A decade of biodiversity change in an estuarine assemblage: fits and starts and natural events

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# Abstract

Anthropogenic activities continue to exert long-term, varied, and increasing pressures on marine ecosystems causing alterations to biological diversity on broad and local scales. Shifts in biodiversity are variable, nuanced and difficult to predict, yet, understanding how communities change through time is crucial for predicting current and future changes to biological systems and the services they provide. We document a decade of biodiversity change in a shallow estuarine nekton community…

# Introduction

Anthropogenic activities continue to exert long-term, varied, and increasing pressures on ecosystems (Steffen et al. 2015) causing alterations to biological diversity on local and global scales. Shifts in biodiversity at local scales are variable and potentially more nuanced than at global scales, but generally local changes manifest primarily as changes to community composition and structure rather than declines in richness (Hillebrand et al. 2018). These shifts in communities through time are difficult to predict, in part, due to the multidimensional nature of biodiversity (Chase et al. 2018). Yet, understanding how communities change through time is crucial for predicting current and future changes to biological systems and ecosystem services.

Explaining the extent and pace of biodiversity change will require identifying the conditions that lead to divergent biological responses to environmental change, both natural and anthropogenic. In particular, it will be important to disentangle the roles of intrinsic (e.g., ecological) and extrinsic (e.g., environmental) drivers of biodiversity change. Intrinsic and extrinsic processes can interact, leading to temporal patterns of biodiversity change that vary in response to environmental change. For example, gradual environmental change over time can lead to gradual community shifts or these shifts may be undetectable or abrupt (Scheffer and Carpenter 2003, Williams et al. 2011).

Disentangling the complexity of drivers and responses in community structure is especially pressing for marine systems. Marine systems have experienced greater changes than other habitats (Antão et al. 2020). Yet, we currently lack linkages between ecological theory, primarily derived from terrestrial systems, and data in marine systems leaving unanswered questions about biodiversity changes in these habitats (Blowes et al. 2019). We propose a framework to explore the nature of biodiversity change in an estuary bay community and connect this change to intrinsic and extrinsic drivers. This research will build towards a more coherent theory of biodiversity change through time (Shoemaker et al. 2020).

Here, we quantified biodiversity changes within a shallow estuarine community over a decade to understand shifts in total species richness, the relative distribution of abundant and rare species, and potential change points in community composition through time…

# Methods

## Sampling area

This study was focused on Terrebonne Bay, located in the northern Gulf of Mexico of Louisiana, USA (2911.200’N, 9036.560’W; Figure S1). Terrebonne Bay is a broad (1,761 km2), shallow estuary (average depth ~2m), separated from the Gulf of Mexico by two barrier island chains and connected by four tidal passes. The bay-estuary complex is part of an abandoned distributary of the Mississippi River and therefore no longer receives significant riverine inputs. Thus, the majority of its freshwater inputs are from the local drainage basin (Bianchi et al. 2009). While water column salinity and density are homogeneous, strong salinity gradients exist seaward from the marsh to the barrier islands (Bianchi et al. 2009). Tides in Terrebonne Bay are diurnal with a semidiurnal component, ranging 20-80 cm (Inoue and Wiseman 2000).

## Trawl sampling

Trawl sampling was conducted as part of the Louisiana Universities Marine Consortium’s (LUMCON) educational outreach program (<https://www.lumcon.edu/education-and-outreach>) from 2009 to 2019. Individual trawls were conducted using *trawl apparatus description…* for 10 - 20 min. To dampen potentially volatile trawl-to-trawl variability, we combined all trawls monthly and therefore report changes based on monthly aggregated trawl sampling.

## Community characterization

Species names were checked for typos and confirmed using the *gni\_parse* function from the *taxize* package (Chamberlain et al. 2020) and further standardized to consistent taxonomic resolution for the entire data series (Supplemental materials). To track trends in species richness through time, we calculated effort-controlled species richness, *Sn*, which provides the expected number of species given a defined number of *n* randomly sampled individuals (Gotelli and Colwell 2001). For annual and monthly *Sn* calculations, *n* was set as the minimum number of individuals sampled. We also calculated the uncorrected accumulation of species over time by filtering species from the data set after first occurrence. We then calculated asymptotic species richness, *Sasymp*, using the Chao1 estimator (Chao 1987, **chao1984?**). This metric is highly correlated with measured richness, *S* (**mcgill2011?**), but attempts to extrapolate the total species richness based on incomplete sampling of the community. We calculated *Sasymp* and *Sn* using the mobr package (McGlinn et al. 2021, **mcglinn2019?**).

