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Joshua Solomon
University of Central Florida

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IDENTIFYING INUNDATION-DRIVEN EFFECTS AMONG INTERTIDAL *CRASSOSTREA VIRGINICA* IN A COMMERCIALLY IMPORTANT GULF OF MEXICO ESTUARY

by

JOSHUA ANDREW SOLOMON
B.S. University of Central Florida, 2011

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ABSTRACT

Sea level rise and changing storm frequency and intensity resulting from climate change create tremendous amounts of uncertainty for coastal species. Intertidal species may be especially affected since they are dependent on daily inundation and exposure. The eastern oyster *Crassostrea virginica* is an economically and biologically important sessile intertidal species ranging from Canada to the Gulf of Mexico. Declines and changes in distribution of oyster populations has forced commercial harvesting to spread from subtidal to intertidal reefs. We investigated the potential responses of intertidal *C. virginica* to sea level rise, and the response of larval settlement to sedimentation which is likely to increase with higher water levels and storm frequency. Inundation was used as a proxy for sea level rise.

We hypothesized four possible outcomes for intertidal oyster reefs as a result of changes in inundation due to sea level rise: (a) intertidal reefs become subtidal and remain in place, (b) intertidal reefs will be lost, (c) intertidal reefs migrate shoreward upslope and remain intertidal, and (d) intertidal reefs will grow in elevation and remain intertidal. To test the plausibility of these four outcomes, oyster ladders were placed at two sites within Apalachicola Bay, Florida, USA. Ladders supported oyster recruitment mats at five heights within the range of intertidal elevations. The bottom-most mat was placed near mean low tide, and the top mat near mean high tide to investigate the effect of tidal inundation time on *C. virginica*. Sediment traps were attached to ladders with openings at equal elevation to the oyster mats. Ladders were deployed for one year starting in June 2012, and again in June 2013, during peak oyster recruitment season. Monthly for six months during year one, sediment was collected from traps, dried to

constant weight and weighed to obtain a monthly average for total sediment at each elevation. At the end of one year, oyster mats were collected from the field and examined for the following responses: live oyster density, mean oyster shell length of live oysters, mean oyster shell angle of growth relative to the benthos, and mean number of sessile competitors. We used AICc to identify the most plausible models using elevation, site, and year as independent variables.

Oyster density peaked at intermediate inundation at both sites (maximum 1740 oysters per m^2), it decreased slightly at the mean low tide, and sharply at the mean high tide. This response varied between years and sites. Mean oyster shell length peaked near mean low tide (6.7 cm), and decreased with increasing elevation. It varied between years and sites. Oyster shell angle of growth relative to the benthos showed a quadratic response for elevation; site but not year affected this response. Sessile competitor density also showed a quadratic response for elevation and varied between sites and years. Barnacles were the primary spatial competitor reaching densities of up to 28,328 barnacles per m^2. Total monthly sedimentation peaked at the lowest elevations, and varied by site, with an order of magnitude difference between sites. Sediment increased with decreasing elevation.

Outcomes a, c, and d were found to be viable results of sea level rise, ruling out complete loss of intertidal reefs. Outcome (a) would be associated with decrease in oyster density and increase in oyster length. Outcome (c) would require the laying of oyster cultch upslope and shoreward of current intertidal reefs, as well as the removal of any hard armoring or development. Outcome (d) remained possible, but is the least likely requiring a balance between sedimentation, oyster angle of growth, and recruitment. This should be further investigated.

A laboratory experiment was designed to test relative impact of varying sediment grain sizes on settlement of *C. virginica* larvae. Previous studies showed that suspended solids resulted in decreased larval settlement when using mixed sediment grain sizes. Predicted storm levels and hurricane levels of total suspended solids were used in flow tanks. Sediment from the field experiment was sieved into seven size classes, the most common five of which were used in the experiment since they represented 98.8% of total mass.

Flow tanks were designed and built that held 12 aged oyster shells, instant ocean saltwater, and sediment. Oyster larvae were added to the flow tanks and allowed one hour to settle on shells. Each run utilized one of the five size classes of sediment at either a high or low concentration. Following the one-hour settlement period, oyster shells were removed from the flow tank and settled larvae were counted under a dissecting microscope. Settlement was standardized by settlement area using Image J. AICc model selection was performed and the selected model included only grain size, but not concentration. A Tukey's post hoc test differentiated <63 μm from 500 – 2000 μm, with the < 63 μm grain size having a negative effect on oyster larval settlement. This indicates that the smaller grain sizes of suspended solids are more detrimental to oyster larval settlement than larger grain sizes.

The oyster ladder experiment will help resource managers predict and plan for oyster reef migration by cultch laying, and or associated changes in oyster density and shell length if shoreward reef growth is not allowed to occur. The laboratory experiment will help to predict the impacts of future storms on oyster larval recruitment. Together this information can help managers conserve as much remaining oyster habitat as possible by predicting future impacts of climate change on oysters.

To Larry, Barbara and Zack Solomon
Thank you for all your support and love.

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CHAPTER 1: GENERAL INTRODUCTION

Sea Level Rise and Oysters

The Intergovernmental Panel on Climate Change (IPCC) predicts sea levels will rise from 20 to 200 cm over the next century (Parris *et al.,* 2012). Rising sea levels, coupled with climate change related change in storm activity and associated alterations to sediment transport, may have impacts on marine and estuarine organisms (Webster *et al.,* 2005, Hoegh-Guldberg and Bruno 2010). The wide range of uncertainty in these predictions calls for research to investigate the effects of changing inundation and sedimentation on coastal species, especially sessile species residing in the intertidal zone.

Crassostrea virginica (eastern oyster) is a sessile estuarine bivalve ranging from the Gulf of Mexico to the Gulf of St. Lawrence in Canada (Buroker 1983). *Crassostrea virginica* is an economically important shellfish around the east and Gulf coasts of the United States where it is harvested as a food resource. Populations of *C. virginica* in the Gulf of Mexico accounted for 69% by weight of all United States oyster fishery landings in 2003 (Turner 2006).

As an estuarine species, *C. virginica* exhibits a wide range of temperature and salinity tolerances. Its temperature tolerance ranges from -2 ℃ to 36℃, and it is considered more susceptible to mortality induced by rapid change in temperature than to temperature itself (Shumway 1996). The salinity tolerance of *C. virginica* is from 0-42.5 ppt, although it most commonly can be found between 5-40 ppt (Shumway 1996). It has a high fecundity (115 million eggs per season per individual) and has widespread dispersal. It is an hermaphroditic organism

which reproduces throughout the year in some parts of its range, and seasonally in other locations (Dame 1976, Buroker 1983).

Crassostrea virginica is also biologically important. This species filters water at a rate of 6.8 L h^{-1}, which has a positive effect on water quality and clarity (Kennedy 1996; Pollack 2013). Oysters also serve as ecosystem engineers, providing three-dimensional reef structure as habitat for mobile fauna and substrate for other sessile invertebrates and macroalgae (Kennedy 1996; Coen, Luckenbach, and Breitburg 1999; Barber, Walters, and Birch 2010). Intertidal oyster reefs serve an additional role of helping to preserve shoreline sediments and vegetation, as well as the shorelines themselves, by significantly reducing wave energy (Scyphers *et al.* 2011, Manis *et al.* 2014).

Hoegh-Guldberg and Bruno (2010) suggest future loss of oyster reefs is an important concern due to both the loss of the oysters and the potential loss of associated biodiversity as a result of decreased habitat complexity. Species potentially affected by loss of intertidal oyster reefs in the northern Gulf of Mexico include commercially important species such as blue crabs, spotted sea trout, shrimp and stone crabs; these are species commonly found and harvested in Apalachicola Bay (Boudreaux, Stiner, and Walters 2006; Edminston 2008, Walters and Birch 2010).

Recent reports document that 85% of shellfish reefs have been lost globally and many of the healthy shellfish bastions that remain may soon be lost as well (Beck *et al.* 2011). Historically, the primary causes of these losses were anthropogenic, specifically pollution and overharvesting (MacKenzie 2007). These declines resulted in not only direct loss to the

economy, but also the indirect loss of ecosystem services provided by oysters. With the already steep declines in shellfish reefs due to anthropogenic causes, the effects of sea level rise (SLR) pose an added threat that needs to be better understood. Inundation frequency is known to have important effects on intertidal species, their competitors, and their predators, but we do not yet know what increased submersion times associated with SLR will have on these interactions. Predator avoidance resulting from daily fluctuations in water levels has been suggested as one of the reasons why intertidal oysters continue to exist, despite the benefits of living subtidally where they can actively filter feed for longer durations (Dame, 1976). Many studies have confirmed inundation frequency as a driver of competition among intertidal sessile organisms, particularly among barnacles, where abundances may relate to larval supply, preference, or resulting in recruitment space being occupied (Grosberg, 1982; Underwood, 1991, Miron, Boudreau and Bourget, 1999; Boudreaux, Walters, and Rittschof, 2009). Likewise, competition with other sessile invertebrates within the intertidal zone may undergo changes with increasing sea levels (Dayton, 1971). Hydrological changes associated with SLR will influence the spatial zones of competition between *C. virginica* and barnacles, the latter which preferentially settle in the areas of higher water motion (Bushek, 1988).

Although almost decadal in occurrence, extreme storm events like Hurricanes Elena and Kate in 1985 resulted in record low oyster landings in Apalachicola Bay (Edmiston 2008). The reefs recovered quickly with the help of management in the form of commercial fishing restrictions, and it has been suggested that seasonal timing of a major storm event may affect the ability of the system to recover (Berrigan 1988, Livingston *et al.* 1999, Edmiston 2008, Oczkowski *et al.* 2011). Co-occurring with SLR, there is an expectation of changing storm

activity, which has the potential to negatively impact many coastal environments (Webster *et al.,* 2005, Hoegh-Guldberg and Bruno, 2010). Winds associated with storm activity have been shown to be positively correlated with increased suspended sediment loads; subsequent concentrations were up to ten times higher than pre-storm loads, and took up to four days to fall to background levels (Liu and Huang, 2009). Previously in Apalachicola Bay, storms have been shown to have extreme effects on total suspended solid (TSS) levels and transport sediment near oyster beds, which is known to have a negative impact on oyster survival (MacKenzie 1983, Lenihan 1999; Livingston *et al.* 1999; Wall *et al.* 2005; Liu and Huang 2009).

Increased sediment loads have been shown to decrease settlement of oyster larvae by increasing mortality in oyster spat less than one month old through abrasion of oyster larvae, or resulting in complete burial during storm events (MacKenzie 1983; Lenihan 1999; Livingston *et al.* 1999; Wall *et al.* 2005). Mixed grain size sediment loads of 8 g/L resulted in significant reductions of oyster settlement (Boudreaux, Walters, and Rittschof 2009). Since sedimentation has been previously identified as playing an important role in oyster recruitment and may increase with increasing storms, developing and understanding a long term sediment grain size profile as it changes with inundation is also an important step towards predicting how changes in sedimentation may affect oysters (MacKenzie 1983, Lenihan 1999, Livingston *et al.* 1999).

Of the many impacts that climate change may have on intertidal oyster reefs, all depend on the amount of time a reef spends inundated. By investigating the effects of time submerged, predictions can be made about intertidal oyster reefs into the future. The effects of inundation

can be studied through manipulation of elevations of oyster recruiting substrate within the present intertidal zone.

A method for manipulating percent time submerged with intertidal oysters was developed and referred to as the "Oyster Ladder", (Figure 1). The oyster ladder was based on the marsh organ design of Dr. James Morris (Morris 2007). Marsh organs were used to experimentally examine effects of inundation on salt marsh plants, particularly *Spartina* and *Juncus* (Morris 2007). From these experiments, the marsh equilibrium model was developed to predict accretion or sediment loss of intertidal marshes. Here, we use oyster ladders to investigate the effects of inundation time and sedimentation on intertidal *C. virginica*.
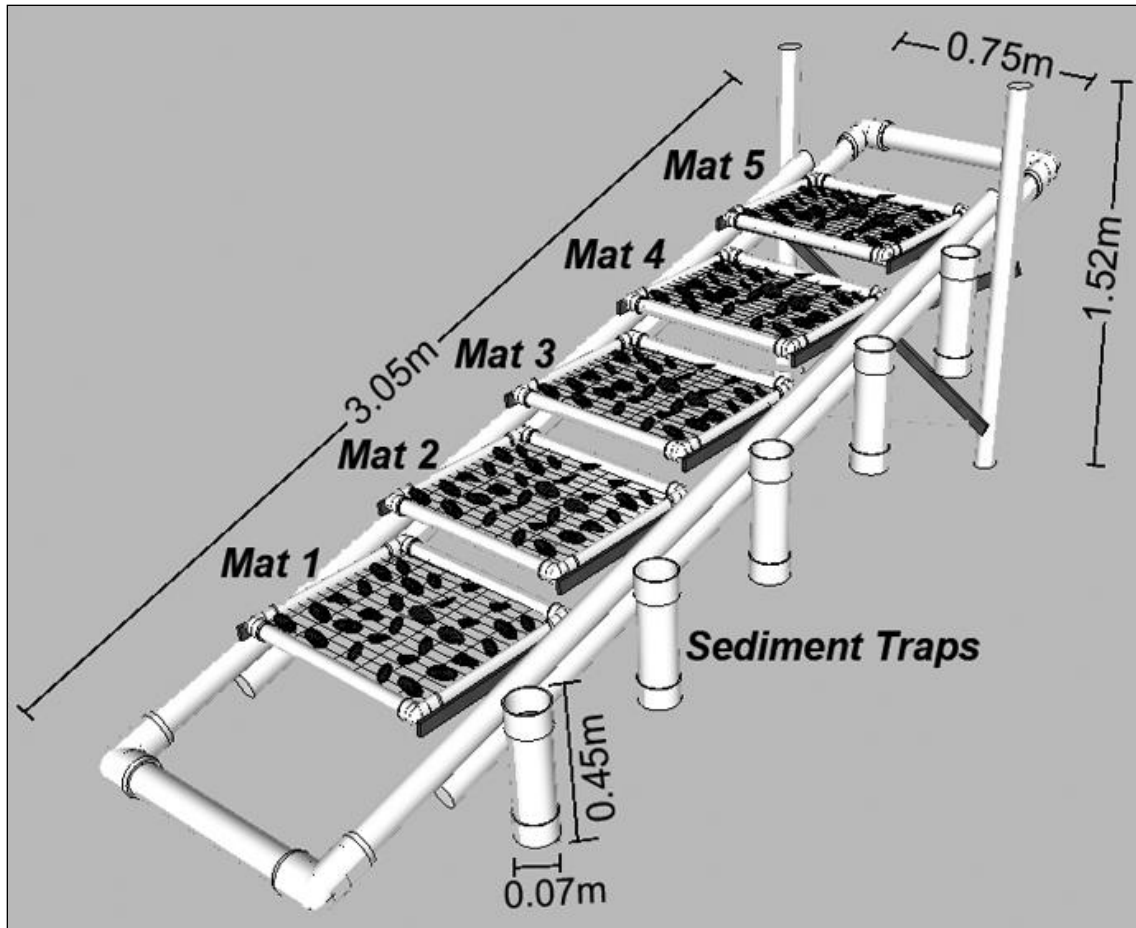
Figure 1.Oyster ladder design showing sediment traps and oyster restoration mats. Dimensions and mat numbers are included.

