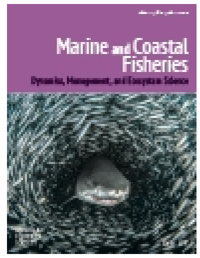

Trends in oyster populations in the northeastern Gulf of Mexico: An assessment of river discharge and fishing effects over time and space

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Trends in oyster populations in the northeastern Gulf of Mexico: An assessment of river discharge and fishing effects over time and space

Manuscript ID: UMCF-2019-0050

Dear Dr. Adkison,

Thank you for the opportunity to revise the manuscript UMCF-2019-0050. We have made extensive revisions throughout based on the Editorial teams comments. We have provided detailed responses to the reviewer and editor questions and comments in the attached document and we feel the manuscript is greatly improved. In the attached document we provide the original comment and then our response in *italics.*

We hope that you find these changes acceptable for publication.

Regards,

Wiliam E. Pine

Reviewer(s)' Comments to Author:

Editor comments

I noticed that the offset of counts for transect length was log-transformed. I may have missed some detail of the analysis, but I would expect that counts would be linearly related to transect length. Please check whether this log-transformation is appropriate given your analysis model.

*We have expanded this discussion in the paper and added additional references. The offset changes the model from modelling counts C, to modelling a rate C/L (where L is the transect length), as the response. Since, these models have a log link, we have log(C/L) = beta0 + beta1 * covariates, which can be rewritten, moving the length to the right hand side, log(C) = log(L) + beta0 + beta1 * covariates. So because the model is using a log link, the values are on log scale. See line 144-167.*

Reviewer: 1

Comments to the Author
Summary: The authors pull together multiple sources of data to investigate patterns of oyster populations and environmental conditions in the Suwannee River region. The statistical methods used are appropriate for drawing inference from these diverse data sources and the data presented and conclusions are valuable to many stakeholders in the region and the field. Given the limited data available, this analysis fills an important gap in our understanding.
Thank you, we appreciate your positive feedback on our study!

General comments: The structure and writing of the paper are clear and easy to follow. The discussion is speculative and wanders from the available data and analyses presented here to discuss general issues affecting oysters that are beyond the scope of the paper. This context is important – but reorganization of the paper is needed to focus on the advancements pertinent to the analysis, and then generalize to interactions with other factors. The modeling and sampling methods should be described in more detail, particularly in reference to figure 3 and the modeled oyster populations, and the time period of oyster surveys. This essential detail seems to be missing from the manuscript. Statistical methods are complex, which may be necessary given the limited data, however this needs to be better justified.
We have added a table in the supplementary materials defining the period (i.e., season and year) when each site and locality were surveyed.

Specific comments:

Abstract:
Line 13: how are inshore intertidal bars becoming like offshore bars? Simply in that they are degraded or are there other structural, biological similarities that inform causes of declines?
We have revised to clarify that the inshore bars are becoming degraded. Line 24-25

Line 16: confusing arrangement suggests a linkage between increasing CV of discharge and oyster fishing effort. Consider revising.
We have deleted this sentence from the abstract.

Data collection line transects: what interval were transects sampled, and over what timeframe? I can't find where the period for oyster surveys is defined. Also winter or summer period is only mentioned in the model methods without definition of how this relates to surveys or other data.
We have added a table in the supplementary material that defines which periods each locality/site was surveyed. In addition, we define the time period (i.e., year and season).

Line 99: minimum? Maybe just a typo or maybe needs to be updated
We have removed the ? after minimum – this was just a typo.

Line 110: How were these selected? Is there evidence that mean daily discharge or extreme events has a greater influence on oyster populations?
We have added text to clarify that these variables were used as a proxy for salinity (line 123).

Line 120: Were all counties pooled for the analysis? I'm curious if there were differences in fishing effort among locations or if the resolution is good enough to address this?
Yes, we have clarified that landings data were combined for the counties. No, the data resolution is not adequate to reflect effort among locations. Line 138-140.

Line 128: the term 'period' is confusing throughout the manuscript. I think this general model description is outlining a method applied to datasets with different sampling intervals and durations, but I found this confusing throughout the manuscript and in the figure captions. particularly in figure 3 with period on the x-axis. Are sampling periods evenly spaced such that the model fit indicates proportional change over time?
Yes, sampling periods are evenly spaced they refer to summer or winter of each consecutive year. We have included a Table in the supplemental files defining each period.

Line 130: Can you provide more justification for using counts and transect length as an offset versus calculating average density?
*We have included additional explanation and references to Zuur (2009 and 2013). Using effort as an offset changes the model from modeling counts, to modeling a rate (count/area) as the response variable. Because each of our transects was a fixed width, the area only changed as a function of transect length. Since these models have a log link, the equation is most simply written as log(count/transect length) = beta 0 + beta 1 * covariates which can be re-written as log(count) = log (transect length) + beta 0 + beta 1 * covariates. Additional advantages of using the actual counts vs. converting the counts and area to densities is that the fitted values and confidence internals do not contain negative values (Zuur et al. 2009). See line 144-167.*

Line 170: what do 'these covariates' refer to? River discharge and fisheries landings? confusing sentence structure

We have dropped this sentence as it was no longer needed given further revisions.

Line 177: are these statistically significant trends? Mean daily discharge and total annual discharge are the same pattern just with transformed data (i.e. divided by 365) – could simplify discussion and reduce the number of figures to select one and focus on that.
We chose to use mean daily discharge throughout the paper and have removed total annual discharge.

Line182-189: Move to methods as justification for using Suwannee River data for all locations.

We have made this change.

Line 245 (and references therein): Kimbro 2017 and Pusack 2017 appear to be the same paper? Double check references.
Yes, Kimbro 2017 and Pusack 2017 are the same paper – the correct citation is Kimbro 2017. We have fixed this in the manuscript and references.

Line 247-259: I appreciate the candid discuss of limitations – what do you think contributed to the strong modeled relationship between oyster count and discharge? It is important to understand why this relationship was observed before extrapolating to whether the relationship is globally relevant.
We do not understand from a mechanistic perspective what drives this relationship.

Line 292: This discussion of factors leading to decline of oysters could benefit from more details from the study. In the methods you mention counting live and dead oysters, but this data does not appear to be used in the analysis. Were there concomitant changes in dead oysters that could support or refute hypotheses about putative causes of decline (like habitat)?
We have not made extensive use of the dead oyster count data, because we are unsure how long the dead shells persist on the oyster bars. We have observed that the dead shells are more likely to wash away in storms than live shells, so we do not know how informative these shell counts are. We simply do not know what other factors led to the decline and feel that discussion beyond what is provided is highly speculative.

Line 316-317: I agree, the use of the fisheries data to explain oyster count when little to none or variable effort occurs in intertidal reefs is tenuous. However, it is of interest to explore whether or not synchrony exists in populations occurring in different habitats that could suggest environmental vs harvest factors driving population changes. The current structure of the analysis doesn't allow for a quantitative comparison, yet some discussion of the needs of this type of analysis seems appropriate.
We have added text (Lines 341-347) expanding on this point.

Figures:

All figs: I recommend redesigning figures for legibility in the final version. Font size is too small, background grids, when present, are distracting.
Figures have been revised.

What is period?
This is addressed by adding the supplemental table

Fig1: Really nice figure!
Thank you.

Fig3: Model seems to poorly predict observations. Many observations outside of the 95% confidence interval – give the relatively low number of surveys this seems like an issue. In Fig. 2 the negative binomial predictions look to accurately model oyster density – can you provide detail why the model might be less accurate in the site-location combinations?

Based on reviewer comments, we switched from using the GLMM to the more widely used MASS package and the likelihood function described in Venables and Ripley (2002). We originally used the

GLMM package because we were exploring the use of random effects and the computational speed of the GLMM package was greater than other packages. However, in revision the use of the likelihood formulation in the MASS package resulted in better model fit to the data. We have revised the results and figures based on this improved fit.

Reviewer: 2

Comments to the Author
I recommend that the article be accepted at this time with minor revisions. The authors investigated the relationships of river discharge and fishing effects over space and time for populations in the US Gulf of Mexico. Overall, this work contributes to further unraveling the complexities behind oyster population flux and decline with implications for conservation management and future research. My suggestions to improve the manuscript are as follows.

General Comments:
1) Be mindful of defining acronyms at first use. There are many instances of undefined acronyms in the text.
We went back through the manuscript to make sure all acronyms were defined the first time that they were used.

2) Go back and check for missing spaces between periods, I note that the authors are using two spaces after the end of a sentence.
We have standardized throughout.

3) Overall, trim the use of significant digits to an appropriate level of precision, such as two to three, e.g., Table 4 estimates and standard errors and p-values throughout the manuscript (e.g. L215 p=9.25e-16 would be sufficient as p<0.01).
We have reduced all numbers to two significant digits throughout.

Abstract:
1) L7 - Do you mean generalized linear mixed effects models? I agree that you are using mixed effects models, yet in the manuscript they are referred to simply as GLM. It is fine to just call these GLM, just decide and stick with that. It would actually be more interesting if the mixed effects are called out specifically in the Data Analysis Methods.
As discussed above, based on these comments we re-evaluated our use of the GLMM package given we did not use a random effect in our final model. We re-analyzed all data using the more common MASS package and this resulted in improved model fit. This led to us updating all results and figures to reflect this improvement in fit.