Beyond actual and expected numbers of species, we calculated additional measures of biodiversity to capture community change through time. We estimated community turnover, the combination of gains and losses relative to total species richness, and the contributions of species gains and losses using the codyn package (Hallett et al. 2020). To quantify changes in the distribution of abundant and rare species, we calculated specific orders of diversity, the percentage of rare species, and evenness in species abundances. An order of diversity, *qD*, where *q* represents a non-negative integer, captures the “effective numbers of species” based on varying degrees of rarity of the species in a community (Hill 1973). We used the the *hill\_taxa* function in the hillR package (Li 2018) to estimate the effective species for diversity order 2 (i.e., *2D*). *2D* is equivalent to the reciprocal of Simpson’s diversity (Simpson 1949) (i.e., 1/Simpson’s index) which emphasizes the importance of dominant (highly abundant) species. At the other end of the abundance spectrum, we calculated the percentage of rare species in the community as the number of species with abundances below a threshold of , divided by the total number of species x 100. Here, *n* is the number of individuals in the sample and the value of 0.05 was chosen because it has been shown to capture rarity well and is generally uncorrelated with other metrics of biodiversity. Lastly, to integrate changes in abundance of dominant and rare species within the community, we calculated the evenness of species abundances with the Gini coefficient (Gini 1921), normalized for differences in species richness among years, (Solomon 1975, Chao and Ricotta 2019), :

where, in a community of *S* species, species’ relative abundances, , are ordered such that for all species of the community. For all metrics, variability was calculated with bootstrapping methods by resampling with replacement 99 times. From these permutations the 2.5% and 97.5% percentiles of yearly statistics were taken to estimate 95% percentile intervals.

We calculated the contribution of each species to community dis/similarity across orders of diversity

## Statistical Analyses

To detect trends in species richness and other dimensions of biodiversity (e.g., turnover, evenness, etc.) we used generalized additive models (GAMs) with a bayesian implementations using the mgcv (**wood2011?**) and brms packages in R (Bürkner 2017, **burkner2018?**). Full models included alinear term for trawl date and smoothing spline terms for month:

where, is the response variable (e.g., richness, turnover, evenness, etc.), is an intercept, a coefficient for trawl date, and represents seasonal smooth functions for month of year. Seasonal terms were fit with cyclic cubic regression splines with smoothing dimension *k* = 12 to allow for continuity between December and January among model years.

# Results

Over the sampling period from 2009 to 2019, 337 trawl-days were performed yielding 1.41e+05 individuals. Among years, total effort generally increased, both in number of trawl-days and individuals counted, from a minimum effort of 18 (2011) to 41 (2017) days and from 2145 (2010) to 2.51e+04 (2016) individuals. In total, 131 unique species were identified and new species were consistently observed throughout the sampling period (Figure S1). Within a calendar year, asymptotic species richness (*Sasymp*) was relatively stable from 2009 to 2012, reaching a minimum value of 41 in 2012. Estimated *Sasymp* increased in 2013 to a series maximum of 133 in 2016. However, given the large differences in effort among years, variability in *Sasymp* may be partly attributable to sampling effects among years. Therefore, we also calculated rarefied richness at 2145 individuals, *S2145*, for each year. Here, effort-controlled species richness, *S2145*, diverged qualitatively from *Sasymp* and was generally constant with an apparent slight increase in more recent sampling years. Overall, *S2145* ranged from 30.9 to 51.4 among all years. Monthly, of rarefied richness averaged 6.6 [range: 2.4–11.1] and exhibited seasonal oscillations, but no detectable trend over time (Figure 1A, Table S1).

