these broad scale and possibly dominant effects therefore require either that local anthropogenic effects be statistically known or better, nonexistent.

Within the Gulf, Florida's Big Bend coastline (Crystal River to Apalachee Bay) supports large expanses (at least 25 km of linear reef) of oyster reef habitat that have existed for thousands of years (Grinnell 1972, Hine et al. 1988, Wright et al. 2005). Unlike the majority of the Gulf coastline, the Big Bend is largely undeveloped, with 30% of the land area and over 60 miles of coastline under conservation protection (Main and Allen 2007). Human population density, impervious surface area, and road density in the Big Bend are among the lowest in Florida and the percent of intact natural land cover is relatively high (Geselbracht 2007). In part due to low development status, the coastal habitat in this region has not been heavily impacted from boat traffic, dredging operations, industrial or residential pollution, eutrophication, and other anthropogenic threats. However, despite this comparatively pristine environment, declines in oyster resources have been suspected by local watermen since the 1970s. An earlier assessment of oyster resources in the Suwannee River Sound suggested that offshore reefs declined between 1972 and 2001 (Bergquist et al. 2006). However, the spatial and temporal extent of this decline is unknown as are possible mechanisms.

To assess trends of oyster habitat in the Big Bend region of Florida, we compared aerial photographs from five time periods between 1982 and 2011. From these data we built maps of the spatial extent and relative condition of oyster resources across this 29-year period. We supplemented our inferences from the imagery with snapshot field surveys during this same time period and extensive ground surveys during 2011 to provide estimates of change in spatial extent of oyster reefs, type of oyster reef, and population structure (proportion live/dead, density, size structure). We conclude with recommendations for prioritizing research and conservation of oyster resources in this unique region of the Gulf.
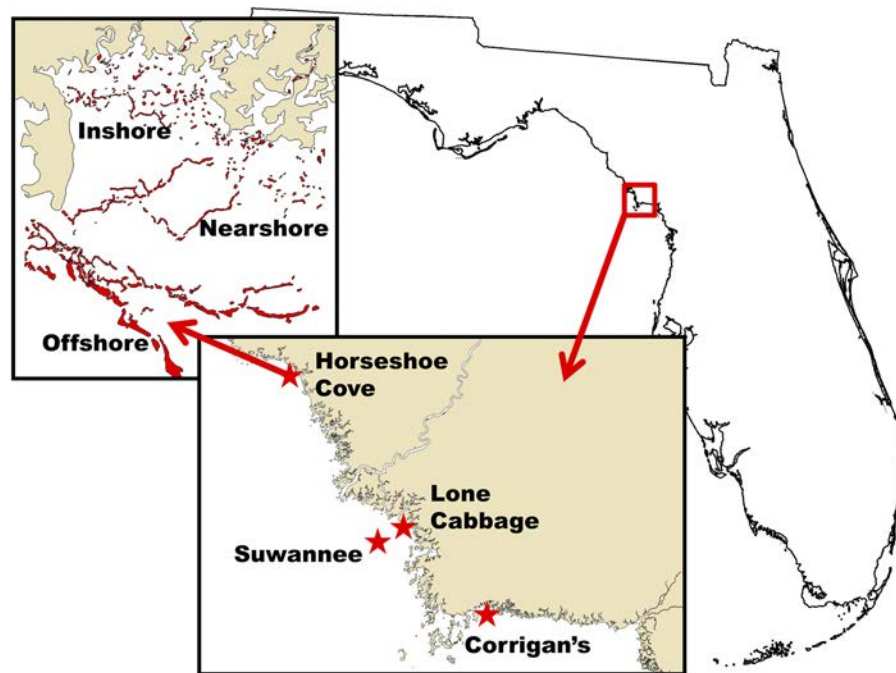
Fig. 1. Map of study area in Florida's Big Bend. The box in the lower left indicates the four focal areas of the historic trend analysis. The box in the upper left shows one example focal area with oyster reefs in red and our ground survey plot stratification design.

METHODS

Study area

Our study area along Florida's Big Bend, stretched from Cedar Key, FL to Horseshoe Beach, FL (Fig. 1). This area has been described as "a siliciclastic, sand-starved, low-wave-energy system dominated by marshes that face the open sea" (Hine et al. 1988). Irregular limestone bedrock topography and ancient sand dunes create unique geology in this region (Hine et al. 1988). The Suwannee River delta is located in the northern half of our study area and provides the majority of surficial fresh water inputs into this coastline and is supplemented by numerous springs and seeps (Wright et al. 2005). Coastal shoreline vegetation communities are dominated by *Juncus* and *Spartina* salt marsh that include many tidal inlets and embayments. Oyster reefs along this coastline are largely intertidal.

Study design

We divided the study area into four focal areas based on proximity to the Suwannee River estuary (Fig. 1). This design allowed for variance in freshwater input with sites closer receiving more stable freshwater inflow compared to sites further from the river mouth.

Data collection

Aerial photographs (resolution = 0.3 m) from 1982 (February 18), 1995 (January 28), and 2001 (November 11) were obtained from the Florida Department of Transportation, Survey and Mapping Office (LABINS 2011). The exact tide height for each year's aerial photography is unknown, but based on comparing known, permanent ground locations the 2001 imagery appears to have been taken at a higher tide level compared to other photos. Due to this tide level, oyster reef estimates for 2001 are likely more conservative compared to the actual number of reefs. We captured digital orthoimagery for 2010 on February 26, during low (−0.15 m) tide at a 0.3 m resolution (Aerial Cartographics of America Inc., Orlando, FL). To help interpret aerial imagery, we used ground photographs from 1995 through 2010 taken within our focal areas.