2) L16 - Sentence starting with "Overall" is confusing, here, yet this linkage is clear in the manuscript text.
We have deleted this sentence.

Intro:
1) Overall, the concept of oyster reefs being intertidal or subtidal AND either inshore, nearshore, or offshore is confusing as presented. Some readers may not know this about oysters.

Perhaps add a sentence stating this explicitly and then lead into the literature examples (L50-53) and that this study focused on intertidal only in all three spatial provinces.
We have added text to clarify the terms intertidal and subtidal as well as inshore, nearshore, and offshore descriptions.

Methods:
1) L94 - add a space between sentences.
Done.

2) L97 - Define acronym.
We have defined the acronym.

3) L99 - Strange occurrence of "?".
We have removed the ? from this sentence.

4) L97,99,101 - Decide if using e.g., # m or #-m.
We have used # m throughout.

5) L110 - Yes, CV is the coefficient of variation, yet should still define the acronym.
We have defined this acronym.

6) L118 and L125 - Hold off on using GLM here, and if you do define the acronym. Rather, flow would be improved to replace use of GLM here with "analysis" and describe in Data Analysis subsection that you used GLM or (GLMM).
We changed these sentences to just say 'analysis' instead of 'GLM analysis'.

7) L127 - call these generalized linear mixed effects models, as in abstract, and define your mixed effects.
We actually used generalized linear models not mixed models, which is why the mixed effects are not defined. We have fixed this throughout the manuscript.

8) L128 - extra space between 2008 and to.
We have removed the extra space.

9) L132 - needs a comma between ". . .function)", and which.
We have added this comma.

10) L135 - define acronym and provide a reference for AIC (Akaike . . .).
We have defined this acronym and added a reference.

Results:
1) L203 - model equation has an extra space and needs a parenthesis.
We have fixed the formatting of this equation and added the extra parenthesis.

2) Starting with L207 - Trim the significant digits used to report the p-values.
These changes have been made throughout

3) L212 - extra space in model equation.

We have removed the extra space.

Discussion:
1) L270 - Isn't there a link between discharge and habitat formation by sedimentation? I see that you get to this in the discussion (L340-341), could you introduce that briefly here? I think this is pretty important to the story.
The role of sedimentation is also unclear. The Wright et al. paper is the only work we are aware of on this topic in Suwannee Sound and in the Big Bend region. Other regions where sedimentation has been assessed including coastal Louisiana are very different because oysters there do not form the same type of clumping reefs as they do in the Big Bend, nor do intertidal oyster bars exist with the same prevalence.

2) L308 - Check use of "subtidal" and "sub-tidal" and choose.
We have used subtidal throughout.

3) L317 - add space between sentences.
We have added a space between sentences.

4) L326-327 - Sentence is unclear, although I know what you are trying to say, I think. Re-write, i.e., are inshore areas becoming more like nearshore and offshore areas in terms of density? Say this directly, and place nearshore before offshore in order.
This sentence has been revised.

5) L328 - Would use of satellite imagery assist with identifying location of new reefs?
We have added text and references to address this.

6) L360 - Extra parenthesis.
We have removed the extra parenthesis.

References:
Review and cross reference, I did not.

Tables and Figures:
1) In general, if acronyms are included in the table fields, define those in the captions.
This has been done throughout.
2) Table 1 - Define GLM acronym in caption. Define AIC in caption, and increase the spacing between fields AIC and Delta AIC.
This has been done throughout.

3) Table 2 - There are waaaaay too many significant digits used here, and it looks sloppy. Reduce to two or three significant digits. Define Std. error.
This has been revised and updated.

4) Table 4 - Same as Table 2.
This has been revised and updated.

5) Increase Figure resolution to 300 dpi for publication.
This has been updated throughout.

Good work, thank you for your contribution
Thank you for the kind words.

ABSTRACT

Within the "Big Bend" region of the northeastern Gulf of Mexico, one of the least developed coastlines in the continental US, intertidal and subtidal populations of Eastern Oyster ("oyster") *Crassostrea virginica* are a critical ecosystem and important economic constituent. We assessed trends in intertidal oyster populations, river discharge, and commercial fishing activity in the Suwannee River estuary within the Big Bend using fisheries independent data from irregular monitoring efforts and publicly available environmental data. We used generalized linear models (GLM) to evaluate counts of oysters from line-transect surveys over time and space. We assessed model performance using simulation to understand potential bias, and then evaluated whether these counts were related to freshwater inputs from the Suwannee River and commercial oyster fishing effort and landings at different time lags. We found intertidal oyster counts have declined over time, and that most of these declines are found in inshore intertidal oyster bars which are becoming degraded. We also found a significant relationship between oyster counts and a one-year lag on mean daily Suwannee River discharge but including commercial fishery trips or landings did not improve model fit. We do not know whether declines in intertidal oyster bars are offset by formation of new oyster reefs elsewhere. These results quantify rapid declines in intertidal oyster reefs in a region of coastline with high conservation value which can be used to inform ongoing and proposed restoration projects in the region.

Many species of oysters of the family Ostreidae are globally recognized as a critical estuarine component where they provide important ecosystem and fishery benefits (Gutiérrez et al. 2003; Coen et al. 2007; Carranza et al. 2009; Grabowski 2012). Large declines in oyster populations have been observed at global (Beck et al. 2011), continental (Zu Ermgassen et al. 2012; Alleway and Connell 2015), regional (Seavey et al. 2011; Wilberg 2011, 2013), and local spatial scales (Pine et al. 2015; Grizzle et al. 2018). These losses have been widely documented including localized extirpations in Australia (Alleway and Connell 2015) and large biomass reductions in the US particularly in the Chesapeake Bay and US Gulf of Mexico regions where the eastern oyster *Crassostrea virginica* is highly valued from cultural, fishery, and ecosystem service perspectives. The US Gulf of Mexico region alone likely supports the world's largest remaining natural oyster reefs (Beck et al. 2011), and these reefs provide about 69% of the US commercial wild eastern oyster harvest (2016 data, see NOAA Fisheries 2019a). Florida has historically supported about 10% of this total but following the collapse of the Apalachicola Bay oyster fishery in 2012 (Pine et al. 2015) this total has declined to about 5% of total US landings (NOAA Fisheries 2019a).

The Suwannee River estuary (Figure 1) is one of the least developed coastal regions in the continental US as more than 30% of the land area and about 100 km of coastline is protected (Main and Allen 2007) and road and human population densities are among the lowest in Florida (Geselbrach 2007; Southwick Associates 2015). Loss of oyster reefs in this area is of conservation concern (Beck et al. 2000) as oyster reefs have large ecological and economic value. In this region, about 13% of private sector employment and 25% of all economic activity is related to natural resources (Southwick Associates 2015) including commercial shellfish harvest. Oyster reefs can form both intertidal and subtidal reefs, and the Big Bend is known for expansive intertidal reefs that occur in shallow water (<1-m depth) and often exposed to air during low tide. These intertidal reefs serve important ecological and hydrological roles in the region. Kaplan et al. (2016) suggested that intertidal oyster reefs in the Big Bend provide a keystone ecosystem service due to their physical orientation as linear chains parallel to the coastline. Likely because of the extremely low gradient of the Big Bend coastline, these parallel chains of reef can be found in series (multiple parallel chains) which may reflect other shoreline levels. We define these parallel chains as inshore oyster reefs, which occur closest to the present shoreline, nearshore reefs which are slightly further from shore, and offshore reefs as the furthest seaward reefs that face the open Gulf of Mexico. Because of this orientation, these reefs help to promote detention of freshwater and modulation of salinity to promote estuarine conditions (Kaplan et al. 2016). Bergquist et al. (2006) and Seavey et al. (2011) identified decadal changes in intertidal oyster reefs in this region. Seavey et al. (2011) used aerial imagery to document a 66% net loss in oyster area from 1982-2011, with offshore intertidal reefs experiencing an 88% loss, nearshore reefs 61% loss, and inshore reefs 50% loss. Reasons for intertidal oyster population decline in this area are unknown, but Seavey et al. (2011) proposed a relationship with changes in freshwater discharge from the Suwannee River leading to cascading increase in frequency of mortality events, eventual loss of nucleation sites for oyster spat, and an irreversible collapse of intact oyster reefs. Small-scale tests of restoring intertidal oyster reefs through construction of nucleation sites have suggested that nucleation sites are indeed limiting this population (Frederick et al. 2016, Kaplan et al. 2016) and larger restoration efforts are now underway. Here, we assess recent trends in intertidal eastern oyster populations ("oyster" hereafter) in the Suwannee River estuary, an area of high conservation value in the "Big Bend" region of the northeastern Gulf of Mexico, using fisheries independent data from irregular monitoring efforts.