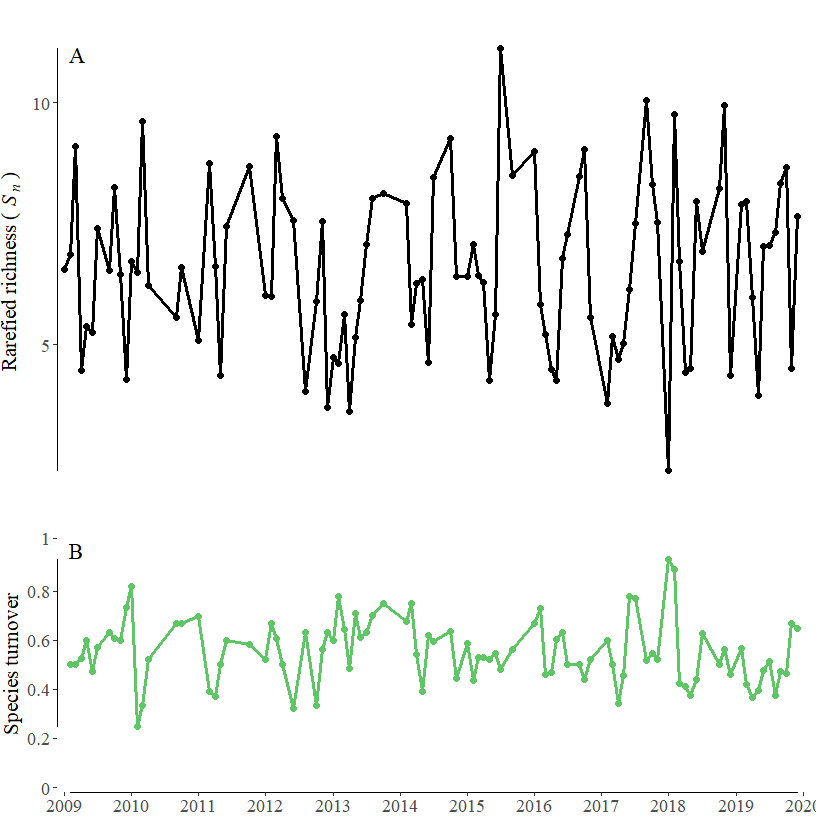


Figure 1. A) Rarefied species richness within the nekton community between the years 2009 to 2019 show variable, but consistent, numbers of species over time. B) Despite no trend in the total number of species, the trawl community showed continual turnover throughout.

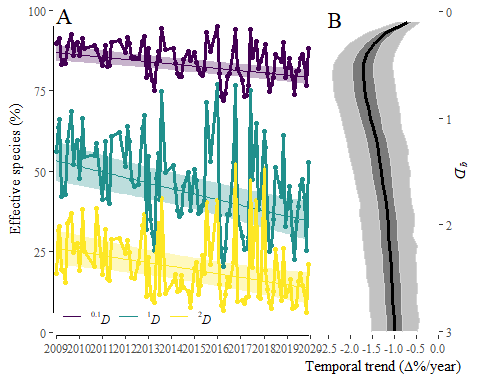


Figure 2. A) Temporal trends in the effective number of species of select orders of diversity (q = 0.1, 1,2). Effective species are presented as percentages of 0D, or species richness. 0.1D highlights the trends in the percentage of species considered very rare, while 1D treats rare and dominant species equally, and 2D highlights the number of dominant species in the community through time. 1D is equivalent to exp(Shannon-Weiner H) and 2D is equivalent to 1/Simpson’s diversity index. B) The estimated temporal trend for qD orders (q = 0.1–3) from conditional effects of time in generalized additive models. The black line represents the mean estimate surrouned by 25th and 75th (dark grey) and 5th and 95th percentiles (light grey) of the posterior distribution.