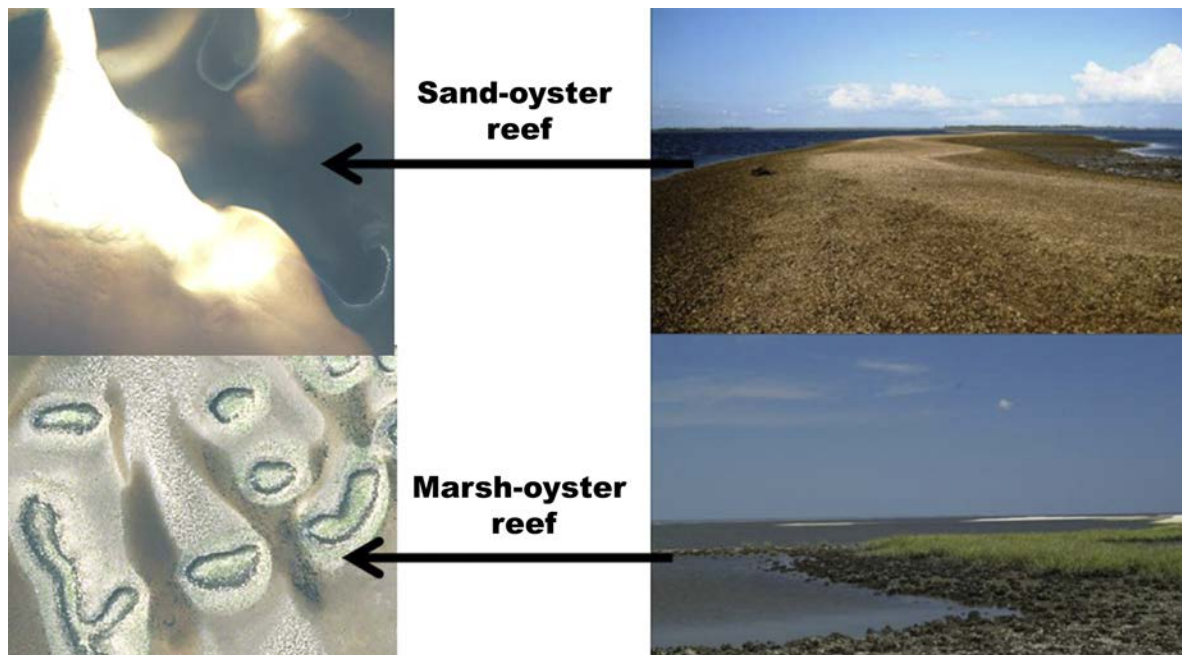From June 2010 to March 2011, we also

Fig. 2. Example of oyster reef classification in both the orthophotographs used to digitize reefs (on the left) and ground photographs from ground truthing (on the right).

conducted intensive ground-based surveys of specific reefs within each of the four focal areas to document reef condition. We did not sample the Suwannee Reef because no intertidal oysters were found at this location in initial ground surveys. At each remaining focal area (Horseshoe Cove, Lone Cabbage, and Corrigan's Reef), we sampled nine oyster reefs (three each at inshore, nearshore, and offshore locations). At each reef, we established a permanent, 0.15-m wide transect oriented to include maximum change in elevation across the reef. We counted all live oysters within the belt transect and counted live/dead ratios within a 0.25 m² quadrat placed at random distances along and away from the transect. We recorded this information during surveys at extreme low tides in June, July, August, October, and December 2010.

To examine the hypothesis that low freshwater discharge from the Suwannee River negatively affected oyster populations through periods of increased salinity (Bergquist et al. 2006), we examined Suwannee River discharge information from 1942 to 2009, from a water gage located seven miles upstream from the river mouth (USGS 2011, USGS Station # 02323500). We also examined the relationship between discharge volume and rainfall on an annual basis using basin-wide averaged rainfall data provided by the Suwannee River Water Management District (Lake City, FL).

Analysis

Aerial photographs were georeferenced and intertidal oyster reefs were hand digitized at a 1:3,000 m scale with a 10-m² minimum mapping unit into three categories: marsh-oyster, sand-oyster and unresolved (Fig. 2). Marsh-oyster was characterized by fine sediment with a surface visibly dominated by *Spartina alterniflora* and oysters occurring as individuals and clumps. Sand-oyster reefs were composed primarily of coarse sand and shell fragment matrix interspersed with oysters of varying densities, and having little or no vegetation and a lighter colored appearance on aerial photos than the marsh-oyster type. The shortest distance from the mainland shoreline to the closest edge of each reef was calculated based on the 2004 Florida Fish and Wildlife Research Institute's Florida Shoreline Map (FGDL 2011). We assigned each reef to one of three distance-to-shore categories
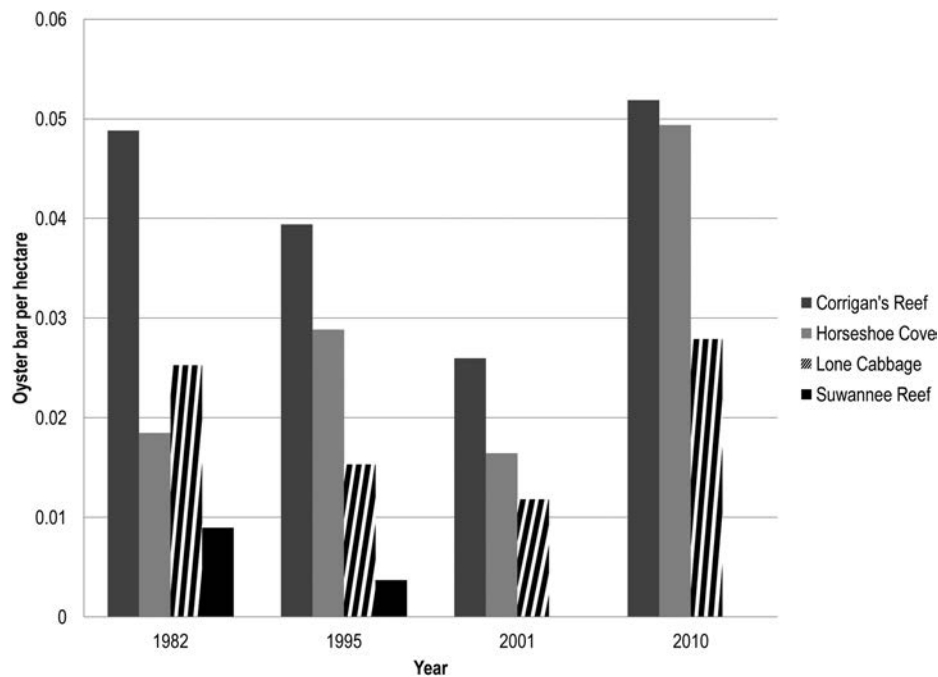
Fig. 3. Total oyster reef per hectare at each focal area for each sample period in Florida's Big Bend.

(inshore, nearshore, offshore) using the Jenks Optimization method in ArcMap 10 (ESRI 2010), which classifies data such that variance within classes is reduced and variance between classes is maximized. We also recorded area, sample year, and reef type for each of the reefs sampled.

Results

Net change in area of oyster habitat

Ground truthing of the 2010 digitized map was based on 20 on-the-ground photos and our 36 field survey sites and showed 100% correct match between these known reefs and our digitized maps in identifying both oyster reefs and classifying reef type. Georeferencing aerial photographs produced horizontal errors between 5.5 to 12.9 m between sample years at any given reef, which is 15 to 30% of the average reef size. To minimize bias, we ignored changes in oyster reef area of less than 0.017 ha in our analysis.