<A>Methods

<B>Study Site. – The Suwannee River estuary in the northeastern Gulf of Mexico (Figure 1) can be divided into three subareas (Orlando et al. 1993), including the lower Suwannee River, upper Suwannee Sound, and lower Suwannee Sound. These shallow (<2-m) regions, fringed by coastal marsh, shell/sand, and oyster bars, are bisected by the Suwannee River and generally bounded to the north by Horseshoe Point and south by Cedar Keys (Orlando et al. 1993; Wright et al. 2005). State and federal partners manage most of the land surrounding the estuary and the 54-km tidally influenced reach of the Suwannee River as conservation land. Suwannee Sound is an open ocean-facing deltaic estuary (Orlando et al. 1993; Wright et al. 2005) and is heavily influenced by discharge from the Suwannee River which provides about 60% of the inflow to the entire Florida Big Bend region (Montague and Odum 1997). Suwannee Sound is the largest estuary within the Big Bend region. The Suwannee River is undammed and free flowing (Benke 1990; Ward et al. 2005), but river discharge may be modified due to surface and sub-surface water withdrawals within the basin (Mattson 2002). Water inputs are from extensive groundwater inflows from the Floridan aquifer and surface water runoff from precipitation. Suwannee River discharge is a major factor influencing monthly, seasonal, and annual variation in salinity in Suwannee Sound (Orlando et al. 1993; Mattson 2002).

In most river basins, river discharge-per-unit-rainfall has increased in recent decades due to watershed changes such as conversion from forest to agriculture or increase in impervious surfaces. In the Suwannee River, discharge has actually declined-per-unit-rainfall possibly due to increasing human use of surface and groundwater (Seavey et al. 2011). Resulting decreased groundwater levels can impact human users in this region (Saetta et al. 2015), but ecosystem impacts are unknown. Climate reconstructions from dendrochronological records for this region suggest a much wider range of precipitation patterns in past centuries than has been observed in recent decades (Harley et al. 2017).

<C>Data collection line transects. – We selected four localities for sampling oysters, (Figure 1) with three in Suwannee Sound (Horseshoe Cove [near the town of Horseshoe Beach], Lone Cabbage Reef, and Cedar Keys [near the town of Cedar Key]) and one in Corrigan's Reef. At each locality, we designated linear groups of oyster reefs as Inshore, Nearshore, or Offshore sites based on their orientation and relative distance from shore. We then randomly chose individual intertidal oyster reefs within each of these sites for sampling (generally 3 unique small reefs within each site and locality). At each of these sampling stations, we then established fixed locations on each oyster reef to conduct line transect sampling to estimate oyster counts and density. Oyster reefs were sampled when tidal heights were less than -0.84 m North American Vertical Datum (NAVD) of 1988 as measured at the National Oceanic and Atmospheric Administration (NOAA) tidal station 8728520 (NOAA 2019b). At this tidal height, intertidal oyster reefs in this area are dewatered, allowing visual counts of oysters with line transect surveys. Transect width was 15.24 cm and transect length was the minimum width of the oyster reef at the tidal height of sampling. The starting point for the transect on the bar was randomly chosen in GIS. Permanent steel rebar posts (0.5 m) were used to mark transect outlines for repeat visits, and global positioning system (GPS) coordinates recorded using a

handheld GPS device. Live and dead oysters were then counted visually along each transect using handheld tally counters and recorded in 2.5 m intervals from the defined transect origin.

<C>*River discharge.* – Because salinity in Suwannee Sound is influenced by Suwannee River discharge, and oyster populations are an estuarine dependent species, we summarized river discharge data using the Suwannee River United State Geological Survey (USGS) gauge 02323500 near Wilcox, Florida. We used the longest continuous data records beginning October 1941-July 2019 to show long-term trends and events in river discharge as a proxy for salinity and summarized river discharge (by convention as cubic feet per second) for each year as mean daily, the variance of daily discharge, and coefficient of variance (CV) of daily discharge. We also calculated these same metrics for the overall time series. We included a locally weighted scatterplot smoothing (LOWESS) line to aid in visually assessing trends in Suwannee River discharge metrics. We assessed how river discharge in year of sampling as well as a 1- or 2-year lag of river discharge influenced oyster counts.

<C>*Commercial fishing and landings.* – We categorized each site as either open or closed to commercial fishing based on harvest zones available from the Florida Department of Agriculture and Consumer Services (FDACS, FDACS 2019). We included fishing as a factor in our analyses to assess whether being in a region open to fishing influenced oyster counts. To examine long-term trends in oyster landings and fishing effort, we obtained and combined annual oyster landings data (oyster meat weight and oyster fishing trips) for the three counties in the Suwannee Sound region (Taylor, Dixie, Levy) from the Florida Fish and Wildlife Conservation Commission (FWC; FWC 2019) for 1986-2018. While landings data for oysters are available prior to 1986, the mandatory trip ticket reporting program was not officially

implemented until 1986. We included the current year and a 1- or 2-year lag of oyster landings and oyster fishing trips in our analyses to assess whether oyster fishing effort in prior years influenced oyster counts.

<C>*Data analyses generalized linear models.* – We initially assumed the count data most likely followed a Poisson or negative binomial distribution, and to assess the distribution of these data, we assumed that count data are discrete and examined the ratio between the variance of the counts and the mean count per site, and graphical representations of predicted vs. observed distributions of count data from each site. We then used generalized linear models (GLM, Bolker et al. 2009) with a negative binomial distribution to assess oyster counts (dependent variable) over period (time variable, a winter or summer period of time of equal length each year, see Table 1 in supplemental files where each period is defined), locality (i.e., Horseshoe, Lone Cabbage etc.), and site (Inshore, Nearshore, Offshore). We assumed that total transect oyster counts were likely to increase with transect length, so we included transect length as an offset of effort (log link function; Zuur et al. 2009; 2013). Using effort as an offset changed the model from modeling counts, to modeling a rate (count/area) as the response variable. Because each of our transects was a fixed width, area only changed as a function of transect length. Since these models have a log link, the equation is most simply described as log(count/transect length) = beta0 + beta 1 * covariates which can be re-written as log(count) = log (transect length) + beta0 + beta 1 * covariates. Additional advantages of using the actual counts vs. converting the counts and area to densities is that the fitted values and confidence internals do not contain negative values (Zuur et al. 2009). We used the best fitting (lowest Akaike information criterion [AIC]; Bolker 2008) model to predict oyster counts by period. All

models were fit using the glm.nb function from the MASS package in R (Venables and Ripley 2002; R Core Team 2018).

We also developed a candidate set of models of biological interest to fit to these data. As an estuarine species, the role of salinity in influencing oyster recruitment and survival is of interest to resource managers (Turner 2006; Buzan et al. 2009; Fisch and Pine 2016). Oyster population status has been considered a metric for estuarine ecosystem health (Bergquist et al. 2006; Coen et al. 2007) and to evaluate minimum flow regulations in the Suwannee River basin (Farrell et al. 2005; Bergquist et al. 2006). We conducted exploratory analyses of how Suwannee River discharge (USGS gauge 02323500), as a proxy for salinity, nutrient inputs, and other factors, influenced counts on oyster reefs. We assessed how mean daily river discharge in year of sampling, or discharge with 1 or 2-year lags influenced oyster counts. All continuous covariates were centered (mean = 0, standard deviation = 1) using the scale function in R before including in each GLM model. The Corrigan's Reef locality is closer in proximity to the Waccasassa River, a small (1242 km^2 watershed compared to 24968 km^2 for the Suwannee River) coastal river with low elevation gradient. We were unsure whether climate driven discharge patterns in the Waccasassa River were the same as the larger Suwannee River basin. River discharge information for the Waccasassa River (detrended to remove tidal influence, USGS station 02313700) is only available for approximately 10 years. We compared patterns in the Waccasassa and Suwannee rivers and found generally similar patterns in discharge. We therefore used the Suwannee River discharge for all analyses.

We assessed whether oyster harvest affected oyster counts by examining whether an area was open or closed to oyster harvest as a factor and whether oyster landings, trips or catch-per-unit-effort for the given year or with a 1 or 2-year lag influenced oyster counts. The relationship between our response variable, oyster counts on intertidal oyster bars, and oyster harvest is complicated. Oysters that grow on intertidal oyster reefs are generally smaller (below minimum legal harvest size limit of 75.2-mm) than subtidal oysters and therefore are not traditionally targeted for harvest. However, these intertidal bars do produce some legal sized oysters, and are often adjacent to harvested subtidal bars. We have observed oyster harvest and culling on intertidal bars particularly in years with high oyster demand (W.E. Pine, *personal observation*). Oyster harvest in prior years may influence oyster counts because oyster harvest removes, disturbs, and fragments shell on oyster reefs. Oyster shell is the dominant substrate on which larval oyster spat settle and recruit, thus harvest could reduce recruitment due to loss of settlement substrate (Powell and Klinck 2007; Pine et al. 2015) and modification of vertical structure. We used a forward selection process where we fit each parameter individually and then retained statistically significant factors ($p<0.05$). Final model comparison was then made with AIC when appropriate.

<C>*Simulations.* – To assess the "informativeness" of our GLM modelling approach (as a type of power analyses, Bolker 2008), we generated 1000 replicate datasets (resampling with replacement) of oyster counts by locality, site, and period and fixed transect length to the transect length used at each oyster reef in the original data. To simplify simulations, we did not simulate data for the covariates of river discharge or fishery landings. We then fit the best fitting (lowest AIC) model without covariates to these data and assessed (1) how many of these 1000 simulations had a negative beta coefficient for period (indicating a decline in oyster counts over time) and (2) the distribution of p-values for the period beta coefficient. This was

done to assess how likely we were to detect both the sign and the significance of a change in oyster counts over period (time) if one were to occur.

