Title: Food Web Response to Foundation Species Change in a Coastal Ecosystem

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Abstract

In the Northern Gulf of Mexico, black mangroves (*Avicennia germinans*) are expanding their range and replacing smooth cordgrass (*Spartina alterniflora*) as the dominant foundation species in estuarine systems. The impact this habitat transition has on the sources of primary production that contribute to the food webs of these areas is as of yet unclear. Here, we used stable isotopes and Bayesian mixing models to determine the contributions of primary production sources to the food webs in Louisiana saltmarshes currently experiencing rapid mangrove encroachment. In addition, we determined how these contributions are altered as a function of foundation species cover, particularly for white shrimp (*Litopeneaus setiferus*). Species primarily rely on algae-derived and water-column derived production, not on production derived from the foundational macrophytes themselves. White shrimp trophic position increased in areas with higher mangrove cover at some locations; shrimp used more water column-derived production and less algae-derived production. Transition from *Spartina* to mangrove-dominated estuarine areas has little effect on the overall pattern of primary producer contribution to food webs in these areas. However, differences in the structural and substrate properties of these foundational species could be altering the way energy moves through food webs.

1. Introduction

In many ecosystems, foundation species can be the primary control on a number of ecosystem functions, including the production of energy, nutrient cycling, and the availability of habitat (Baiser et al., 2013; Ellison et al., 2005; Van der Putten, 2012). Foundation species are typically primary producers, with the notable exception of certain aquatic invertebrates (e.g. corals and bivalves), that create the physical setting used by consumers in an ecosystem. The literature is replete with the non-trophic effects of foundation species, from altering micro-climates to whole system effects on biodiversity and species distributions (Allesina and Pascual, 2009; Baiser et al., 2013; Martin and Goebel, 2013). However, we know less about effects that foundation species change exerts on food webs.

In coastal ecosystems, foundation species such as seagrasses, saltmarsh cordgrass, and mangroves, were most often thought to contribute to food webs via the detrital pathway, giving rise to the phrase "Detritus Based Ecosystems" (Odum et al., 1982; Odum and Heald, 1975; Zieman et al., 1984). While that view is still widely accepted, recent work paints a more complex picture showing that epiphytic and benthic microalgal sources are often the dominant sources of primary production in these systems (Nelson et al., 2012, 2015; Odum and Heald, 1975). Regardless if foundation species contribute to the food web via the detrital pathway, or by providing structure that supports epiphytic production, change in the dominant foundation species may alter food web structure or energy flow.

Black mangroves (*Avicennia germinans*) are expanding into northern Gulf of Mexico marshes that have historically been dominated by smooth cordgrass (*Spartina alterniflora).* Although *A. germinans* has occurred periodically in the northern Gulf of Mexico (Odum et al., 1982; Stuart et al., 2007), since 1986 black mangrove habitat has increased nearly 25-fold in Louisiana alone (Michot et al., 2010; Perry and Mendelssohn, 2009). These expansions are catalyzed by milder winters, increased water temperature, and drought induced dieback of *S. alterniflora* (Comeaux et al., 2012; Osland et al., 2013). Each of these drivers are linked to climate warming, thus expansion of black mangroves will likely continue (Armitage et al., 2015; Cavanaugh et al., 2014).

S. alterniflora-dominated wetlands in the northern Gulf of Mexico, particularly those in Texas and Louisiana, are critical nursery areas for a number of species including commercially important penaeid shrimp, white shrimp (*Litopenaeus setiferus*) and brown shrimp (*Farfantepenaeus aztecus*) (Zimmerman et al. 2000, Baker et al. 2014). Quantitative sampling of estuarine habitats supports this notion with the highest densities of brown shrimp and white shrimp, 10.4 m^{-2} and 10.3 m^{-2}, respectively, in polyhaline *S. alterniflora* marsh edge, compared with densities of 3.9 m^{-2} and 5.0 m^{-2} in mixed vegetation marsh edge (Minello 1999). Although these results suggest continued conversion of *S. alterniflora* habitat to *A. germinans* habitat would decrease production of panaeid shrimp, our current understanding is limited.

In this study we used stable isotope analysis and Bayesian mixing models to determine the contribution of the primary production sources to the food web in a southern Louisiana saltmarsh to determine the contribution of mangrove production to the food web. Mangrove derived organic matter is more depleted in ^{13}C, typically ~28 ‰ δ^{13}C, relative to organic matter fixed by *Spartina,* typically ~15 ‰ δ^{13}C (McKee et al., 2002; Peterson and Fry, 1987). The difference is due to isotope fractionation difference in the C3 photosynthetic pathway used by mangroves and the C4 photosynthetic pathway used by *Spartina* (Fry, 2007). Therefore, if mangrove-derived production is being incorporated into the food web we would anticipate organisms using incorporating that material to have more depleted carbon isotope values than their counterparts in areas dominated by *Spartina*. We also examined trophic metrics for the dominant species of penaeid shrimp at two sites, which differed in mangrove cover, to determine if mangrove habitat food webs differ from *Spartina*-dominated food webs due to potential structural or geomorphic differences in each habitat. We hypothesized that mangrove habitat will contribute to the food web, replacing saltmarsh *Spartina* contributions to the detrital energy pathway.