Study Site

Apalachicola Bay is situated in Franklin County on the Florida Panhandle. The oyster industry, as we know it today with collection occurring by hand tonging, began in 1836. As early as 1895, surveys of Apalachicola Bay acknowledged the problem of oyster harvesting without concern for conservation of the resource, and instituted the first regulations on over-harvesting (Whitfield 1977).

Since then, oysters have continued to drive the culture of the region and provide the basis

for ecotourism in Franklin County (City of Apalachicola Website 2015). The Apalachicola

National Estuarine Research Reserve (ANERR), founded in 1979, encompasses 99,862 ha, is

located in Franklin, Gulf, and Liberty Counties and includes 80,000 acres of submerged land

(Edminston 2008). Its water is maintained for the designated use of shellfish propagation or

harvesting; as such, both sites used are classified by the Florida Department of Environmental

Protection (DEP) as Class II waters (Isphording, 1985; Florida Administrative Code, 2006).

In early 2012, the Apalachicola region was reported as one of the most healthy oyster

populations in the United States, with health being defined as achieving full estuary filtration

within one tidal cycle (Zu Ermgassen *et al.* 2013). Apalachicola Bay historically accounted for

90% of the Florida oyster fishery, and 10% of the national total (Livingston 1984). These

harvests were historically high, with up to 1200 bushels per acre harvested annually from

subtidal reefs (Edminston 2008). Oysters in Apalachicola Bay are overwhelmingly harvested

from subtidal reefs, which represent 93.5% of mapped oyster reef acreage (M. Donnelly,

unpublished data).

In July 2012, the Florida Department of Agriculture and Consumer Services (FDACS)

issued a report indicating that most commercially harvested subtidal oyster reefs in Apalachicola

Bay had severely decreased populations and recommended a fishing closure (FDACS 2012).

Instead, an executive order was issued by Florida Fish and Wildlife Commission to lower

harvesting limits (Sempsrott *et al.* 2012). In an attempt to identify causes of the collapse, the

Apalachicola Bay Oyster Situation Report was released in April 2013, summarizing work done

by multiple institutions to describe the state of Apalachicola Bay during the "collapse of the

oyster fishery" (Florida Sea Grant College Program 2013). The authors reported decreased subtidal oyster harvests resulted from significant decreases in oyster recruitment and survival. They suggested high salinity due to low discharge from the Apalachicola River was a primary cause of mortality, and parasitism as a negative factor of unknown magnitude. Overfishing was specifically dismissed as an ongoing problem if current size limits "continue[d] to be" enforced.

In 2014, new restrictions were placed on oyster harvesting in Apalachicola Bay. Starting on the first of June, there was a 75% reduction in recreational oyster harvest limits from 20 gallons of culled oysters to five per harvester per day. At the same time, a 60% decrease in the commercial bag limit from 20 to 8 was implemented. These changes occurred in tandem with a decrease in allowable harvesting days.

To date, reports and most research in Apalachicola Bay have focused on the commonly harvested subtidal oyster populations, and have not considered intertidal oysters; current harvesting laws do not differentiate between intertidal and subtidal oysters . While intertidal oyster reefs account for only 6.5% of oyster coverage in the bay, they were historically thought to represent populations that had less harvesting pressure than subtidal reefs (M. Donnelly, unpublished). However, increased intertidal harvesting has been observed in East Cove in recent years (J. Hodson, St. George Island State Park, pers. comm.). As anthropogenic pressure increases on intertidal oysters, both directly through harvesting, and indirectly through sea level rise, it is important that we assess these impacts and the resilience of *C. virginica*.

CHAPTER 2: DETERMINING THE RESPONSE OF RECRUITMENT AND GROWTH OF INTERTIDAL OYSTERS TO VARYING ELEVATIONS

Methods:

To determine the response of *C. virginica* recruitment and growth at varying elevations within the intertidal zone, oyster ladders were developed; they are a method for manipulating percent time submerged with intertidal oysters (Solomon *et al.* 2014). Each oyster ladder consisted of 6 cm (two-inch) PVC, wood and galvanized steel framework, measuring 3.05 m long by 0.76 m wide, and standing 1.52 m tall (Figure 1).

Each ladder suspended five oyster recruitment mats made of aquaculture-grade plastic mesh (Vexar) with 1.5 cm openings. Each mat measured 0.25 m² and had thirty-six drilled, aged local oyster shells attached with 20 cm plastic zip ties (50 lb. test) (Figure 1). Below each mat, a base of corrugated plastic was secured; this provided a stable, solid surface for the mat. Oyster shells were equally spaced in 6 x 6 arrays oriented perpendicular to the substrate, similar to the orientation of live oysters on intertidal oyster reefs (Grinnell 1974; Stiner and Walters 2008). Mean total available oyster shell substrate per recruitment mat ($\pm$ SE) was 5273 $\pm$ 122 cm (146 $\pm$ 3 cm per shell) (n=200 shells) (Solomon *et al.* 2014). Oyster recruitment mats have been shown to provide suitable substrate for oyster recruitment (Wall *et al.* 2005; Birch and Walters 2012). Oyster recruitment mats were spaced apart equally vertically within the ladder at intervals of 33 cm, between the mean high tide and mean low tide water levels. Ladders additionally supported sediment traps at each level adjacent to the recruitment mats.

At each study site, five oyster ladders were deployed in a row, two meters apart from one another, facing ninety degrees from the shoreline. Ladders were anchored with cinderblocks and rebar and were leveled with one another. Additionally, each mat was vertically aligned with corresponding mats on the other four ladders relative to water level as closely as possible (Solomon *et al.* 2014).

Two sites within the ANERR were used in this study (Figure 2). Both were chosen for their proximity to intertidal oyster reefs and for ease of access. The first site (ANERR) was located beachside of the ANERR Education/Visitor Center in the town of East Point, and was 15 meters from a live intertidal oyster reef (Figure 2). The nearest subtidal oyster reef was the Cat Point oyster bar, 1.5 km SSE of the experimental site. The second site (ASP) was located on the north side of St. George Island near the St. George Island State Park eastern boat ramp in East Cove, and was 10 meters from live intertidal oyster reefs. ANERR and ASP were 9 km east and 21 km southeast from the mouth of the Apalachicola River, respectively.
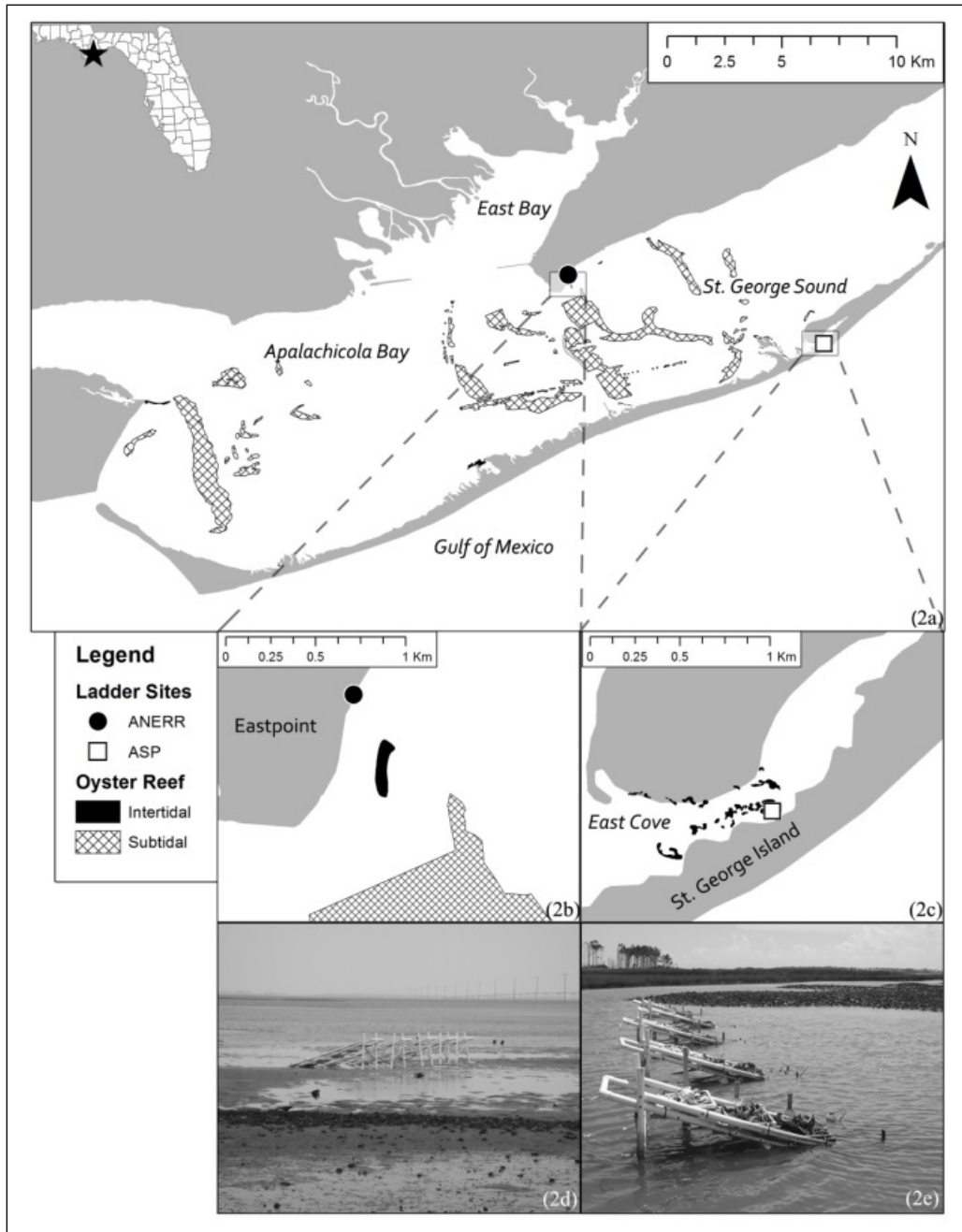
Figure 2. Locations of sites: ANERR (solid circles), ASP (white square), and previously mapped oyster reefs within Apalachicola Bay, Florida. 2b: Inset of ANERR site on the shoreline of Eastpoint, FL nearby to both intertidal and subtidal oyster reefs. 2c: Inset of site within East Cove adjacent to intertidal oyster reefs. 2d: South-southwest view of ANERR oyster ladders, intertidal reef in foreground. 2e: West view of ASP oyster ladders showing intertidal reef in background. (Figure originally from Solomon *et al.* 2014).

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Oyster recruitment mats were deployed on the oyster ladders in June 2012 and June 2013. Trials lasted for twelve months and deployment coincided with annual peak oyster recruitment season in Apalachicola Bay (J. Harper pers. comm.). Monitoring of each recruitment mat occurred at the end of twelve months and included oyster density, mean shell length of live oysters, density of sessile competitors, and oyster shell angle of growth relative to the benthos. Elevation of each oyster mat was recorded by the Coastal Hydroscience Analysis Modeling & Predictive Simulations (CHAMPS) Laboratory at UCF utilizing real time kinematic techniques and GPS equipment.

Collection of sediment occurred monthly for six months from June 2012 to January 2013 via sediment traps attached to oyster ladders (Figure 1). Traps were built from PVC (45.7 cm length, 7.6 cm diameter), the bottom end was capped, and the upper end held a 7.6 cm wide Nalgene funnel that held in place with a PVC coupling. The sediment traps had a 6:1 ratio of length to diameter, within the 5:1 – 10:1 range of recommended ratios to maximize sediment retention (Bloesch and Burns 1980). Funnel traps of this type have been determined to have 65% efficiency (Gardner 1980). Oyster ladders suspended the sediment traps with their openings level to the associated oyster recruitment mat (Figure 1). Five sediment traps were installed on three ladders at each site (15 per site). For sediment collection, each sediment trap was removed from the oyster ladder and sediment was emptied into a plastic container. The sediment was taken to the ANERR laboratory, placed inside a 1300 watt drying oven (Econotherm) at 85°C, and dried to constant weight signaling that there was no additional evaporation occurring. Total monthly weights were measured with a microbalance (Fisher ALF64) accurate to 0.0001g.

Analysis:

Using RStudio (2012), I conducted a series of multiple regressions for each of the response variables (oyster density, oyster length, oyster angle, competitor density, and monthly total sedimentation). I included elevation, site, and year as predictor variables, if applicable, as well as all possible interactions, so that I could evaluate potential site or year effects in addition to elevation. Following this I used AICc to evaluate all combinations of predictor variables listed above as well as quadratic fit for elevation (m). The model with the smallest AICc was chosen as the most plausible model, unless a more simple model with a ΔAICc $\leq$ 4 existed (Burnham and Anderson 2002).

Predictions & Interpretations:

Oyster Density

Based on preliminary data from Solomon, Donnelly, and Walters (2014), I expected oyster density, oyster length, sessile competitor density, and mean total sedimentation to differ significantly with elevation, as a result of variation inundation regime. Specifically, I expected oyster density to peak at intermediate elevations (Figure 3a); this is in keeping with literature which suggests that benefits to intertidal organisms stem from balancing submerged predation threat, with ability to feed, and decreased temperature variability (Dame 1976). Here I expected to see a quadratic relationship between density and elevation, with site not retained as a significant variable.