<A>Results

<B>Trends in Suwannee River discharge

We found generally declining trends in mean daily discharge, stable trends in daily discharge variance, and increasing trends in the CV of daily discharge (a measure of volatility) since October of 1941 (Figures 4 and 5). Since 2010, mean daily discharge has been below the 1941-2018 average in six of the last nine years, near average for two years, and above average for one year (Figure 5).

<B>Commercial fishing and landings

During 2010-2019 commercial oyster landings, trips, and catch-per-trip were variable with a large increase in landings and trips in 2016, and then a decline in 2017 (Figure 6). This increase in landings and trips equaled the third highest values for the 1986-2019 time period (Figure 6). Catch-per-trip has generally trended down since 2010 (Figure 6).

<B>Evaluating distribution of data

Based on (1) our use of count data, (2) variance of oyster counts exceeding the mean, (3) high dispersion, and (4) visual assessment of observed oyster counts vs. predicted counts based on a negative binomial distribution (Figure 2), we concluded a negative binomial distribution to be a reasonable fit to the observed data and used this distribution for each GLM model.

<B>GLM analyses

For our simulations, we found that our best fit model without covariates (period*locality+site+offset(log(transect length))) was informative both in terms of the direction (Figure S1) and significance (Figure S2) of the beta terms. Of our 1000 simulated data sets, all (100%) had a negative beta parameter for period indicating a decline in oyster counts. We also found that the distribution of p-values was generally centered around 0.03 (Figure S2), which was higher than the p-value estimated for the original data ($p=0.005$). Of the 1000 simulations, 847 p-values were less than alpha = 0.05 (85%). These results suggest our model is informative and reliable in detecting change in oyster counts over time.

The top GLM models (lowest AIC) included a combination of period, site, and locality as additive or interaction terms, and these models were very similar in AIC value (Table 1; delta AIC = 1.68 across top three models). The top model (period*locality+site+offset(log(transect length))) allowed for a unique slope by period and locality. We found oyster counts to differ across time ($p=0.000676$, Table 2, Figure 3) and we found that nearshore sites differed from inshore sites ($p < 0.01$, Table 2, Figure 3). We found a locality effect only for Corrigan's Reef ($p = 0.02$, Table 2). Adding covariates of biological and management interest to this model improved fit (Table 3), and best fit was found with a one-year lag on mean daily discharge. A simple ANOVA between the top model with and without a river discharge covariate was significant ($p < 0.01$). Including mean daily discharge in the model again led to significant period and site effects, with Corrigan's Reef the only locality effect while mean daily discharge was highly significant ($p < 0.01$; Table 4). Including landings, trips, or open/closed harvest status as a category was not an improvement in model fit over including river discharge alone.

<A>Discussion

We documented declines in intertidal oyster reefs in a region of the US Gulf of Mexico that has low human population density, large areas of protected coastal and submerged lands, and regulated oyster harvests – all factors that suggest high likelihood of viable oyster populations compared to other regions within eastern oyster native range. Declines in oyster populations and the loss of associated ecosystem services and fishery resources in this region is therefore of significant conservation concern. Causal factors for oyster population declines across their range are often not clear owing to complex interactions between fishery harvests (Wilberg et al. 2011), oyster habitat (Wilberg et al. 2013; Pine et al. 2015), changes in water quality and quantity (Seavey et al. 2011; Fisch and Pine 2016), disease dynamics (Powell et al. 1992), and other unknowns. These same factors can be influenced in multiple and uncertain directions by changing climate (Mulholland et al. 1997; Gazeau et al. 2007; Miller et al. 2009) and associated sea-level rise.

In our assessment, we found a relationship between mean daily discharge one year prior and intertidal oyster population counts (Table 4, Figure 7). The reported relationships between river discharge and oyster population responses are various, complicated, and unclear, from ecological, management, and legal perspectives (La Peyre et al. 2009; Buzan et al. 2009; Fisch and Pine 2016, US Supreme Court 2018). Because of their preference for intermediate salinities, oyster growth and survival can be expected to be responsive to flood, drought, or other factors influencing river discharge. These same conditions may also influence the likelihood of mortality from disease (La Peyre et al. 2003; 2009) or marine predators and parasites (Kimbro et al. 2017; Pusack et al. 2019), which may reinforce negative effects due to physiological costs of inappropriate salinities.

While we found a positive relationship between mean daily discharge and intertidal oyster counts one year later, this does not mean that higher river discharge universally leads to more oysters. During 2010-2019 we observed years with low discharge, and only infrequently encountered years of high discharge. Because of this restricted observed range of discharge during our period of oyster count collection, we could not document the relationship between higher average discharge and oyster counts. Figure 7 must be carefully considered (as it may be misleading) as there are many factors in addition to river discharge that could be limiting factors for oyster populations. Indeed, higher river discharge levels can lead to lower salinity and lower spat production (Chatry et al. 1983) for many of the same reasons that high salinity can be deleterious (Kimbro et al. 2017; Pusack et al. 2019). Thus, the relationship between river discharge and oyster counts is not universally representative across all discharge values and is highly dependent on other factors including availability of suitable substrate.

This paper demonstrates a relationship between river discharge and oyster counts, but freshwater inputs are just one of several factors likely necessary for resilient oyster populations. A key limiting factor for oyster spat distribution in Suwannee Sound is the availability of suitable substrate for oyster spat settlement and growth (Frederick et al. 2016). Frederick et al. (2016) demonstrated in a small pilot project that the placement of limestone boulders on a section of the degraded Lone Cabbage oyster reef led to increased oyster spat and oyster recruitment on the reef site. This demonstrates the necessity of having suitable substrate for oyster spat settlement and reef growth which is at present being tested on a larger scale and may be important in other Florida estuaries (Pine et al. 2015). Overall, the limiting factors for oyster reef creation, persistence, collapse, restoration, and recovery remain unclear.

Oyster disease, parasites, and predators have existed in this (and other) systems for much longer than the 60+ years of river discharge records available for the Suwannee River. Climatological assessments over the scale of centuries suggest that the Suwannee River basin overall has experienced periods of much drier conditions (Harley et al. 2017) particularly during the 16th and 18th centuries, with river discharge likely less than 20% of the mean estimated from the instrument period of record - yet oyster populations survived in this region. Oyster reefs in and around Lone Cabbage reef have persisted for 2800-4000 years (Grinnel 1972; Wright et al. 2005) including time with extensive human occupation and oyster harvest (Sassaman et al. 2017). One key concern is that while oyster populations may have recovered historically from episodic mortality due to drought, disease, or other factors, this resilience may have declined. Examples of resilient processes would include buffering of salinities by reef structures (Kaplan et al. 2016), or recolonization through oyster metapopulation dynamics, or presence of a large, persistent capital of settlement substrate (Pine et al. 2015). If resilience has declined in Big Bend oyster reefs, and disturbance continues to occur, these conditions may foment an increased risk of hysteresis where multiple “states” of oyster populations may exist across similar environmental conditions. Modeling efforts by Pine et al. (2015) suggest that in absence of suitable substrate for settlement and growth, even with “average” recruitment levels of Apalachicola Bay oyster populations were not predicted to reverse declining population trends. Given the recent, rapid collapse of oyster populations across many Gulf of Mexico estuaries, the loss of resilience is of central ecological and management concern. This study demonstrates that even with relatively few anthropogenic stressors in a highly protected coastal environment oyster populations may be at risk of rapid change.

Our assessment of trends in Suwannee River discharge metrics over the instrument period of record suggests increasing volatility in river discharge (CV) and an overall downward trend in river discharge. The reasons for these trends are unknown, but an examination of trends in the Palmer Drought Severity Index for the southeast Georgia and north Florida regions covering the Suwannee River basin suggest rainfall drought has occurred several times in this region since 2010 (Figure S3a). There is also evidence that the discharge/rainfall ratio has been declining (Seavey et al. 2011) or that evapotranspiration is increasing (or both) possibly influencing temporal trends in discharge. The relationship between frequency and severity of drought and oyster reef resilience is an important area of future research.

We are unable to determine an age-structure for oyster populations, so we do not know if oyster counts represent multiple oyster year-classes or not. This is important because it would help to determine whether lower counts are a function of year-class failure in the year of low river discharge, or if multiple year-classes were affected. Other than the irregular monitoring effort we report here, fishery independent data for oyster populations in Suwannee Sound are absent. Since we only sampled intertidal reefs, we also do not know if these dynamics extend to inter and subtidal oysters of multiple age classes and sizes which may be affected by these same factors. Our only other line of inference for both inter-and subtidal population trends over this time are from landings data. These data suggest overall declines in landings and catch-per-effort in the years following the implementation of the trip ticket program in 1986. Over the same time period as these monitoring efforts, oyster landings and effort have increased, and catch per unit of effort has generally declined. In our study, neither harvest status (open/closed) nor annual landings or effort influenced oyster counts. This may suggest that fishing plays less of a role in these intertidal oyster bars than climate-related factors such as river discharge. The interpretation of this result is complicated result because it is unclear how much harvest occurs on intertidal reefs even in areas open to harvest. In addition to traditional harvest, state funded programs that relocate oysters from intertidal to subtidal areas ("relay") have been used as an approach to increase oysters available for harvest in our study area The net effect of both traditional harvest on legally open reefs, and directed harvest through relay programs on closed reefs is unknown. The effects of fishing on oyster populations both through direct harvest or indirect effects (i.e., discard mortality, loss of spawning stock biomass or shell area) is an area requiring substantial future work.