Consistent with the pattern of continued accumulation of new species throughout the sampling series and relatively stable effort-controlled richness, species gains (0.28 0.17 SD) and losses (0.28 0.17 SD) generally balanced over time. Total turnover was variable but relatively stable (0.55 0.13 SD) and exhibited no detectable trend or coherent seasonal component (Figure 1B). Species turnover was likely confined to species with moderate relative abundances. While we observed declines in the effective number of species for highly rare (0.1D; conditional effects -0.002, 95% CI: -0.003—0.001) and highly abundant species (2D; -0.003, 95% CI: -0.005—0.001), declines were greater for diversity orders describing moderately abundant species (0.5D; -0.005, 95% CI: -0.007—0.003, Figure 2). These changes in the distribution of relative abundances within the community led to a decrease in the community evenness through time (Figure X). Gini coefficients normalized for species richness varied from 0.055 to 0.448 and exhibited estimated declines from initial values of 0.226 (0.182–0.27 95% CI) to 0.129 (0.088–0.169 95% CI) in 2019.

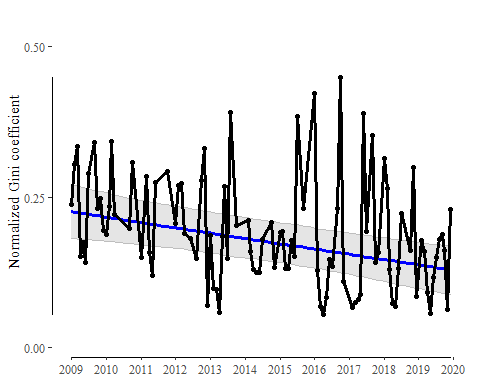


Figure 4. Evenness in species’ relative abundances normalized to species richness varied seasonally and exhibited a moderate decrease through time. The blue line represents the mean estimated trend surrounded by the 5th and 95th posterior percentile