2. Materials and Methods

2.1 Site Description

All samples were collected near Port Fourchon, Louisiana (29.10°N, 90.19°W) between August-September 2016 during flooding tides (Fig. 1). The marsh and mangrove area are microtidal habitats with a mean tidal range of ~0.37 m. The black mangrove and smooth cordgrass are the dominant plant species. Each site varied in the proportional coverage of the two dominant macrophytes. Sampling locations were spatially distributed along the mangrove-marsh ecotone to capture varying levels of black mangrove abundance in marsh areas.

2.2 Habitat Estimation

Habitat cover was estimated by classifying areal satellite imagery in ArcMap (10.4.1). Satellite images of each bay were taken from Google Earth, georeferenced and clipped to the study area. Using ArcMap's Image Classification tool, a training file was constructed by drawing polygons around known saltmarsh and mangrove areas, as well as areas of water. This training file was used to classify all areas throughout the clipped satellite image as one of these three habitat categories using a Maximum Likelihood Estimation method. Sampling locations were imported and georeferenced, and layered onto the classified image. Buffers of 400 m diameter were made around each sampling location, and the amount of each habitat category within each buffer was determined by clipping the classified image layer to these buffers. This area was chosen because it is an average home range of white shrimp while in the marsh (Rozas and Minello, 1997).

2.3 Sample Collection

Samples of nekton in salt marsh and black mangrove habitats were collected using a 1-m^2 drop sampler following the method described by Zimmerman et al. (1984). Two persons positioned the sampler over a sample site by guiding the boat from the stern, and the third person on the boat released the drop sampler, rapidly enclosing the sample area. After the cylinder was dropped and secured in position, the location of each sample site was determined using a GPS unit.

After all vegetation was removed, we collected nekton captured in the drop sampler with dip nets and by pumping the water out of the sampler through a 1-mm mesh net. Once the sampler was completely drained, any animals remaining on the sediment surface were removed by hand. Animal samples for stable isotope analysis were sorted and placed on ice. Subsamples of mangrove leaves and Spartina stems were taken by hand and placed on ice. Epiphytic algae growing on plant roots and stems were sampled by removing a section of the whole plant and placing them on ice. Water samples were collected adjacent to drop sites and placed on ice for determination of particulate organic matter isotope values. All samples were frozen at -20 ° C in the laboratory prior to processing.

2.4 Stable Isotope Analysis

We used the stable isotope ratios of $^{13}C/^{12}C$, $^{15}N/^{14}N$, and $^{34}S/^{32}S$ to determine the relative contributions of primary production sources in our food web. All plants fix carbon from the same atmospheric reservoir of CO_2 that is currently -8 ‰ $\delta^{13}C$. In coastal ecosystems carbon stable isotope values can be most useful in differentiating between C3 plants, such as mangroves, which fix carbon with a net fractionation of about -20 ‰ relative to the atmosphere and C4 plants, such as tropical and temperate salt tolerant grasses, which have a net fractionation of about -5 ‰ (Fry 2007). With some notable exceptions, primary production in many coastal ecosystems is nitrogen limited (Howarth and Marino, 2006; Sundareshwar et al., 2003). As a result the primary producers in coastal systems typically have lower $\delta^{15}N$ values than their terrestrial counterparts (Fry 2007). In food web studies nitrogen stable isotopes are used primarily as a trophic level indicator because of the measurable fractionation (+0.9-4.0 ‰) associated with trophic transfers (Hussey et al., 2014). Sulfur is one of the most under used, but potentially powerful stable isotopes for tracing production through coastal food webs. In the marine environment the sulfate used by water column primary producers is derived from the large well mixed reservoir of sulfate that has a typical value of 21 ‰ $\delta^{34}S$ (Fry 2007). Sulfate reduction in coastal sediments has are large fractionation factor (30-70 ‰) (Chanton et al., 1987). This large difference in isotope values can be used as an indicator of benthic vs pelagic derived organic matter (Nelson et al., 2015, 2012).