We digitized 3,800 total oyster reefs across all sampling years with an average area of 0.19 ha (SD = 0.58) and mean distance from the mainland of 351 m (SD = 586). Offshore reefs averaged 1837.56 m (SD = 816.40), nearshore reefs averaged 490.42 m (SD = 350.74), and inshore reefs

averaged 86.84 m (SD = 129.32) from the shoreline. Across focal areas and years, Corrigan's Reef had the highest oyster reef density (0.17 reef/ha), followed by Lone Cabbage (0.13 reef/ha), Horseshoe Cove (0.08 reef/ha), and Suwannee Reef (0.01 reef/ha). Though we expected to see more oyster reef area in 2001 compared to other years due to high tide level in the imagery, all sites—except Horseshoe Cove—showed a declining trend in total oyster habitat from 1982 thru 2001, followed by an apparent increase in 2010 (Fig. 3). This apparent increase in the last decade of the study was an artifact driven by a conversion of high-relief reefs with high oyster densities to reefs with low-relief dominated by sand and dead shell. Thus, the apparent spreading of these reefs was actually a final stage of oyster reef loss which we refer to as "collapse" (Fig. 4). Based on tracking individual reefs, we identified a 66% net loss of oyster reef area from 1982 to 2010 (Table 1). Loss of reef area among focal areas varied between 49% and 100%, with 30% to 100% of that loss due to collapse.

Dynamics of change in oyster habitat

Offshore reefs lost the most area (88%), followed by nearshore (61%) and inshore (50%)
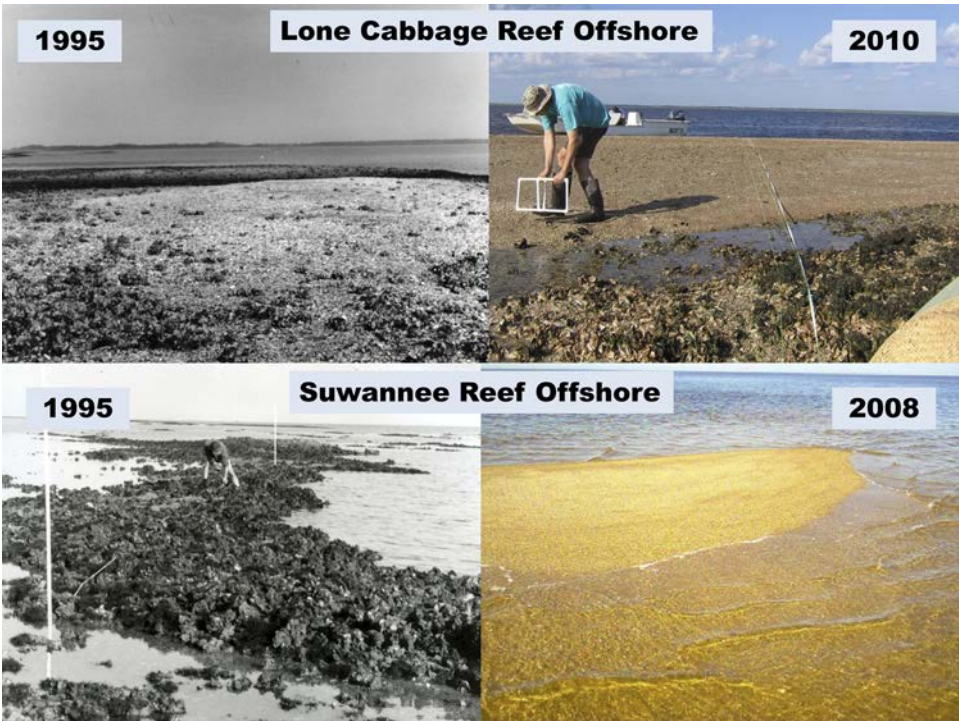
Fig. 4. Examples of off-shore oyster reefs photographs from 1995 compared to more recent conditions on the ground in Florida's Big Bend.

(Table 1). Further, reef collapse was more common offshore (100% of reefs) compared to nearshore and inshore reefs (37%). Across the 28 years of our data, offshore areas were the most susceptible to loss—Suwannee lost 100% of offshore reefs, Lone Cabbage lost 77%, Corrigan's Reef lost 43%, and Horseshoe Cove offshore reefs increased by 30% (Fig. 5). This decline in offshore oysters was also observed in our field surveys and ground photos (Fig. 4). During 2010, we found the highest oyster densities at inshore sites (about 40–50 oysters/m^2) and lowest (and most variable) at offshore sites (generally 3–30 oysters/m^2) across all focal areas. Proportion of oysters that were alive was generally >50% across all focal areas and sites, with the highest proportion of live oysters generally found in inshore areas (upwards of 80%) and lowest proportion found offshore (~40–50%). Nearshore and inshore reefs also decreased over the 28 years examined, though we found modest increases among marsh-oyster reefs in 2010 (described below).

Oyster reef types were not evenly distributed or impacted across the study area over time.

Table 1. Net loss of oyster reef area from 1982 to 2010 in sampled areas of Florida's Big Bend, displayed by focal area, oyster reef type, and distance-to-shoreline. "Collapse" loss describes oyster reefs that experienced erosion and submergence over time. "Total loss" includes collapsed reefs and those that disappeared between time steps without evidence of erosion/submergence.

Characteristic	Total Loss (ha)†	Collapse (ha)‡
Focal area		
Horseshoe Cove	16.68 (49)	13.50 (81)
Long Cabbage	40.54 (73)	12.25 (30)
Corrigan's Reef	61.08 (65)	23.78 (39)
Suwannee Reef	5.74 (100)	5.74 (100)
Total	124.05 (66)	55.27 (45)
Distance-to-shoreline category		
Inshore	34.37 (50)	25.05 (37)
Nearshore	36.3 (61)	22.44 (37)
Offshore	53.38 (88)	53.38 (100)
Oyster reef type		
Marsh-oyster	5.17 (32)	4.77 (92)
Sand-oyster	84.12 (74)	40.69 (48)
Unresolved	32.82 (56)	9.38 (30)