Seavey et al. (2011) documented large declines of about a 66% net loss in oyster reef area in the Suwannee Sound region from 1982-2011. This work documented highest declines in offshore reefs with about an 88% decline, followed by nearshore reefs (-61%), and inshore (-50%). Our oyster density results over time and space also show declines in oyster counts with the largest declines occurring in inshore areas, which may be becoming more similar to offshore and nearshore regions based on counts. (Figure 3). What is not known is whether these inshore losses are offset by formation of new reefs elsewhere, although this could possibly be assessed through satellite, drone based, or other surveys (Grizzle et al. 2018; Windle et al. 2019). Seavey et al. (2011) reported inland colonization of salt marsh by oysters in inshore areas of Suwannee Sound, but those increases did not offset net losses experienced in nearshore and offshore reefs. Successional habitat processes have been observed in this region with the conversion of coastal forest to marsh as well as loss of coastal forest communities over the course of decades (Geselbracht et al. 2011; Raabe and Stumpf 2016). At longer time scales, oyster reef distribution along the west coast of Florida has been shown to be quite dynamic in time and space, with Locker et al. (2016) documenting fossilized oyster communities in what is now 116-135 m of water along the central west-Florida shelf. Hine et al. (1988) described the complex interactions between geology, currents, and the formation and persistence of oyster reefs along the west coast of Florida and suggested that seaward oyster reefs are the ones most susceptible to degradation due to higher salinity levels, marine predators, and wave action. These predictions were supported by Wright et al (2005) who identified that most of the oyster bars in Suwannee Sound developed from deltaic sediment deposits. Seavey et al. (2011) showed that once an oyster reef degrades to the point of losing the covering of shell, the likelihood of that reef reforming and persisting is very low, at least over a period of a decade. This scenario was reinforced by the findings of Frederick et al. (2016) who showed experimentally that addition of limestone substrate to the degraded Lone Cabbage reef resulted in a rapid and substantial recruitment of oysters.

<B>Implications

Our findings suggest that landscape level factors including trends in river discharge likely influence intertidal oyster populations, but the mechanisms are not known. From a freshwater management perspective, river basin level planning efforts in terms of minimum flows and levels are in place or underway to inform water management decisions within the Suwannee River basin (Suwannee River Water Management District [SRWMD] 2019). Long-term forecasts of water demand in areas near the Suwannee Basin and across north Florida and southeast

Georgia suggest increased demand and lower ground water levels (see https://northfloridawater.com/). In both cases the time horizons for decision making and implementation of large-scale water infrastructure projects is likely longer than the time scale (<10 years) documented here of oyster population change in Suwannee Sound. At shorter monthly or annual time scales, there is potential for expanded restoration actions that would possibly both increase oyster populations by providing substrate, and at the same time reduce loss of freshwater through coastal impoundment (Frederick et al. 2016). However, these restoration programs are expensive (>$1m/km for Suwannee Sound) and seem unlikely at least at the scale of restoration needed to replace estimated losses of oyster habitat. At century time scales, sea-level rise may negate many short-term benefits of reef restoration because reefs may become inundated with higher salinity water. Observed sea-level rise in this region based on a 100-year record is on average about 2.13 mm/yr (95% CI 1.95-2.31 mm/year; Figure S3c) but the observed rate in recent years is higher (Figure S3c). Simply put, restoration efforts could be swamped by rising sea-level regardless of river discharge conditions.

There are at least two options going forward from a management perspective, but neither is a clear choice as to which is “best” in terms of long-term viability of oyster reefs in Suwannee Sound. One option is to evaluate ongoing restoration efforts (Frederick et al. 2016) and if these are successful, work to implement similar programs at larger spatial scales to replace substrate and ecosystem function that is being lost with declining oyster reefs. The second is to assess whether this landscape is simply undergoing a successional process as has happened in the past. This succession could involve the migration of oyster reefs following change in sea levels, as they have occurred previously (Locker et al. 2016; Sassaman et al. 2017)

– perhaps now at a faster rate and with people recording observations in close to real time. Given large areas of undeveloped public land and low shoreline gradient in this region, the potential certainly exists for migration of oyster habitat into what is at present inland areas. However, this migration would occur at the cost of these inland habitats – which may be inevitable under several sea-level scenarios (Geselbracht et al. 2011). These types of decisions, to implement restoration for short-term gain to delay long-term losses due to sea-level rise, are among the most complicated management decisions to be addressed in both the natural and built environments in upcoming decades. Whether decisions are made, and actions taken before irreversible losses of oyster resources occurs in Suwannee Sound remains unknown.

<A>Acknowledgements

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TABLE 1. Model selection table for GLM (Generalized Linear Model) models of oyster count data from intertidal reefs in the Big Bend of Florida, without covariates. AIC (Akaike Information Criteria), Delta AIC, and AIC Weights are provided to inform comparisons of model statistical fit to data.

Model	Number of parameters	AIC	Delta AIC	AIC Weight
Period * locality + site	11	3185.65	0.00	0.94
Period + site	5	3192.36	6.71	0.03
Period + locality + site	8	3193.41	7.76	0.02
Period * site	7	3196.27	10.62	0.00
Period + locality * site	14	3196.62	10.97	0.00
Period * site + locality	10	3197.27	11.63	0.00
Period + locality	6	3259.43	77.78	0.00
Period	3	3263.49	77.84	0.00
Period * locality	9	3263.51	77.86	0.00

TABLE 2. Model results for the best fitting GLM (Generalized Linear Model) model without covariates (Table 1) of oyster counts on intertidal reefs in the Big Bend of Florida, where oyster counts = period * site + locality + offset(log(transect length)). Parameter estimates are on log scale.

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	5.18	0.38	13.57	< 0.01
Period	-0.10	0.03	-2.79	0.005
Nearshore site	-1.57	0.21	-7.38	< 0.01
Offshore site	-1.85	0.21	-8.99	< 0.01
Corrigan’s Reef	-0.06	0.43	-0.14	0.89
Horseshoe Beach	-0.38	0.43	-0.89	0.37
Lone Cabbage	-1.21	0.42	-2.87	<0.01
Period: locality Corrigan’s Reef	0.03	0.05	0.60	0.55
Period: locality Horseshoe Beach	-0.001	0.05	-0.02	0.98
Period: locality Lone Cabbage	0.11	0.004	2.76	< 0.01

TABLE 3. Model selection table assessing improvements in the fit of best fit GLM (Generalized Linear Model) model from Table 1 (oyster counts = period * locality + site + offset(log(transect length))) with the addition of covariate described.

Covariate description	Number of parameters	AIC	Delta AIC	AIC Weight
Mean annual daily discharge with one-year lag	12	3154.37	0.00	0.50
Annual landings with two-year lag	12	3175.76	21.38	0.00
Annual discharge year of count	12	3176.98	22.61	0.00
Annual trips with two-year lag	12	3178.02	23.64	0.00
Annual landings year of count	12	3178.90	24.53	0.00
Annual trips year of count	12	3184.47	30.10	0.00
No covariates	12	3185.65	31.27	0.00
Harvest in year of count	12	3185.86	31.49	0.00
Annual discharge with two-year lag	12	3186.51	32.13	0.00
Annual trips with one-year lag	12	3186.89	32.51	0.00
Landings with one-year lag	12	3187.05	32.68	0.00

TABLE 4. Model results for the best fitting GLM (Generalized Linear Model) model (Table 3) of oyster counts on intertidal reefs in the Big Bend of Florida where oyster counts = period * locality + site + mean daily discharge with one-year lag + offset(log(transect length)). Parameter estimates are on log scale.

	Estimate	Standard Error	z value	Pr(>|z|)
Intercept	5.59	0.37	15.23	< 0.01
Period	-0.12	0.03	-3.84	< 0.01
Nearshore site	-1.67	0.20	-8.33	< 0.01
Offshore site	-2.15	0.20	-11.03	< 0.01
Corrigan's Reef	-0.16	0.41	-0.40	0.69
Horseshoe Beach	-0.60	0.41	-1.47	0.14
Lone Cabbage	-1.52	0.40	-3.80	< 0.01
Mean daily discharge with one-year lag	0.56	0.08	6.88	< 0.01
Period: locality Corrigan's Reef	0.04	0.04	0.99	0.32
Period: locality Horseshoe Beach	0.01	0.04	0.22	0.83
Period: locality Lone Cabbage	0.12	0.04	3.21	0.001

Table S1. Period surveyed for each locality and site combination.