<u>Oyster Shell Length</u>

Oyster shell length was expected to be inversely related to elevation, as seen with the linear trend in my preliminary experiment (Figure 3b). While oyster density was lower at higher inundations, potentially due to predation, those surviving had the opportunity to spend more time submerged and actively feed, resulting in additional growth. Therefore I expected shell length to have an inverse linear relationship with elevation, with site not retained as a significant predictor variable.
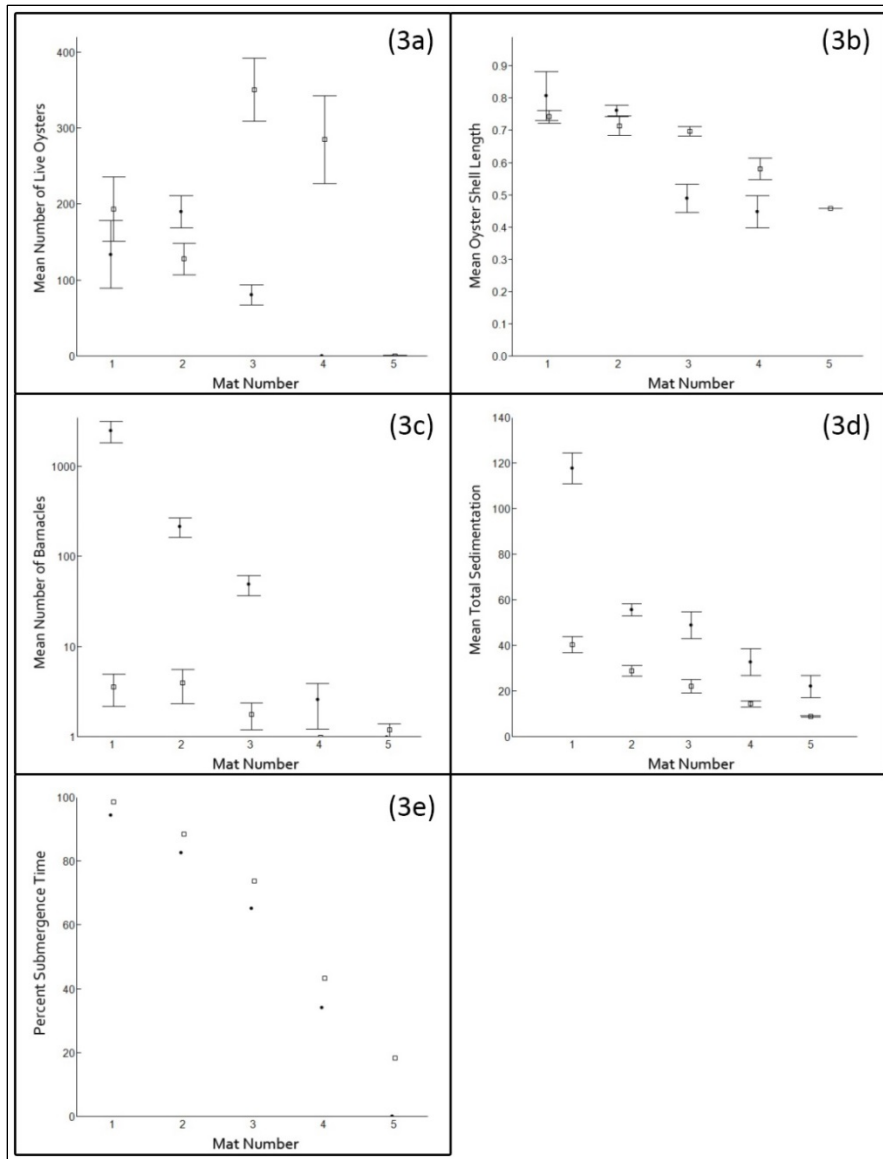
Figure 3.Adapted from Solomon, Donnelly, and Walters (2014). Results of six weeks of oyster recruitment and growth at sites ANERR (solid circles) and ASP (open squares) during June and July 2011. 3a: Mean number of oysters recruited per oyster recruitment mat ± SE by mat number from low to high elevation. 3b: Mean oyster shell length ± SE (cm) by percent submergence; no point appears for ANERR mat 5 as a result of no live oysters at that mat height. 3c: Log of mean number of barnacles recruited per oyster recruitment mat ± SE by percent submergence time. 3d: Total sediment (g) captured by sediment traps ± SE by percent submergence time. 3e: Percent submergence time by mat number; mat 1 was the lowest elevation, while mat 5 represented the highest elevation.

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Oyster Shell Angle of Growth Relative to the Benthos

Preliminary examination of angle of growth relative to the benthos did not result in significance with relation to inundation when mean oyster length was <1 cm during the six week preliminary trial. As a result of an inverse relationship between sedimentation and elevation seen previously (Figure 3d), I expected oysters at lower elevation to exhibit an angle of growth relative to the benthos higher than oysters at higher elevation. This high angle of growth would decrease their likelihood of burial in sediment. I did not expect site to be retained as a significant variable.

Density of Sessile Competitors

Density of sessile competitors showed different trends at each site during preliminary work and these trends were an order of magnitude in difference (Figure 3c). Here, I expected to see high variability between sites, with higher barnacle recruitment at site ANERR than at ASP as seen in the six week preliminary trial. This was postulated to result from variation in hydrology due to presence and absence of shielding land masses (Solomon, Donnelly, and Walters 2014) (Figures 2b, 2c). Additionally, I expected to need to log transform data, due to the order of magnitude differences in recruitment in preliminary work.

Total Sedimentation

I predicted mean total sedimentation to have an inverse relationship with elevation as seen in preliminary research (Figure 3d). I also expected site to be retained as a significant variable, with sediment traps at ANERR collecting more sediment than at ASP.

By utilizing the above information, I made interpretations as to the likely changes that intertidal oyster reefs will undergo as a result of sea level rise. A generalized list of possibilities for intertidal oyster reefs following sea level rise is presented in Figure 4. The sub-figures represent four major general outcomes for intertidal *C. virginica* in Apalachicola Bay, and a representation of a current intertidal oyster reef (Figure 4a): (a) change from intertidal to subtidal (Figure 4b), (b) loss of current intertidal reefs (Figure 4c), (c) shoreward migration of intertidal reefs (Figure 4d), (d) accretion and increase in elevation of intertidal reefs to keep pace with sea level rise (Figure 4e). With any of these generalized outcomes, it would be possible to see additional increases or decreases in density and or mean length of oysters; those extensive possibilities are not outlined in the figure. I did not expect to be able to choose a single outcome as the most likely following sea level rise, however, feasible outcomes and unlikely outcomes should be identified. Additionally, I expected to be able to predict what changes in oyster density and length, if any, will accompany the outcomes.
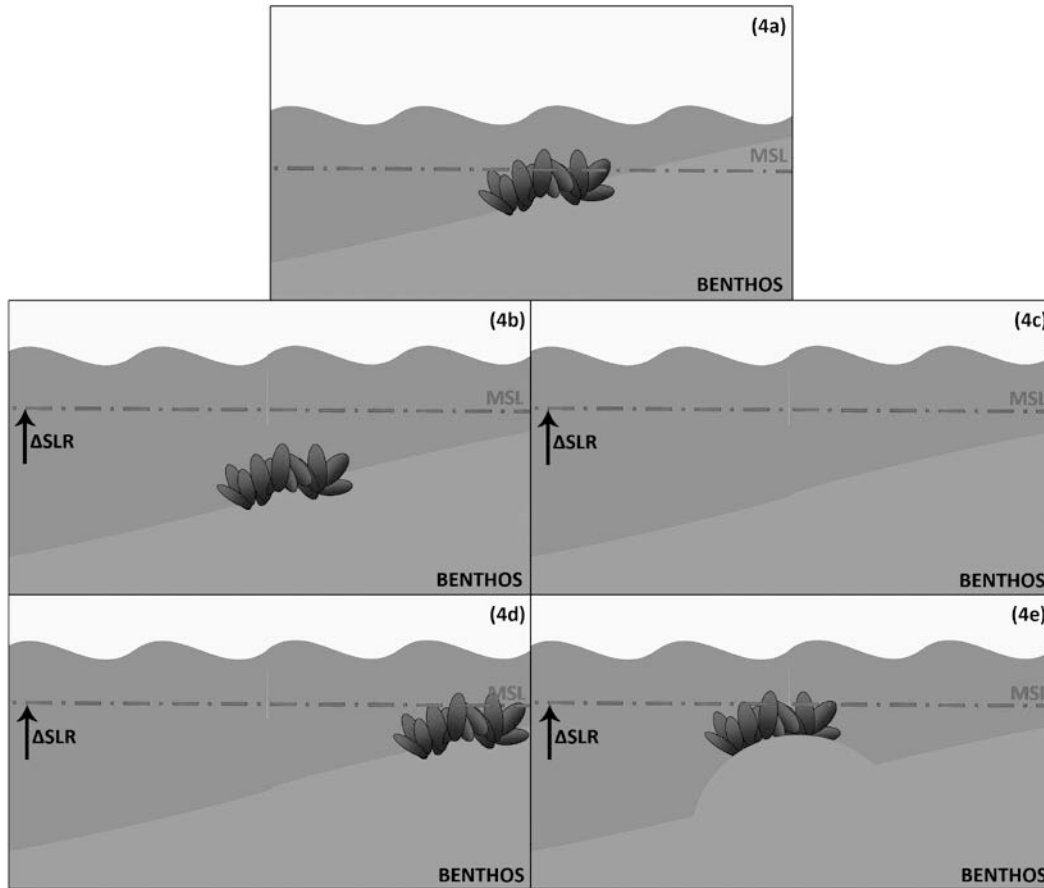
Figure 4. Generalized possible outcomes for intertidal oyster reefs following increase in mean sea level. 4a: Current state of intertidal oyster reef. 4b: Intertidal oyster reefs remain at the same location, effectively becoming subtidal oyster reefs. 4c: Intertidal oyster reefs are lost. 4d: Intertidal oyster reefs move shoreward as oysters continue to recruit and remain within the intertidal zone, this requires appropriate substrate shoreward of current reefs. 4e: High levels of sediment accretion combined with ongoing oyster recruitment results in intertidal oyster reefs remaining in place and gaining elevation to remain intertidal.

Outcome one (Figure 4b), the intertidal reef slowly becomes a subtidal reef, could be retained as a possibility if oysters recruit and survive at the lowest elevations, effectively becoming a subtidal reef. Based on our data this would most likely manifest with decreased oyster density and increased shell length (Figures 3a, 3b). This possibility would not require the addition of settlement substrate (cultch) to current intertidal reefs.

Outcome two (Figure 4c) results in the loss of current intertidal oyster reefs. This possibility can be retained if oysters grown at the lowest elevations have extreme decreases in density to the point of complete loss as a result of either increased predation or burial by increased sedimentation. Our data do not show this outcome as likely since the near subtidal mats did have surviving oyster recruits (Figure 3a).

Outcome three (Figure 4d) is the result of shoreward (upslope) migration of current intertidal reefs to remain intertidal. This possibility requires the presence of oyster recruitment at high elevations on the oyster ladders, as well as the caveat of requiring additional settlement substrate (cultch) shoreward of current reef boundaries. These shoreward areas adjacent to the reefs are currently soft sediment which is not a suitable settlement substrate. Preliminary data showed a sharp decrease in oyster recruits at the highest elevations due to oyster ladder placement, this experiment's oyster ladder placement allowed recruitment up to the mean high water line. Preliminary data therefore do not offer any powerful insight for or against the likelihood of this scenario.

Outcome four (Figure 4e) results from accretion of sediment at a level high enough to increase reef elevation at a pace close to rising sea levels, while not resulting in burial and subsequent death of oysters. Preliminary data show increasing sedimentation levels with increasing depth (Figure 3d). However, this possibility requires a balance is achieved between sedimentation rate and sea level rise, as well as sedimentation rate and oyster survival. Oyster angle will provide insight here, since high oyster angles necessarily create more turbulence which results in additional sedimentation. Therefore, if I see oyster angle of growth is not correlated with elevation, then that would make outcome four an unlikely scenario.

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Results:

      Oyster density exhibited an overall quadratic trend that peaked in the mid to low intidal zone around -0.4 m (NAVD88), as can be seen in the generalized trend (Figure 5). To normalize the distribution of oyster density, a squareroot transformation was used, and uneven variance was addressed by weighting the linear model by elevation.

Model selection by lowest AICc in R resulted in a best model of:

$$sqr(OysterDensity) = Elevation * Year + Elevation^2 * Year \qquad (1)$$

with $p < 2.2 \times 10^{-16}$ and $R^2a = 0.7252$ (Figure 6, Table 1). The model includes individual effects of year, elevation, and year interaction with the quadratic. The dependent variable histogram, AIC Table of the top five models, parameter estimates of the chosen model, and residual plot of the chosen model are included in Appendix I.
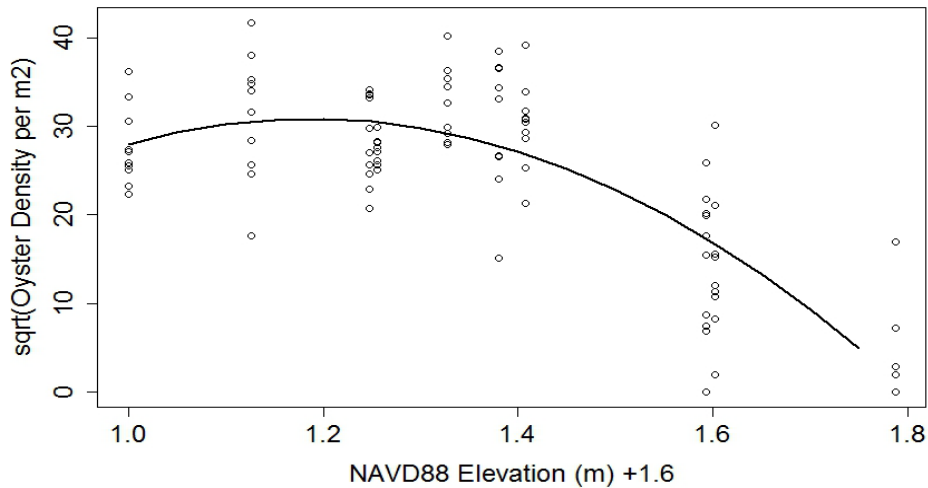
Figure 5. A quadratic plot of the relationship between elevation and oyster density that does not include effects of site or year.
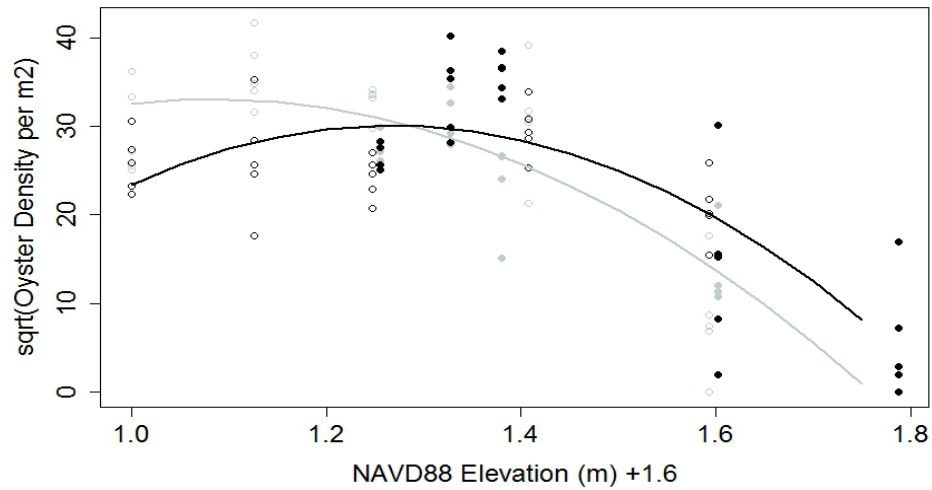
Figure 6.Plot of selected model, m67, predicting mean oyster shell density as a function of elevation. Year one is in grey, and Year two is in black. Sites are pooled due to lack of effect.