† Values in parentheses are percentages of 1982 oysters.
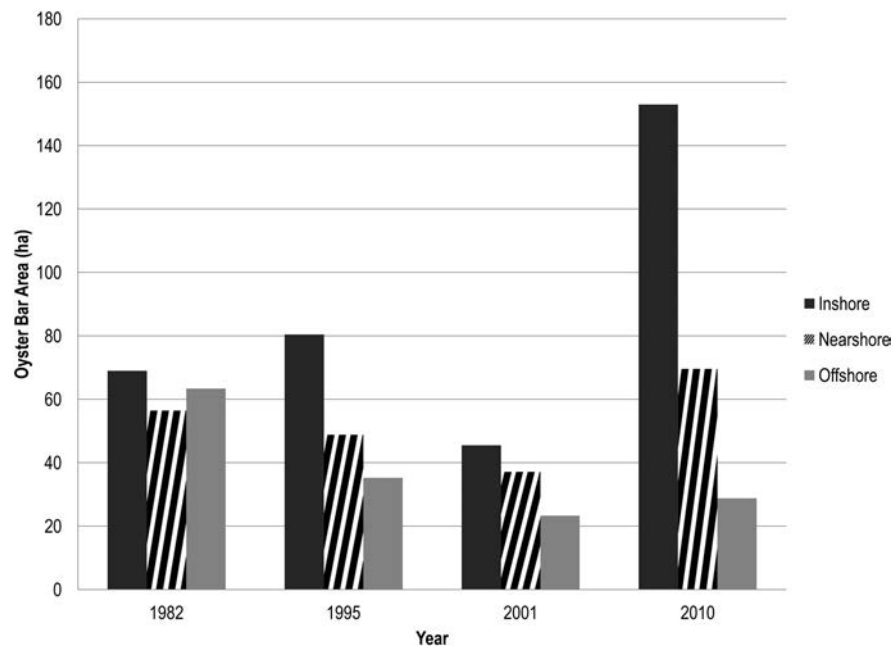‡ Values in parentheses are percentages of total loss.

Fig. 5. Total oyster reef area at each distance-to-shore category for each sample period in Florida's Big Bend.

Marsh-oysters composed 38% of inshore reefs, 21% of nearshore reefs, and none of the offshore reefs. Sand-oysters were 61% of inshore reefs, 79% of nearshore, and 100% of offshore reefs. Because offshore reefs experienced the most loss, they contributed much to the loss of sand-oysters over all. We found that between 1982 and 2010, 74% of sand-oyster reef area was lost, followed by unresolved reefs (56%) and marsh-oyster reefs (32%) (Table 1). The number of sand-oyster reefs decreased by 10–16% over each time step 1982 to 2001 and didn't change in 2001 to 2010. Total sand-oyster reef area in 1982 was 112.16 ha, followed by 87.61 ha in 1995, 44.81 ha in 2001, and 142.60 ha in 2010. Between 1982 and 2001, the number of marsh-oyster reefs was relatively steady between 262 to 303 reefs, then increased 37% in 2010. Marsh-oyster reef area slowly increased from 16.05 ha in 1982 to 36.95 ha in 1995, 25.54 ha in 2001, and 56.40 ha in 2010. However, marsh-oyster habitat type remained a relatively small proportion of the total oyster reef area throughout the study.

Inland movement

The distance from the mainland decreased for all reef types over time. Over the entire study period, sand-oyster reefs were generally further from shore (average = 489 m, SD = 678.3) compared to marsh-oysters (average = 134.1 m, SD = 225.2). From 1982 to 2010, the mean distance from shore to sand-oyster reefs decreased from 601.7 m (SD = 802.3) to 403.9 m (SD = 557.8). Off-shore reefs did not show any decrease in distance because they were nearly all lost and did not have new habitat to colonize. Distance from shore to marsh-oyster reefs decreased an average of 60 m over time (1982: 162.0 m (SD = 303.4), 1995: 165.2 (SD = 246.2), 2001: 117.7 (SD = 187.1), 2010: 108.6 m (SD = 159.8). A Kruskal-Wallis rank sum test found significant differences in the marsh-oyster reef distance over time (K-W chi-squared: 9.76, df = 3, p-value = 0.02).

Changes in Suwannee River discharge

We examined discharge volume for the Suwannee River (at Wilcox station) collected from 1957 to 2008 and rainfall data collected from 1941 to 2008. The relationship between annual discharge volume and annual basin-wide rainfall was not constant, with a significantly lower annual yield ratio (annual discharge/annual total rainfall, all stations) during the period 1995 to 2008 (x = 1.991 cu m/cm rainfall, SD = 0.81, n = 14) than in the previous 38 yr (x = 2.77 cu m/cm
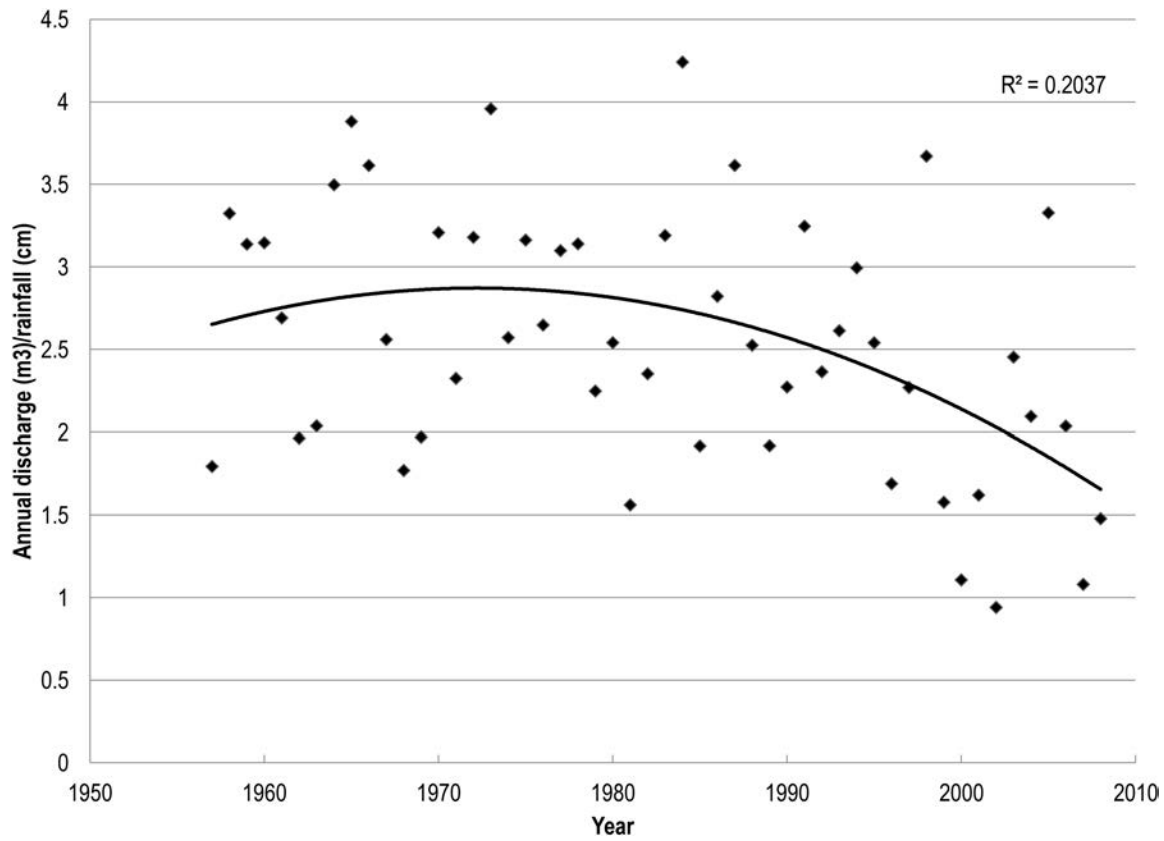
Fig. 6. Annual freshwater discharge/annual rainfall in the Suwannee River drainage basin, 1957–2008.