Locality	Site	Period	Time
CK	I	1	Summer 2010
CK	I	6	Winter 2012-2013
CK	I	17	Summer 2018
CK	N	1	Summer 2010
CK	N	6	Winter 2012-2013
CK	N	17	Summer 2018
CK	O	1	Summer 2010
CK	O	6	Winter 2012-2013
CK	O	17	Summer 2018
CR	I	1	Summer 2010
CR	I	2	Winter 2010-2011
CR	I	3	Summer 2011
CR	I	6	Winter 2012-2013
CR	I	17	Summer 2018
CR	N	1	Summer 2010
CR	N	2	Winter 2010-2011
CR	N	3	Summer 2011
CR	N	6	Winter 2012-2013
CR	N	17	Summer 2018
CR	O	1	Summer 2010
CR	O	2	Winter 2010-2011
CR	O	3	Summer 2011
CR	O	6	Winter 2012-2013
CR	O	17	Summer 2018
HB	I	1	Summer 2010
HB	I	2	Winter 2010-2011
HB	I	3	Summer 2011
HB	I	6	Winter 2012-2013
HB	I	17	Summer 2018
HB	N	1	Summer 2010
HB	N	2	Winter 2010-2011
HB	N	3	Summer 2011
HB	N	6	Winter 2012-2013
HB	N	17	Summer 2018
HB	O	1	Summer 2010
HB	O	2	Winter 2010-2011
HB	O	3	Summer 2011
HB	O	17	Summer 2018
LC	I	1	Summer 2010

LC	I	2	Winter 2010-2011
LC	I	3	Summer 2011
LC	I	6	Winter 2012-2013
LC	I	16	Winter 2017-2018
LC	I	17	Summer 2018
LC	N	1	Summer 2010
LC	N	2	Winter 2010-2011
LC	N	3	Summer 2011
LC	N	6	Winter 2012-2013
LC	N	16	Winter 2017-2018
LC	N	17	Summer 2018
LC	O	1	Summer 2010
LC	O	2	Winter 2010-2011
LC	O	3	Summer 2011
LC	O	6	Winter 2012-2013
LC	O	7	Summer 2013
LC	O	10	Winter 2014-2015
LC	O	11	Summer 2015
LC	O	14	Winter 2016-2017
LC	O	16	Winter 2017-2018

Figure 1. Map of the study area, showing locations of sampling sites within localities of major oyster reef complexes. Within each locality, note that transects were placed on reefs representing a gradient from inshore to offshore. For offshore reefs, note the coastwise orientation and linearity of reefs.

Figure 2. Histogram of probability density function (y-axis) of live oysters counted (x-axis) on intertidal reefs in Suwannee Sound, Florida. The red line represents the predicted density of oyster counts if these data follow a negative binomial distribution.

Figure 3. Predicted oyster counts using the best-fit negative binomial model offset by transect length from each locality CK = Cedar Key, CR = Corrigan's reef, HB = Horseshoe Beach, and LC = Lone Cabbage based on data from 2010-2019. Colored lines represent Inshore (red), Nearshore (blue), and Offshore (green) sites within each locality. Shaded regions represent 95% CI on the predicted values.

Figure 4. Mean daily discharge by year (panel A) and associated variance (panel B) and CV (panel C) of daily discharge for the Suwannee River measured at USGS Wilcox gauge from October 1941 to December 2018. Red LOWESS (Locally Weighted Scatterplot Smoothing) line provided to show general trends in discharge. Blue dashed line is the average mean daily discharge, variance, or CV from 1941-2018.

Figure 5. Mean daily discharge by year (panel A) and associated variance (panel B) and CV (panel C) of daily discharge for the Suwannee River measured at USGS Wilcox gauge from January 2010 to December 2018. Red LOWESS (Locally Weighted Scatterplot Smoothing) smoothing line provided to show general trends in discharge. Blue dashed line is the average mean daily discharge, variance, or CV from 1941-2018.

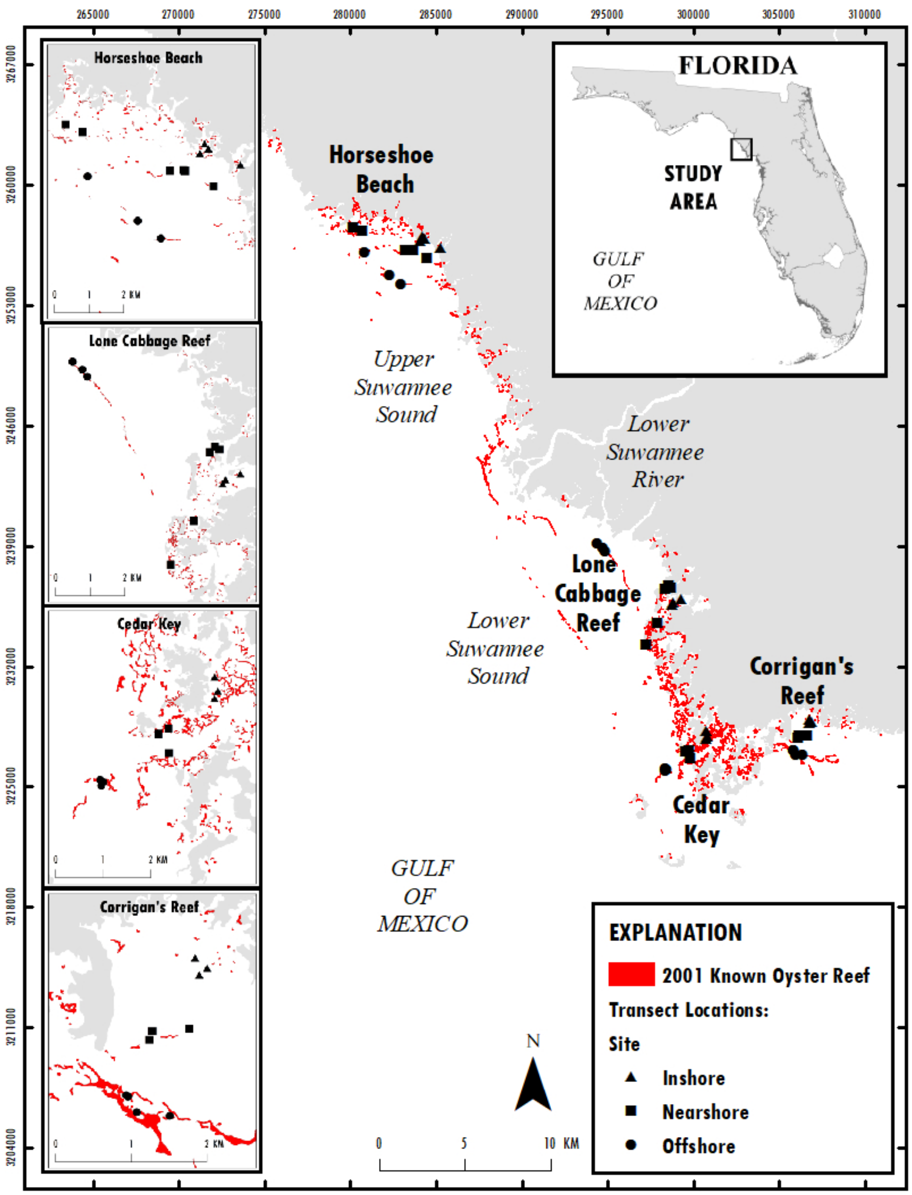
Figure 6. Oyster landings (whole meat weight, panel A), oyster fishing trips (panel B), and oyster catch per trip (CPUE, panel C) for Suwannee Sound, Florida (Levy, Dixie, Taylor counties) from 1986-July 2019. Data for 2018 and 2019 are provisional.

Figure 7. Predicted oyster counts using the best-fit negative binomial model offset by transect length including mean daily discharge with a one-year lag as a covariate. Shaded regions represent 95% CI on the predicted values.

Figure S1. Predicted oyster counts using the best-fit negative binomial model offset by transect length (oyster counts = period * locality + site + offset(log(transect length))) fit to 1000 simulated data sets (black lines) for all localities combined based on data from 2010-2019. Solid blue line is predicted values fit to observed (actual) field data.

Figure S2. Kernel density plot (y-axis) and p-value (x-axis) for the “period” beta term fit to the model oyster counts = period * locality + site + offset(log(transect length)) from 1000 simulated datasets.

Figure S3. Panel A: Monthly Palmer drought severity index (y-axis) for north Florida (red line) and southeast Georgia (black line) by year (x-axis). Negative values indicate periods of drought and positive values periods of higher soil moisture. Data from NOAA 2019c. Panel B: Monthly mean sea level (y-axis, solid black line) over year (x-axis) from NOAA station 8727520, Cedar Key, Florida with a linear model (dotted black line) plotted for reference. Average seasonal cycle removed by NOAA (NOAA 2019b).