Table 1.ANOVA Table for selected model, m67, predicting mean oyster density as a function of elevation. N_E abbreviation represents linear elevation, and N_E2 represents the elevation quadratic.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
N_E	1	9121.8	9121.8	183.4621	2.20E-16
Year	1	87.5	87.5	1.7588	0.18816
N_E2	1	2653.4	2653.4	53.3662	1.13E-10
N_E:Year	1	673.9	673.9	13.5547	0.0004
Year:N_E2	1	47.5	47.5	0.9551	0.33108
Residuals	89	4425.1	49.7		
Total	94	17009.2			

Mean shell length of live oysters aggregated by site and year shows an almost linear negative correlation between elevation and mean shell length, with the shells at the lowest elevations being the largest after 12 months (Figure 7). Oyster shell length exhibited a normal distribution, but uneven variance was addressed by weighting the linear model by elevation. Model selection by lowest AICc in R resulted in a best model of:

$$OysterShellLength = Elevation * Year * Site + Elevation^2 * Site * Year \qquad (2)$$

with $p < 2.2 \times 10^{-16}$ and $R^2 a = 0.8833$ (Figure 8, Table 2). The model includes individual effects of

year, site, elevation, and quadratic elevation, as well as year site interactions, elevation year

interactions, elevation site interactions, site quadratic elevation interactions, and year site

elevation interactions. The year site interactions are apparent in the detailed plot which includes

both factors, it shows a change in inflection between sites, and slope between years. The

dependent variable histogram, AIC Table of the top five models, parameter estimates of the

chosen model, and residual plot of the chosen model are included in Appendix I.

Figure 7. A quadratic plot of the relationship between elevation and mean shell length of live oysters. The plot does not include effects of site or year.

Figure 8. Plot of chosen model, m10, predicting mean oyster shell length as a function of elevation. Year one is in grey, and Year two is in black. Solid lines represent site ANERR, and dotted lines represent site ASP.

Table 2. ANOVA table of selected model, m10, predicting mean oyster shell length as a function of elevation. N_E abbreviation represents linear elevation, and N_E2 represents the elevation quadratic.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
N_E	1	9645.1	9645.1	460.4867	2.20E-16
Year	1	1.4	1.4	0.0658	0.79826
Site_ID	1	20.9	20.9	0.9989	0.32071
N_E2	1	7.5	7.5	0.3601	0.55021
N_E:Year	1	2.4	2.4	0.1148	0.73565
N_E:Site_ID	1	406.5	406.5	19.4076	3.37E-05
Year:Site_ID	1	927.5	927.5	44.2813	3.72E-09
Year:N_E2	1	376.9	376.9	17.9952	6.11E-05
Site_ID:N_E2	1	459.6	459.6	21.9446	1.19E-05
N_E:Year:Site_ID	1	344.2	344.2	16.4349	0.00012
Year:Site_ID:N_E2	1	20.5	20.5	0.9766	0.32615
Residuals	77	1612.8	20.9		
Total	88	4267.2			

Oyster shell angle of growth relative to the benthos aggregated by site and year shows an almost linear negative correlation between elevation and mean angle of growth, with shells at the

lowest elevations growing at the highest angles (nearer to vertical, $> 50°$) and the highest

elevations showing the lowest angles (nearer to horizontal or parallel to the benthos, $< 30°$)

(Figure 9). Oyster shell angle exhibited a normal distribution; uneven variance was addressed by

weighting the linear model by elevation. Model selection by lowest AICc in R resulted in a best

model of:

$$OysterAngle = Elevation + Site \qquad (3)$$

with $p < 4.579\text{x}10^{-5}$ and $R^2a = 0.1889$ (Figure 10, Table 3). The model includes elevation and

site (Figure 11). The detailed plot shows the varied slope between sites, and does not include

year since it was not retained as a predictor variable. The dependent variable histogram, AIC

Table of the top five models, parameter estimates of the chosen model, and residual plot of the

chosen model are included in Appendix I.

Figure 9. A linear plot of the relationship between elevation and mean oyster angle of growth
form the benthos, the plot does not include effects of year.
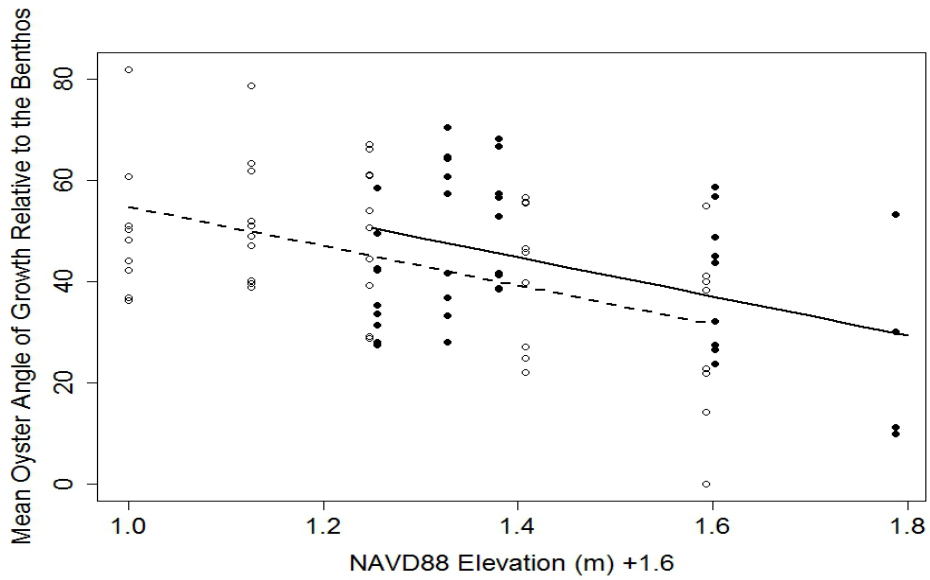
Figure 10. Plot of chosen model, m6, predicting angle of oyster growth relative to the benthos as a function of elevation. Solid lines represent site ANERR, and dotted lines represent site ASP. Years are pooled due to lack of effect from year.

Table 3. ANOVA table of selected model, m6, predicting angle of oyster growth relative to the benthos as a function of elevation. N_E abbreviation represents linear elevation.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
N_E	1	5914.2	5914.2	19.8345	2.53E-05
Site_ID	1	793.4	793.4	2.6608	0.1065
Residuals	86	25643.3	298.2		
Total	88	32350.9			
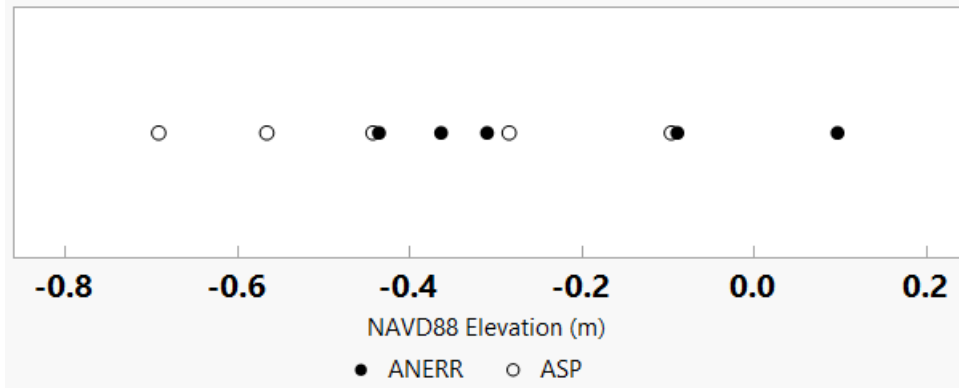
Figure 11. A plot of elevations sampled at each site, showing overlap between -0.44 m to -0.1m.

Sessile competitors that were visible were represented overwhelmingly by barnacles

(*Balanus eburneus, Balanus amphitrite*) (>99%). Barnacle densities varied by over 5 orders of

magnitude between some elevations and sites, with the majority of barnacles appearing at site

ANERR. A log transformation was employed to get closer to a normal distribution, after other

transformations were used as well as poisson and quasipoisson distributions. However, these did

not result in improved distributions or fit. An aggregated quadratic fit of the data combined by

site and year show a barnacle minimum in the mid-intertidal zone around -0.2 m. However, this

is an artifact of the high variation between sites and years (Figure 12). A detailed plot shows a

minor version of that trend at site ASP, and a very different trend at site ANERR where barnacle

density was negatively correlated with elevation. Model selection by lowest AICc in R Resulted

in a best model of:

$$log(BarnacleDensity) = Elevation + Elevation^2 + Site + Year \qquad (4)$$

with $p = 9.072 \times 10^{-13}$ and $R^2a = 0.4879$ (Figure 13, Table 4). The model includes elevation, the

quadratic, site and year. The dependent variable histogram, AIC Table of the top five models,

parameter estimates of the chosen model, and residual plot of the chosen model are included in
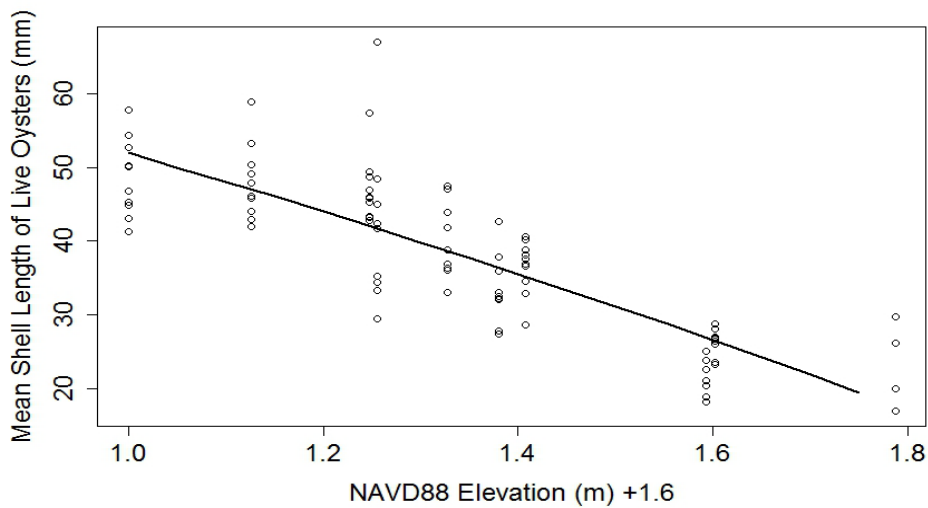
Appendix I.
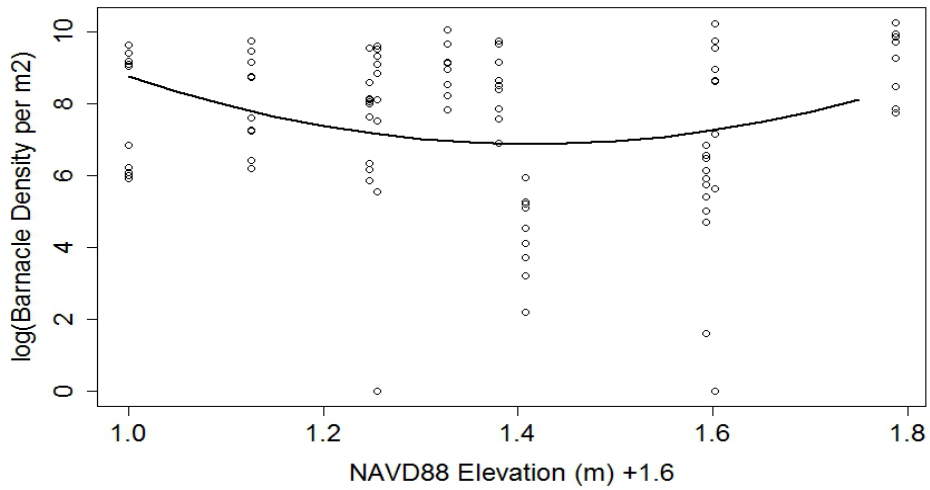
Figure 12. A quadratic plot of the relationship between elevation and barnacle density that does not include effects of site or year.
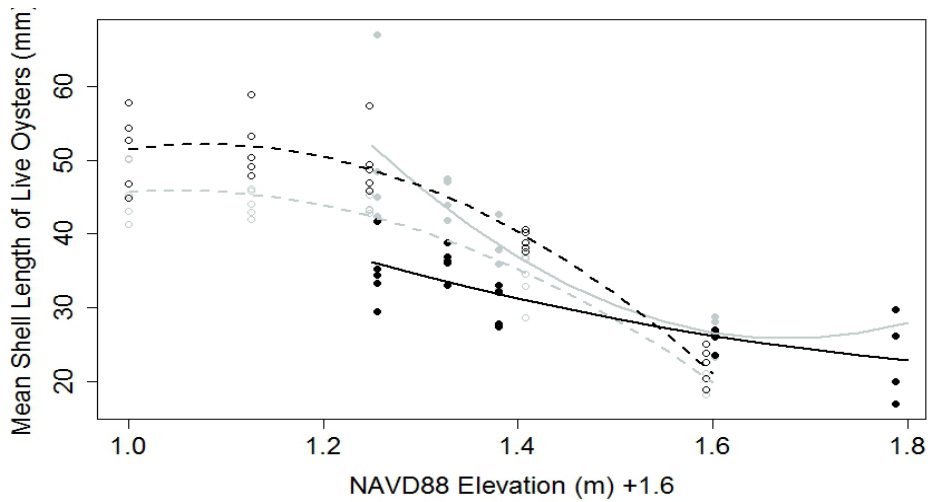

.
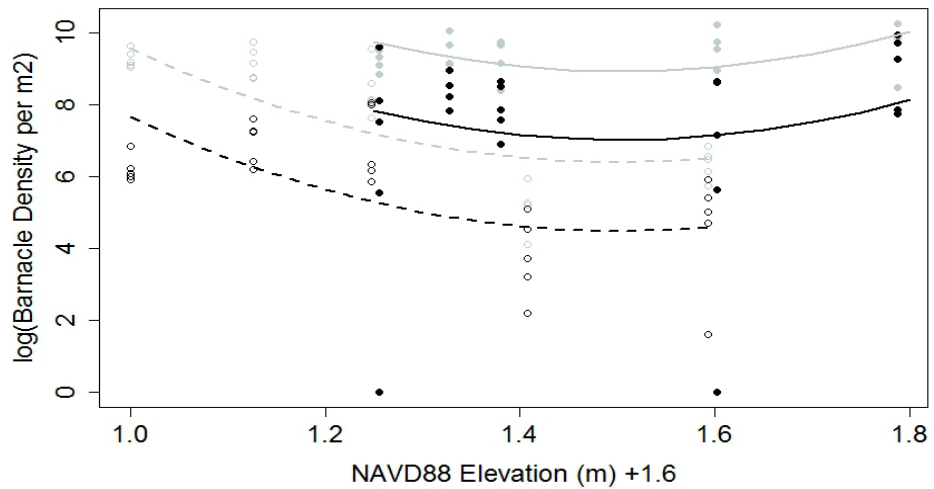
Figure 13. Plot of chosen model, m52, predicting barnacle density as a function of elevation. Year one is in grey, and Year two is in black. Solid lines represent site ANERR, and dotted lines represent site ASP.