rainfall, SD = 0.65, n = 38; log-transformed data, t = 4.02, df = 50, p < 0.0001, Fig. 6). Average annual rainfall was not statistically different during these two periods (t = 0.17, p > 0.50). We also found that low discharge events (<1 SD below period of record monthly mean lows) were significantly more common during the period 1995 to 2008 (4.23 months/yr) than during the previous 55 years (0.42 months/yr, chi squared = 135.5, p ≪ 0.0001, Fig. 7).

DISCUSSION

Overall, we found a decrease of 124 ha of oyster habitat between 1982 and 2010 in the Big Bend of Florida, with a monotonic, nonreversing decline over time. This decrease was not trivial, as it represents a net 66% decline of oyster reef habitat. The pattern of loss was highly nonrandom, with offshore and sand-oyster reefs experiencing the greatest decline, and decreased losses closer to shore. At inshore reefs, marsh-

oyster reefs increased over this time period (mostly due to new reefs forming), but this expansion was not sufficient to offset the losses at offshore and sand-oyster reefs. We consider the loss of offshore sand-oyster reefs ecologically very significant for a number of reasons. First, these reefs have existed for 2,800 to 4,000 years (Grinnell 1972, Wright et al. 2005), suggesting that something fundamental has changed to induce such a sudden (30–40 yrs) decline. Second, these offshore reefs are functionally important as fringing reefs, reducing wave action in nearshore and inshore areas during storms (Grinnell 1972, Coen et al. 2007), and acting as a linear, coastwise dam for entrainment of sediment and freshwater (Grinnell 1972, Wright et al. 2005). Third, according to local watermen, in recent history these reefs were the most productive for local fisheries, producing high densities of large-sized oysters compared to reefs closer to shore. Understanding the mechanisms behind this rapid loss is therefore important to the
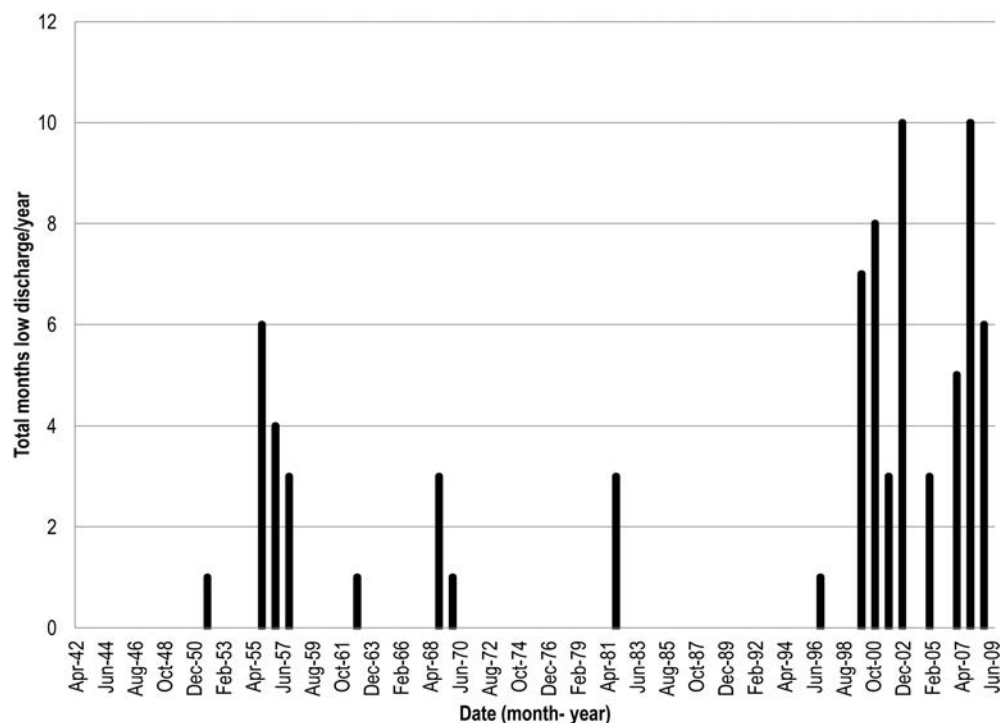
Fig. 7. Number of months low discharge (<1 SD below period of record monthly mean) from the Suwannee River, 1942–2009.

What factors are likely driving changes in oyster resources in the Big Bend?

Overharvest is a leading threat to oysters worldwide (Beck et al. 2011). The long history of oyster harvest in the Big Bend area began with Native Americans and was continued by European settlers, who developed a commercial fishery in the late 1800s (Arnold and Berrigan 2002), harvesting around 66 metric tons of oyster meat annually (Ingle and Dawson 1953). Over time annual harvest has fluctuated; the annual harvest dipped in the 1950s (Ingle and Dawson 1953) and then rose up to about 231 metric tons of oyster meat in 1985, where it remained until the early 1990s when annual harvests dropped below 68 metric tons (Arnold and Berrigan 2002). From 1995 through 2009, the annual oyster harvest did not rise above 68 metric tons (Sturmer 2010). The drop in oyster landings in the early 1990s is probably explained by two major economic and regulatory events in the late

1980s and early 1990s (Colson and Sturmer 2000). In 1991, the Florida Department of Labor and Employment Security initiated a job-retraining program to promote shellfish aquaculture (Colson and Sturmer 2000). This program heralded a switch among the fishing industry from oysters and other marine species to hard clam aquaculture, which is a more profitable and stable industry and is now the primary source of income for coastal residents in our study area (Colson and Sturmer 2000). Regulatory change in the oyster harvest began in 1987, when the Florida Department of Agriculture and Consumer Services, Division of Aquaculture began closing shellfish harvesting areas due to increasing levels of fecal coliform bacteria (FL Statute 597.020), an indicator for human pathogens that does not reduce oyster viability. Closed oyster reefs made up 14–79% (closed areas within each focal area was 14% Corrigan's Reef, 79% Horseshoe Cove, 0% Suwannee Reef, and 25% Lone Cabbage) of our study area. Although we may never know the effect of harvest history on oyster populations in this area due to a lack of

monitoring, several lines of evidence suggest that oyster reef collapse was essentially independent of harvest effects. First, oyster decline in this study was observed across closed and open harvest areas. Second, the fishery was historically maintained under higher levels of harvest than those occurring during the period of reef decline. Third, it is important to note that the recent decline in harvest was probably more strongly driven by economic and regulatory dynamics than decline in the resources. For these reasons, we believe that harvest is not a primary driver of the oyster decline shown in our results.