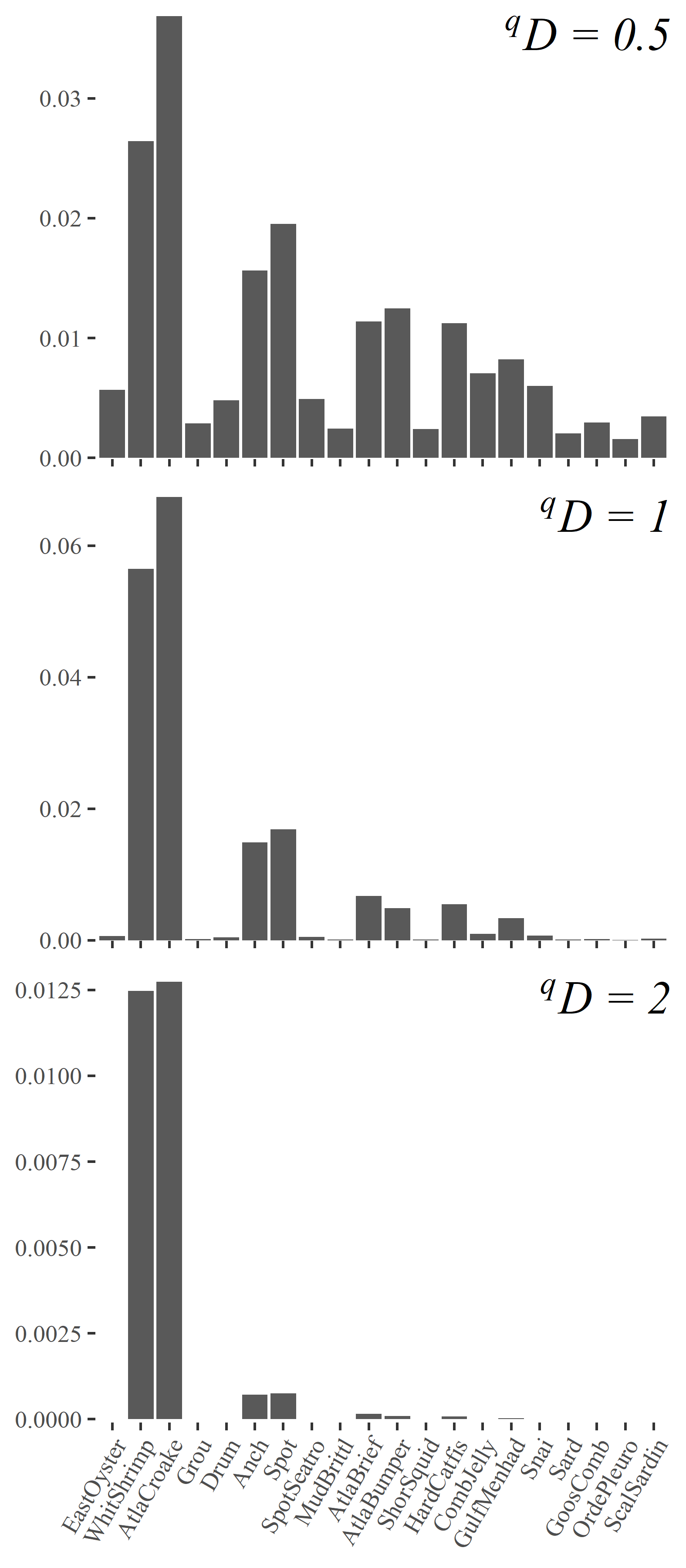


Figure 5.

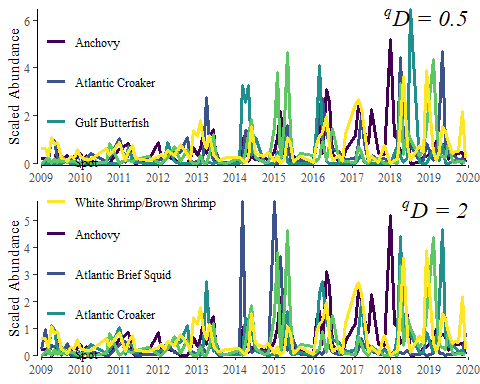


Figure 5. Scaled abundance of the species with the largest contribution to community dissimilarity within the timeseries at orders of diversity q = 1 (top) and q = 2 (bottom).

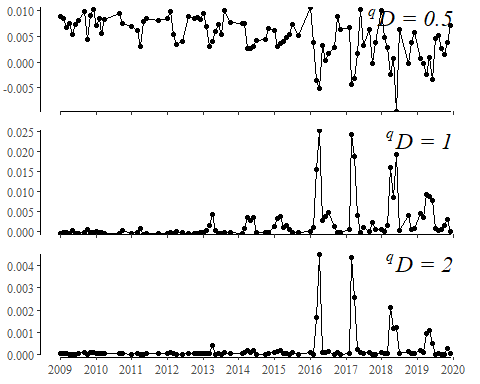


Figure 6. The contribution of individual trawl-dates to dissimilarity of the entire timeseries for diversity order q = 0.5 (top), q = 1 (middle), and q = 2 (bottom).

Changes in the estuarine community, in both rare and common species, were not evenly distributed among taxa (Figure 5). For example, dissimilarity in rarer species (i.e., low diversity orders, *0.1D*), was contributed by a relatively large number of species (~5 contibuted 1% to total dissimilarity) and individual species effects were relatively diffuse (largest contribution was 1.1). On the contrary, few species contributed to dissimilarity in more abundant species (~4 contribute 1% to total dissimilarity) and two taxonomic groups contributed `~90% to total dissimilarity (Penaeid spp. and *Micropogonias undulatus*).

Further, community changes were not equally distributed through time (Figure 6). New

# Discussion

# Acknowledgements

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# Appendix

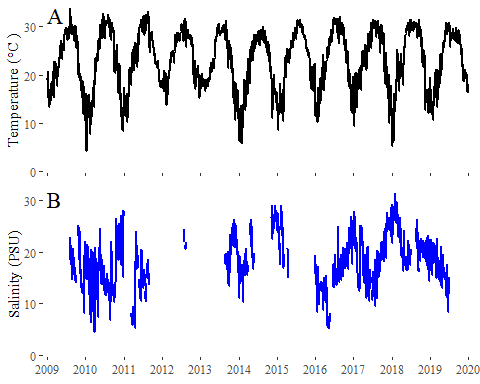


Figure S2. Time series of environmental variables a) water temperature and b) salinity measured at the Terrebonne Bay environmental monitoring station (XX N, XX W). Data were provided by the Environmental Monitoring department of LUMCON. Periods of no data in the salinity series represent periods of no data due to storm damage to monitoring stations.