Table 4. ANOVA Table for selected model, m52, predicting barnacle density as a function of elevation. N_E abbreviation represents linear elevation, and N_E2 represents the elevation quadratic.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
N_E	1	0	0	0.0001	0.99169
Year	1	104.59	104.586	29.0404	5.64E-07
N_E2	1	47.45	47.448	13.175	0.00047
Site_ID	1	171.85	171.846	47.7167	6.79E-10
Residuals	90	324.12	3.601		
Total	94	648.01			

Total monthly sedimentation varied by an order of magnitude between the two sites with ANERR receiving the majority of the sediment (Figure 14). Both sites showed a negative correlation between elevation and sedimentation, with the lowest elevations receiving the most sediment. A log transformation was used on the sediment (g) to more closely approximate a normal distribution. A detailed plot shows the difference between the two sites. Year was not used as a variable since all sediment collection occurred within a 6-month period in year one. After weighting by elevation to account for uneven variance, model selection by lowest AICc in R resulted in a best model of:

$$log(TotalSedimentation) = Elevation + Site \qquad (\,5\,)$$

with $p < 2.69\text{x}10^{-14}$ and $R^2a = 0.6659$ (Figure 15, Table 5). The model includes site and elevation. The dependent variable histogram, AIC Table of the top five models, parameter estimates of the chosen model, and residual plot of the chosen model are included in Appendix I.
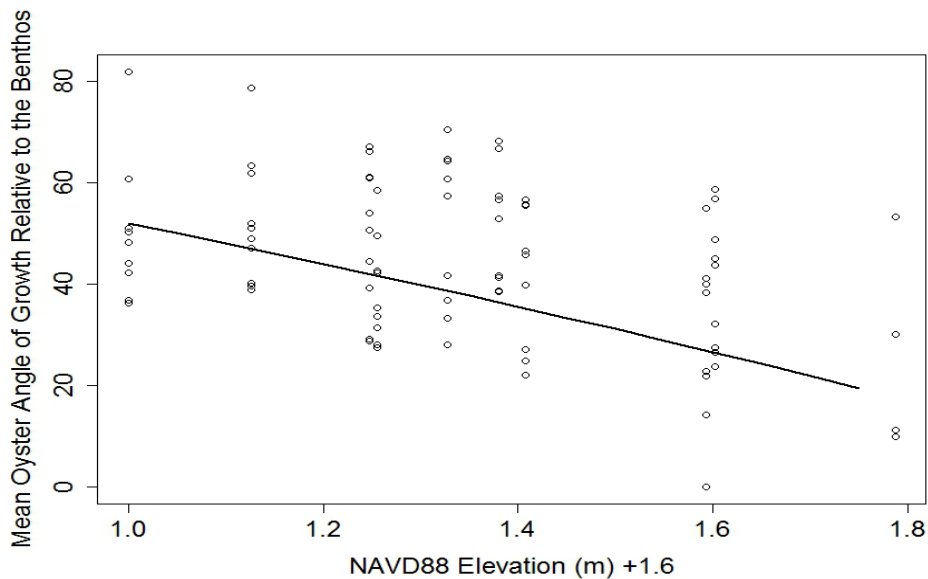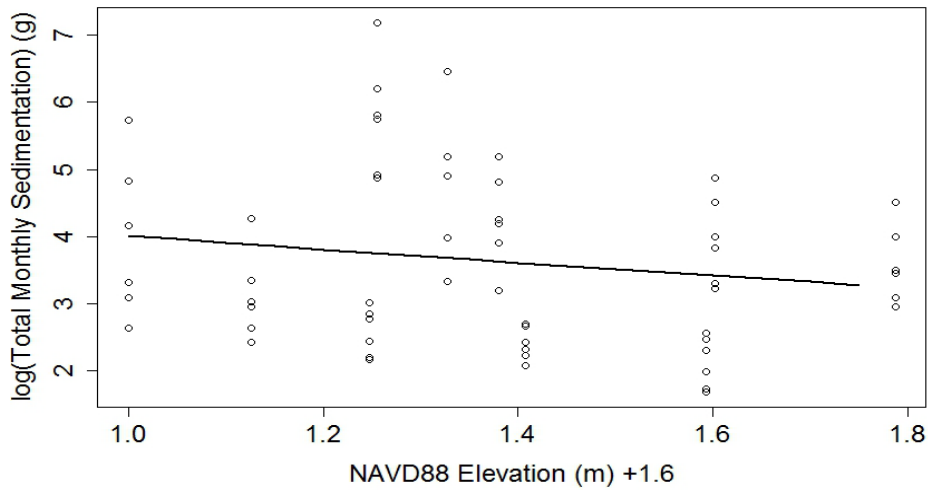
Figure 14. A linear plot of the relationship between elevation and mean total sedimentation.
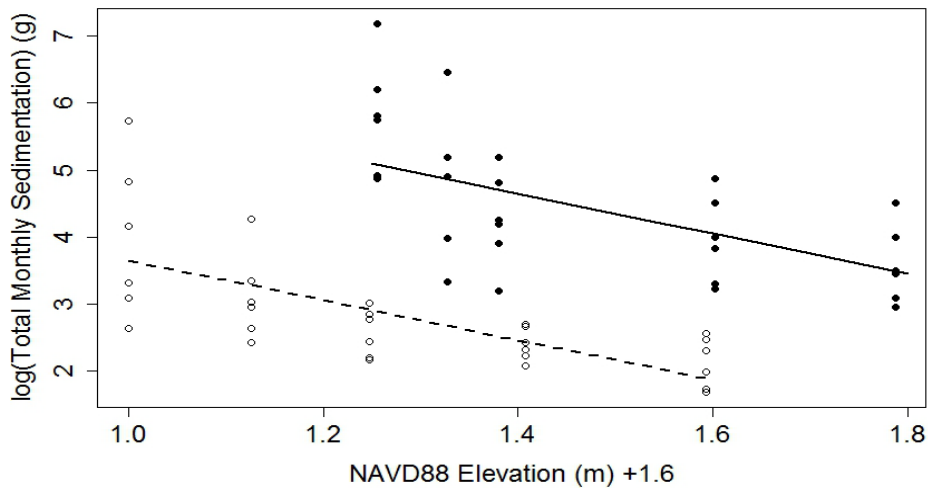
Figure 15. Plot of chosen model, m8, predicting total sedimentation as a function of elevation. Solid lines represent site ANERR, and dotted lines represent site ASP.

Table 5. ANOVA table of selected model, m8, predicting total sedimentation as a function of elevation. N_E abbreviation represents linear elevation, and N_E2 represents the elevation quadratic.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
N_E	1	3.93	3.93	5.273	0.02536
Site	1	80.754	80.754	108.338	8.49E-15
Residuals	57	42.487	0.745		
Total	59	127.171			

Discussion:

Oyster density, oyster shell length, and oyster shell angle of growth relative to the benthos significantly responded to elevation. Two other factors, barnacle recruitment and sedimentation, both associated with indirect effects on oyster recruitment and growth, also had significant response to elevation. These responses resulted from the direct impact of changing inundation as well as a multitude of other indirect effects including predation, competition, and sedimentation, all associated with the changed inundation.

As expected, oyster density had a quadratic response to elevation peaks at about 1.2 m NAVD88 elevation when both sites are included. Both effect of site and year are included in the model. With their inclusion, we continue to see a quadratic response of oyster density to elevation, but with a clear interaction between site and year. Oyster density at intermediate to low elevations increased at site ANERR from the 2012-2013 seasons to the 2013-2014 seasons, while they decreased at ASP during the same time periods. These lower than intermediate elevations are representative of sea level rise < 0.5m, and while there was variation between years at both sites with regard to oyster density, the general shape of the function stayed the same. Specifically, the peak oyster density continued to be at intermediate elevations.

The reasons why intertidal oysters grow in the intertidal are well studied. Dame (1976) found that intertidal oysters in the southeastern United States remain intertidal as a response to local predation, since many subtidal oyster predators utilize the intertidal zone, and then retreat with the outgoing tide (Dame and Patten 1981). These predators include mud crabs (*Panopeus sp.*) and blue crabs (*Callinectes sp.*), both voracious predators of oysters that were found on

submerged oyster recruitment mats in our preliminary study and this study (Seed 1980, Grabowski and Powers 2004, Solomon, Donnelly, Walters 2014). The peak in oyster recruitment in the mid-low elevations within the intertidal zone likely results from a balance between needing to spend time inundated to feed, and predation risk from these and other subtidal predators when submerged.

The differences in oyster density between sites may be driven by the uneven distribution of sampling by elevation between the two sites, with ladders at site ANERR having elevation 0.2 m above site ASP (Figure 11). Additionally, there is likely variation in inundation regimes at the two sites as a result of their locations within the bay. This could also have contributed to the differences in oyster density between the sites in an additive interaction with variation in elevation. Future studies of this kind should include additional sites with their elevations more perfectly aligned, or utilize hydrological modeling to use inundation as a predictor variable rather than elevation.

Oyster shell length initially appeared to show the hypothesized linear increase with decrease in elevation (Figure 7), however the selected model and detailed plots show a quadratic relationship between elevation and mean shell length (Figure 8). This overall trend of increasing shell length with depth fits the life history of oysters which require submergence to filter-feed and thus to grow. Identifying the elevation level within the intertidal associated with larger oysters has important repercussions since larger oysters are more efficient filter feeders and have a higher reproductive output (Walne 1972, Choi *et al.* 1993). It is important to note that the elevations with the largest mean shell length were not the inundations with highest oyster density, so there is a tradeoff between oyster size, recruitment and survival.

The difference in oyster shell length between sites is clear with the change in sign of the quadratic, for each with site ANERR showing a positive quadratic, and ASP showing a negative quadratic. Mean shell length showed differential variation between sites across years (the two growing seasons), with site ANERR having lower overall mean shell length in the second season, and site ASP showing increased mean shell length. Interestingly, the increased shell length corresponded with decreased density at the same site and vice versa. This may indicate that variation in changes of mean shell length after one year of recruitment and growth may be the result of variation in competition.

Oyster shell angle of growth relative to the benthos had a significant response to variation in elevation as hypothesized, since shell lengths reached a high enough mean for the oysters to differentiate their angle of growth from the angle of their substrate. The overall trend described by a simple quadratic appeared almost linear, with low elevation being associated with high angle and high elevation being associated with low angle (Figure 9). The model and detailed plot showed no effect of year, but an effect of site and site interactions with elevation. The interaction is particularly clear from the intersecting quadratic regression lines.

This variation in oyster angle of growth relative to the benthos can be interpreted two ways. First, oysters may have a plastic response in growth angle to varying inundation resulting from their elevation within the intertidal. Specifically, oysters in the low intertidal grew at higher angles of growth relative to the benthos, which would make death by burial in sediment less likely and increase their individual fitness. Oysters in the high intertidal zone would grow at low angles to maximize their time spent inundated and filter feeding. Moore (1934) showed that limpets regulated their drying in-between inundation events by adjusting their shell growth and

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length as a response to elevation within the intertidal zone, so adjustment of shell growth within the intertidal is not a novel concept. The second interpretation becomes more obvious when the selected model is utilized to plot separate regressions for each site. In this case, peak angles coincide with peak oyster densities at elevations around 1.2 m at site ASP; the trend also occurs to some degree at site ANERR around 1.4 m elevation. This would indicate an increase in oyster angle of growth as a response to increased oyster density, which is also an intuitive interpretation. Further work is needed to identify whether oyster angle of growth relative to the benthos is a response to density or elevation within the intertidal zone.

Barnacle density showed a positive quadratic response to elevation after log transformation. A quadratic plot of the aggregated data showed only a slight increase in barnacle density with depth (Figure 12). Site ANERR showed an overall higher concentration of barnacles than site ASP in both years (Figure 13), in keeping with the predictions based on preliminary data of Solomon, Walters, and Donnelly (2014).

Site ANERR also showed an almost flat positive quadratic regression, indicating high barnacle recruitment in both the high and low intertidal zones, with moderate recruitment in the intermediate intertidal zone. Site ASP showed increasing barnacle recruitment with decreasing elevation in keeping with data from the preliminary six-week study. Both sites showed a two order of magnitude decreased barnacle recruitment across all elevations. While the selected model was highly significant, it does not readily explain barnacle recruitment, but rather indicates differences in trends between both years and sites. Since barnacles are an important competitor of oysters for settlement space (Bushek 1988, Wall *et al.* 2005), they are still of

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concern, but additional work would be required to predict densities of barnacle recruitment in the intertidal zone.