Although eastern oyster populations can tolerate a wide range of salinities for short periods, they are vulnerable both to high and low salinity levels (White and Wilson 1996). Bergquist et al.(2006) suggested that droughts and associated increases in salinity might be important in explaining losses of reefs in Suwannee Sound. We suspect that the increased variability in freshwater input as represented in the discharge and rainfall data from the Suwannee River may have impacted the oysters in our study area over the last 28 years as salinity is known to influence recruitment survival and disease resistance in Eastern oyster populations (White and Wilson 1996).

In the non-embayed, shallow, highly karstic region we studied, salinities can be strongly affected by several factors including freshwater inputs, complex local currents, and local offshore springs. Although there are several salinity monitoring stations along the coast, these are generally spatially distinct, often offshore, and have short time periods of available data. In the absence of direct measurement of salinities, freshwater inputs are probably the best proxy for inferring salinity dynamics. The Suwannee River is the major source of freshwater in this region, historically producing the largest pulses of freshwater during spring months and during tropical storm activity in late summer. The period of greatest declines in oyster habitat during the study period coincided with a more than nine-fold increase in the incidence of low-flow events in the Suwannee, and a significant negative change in the relationship between discharge and rainfall. Since annual rainfall has not changed significantly during the period of study, these characteristics suggest that usage or reten-

tion or redistribution of freshwater by human users is the main driver of the reduced discharge of the Suwannee.

We consider the coincidence of sharply reduced freshwater discharge and declines in oyster habitat to be suggestive of a possible relationship, but not diagnostic. However, two other observations lend support to existence of a mechanistic relationship. First, we saw a dramatic difference both in total area and in robustness and density of oysters between inshore and offshore habitat. Although river discharge is the dominant parameter in freshwater inputs, the region is quite karstic and a significant amount of freshwater inputs may come from seepage and overland flow from extensive coastal and inland wetlands (Raabe and Bialkowska-Jelinska 2007). This more diffuse freshwater has a very short plume from the land's edge, and a relatively weak zone of influence. Seepage and overland flow therefore, probably buffer inshore reefs from salinity changes more than offshore reefs. Second, it is known that springs and seeps of varying sizes exist in the coastal zone (Raabe and Bialkowska-Jelinska 2007, 2010) including adjacent to the Corrigan's Reef complex, which has a high degree of persistence over this time period relevant to other regions we studied which is surprising given its distance from the Suwannee River mouth. These three features (temporal coincidence of declines in oyster habitat with reduced discharge, resilience of inshore reefs, and resilience of reefs close to freshwater) are consistent with the idea that persistence of oyster communities in this region are driven by pulsed access to freshwater.

We propose that extended periods of high salinity are likely to have stressed oyster populations, particularly on offshore reefs, to the extent that the physical structure of reefs was affected by mortality of older oysters and loss of significant recruitment. Oyster reef growth and expansion is predicated on successful settlement and growth of new larvae (spat) on physical structure (a nucleation site). Often this structure is an existing oyster reef such that spat settle and grow among older age classes of oysters. As these older oysters die, their shells continue to offer high quality habitat for settlement and growth of spat and high survival to adulthood. Once these bioherms are weakened due to a loss

of spat, increased mortality of adults, or both, the fundamental structure of the oyster reef as a settlement site for spat is lost, increasing the likelihood that the remaining oyster shell (settlement sites) will be dispersed by wave action making the oyster reef much less resilient to wave action, particularly during storm events. Since most oyster reefs in our study area are built on riverine sediments (Wright et al. 2005), the breakup of oyster structure would likely trigger a spreading of sediment, and loss of vertical profile. Once this chain of events occurs, an offshore oyster reef would be difficult to re-establish since little appropriate substrate remains upon which spat can recruit and survive. Our incidental observations during 2010 indicate that spat do often arrive on offshore reefs in high densities, but that they do not survive in the shifting sediments, which are poor nucleation sites and also offer no refugia from predators.

During the last 28 years sea-level rose 5 cm in our study site (NOAA 2010), which also likely contributed to the decline of oyster reefs in the Big Bend. Due to the extremely low coastline gradient in this area, small increases in sea level can lead to widespread changes in the ecology and sedimentary geology of this area. Hine et al. (1988) noted that the Big Bend region had undergone submergence as a result of sea level rise during the past 5,000 years and that recent tide-gauge data indicate that submergence is continuing and increasing "to a pace four times the radiocarbon-based rate (4 cm/100 yr)". Cedar Key has a nearly 100 year record of tide-gauge data, indicating that the annual increase is 1.8 (±0.19) mm/yr (NOAA 2010). Updating the sea-level rise rates reported by Hine et al. (1988) and Hicks and Debaugh (1983) with data through 2006 shows that the observed rate from the NOAA tide-gauge station is now about 4.5 times the radiocarbon-based rate reported in Hine et al. (1988) and the gauge data reported by Hicks and Debaugh (1983). Further, the estimate for future sea-level rise for Cedar Key over the next 70 years is 3.6 mm/yr (Walton 2007), which could increase submergence greatly and accelerate oyster reef decline.

Sea-level rise has likely combined with storms to enhance wave energy during storm events, leading to increased reef erosion during storm events over time. In fact, sea-level rise, stormi-ness, and drought have all been implicated in the loss of many coastal biotic communities throughout the Gulf of Mexico, including forests (O'Brien et al. 1994, Denslow and Battaglia 2002), coral reefs (Lidz and Shinne 1991, Jokiel and Brown 2004), salt marsh (Reed 1990, Silliman et al. 2005, Zedler 2010), and other coastal communities (Ross et al. 2000). In our study area, drought (Desantis et al. 2007) and storms (Williams et al. 2003) also have been documented to work in concert with sea-level rise to increase soil salinity, leading to vegetation die-off. One particular extratropical storm in 1993 brought a water surge of 2.5 m into Waccassassa Bay (NCDC 1993) and caused significant dieback of forest tree species with high sensitivity to increased salinity (Williams et al. 2003). This storm was also implicated in stories from local watermen as the threshold event that broke up several stressed off-shore reefs in our study area.