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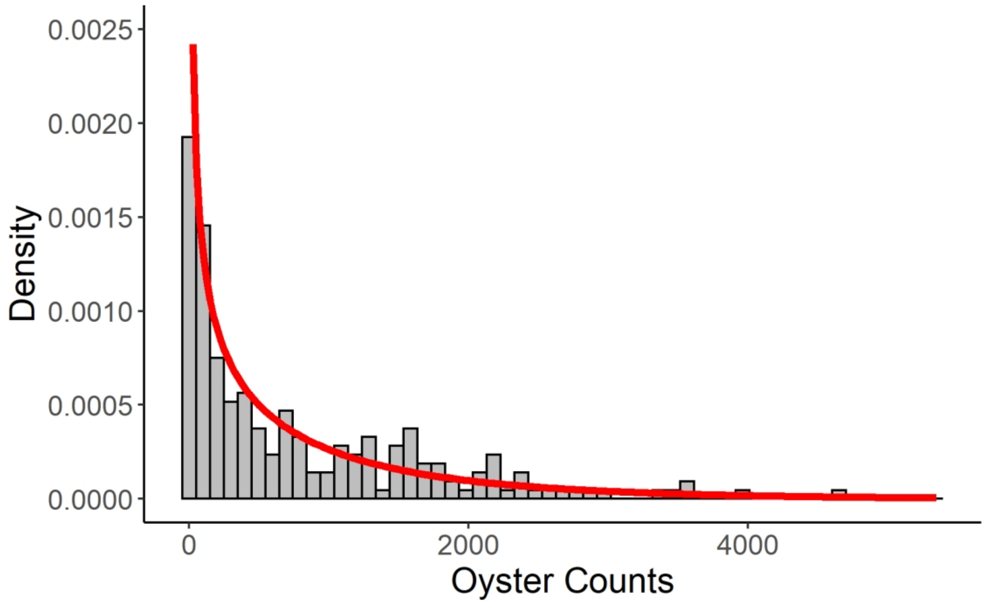

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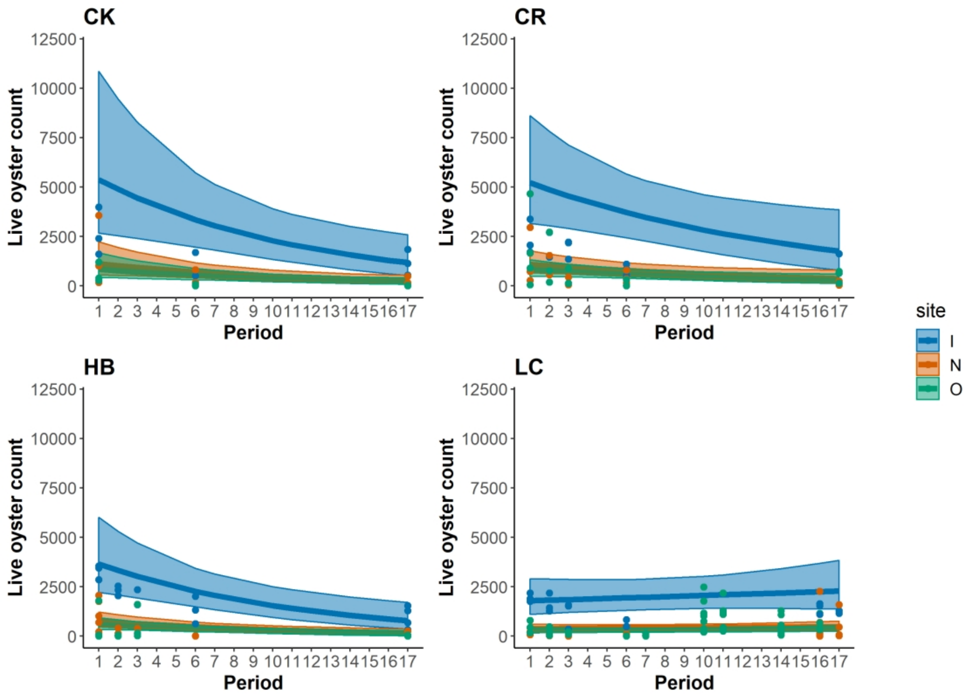

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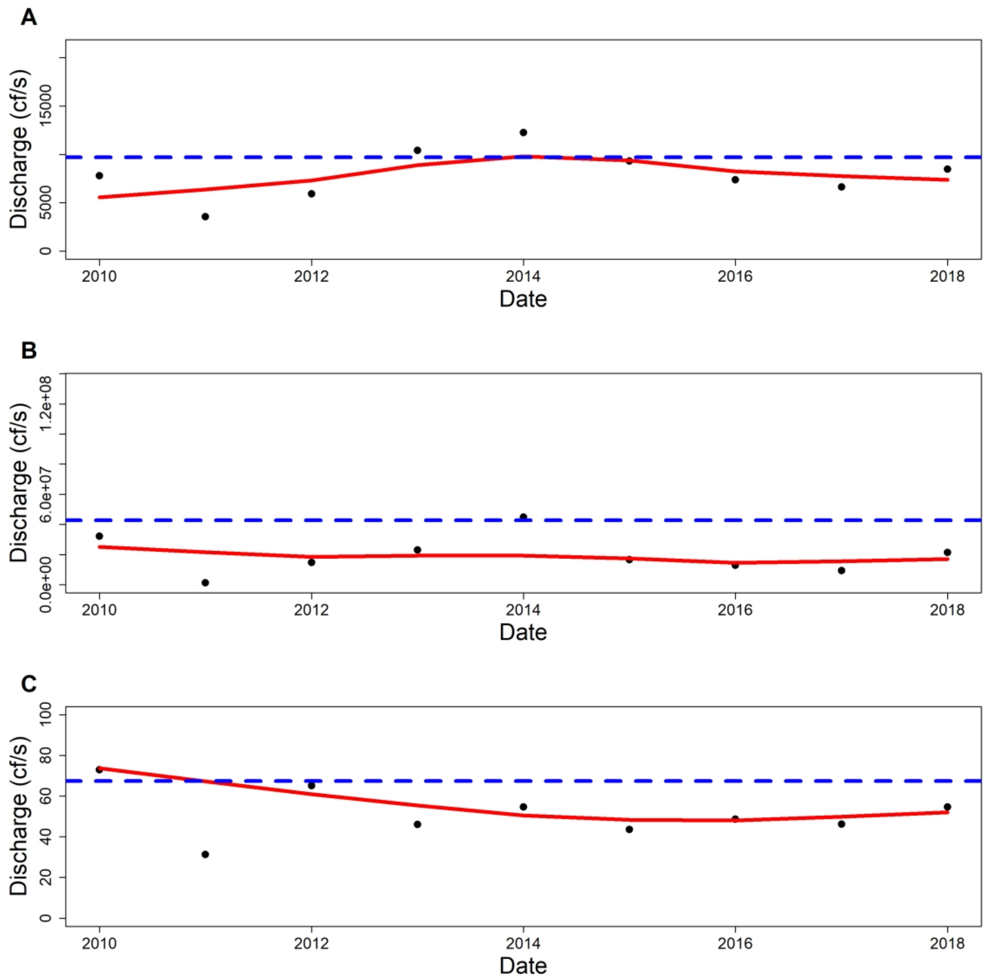

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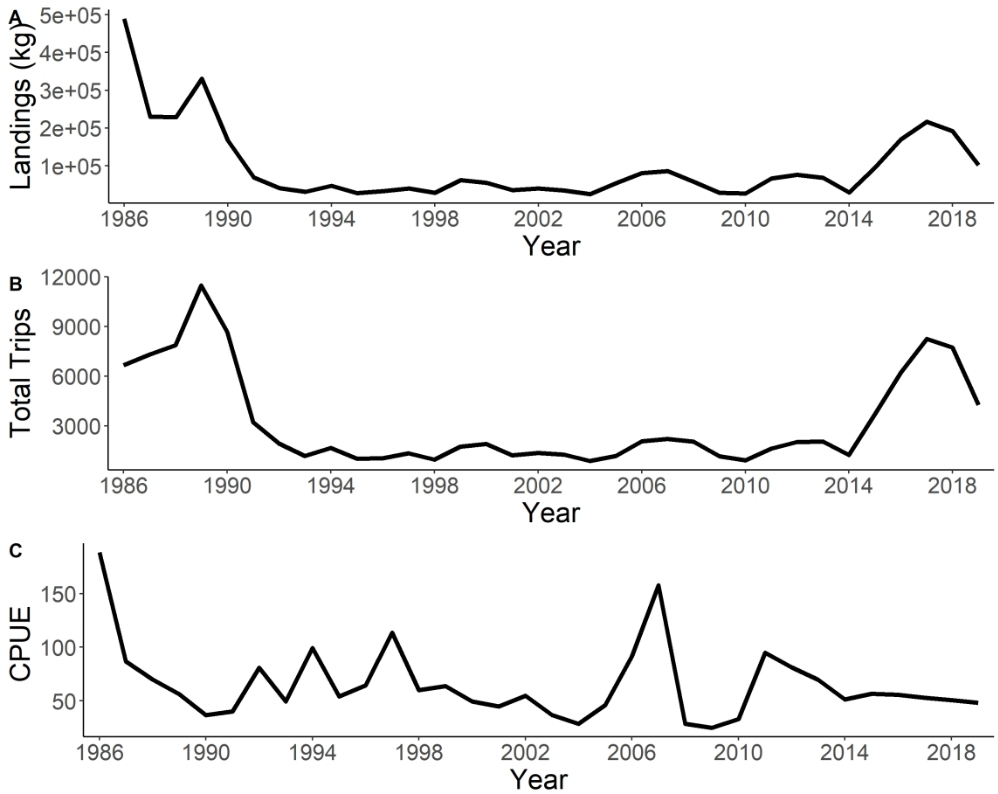