Total sedimentation was expected to increase as a quadratic with decreased elevation, and vary between sites based on preliminary work. As predicted the log of total sedimentation in grams increased with decreased elevation, with site ANERR having much higher sedimentation than site ASP. These results are consistent with the 6-week study by Solomon, Donnelly and Walters (2014), and their findings which suggest that site ANERR may have higher sedimentation as a result of being 12 km closer to the mouth of the Apalachicola River than site ASP. The paper also acknowledged additional protection afforded to site ASP from land resulting in decreased fetch and decreased resuspsension of surficial sediments during storm winds (Chanton and Lewis 2002, Solomon, Donnelly, Walters 2014). These sediment levels can have important effects on oysters through burial of available substrate, and abrasion by sediment particles (Mackenzie 1983, Lenihan 1999, Wall *et al.* 2005). By showing variation in sedimentation across the elevation gradient of the intertidal, we would predict these effects to be more pronounced for oysters in the low intertidal, particularly burial.

With insight into the response of these five factors with respect to elevation within the intertidal zone, we can revisit the potential outcomes discussed in our predictions (Figure 4). Outcome (a) (Figure 4b), suggesting that intertidal reefs slowly becoming subtidal, remains a possible outcome for intertidal reefs in the areas we studied. It remains a viable outcome in Apalachicola Bay because oyster density did not drop off at low elevations, never falling below 400 live oysters per m^2. Furthermore, reefs remaining in place would not require additional intervention. If this outcome manifests it would likely be associated with increased oyster shell

length and decreased oyster density. Outcome (b) (Figure 4c), the loss of intertidal reefs, can be rejected as a possibility within the range of elevation change examined in this study (~0.4 m), as oyster recruitment and survival continued at the lowest elevations. Outcome (c) (Figure 4d), the shoreward (upslope) migration of current intertidal reefs to remain intertidal also remains a possibility, with some anthropogenic caveats. It requires continued oyster recruitment at near mean high water on the oyster ladders, which was observed up to ~0.4 m above the current intertidal reef elevation, although at decreased levels. Caveats would include the requirement of a natural upward slope shoreward of intertidal oyster reefs without hard armoring or development and the addition of oyster cultch early enough to allow recruitment, but not so early as to be first buried by sedimentation. Outcome (d) (Figure 4e), high levels of sediment accretion combined with ongoing oyster recruitment results in intertidal oyster reefs remaining in place and intertidal at a higher elevation than they currently reside, cannot be discarded. This outcome's continued possibility comes together as a synthesis between sedimentation increasing with low elevation, and oyster angle increasing with low elevation within the intertidal. With this data we would expect that, as sea level rises, sedimentation at the newly low areas of the reef will increase, as will the length the oysters grow. Due to the gregarious nature of oysters, this may allow reefs to increase in elevation.

CHAPTER 3: DETERMINING THE RESPONSE OF OYSTER LARVAL SETTLEMENT TO EXPOSURE TO SUSPENDED SOLIDS PRESENT IN APALACHICOLA BAY

Methods:

To determine the response of oyster laval settlement to varying grain sizes of suspended solids present in Apalachicola Bay, I combined grain size data from sediment traps on oyster ladders (Figure 1), with laboratory oyster larval settlement experiments. Sediment collected over six months during the oyster ladder experiment was sieved into its grain size categories by ATSM standards into seven size classes: <63µm, 63-125 µm, 125-250 µm, 250-500 µm, 500-2000 µm, 2000-4000 µm and >4000 µm. Mass of each grain size class was determined for each sample by weighing on a microbalance (Fisher ALF64) accurate to 0.0001g.

Grain sizes of 2000-4000 µm and >4000 µm were eliminated from experiments since they require flow speeds of over 50 cm/s to erode and transport, and these were not speeds achievable with laboratory techniques used (Hjulstrom 1935). Despite their large size, they represented only 1% and 0.2%, respectively, of the total mass of sediment collected.

A preliminary multiple regression was performed with elevation as an independent variable, and logit transformed percent composition by mass of each of five grain sizes (<63µ, 63-125 µ, 125-250 µ, 250-500 µ, 500-2000 µm). Percent of total composition from each grain size was found to vary significantly with elevation at each site $p < 0.0001$ in all cases.

All oyster larval settlement experiments examining effects of suspended sediments took place in eleven recirculating flow tanks (volume: 80L) at a flow speed of 5 cm/s tank (Wall *et al.* 2005). By using the 5 cm/s flow speed used by Wall *et al.* (2005), we can compare our results

with previous experiments, indicating negative correlation between suspended sediment and oyster settlement. Flow tanks produced by Fish Tanks Direct were based on the flow tank design in Tamburri *et al.* (1996). The settlement zone of the flow tank measured 25.4 cm wide by 55.9 cm long and held twelve disarticulated oyster shells. Oyster shells were allowed to develop a biofilm over 14 days in an aquarium in 35 ppt saltwater (25% Mosquito Lagoon, FL, 75% Artificial Instant Ocean™). In previous oyster settlement studies, Wall *et al.* (2005) and Boudreaux *et al.* (2006) placed shells in Mosquito Lagoon for 14 days to develop a biofilm. Mean total available oyster shell substrate per twelve shells (± SE) was 877 ± 114 cm. Water movement was controlled by a motorized acrylic paddle wheel attached to a geared 12V DC motor. Aquariums were located at the University of Central Florida (UCF) Biology Field Building.

The experiment investigated the effects of individual grain sizes at both high and low concentrations. Treatments included low and high total suspended solids (TSS) concentrations (54.3 mg/L, 165 mg/L), and five grain size classes (<63μ, 63-125 μ, 125-250 μ, 250-500 μ, 500-2000 μ). Low and high sediment concentrations for Apalachicola Bay were obtained from Chen *et al.* (2009) and represented normal storm TSS, and extreme high storm TSS during Hurricane Frances. This resulted in 10 treatment combinations, as well as a diagnostic control with no sediment. Each treatment combination and diagnostic control were replicated 4 times for a total of 44 runs.

Oyster larvae were obtained from Research Aquaculture, Inc. on the day of the trials and transported to UCF in aerated 35 ppt saltwater. Larvae were observed under a dissecting

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microscope to confirm that over 50% of the larvae were visibly active (swimming or crawling).

Flow tanks were filled before each trial with 35 ppt artificial saltwater (Instant Ocean™), the

same salinity from which larvae were cultured and shells developed biofilm. Paddle wheels were

brought to speed after filling, and before shells were placed into the tank. Just before each trial,

twelve haphazardly chosen oyster shells were placed into the settlement zone of the tank, and the

treatment sediment was poured over the surface of the settlement zone. A run began when oyster

larvae were added to the flow tank by being poured in slowly (5 seconds) from a beaker, and

ended after sixty minutes (Wall *et al.* 2005).

Following each run, shells were removed from the flow tanks and allowed to dry. All

were then examined under a dissecting microscope to quantify settled oyster larvae. Larvae were

considered settled if their foot was attached to the substrate shell (Turner *et al.* 1994). Flow tanks

were cleaned with deionized water and dried between each trial. Following the counting of

settled larvae, shells were photographed on a copy stand and Image-J was utilized to determine

total available substrate for each of the runs. Oyster larval settlement was standardized by

dividing the number of settled larvae by total available substrate. Using R, AICc model selection

was used to determine the best independent variables for predicting larval settlement per unit

area.

Predictions:

Although previous research showed effects of sedimentation with much higher mixed

grain size sediment concentrations 8 g/L and 16 g/L (Wall *et al.* 2005, Boudreaux *et al.* 2006), I

hypothesized a decrease in larval settlement with increased sediment loads using 54.3 mg/L and

165 mg/L. With respect to grain size, I hypothesized smaller grain sizes would have the strongest effect of preventing settlement, since by volume they will be both more likely to stay in suspension and more numerous, therefore the most likely to interact with the larvae.

Results:

Larval settlement in the flow tanks reached a minimum with the <63µm sediment, followed by 63µm, 125µm, 250µm, and 500µm (Figure 16). Concentration of sediment did not show an effect between the concentrations tested. A squareroot transformation was used on oyster larval settlement per cm^2 to approximate a normal distribution. Model selection by lowest AICc in R resulted in a best model of:

$$sqroot(SettledSpatPermm2) = Size \qquad (6)$$

with p < 0.02909 and R2a = 0.1744 (Figure 16. Table 6). The model included only grain size. The dependent variable histogram, AIC Table of the top five models, parameter estimates of the chosen model, and residual plot of the chosen model are included in Appendix I. Model residuals were less than ideal, showing heteroscedasticity despite attempts to correct with multiple transformations; this is probably an artifact of a small sample size. A Tukey's post hoc test differentiated only the <63 µm size range from the >500 µm size range, with the <63 µm resulting in less settlement than the >500 µm.
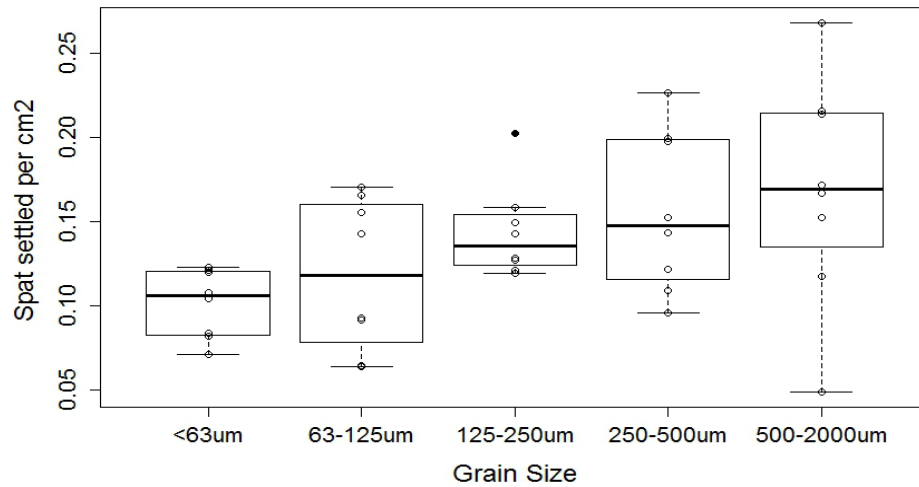
Figure 16. Box plot of chosen model for predicting oyster larval settlement when exposed to varying sizes of sediment. Solid lines represent site ASP, and dotted lines represent site ANERR.

Table 6. ANOVA table of selected model, m3, for predicting oyster larval settlement when exposed to varying sizes of sediment.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
Size	4	0.0244	0.006092	3.06	0.02909
Residuals	35	0.0697	0.001991		
Total	39	0.094			

Discussion:

The model selected by lowest AICc resulted in a single term of grain size which

represented grain size range. The low and high concentrations which represented storm and

hurricane levels of TSS in Apalachicola Bay did not have an effect. While these were much

lower than the concentrations tested by Wall *et al.* (2005) and Boudreaux *et al.* (2006), it

suggests that, in Apalachicola Bay, sediment concentration alone within normal storm ranges

was not enough to decrease settlement. However, the earlier studies did not separate or test

specific grain sizes, and grain sizes of less than <63 µm which may be eroded by flow speeds

over 1 m/s, but require a drop to below 0.1 cm/s to re-deposit. This means that following a storm,

the most detrimental grain size range are the smallest particles which take the longest to leave

suspension. However, because of consolidation resulting from high packing efficiency, these

particles will also resist re-suspension once settled. While this data make sense conceptually, this

experiment should be revisited either removing concentration as a factor or increasing number of

replicates to increase power and potentially be able to better differentiate specific effects on

larval settlement as a function of grain size.

CHAPTER 4: CONCLUSIONS

In the face sea level rise, it seems that intertidal oyster reefs in Apalachicola Bay are not in danger of complete loss. In the simplest terms, looking at new oyster recruitment within the intertidal under future sea level rise is as simple as decreasing elevation on the oyster ladder equal to the increase in sea level.

However, depending on which possible outcome(s) for intertidal oyster reefs occur, reefs may become subtidal, migrate shoreward, or rise in elevation remaining intertidal. Each of these possibilities has potential for associated changes in oyster density and mean shell length, some have the added caveats of pre-laying cultch, or removing hard armoring. Each possibility also has the potential for change in the ecosystem services provided by intertidal oyster reefs, as well as varying commercial value. Additional research is needed to identify the likelihood of each of these possible outcomes in Apalachicola Bay, and to understand the economic and biological ramifications in detail.

In addition to sea level rise which will have direct impact on all the responses studied with the oyster ladder, we will also have indirect effects resulting from climate change. One of these effects, changing storm frequency and intensity, may have additional impacts on oyster recruitment through the suspension of sediment in bay waters. Information we glean, such as this information on relative effects of sediment grain sizes in suspension, can lead to making more informed predictions about future storm events. By combining this information with sediment transport models during storms and river discharge predictions, detrimental effects to oyster larvae can be identified, particularly during Apalachicola Bay's peak oyster recruitment season

in mid-summer. This would be useful for assessing future stocks when allowing for changes in storm intensity and frequency. Additionally, the most detrimental class of sediment grain size is relevant to managers of the upstream Jim Woodruff Dam, which has limited control over the TSS of its output water.

The oyster population crash that occurred in Apalachicola Bay in 2012, during the first year of this study, further increases the importance of this topic. Following the crash, a new harvesting pressure was placed on intertidal oyster reefs in Apalachicola Bay, which historically were not harvested. There was, however, no harvesting from the oyster ladders. While oyster recruitment mats supply ideal substrate, this study provides insight to what unharvested intertidal oyster growth may look like with supplied substrate. This information can be utilized to produce idealized specifics on density and lengths of intertidal oysters to be incorporated into future habitat suitability modeling efforts in order to make them more relevant to managers that are focused on sustainable harvesting.

With shellfish habitat on the decline worldwide, it is important to work to conserve as much remaining habitat as possible. Conservation is especially important in the case of intertidal reefs in Apalachicola Bay, which already account for only ~6% of reef coverage. By considering possible outcomes for intertidal reefs, we can better prepare for future change, and be better equipped to meet our conservation goals.

APPENDIX:
MODEL SELECTION

Oyster Density

Figure 17. Histogram of squareroot transformed oyster density per m^2.

Table 7. AIC Table of top 5 models and null model predicting squareroot transformed oyster density per m^2.