The severity and pattern of climate change impacts in this region are closely linked to topography. Hine et al. (1988) identified morphological features of the Big Bend that are formed and influenced by the interactions between sediments, underlying geology, and freshwater discharge. Hine et al. (1988) reasoned the oyster reefs were maintained via (1) the availability of hard substrate for oyster-reef nucleation; (2) reduced salinities which discourages oyster predators; and (3) strong tidal currents (which are oriented laterally along this coast) which increase available food resources for oysters. After proposing the geological succession model that we confirmed with our analysis, the authors postulated that "...as sea level continues to rise, the outer bioherms [organic bar in a mound shape] experience rising salinity. Eventually, the linear shell mounds can no longer support oyster growth due to increased predator infestation. Many shells composing the deeper, outer bioherms are highly degraded and biologically corroded (numerous Clionid sponges). In addition to bioerosion, these outer bars are exposed to open wave attack, resulting in shell dispersal and causing general morphological degradation of the entire feature." This speculation appears, according to our analysis, to be playing out in the Big Bend region and if climate change predictions prove to be correct, is likely to play out in a larger, more dramatic manner in the

future.

Recommendations for prioritizing research and conservation of oyster resources

While our hypothesized chain of events is currently the most likely explanation for observed changes in oyster reef communities in the Big Bend region of Florida, the evidence we offer is correlative and non-experimental. We suggest that field experiments may offer insight into oyster reef structural processes and that these experiments be designed to inform restoration strategies by testing importance of freshwater input, reef structure, and reef elevation. Experimental restoration could include testing various reef structure building methods across a gradient of distance to shoreline and distance to known freshwater sources. This would enable an exploration of the relative importance of freshwater versus reef structure in establishing and maintaining healthy oyster habitat.

Our study suggests that even in the absence of major coastal development and anthropogenic stressors, oyster habitat may be at considerable risk in the Gulf, a globally important region for oysters (Beck et al. 2011). In this case, it seems most likely that increasing human uses of freshwater inland may be an important factor resulting in habitat loss. Global climate change and increased development is expected to raise sea-level, limit freshwater availability, and increase storm intensity in Florida's near and long-term future (Twilley et al. 2001, Purtlebaugh and Allen 2010). Planning for the conservation of oyster habitat in the Gulf should include scenarios that encompass the interaction of global change, and local stressors of human origin.

ACKNOWLEDGMENTS

LITERATURE CITED

Arnold, W. S. and M. E. Berrigan. 2002. A summary of the oyster (*Crassostrea virginica*) fishery in Florida. A Report to the Division of Marine Fisheries, Florida Fish and Wildlife Commission, St. Petersburg, Florida, USA.

Atlantic States Marine Fisheries Commission (ASMFC) 2007. The importance of habitat created by shellfish and shell beds along the Atlantic coast of the U.S. Atlantic States Marine Fisheries Commission, Washington, D.C., USA.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J. Edgar, B. Hancock, M. C. Kay, H. S. Lenihan, M. W. Luckenbach, C. L. Toropova, G. F. Zhang, and X. M. Guo. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61:107–116.

Becnel, T. 2010. No oil among Apalachicola Bay's oysters, but no relaxing, either. Herald-Tribune. Apalachicola, Florida, USA. August 6, 2010. http://www.heraldtribune.com/article/20100808/ARTICLE/8081064?p=1&tc=pg

Bergquist, D. C., J. A. Hale, P. Baker, and S. M. Baker. 2006. Development of ecosystem indicators for the Suwannee River estuary: Oyster reef habitat quality along a salinity gradient. Estuaries and Coasts 29:353–360.

Berrigan, M. E., T. Candies, J. Cirino, R. J. Dugas, C. Dyer, J. Gray, T. Herrington, W. R. Keithly Jr., R. Leard, J. R. Nelson, and M. Van Hoose. 1991. The oyster fishery of the Gulf of Mexico, United States: a regional management plan. No. 24. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi, USA.

Borsje, B. W., B. K. van Wesenbeeck, F. Dekker, P. Paalvast, T. J. Bouma, M. M. van Katwijk, and M. B. de Vries. 2011. How ecological engineering can serve in coastal protection. Ecological Engineering 37:113–122.

Buzan, D., W. Lee, J. Culbertson, N. Kuhn, and L. Robinson. 2009. Positive relationship between freshwater inflow and oyster abundance in Galveston Bay, Texas. Estuaries and Coasts 32:206–212.

Cappiello, D. 2011. House passes bill to speed offshore drilling process. Huffington Post. May 5, 2011. http://www.huffingtonpost.com/2011/05/05/house-offshore-drilling-bill_n_858271.html

Carranza, A., O. Defeo, and M. Beck. 2009. Diversity, conservation status and threats to native oysters (*Ostreidae*) around the Atlantic and Caribbean coasts of South America. Aquatic Conservation: Marine and Freshwater Ecosystems 19:344–353.

Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers, and S. G. Tolley. 2007. Ecosystem services related to

oyster restoration. Marine Ecology Progress Series 341:303–307.

Colson, S. and L. N. Sturmer. 2000. One shining moment known as clamelot: the Cedar Key story. Journal of Shellfish Research 19:477–480.

Denslow, J. S. and L. L. Battaglia. 2002. Stand composition and structure across a changing hydrologic gradient: Jean Lafitte National Park, Louisiana, USA. Wetlands 22:738–752.

Desantis, L. R. G., S. Bhotika, K. Williams, and F. E. Putz. 2007. Sea-level rise and drought interactions accelerate forest decline on the Gulf Coast of Florida, USA. Global Change Biology 13:2349–2360.

Eastern Oyster Biological Review Team (EOBRT) 2007. Status review of the eastern oyster (Crassostrea virginica). Report to the National Marine Fisheries Service, Northeast Regional Office. February 16, 2007. NOAA Technical Memorandum NMFS F/SPO-88.

Eggleston, D. B., W. E. Elis, L. L. Etherington, C. P. Dahlgren, and M. H. Posey. 1999. Organism responses to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna. Journal of Experimental Marine Biology and Ecology 236:107–132.

Environmental Systems Research Institute (ESRI) 2010. ArcMap 10. Environmental Systems Research Institute, Redlands, California, USA.

Florida Geographic Data Library (FGDL) 2011. 2004 Florida Shoreline Map. Florida Fish and Wildlife Research Institute. http://www.fgdl.org/

Geselbracht, L. 2007. Conservation action plan for marine and estuarine resources of the Big Bend Area of Florida. The Nature Conservancy, Florida Chapter. conpro.tnc.org/968/big_bend_conservation_action.../download_public

Goodbred, S. L. and A. C. Hine. 1995. Coastal storm deposition: Salt-marsh response to a severe extratropical storm, March 1993, west-central Florida. Geology 23:679–682.

Grinnell, R. S., Jr. 1972. Structure and development of oyster reefs on the Suwannee River delta, Florida. Dissertation. State University of New York, Binghamton, New York, USA.