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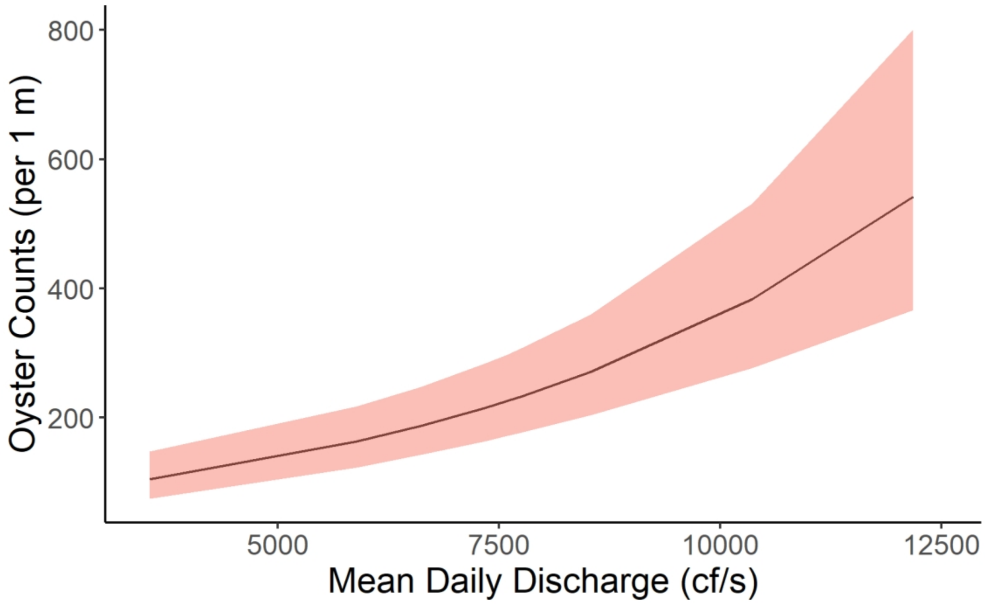

Figure 7. Predicted oyster counts using the best-fit negative binomial model offset by transect length including mean daily discharge with a one-year lag as a covariate. Shaded regions represent 95% CI on the predicted values.

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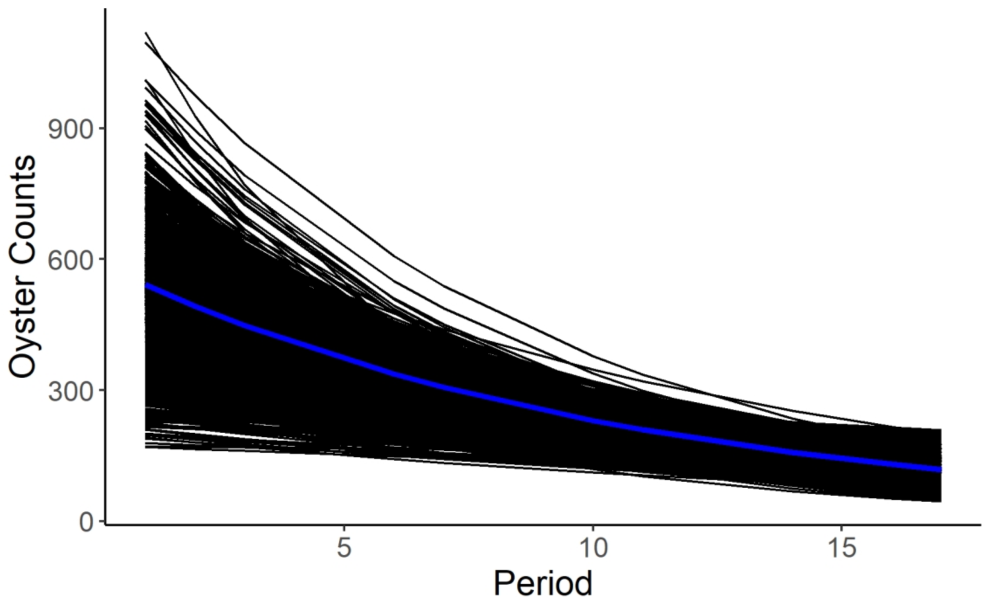

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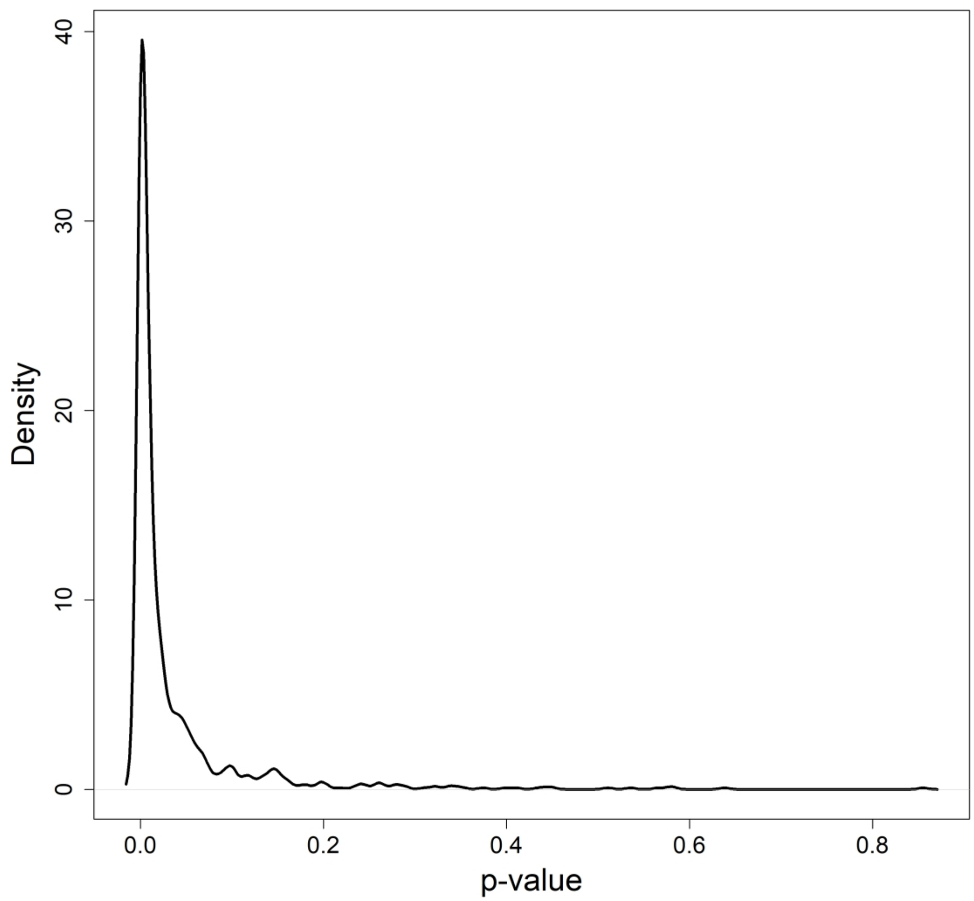

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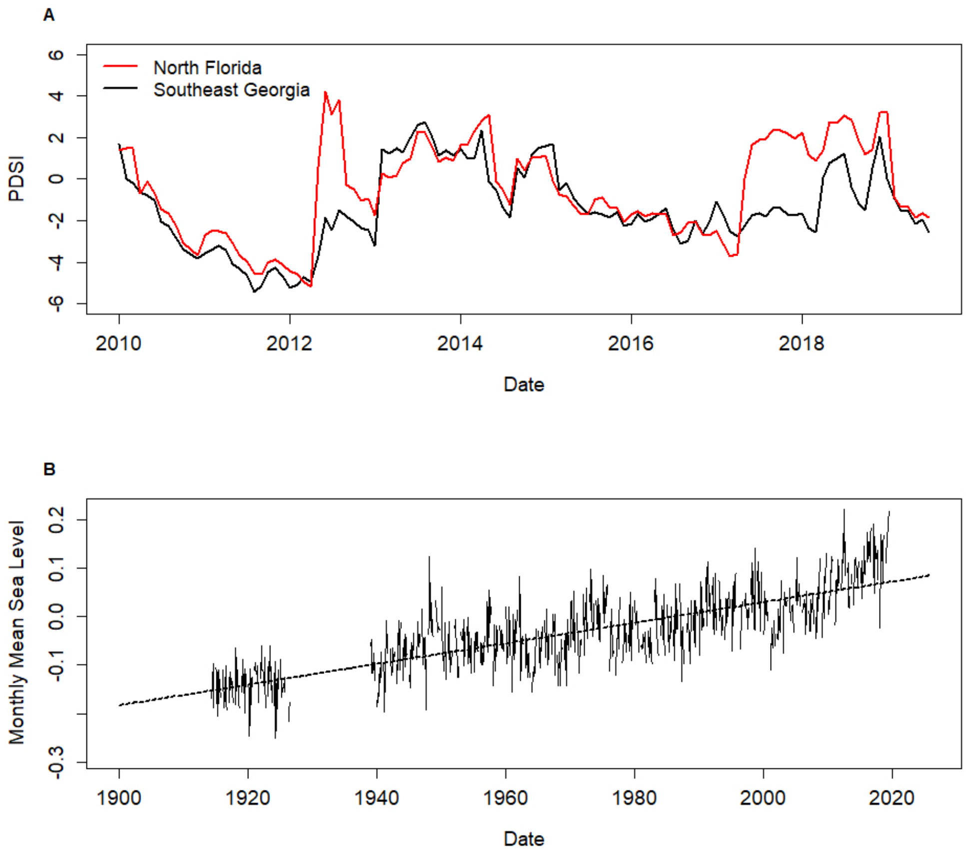

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