#	Model	AICc	dAICc	df	weight
m10	sqrSpat~N_E*Year*Site_ID+N_E2*Year*Site_ID	618.7	0	13	0.7349
m67	sqrSpat~N_E*Year+N_E2*Year	621.4	2.7	7	0.1948
m24	sqrSpat~N_E*Year+N_E2*Year+Site_ID	623.5	4.8	8	0.0682
m41	sqrSpat~N_E+Site_ID+N_E2+Year*Site_ID	631.2	12.5	7	0.0014
m52	sqrSpat~N_E+Year+N_E2+Site_ID	633.1	14.4	6	<0.001
m0	Null	726.1	108.4	2	<0.001

Table 8. Parameter estimates of m67 predicting squareroot transformed oyster density per m^2.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-51.42	32.05	-1.604	0.11216
N_E	156.07	46.16	3.381	0.00107
Year2	-69.56	44.45	-1.565	0.12121
N_E2	-72.09	16.33	-4.415	2.83E-05
N_E:Year2	82.36	63.81	1.291	0.20015
Year2:N_E2	-21.98	22.5	-0.977	0.33108
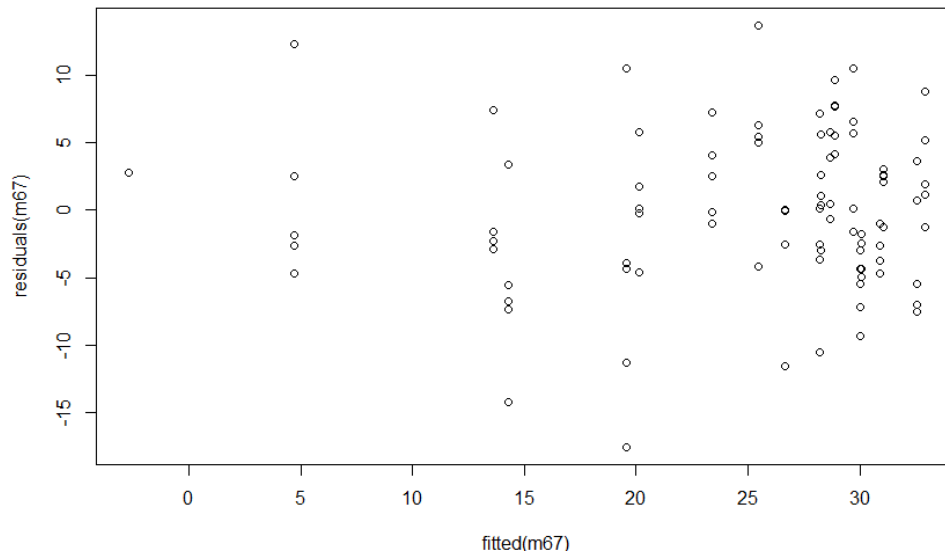
Figure 18. Residuals of m67, predicting squareroot transformed oyster density per m^2.

Barnacle Density
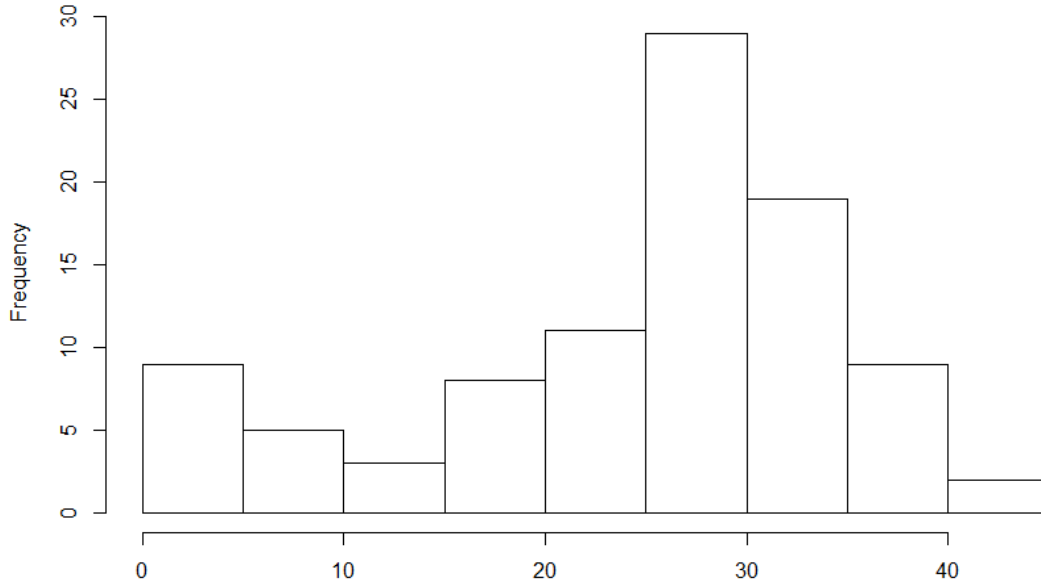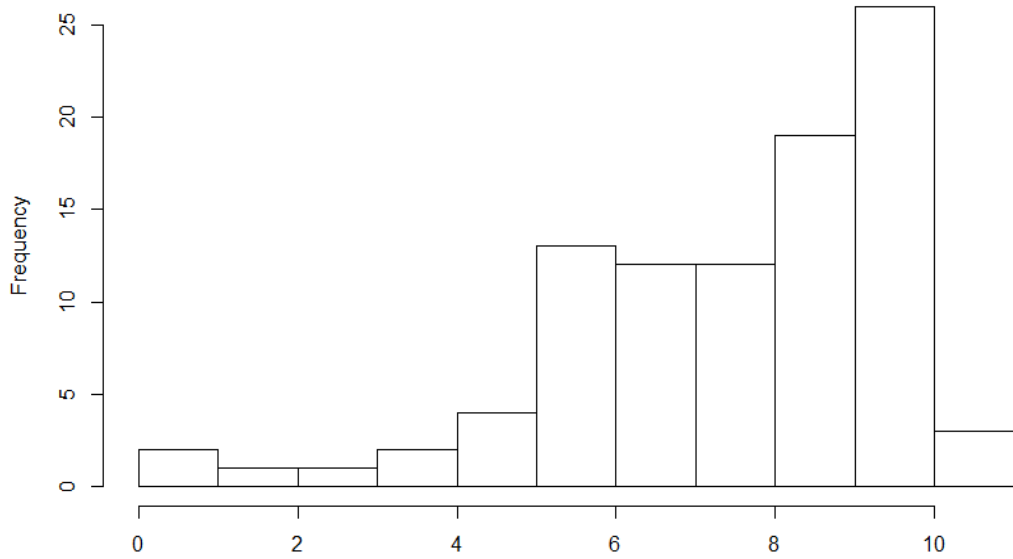

Figure 19. Histogram of log transformed barnacle density per m^2.

Table 9. AIC Table of top 5 models and null model predicting log transformed barnacle density per m^2.

	Model	AICc	dAICc	df	weight
m52	logBarn~N_E+Year+N_E2+Site_ID	370.7	0	6	0.6279
m41	logBarn~N_E+Site_ID+N_E2+Year*Site_ID	373	2.3	7	0.1956
m24	logBarn~N_E*Year+N_E2*Year+Site_ID	374.4	3.7	8	0.0987
m1	logBarn~N_E*Year*Site_ID	375	4.3	9	0.0746
m10	logBarn~N_E*Year*Site_ID+N_E2*Year*Site_ID	382	11.2	13	0.0023
m0	Null	422.4	52.4	2	<0.001

Table 10. Parameter estimates for m48, predicting log transformed barnacle density per m^2.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	37.2545	6.0758	6.132	2.27E-08
N_E	-37.6873	8.6259	-4.369	3.33E-05
Year2	-1.9098	0.3341	-5.717	1.39E-07
N_E2	12.5354	3.0288	4.139	7.85E-05
Site_IDASP	-2.5407	0.3678	-6.908	6.79E-10
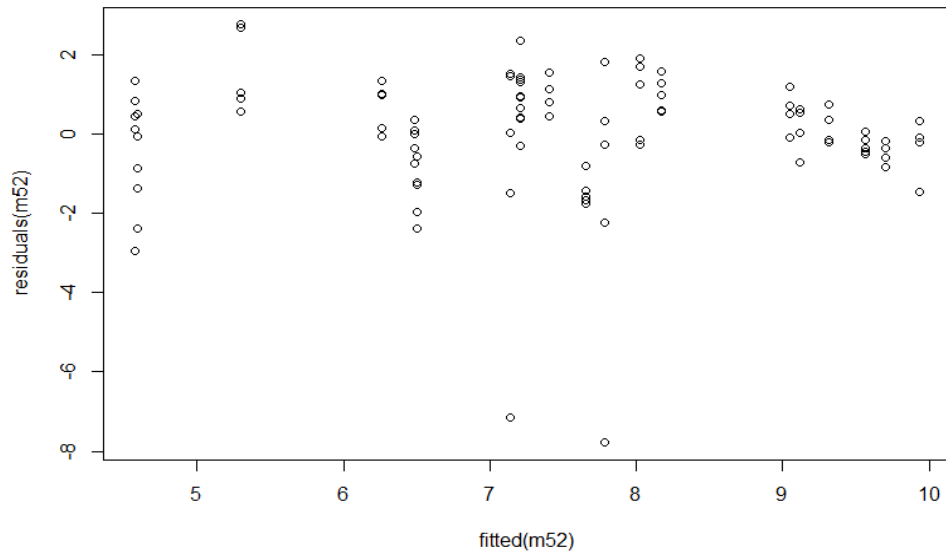
Figure 20. Residuals of m52, predicting log transformed barnacle density per m^2.

Oyster Length
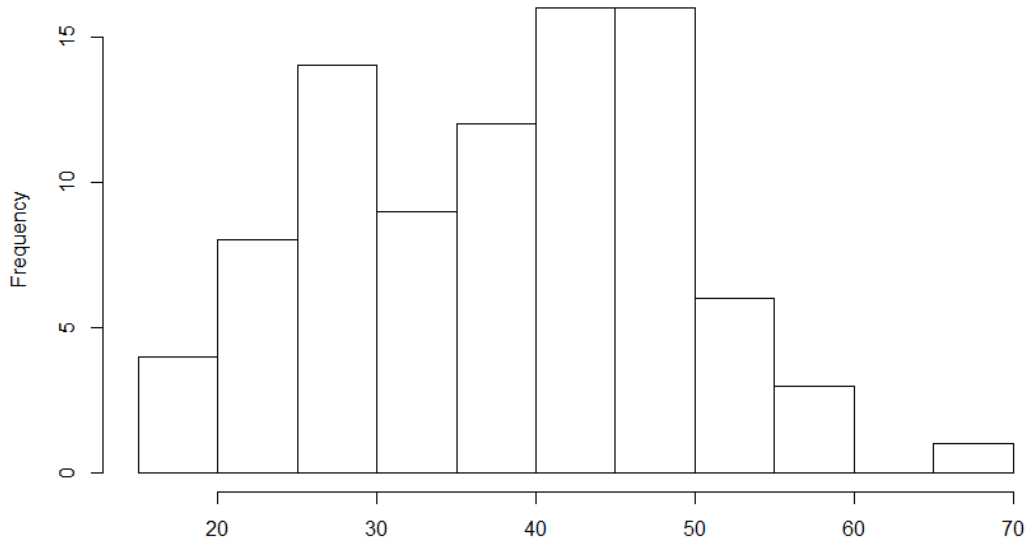
Figure 21. Histogram of mean spat size.

Table 11. AIC Table of top 10 models and null model predicting mean spat size.

	Model	AICc	dAICc	df	weight
m10	SpatSize~N_E*Year*Site_ID+N_E2*Year*Site_ID	515.8	0	13	1
m1	SpatSize~N_E*Year*Site_ID	545.4	29.6	9	<0.001
m70	SpatSize~N_E*Site_ID+N_E2*Site_ID	558.9	43.1	7	<0.001
m3	SpatSize~N_E+Year*Site_ID	563.9	48	6	<0.001
m41	SpatSize~N_E+Site_ID+N_E2+Year*Site_ID	566.1	50.3	7	<0.001
m0	Null	678.4	162.6	2	<0.001

Table 12. Parameter estimates for m10, predicting mean spat size.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	429.21	172.96	2.482	0.01526
N_E	-481.03	241.66	-1.99	0.05009
Year2	-314.09	185.53	-1.693	0.09452
Site_IDASP	-475.81	177.1	-2.687	0.00884
N_E2	143.4	83.71	1.713	0.09071
N_E:Year2	390.87	257.67	1.517	0.13337
N_E:Site_IDASP	657.97	248.87	2.644	0.00993
Year2:Site_IDASP	281.44	193.06	1.458	0.14896
Year2:N_E2	-121.76	88.68	-1.373	0.17375
Site_IDASP:N_E2	-228.02	86.74	-2.629	0.01034
N_E:Year2:Site_IDASP	-323.77	270.74	-1.196	0.23541
Year2:Site_IDASP:N_E2	93.07	94.18	0.988	0.32615
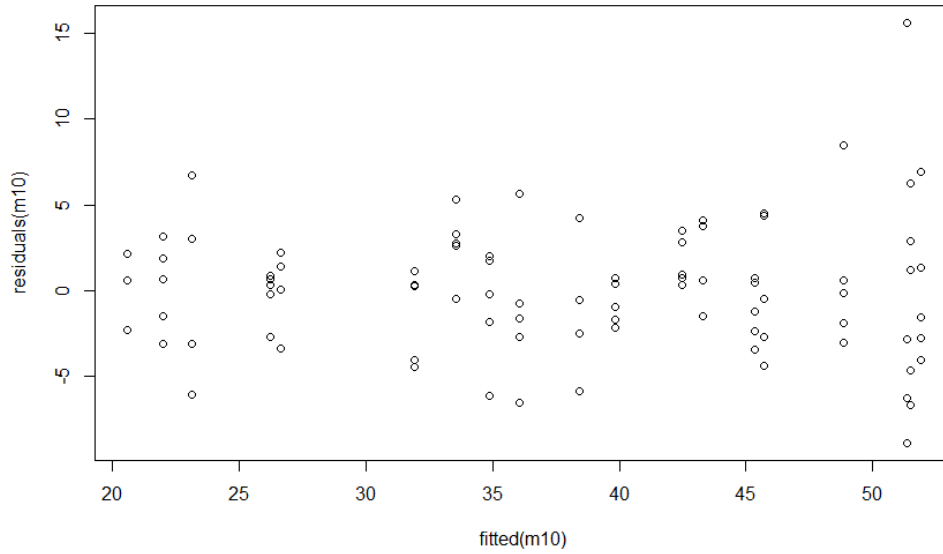
Figure 22. Residuals of m42, predicting mean spat size.