Hicks, S. D. and H. A. Debaugh, Jr. 1983. Sea level variations for the United States, 1855-1980. National Ocean Survey 170. Rockville, Maryland, USA.

Hine, A. C., D. F. Belknap, J. G. Hutton, E. B. Osking, and M. W. Evans. 1988. Recent geological history and modern sedimentary processes along an incipient, low-energy, epicontinental-sea coastline: Northwest Florida. Journal of Sedimentary Petrology 58:567–579.

Hulathduwa, Y. D. and K. M. Brown. 2006. Relative importance of hydrocarbon pollutants, salinity and tidal height in colonization of oyster reefs. Marine Environmental Research 62:301–314.

Ingle, R. M. and C. E. Dawson. 1953. A survey of the Cedar Key area. State of Florida, Board of Conservation, Division of Oyster Culture. Technical Series number 9. Tallahassee, Florida, USA.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Jokiel, P. L. and K. M. Brown. 2004. Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. Global Change Biology 10:1627–1641.

Kirby, M. X. 2004. Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. Proceedings of the National Academy of Sciences of the United States of America 101:13096–13099.

Land Boundary Information System (LABINS) 2011. On-line survey information and maps for the state of Florida. Florida Department of Environmental Protection. http://data.labins.org

Levinton, J., M. Doall, D. Ralston, A. Starke, and B. Allam. 2011. Climate change, precipitation and impacts on an estuarine refuge from disease. PLoS One 6.

Lidz, B. H. and E. A. Shinne. 1991. Paleoshorelines, reefs, and a rising sea: south Florida, USA. Journal of Coastal Research 7:203–229.

Main, M. B. and G. M. Allen. 2007. Florida's environment: North central region. Wildlife Ecology and Conservation Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida, USA.

Mearns, A. J., D. J. Reish, P. S. Oshida, M. Buchman, T. Ginn, and R. Donnelly. 2007. Effects of pollution on marine organisms. Water Environment Research 79:2102–2160.

National Climatic Data Center (NCDC) 1993. The big one!—May 14, 1993 update. National Oceanic and Atmospheric Administration, Ashville, North Carolina, USA. http://www.erh.noaa.gov/aly/Past/tr9301.pdf

National Marine Fisheries Service (NMFS) 2011. NMFS Landings Data, 2009 Gulf States Oyster Data. http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html

National Oceanic and Atmospheric Administration (NOAA) 2005. NOAA fisheries service considers listing eastern oyster as threatened or endangered. Press release NOAA05-063. http://www.nefsc.noaa.gov/press_release/2005/ma0507.pdf

National Oceanographic and Atmospheric Administration (NOAA) 2010. Mean sea level trend, station 8727520, Cedar Key, Florida. National Ocean Service http://co-ops.nos.noaa.gov/sltrends/sltrends_station.shtml?stnid=8727520

Ning, Z. H. and K. Abdollahi. 2003. US National assessment of the potential consequences of climate variability and change. Climate change and its consequences on the Gulf Coast Region of the US. Southern University, A&M College, U.S. Environmental Protection Agency. http://www.usgcrp.gov/usgcrp/nacc/gulfcoastworkshop.htm#intro

O'Brien, J. J., L. D. L. Sternberg, and M. S. Ross. 1994. Sea-level rise and the reduction in pine forests in the Florida Keys. Ecological Applications 4:144–156.

Purtlebaugh, C. H. and M. S. Allen. 2010. Relative abundance, growth, and mortality of five age-0 estuarine fishes in relation to discharge of the Suwannee River, Florida. Transactions of the American Fisheries Society 139:1233–1246.

Raabe, E. A. and E. Bialkowska-Jelinska. 2007. Temperature anomalies in the Lower Suwannee River and tidal creeks, Florida, 2005. U.S. Geological Survey Open-file report 2007–1311.

Raabe, E. A. and E. Bialkowska-Jelinska. 2010. Thermal imaging of the Waccasassa Bay Preserve: image acquisition and processing. U.S. Geological Survey Open File Report 2010–1120.

Reed, D. J. 1990. The impacts of sea-level rise on coastal salt marshes. Progress in Physical Geography 14:465–481.

Ross, M. S., J. F. Meeder, J. P. Sah, P. L. Ruiz, and G. J. Telesnicki. 2000. The Southeast Saline Everglades revisited: 50 years of coastal vegetation change. Journal of Vegetation Science 11:101–112.

Silliman, B. R., J. Van de Koppel, M. D. Bertness, L. A. Staton, and I. A. Mendelssohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science 310:1803–1806.

Sturmer, L. N. 2010. Clam culture industry. Big Bend Oyster Working Group Meeting Presentation. April 11, 2011. Cedar Key, Florida, USA. http://floridarivers.ifas.ufl.edu/oyster.htm

Twilley, R. R., E. J. Barron, H. L. Gholz, M. A. Harwell, R. L. Miller, D. J. Reed, J. B. Rose, E. H. Siemann, R. G. Wetzel, and R. J. Zimmerman. 2001. Confronting climate change in the Gulf Coast region: prospects for sustaining our ecological heritage. Union of Concerned Scientists, Cambridge, Massachusetts, and Ecological Society of America, Washington, D.C., USA.

United States Geological Survey (USGS) 2011. National water information system: web interface. http://waterdata.usgs.gov/nwis/dv/?site_no=02323500&PARAmeter_cd=00060

Wall, L. M., L. J. Walters, R. E. Grizzle, and P. E. Sacks. 2005. Recreational boating activity and its impact on the recruitment and survival of the oyster Crassostrea virginica on intertidal reefs in Mosquito Lagoon, Florida. Journal of Shellfish Research 24:965–973.

Walton, T. L., Jr. 2007. Projected sea level rise in Florida. Ocean Engineering 34:1832–1840.

White, M. E. and E. A. Wilson. 1996. Predators, pests and competitors. Pages 559–580 in V. S. Kennedy, R. I. E. Newell, and A. F. Eble, editors. The eastern oyster, Crassostrea virginica. Maryland Sea Grant College, College Park, Maryland, USA.

Williams, K., M. MacDonald, and L. S. L. Sternberg. 2003. Interactions of storm, drought, and sea-level rise on coastal forest: a case study. Journal of Coastal Research 19:1116–1121.

Wright, E. E., A. C. Hine, S. L. Goodbred, and S. D. Locker. 2005. The effect of sea-level and climate change on the development of a mixed siliciclastic-carbonate, deltaic coastline: Suwannee River, Florida, USA. Journal of Sedimentary Research 75:621–635.

Zedler, J. B. 2010. How frequent storms affect wetland vegetation: a preview of climate-change impacts. Frontiers in Ecology and the Environment 8:540–547.