Oyster Angle of Growth
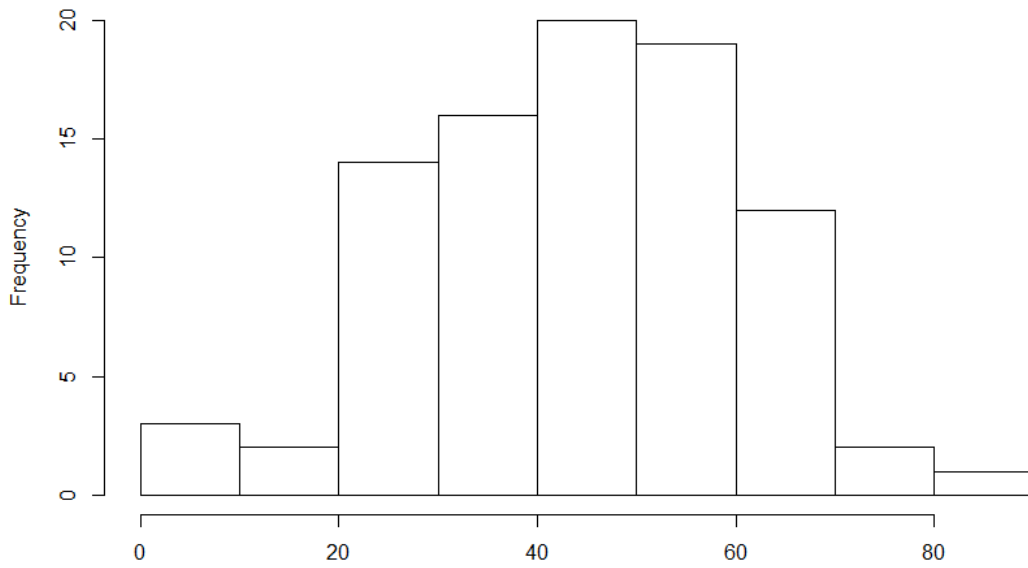
Figure 23. Histogram of mean spat angle of growth relative to the benthos.

Table 13. AIC Table of top 5 models and null model predicting mean spat angle of growth relative to the benthos.

	Model	AICc	dAICc	df	weight
m70	SpatAng~N_E*Site_ID+N_E2*Site_ID	736.2	0	7	0.5338
m6	SpatAng~N_E+Site_ID	740	3.8	4	0.0781
m9	SpatAng~N_E	740.5	4.4	3	0.0599
m2	SpatAng~N_E+Year+Site_ID	740.7	4.5	5	0.0555
m52	SpatAng~N_E+Year+N_E2+Site_ID	740.8	4.7	6	0.0511
m0	Null	750.9	14.7	2	<0.001

Table 14. Parameter estimates for m6, predicting mean spat angle of growth relative to the benthos.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	99.003	12.067	8.205	2.04E-12
N_E	-38.718	8.165	-4.742	8.32E-06
Site_IDASP	-5.533	3.392	-1.631	0.1
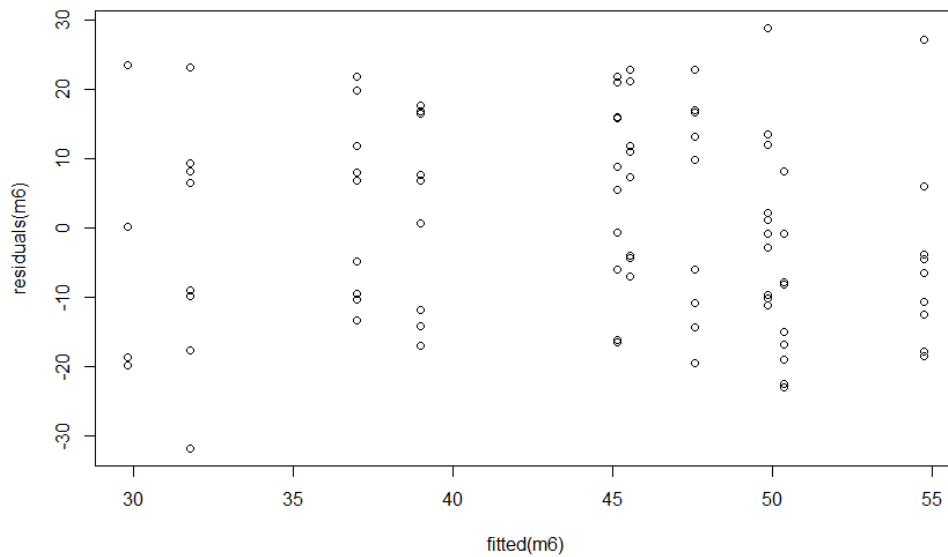
Figure 24. Residuals of m6, predicting mean spat angle of growth relative to the benthos.

Total Monthly Sedimentation
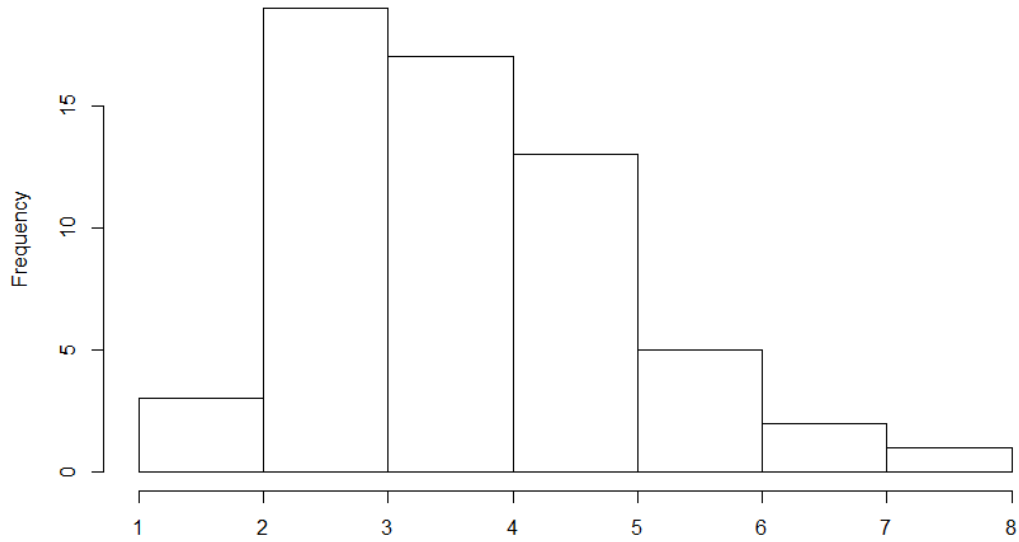
Figure 25.Histogram of mean total monthly sedimentation.

Table 15. AIC Table of 5 models and null model predicting mean total monthly sedimentation.

	Model	AICc	dAICc	df	weight
m2	logTsed~N_E*Site+N_E2*Site	139.1	0	7	0.43
m8	logTsed~N_E+Site	139.8	0.8	4	0.29
m9	logTsed~N_E+N_E2+Site	141	1.9	5	0.17
m5	logTsed~N_E*Site	141.8	2.7	5	0.11
m7	logTsed~Site	170.2	31.2	3	<0.001
m0	Null	203.7	65.1	2	<0.001

Table 16.Parameter estimates for m8, predicting mean total monthly sedimentation.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	26.207	6.7	3.911	0.00026
N_E	-25.913	8.856	-2.926	0.00498
SiteASP	-7.452	2.197	-3.392	0.00129
N_E2	7.427	2.889	2.571	0.01288
N_E:SiteASP	3.704	1.544	2.4	0.01983
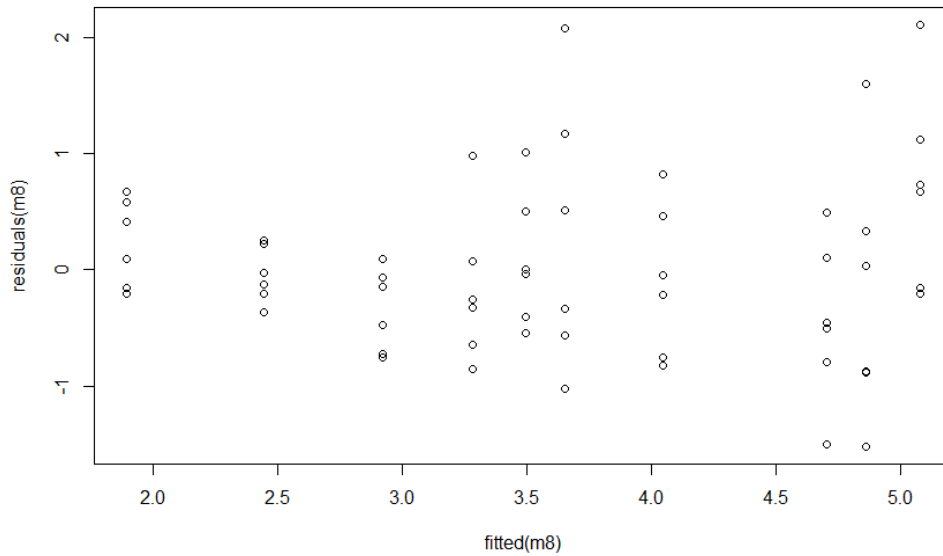
Figure 26. Residuals of m3, predicting mean total monthly sedimentation.

Larval Settlement in Flow Tank
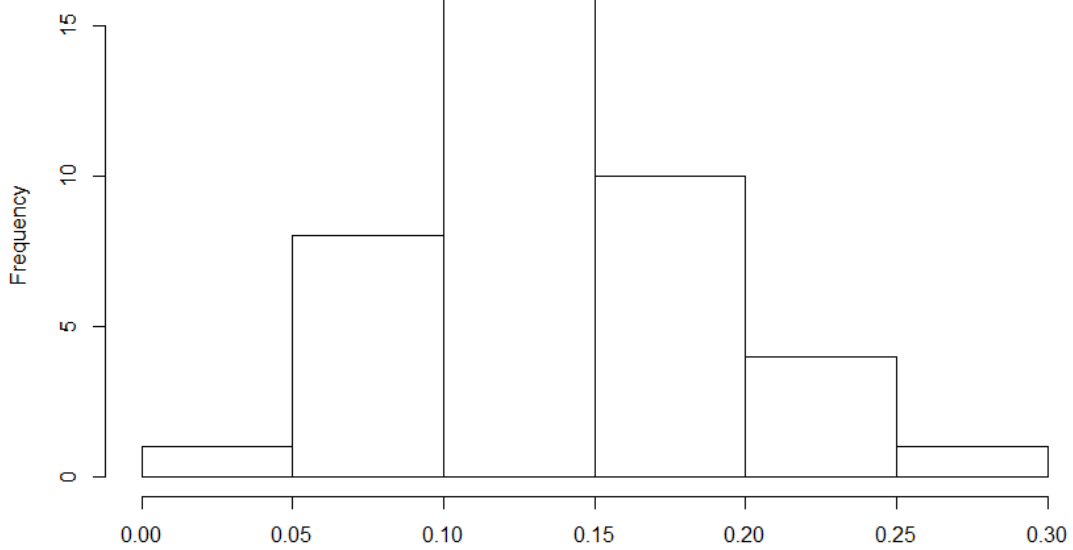
Figure 27. Histogram of squaroot transformed spat settlement per cm^2 of substrate.

Table 17. AIC Table of 6 models and null model predicting squaroot transformed spat settlement per cm2 of substrate.

	Model	AICc	dAICc	df	weight
m3	sqrspatcm2~Size	-128	0	6	0.6228
m4	sqrspatcm2~HighLow+Size	-125	2.3	7	0.1984
m0	Null	-125	3.2	2	0.1275
m2	sqrspatcm2~HighLow	-122	5.3	3	0.0446
m1	sqrspatcm2~HighLow*Size	-116	11.3	11	0.0022
m5	sqrspatcm2~HighLow*Size+HighLow	-116	11.3	11	0.0022
m6	sqrspatcm2~HighLow*Size+Size	-116	11.3	11	0.002

Table 18. Parameter estimates for m3, predicting squaroot transformed spat settlement per cm^2 of substrate.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.14362	0.01577	9.104	9.31E-11
Sizes250	0.01227	0.02231	0.55	0.5857
Sizes500	0.02586	0.02231	1.159	0.2543
Sizes63	-0.02523	0.02231	-1.131	0.2658
Sizesl63	-0.04194	0.02231	-1.88	0.0685

Figure 28. Residuals of m3, predicting squaroot transformed spat settlement per cm^2 of substrate.

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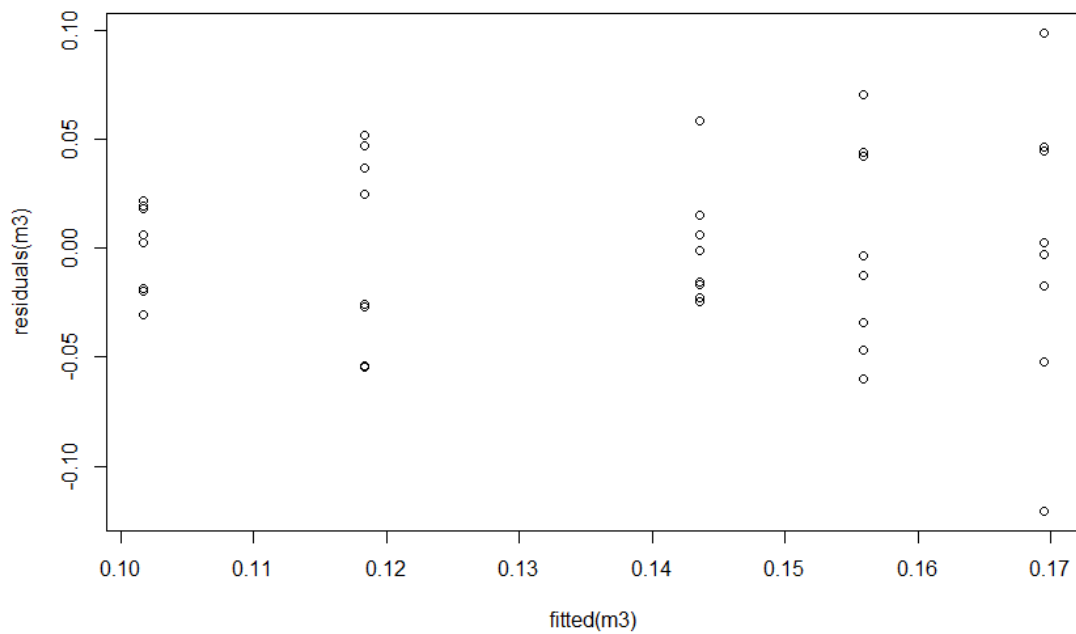Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., & Guo, X. (2011). Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience*, *61*(2), 107-116.

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