In the laboratory, muscle tissue samples were extracted from all animals, rinsed with deionized water, dried at 50 ºC for 48 hours, ground, and wrapped in tin capsules. Plant tissue samples were rinsed in deionized water and then dried, ground, and wrapped. Epiphyte samples were gently scraped from the surface of the plant substrate they were attached to and rinsed with deionized water. A subsample of epiphyte material was rinsed with 10 % HCL solution to determine if acid washing was required. We determined the epiphytes did not contain carbonate when none of the samples produced bubbles (Nelson et al. 2015). The epiphyte samples were then dried, ground, wrapped for analysis. The samples were shipped to the Washington State University Stable Isotope Core Facility for C, N, and S content and stable isotope analysis. Carbon, nitrogen, and sulfur isotope values were calculated using the standard formula (Fry, 2007). PeeDee Belemnite (PDB), atmospheric nitrogen, and Canyon Diablo Troilite (CDT) were used as the reference standards for C, N, and S, respectively. No C:N ratio was above 3.5; therefore, no lipid correction was applied (Nelson et al., 2013; Post et al., 2007). Source isotope values are summarized in Table 1.

The relative contribution of each organic matter source to each species was derived using a Bayesian mixing model that included all three isotopes (CNS) for the producers and consumers. All stable isotope data were analyzed in R (v 3.5.1, R Development Core Team) using the package

MixSIAR (v 3.1.7, (Semmens et al., 2014)). The fractionation factors for used in the model were 0.9 ± 0.3 for carbon, 2.9 ± 0.5 for nitrogen, and 0.5 ± 0.2. Models were run in three chains with 1,000,000 iterations and a burn-in of 500,000 to allow for adequate model convergence. An elemental analyzer determined the concentration of each element in the primary producers. These values were used to determine the concentration-dependent mean proportional contributions of each source were calculated for each individual. From these source contributions, the trophic position of each individual was calculated according to the following formula:

Equation 2:

$$TL = \frac{\delta^{15}N_{ind} - \sum(\delta^{15}N_{source} * mean\ \%\ cont_{source})}{\Delta\delta^{15}N} + 1$$

where $\Delta\delta^{15}N$ = 2.9 ± 0.5, $\delta^{15}N_{ind}$ is the nitrogen value of an individual consumer, $\delta^{15}N_{source}$ is the nitrogen value of each particular source of primary production, and % $\text{cont}_{\text{source}}$ is the proportion contribution of each source to the consumer diet (Nelson et al., 2015; Hussey et al., 2014; Wilson et al., 2009a). Source contributions are summarized in Table 3, Fig. 3.

2.5 Shrimp Caloric Content

Ten whole shrimp from each site were dried and ground as described in section 2.4. For each homogenized individual, two subsamples of 0.15-0.20g were taken for calorimetry analysis. Each ground subsample was placed in a crucible in a pre-cleaned Parr 1109A semi-micro oxygen combustion vessel. The vessels were then pressurized with oxygen to 206.8-241.3 kPa and placed in 450ml of deionized water in insulated calorimeter jacket. The caloric content was determined using a Parr 6725 bench top calorimeter. Each sample was run twice to ensure replicate measurements were within 250 calories of each other.

3. Results

3.1 Stable Isotope Values

The isotope values we observed for the primary producers that made up the end members of the mixing model were typical of other studies in the region (Fry et al., 2003; Nelson et al., 2012). The *Spartina* end member had a mean $\delta^{15}N$ value of 6.6 ± 0.6, $\delta^{13}C$ of −14.5 ± 0.3, and $\delta^{34}S$ of -5.9 ± 2.0. Carbon, nitrogen, and sulfur isotope values for mangrove leaves were more depleted than *Spartina*, $\delta^{13}C$ -26.3 ± 1.1, $\delta^{15}N$ 4.9 ± 0.1, and $\delta^{34}S$ -8.9 ± 2.8. The water column end member particulate organic matter (POM) had a mean $\delta^{15}N$ value of 6.7 ± 0.8, $\delta^{13}C$ of -22.1 ± 0.8, and $\delta^{34}S$ of 18.7 ± 1.5. The benthic algae had a mean $\delta^{15}N$ value of 3.1 ± 1.4, $\delta^{13}C$ of −16.1 ± 2.1, and $\delta^{34}S$ of 4.1 ± 3 (Table 1).

Stable isotope values were determined for nine different nekton species (Table 2). Carbon isotope values ranged from -20.17 ‰ for brown shrimp to -15.87 ‰ for striped mullet (*Mugil cephalus*). We observed a fairly narrow range in nitrogen isotope values from 7.93 ‰ for blue crabs (*Callinectes sapidus*) to 11.38 ‰ for silversides (*Menidia menidia*). Although both dominant macrophytes had negative $\delta^{34}S$ (-8 to -5 ‰), all animals were enriched by more than 10 ‰ from 6.30 ‰ for mojarra (*Eucinostomus sp.*) to 13.57 ‰ for silversides.

3.2 Mixing Model Results

Benthic algae and water column POM accounted for 74 % or more of the production to all species in the food web (Table 2). *Spartina* was the primary macrophyte contributor to the food web, according to the mixing model, contributing ~8-25 % of energy to consumers. Mangrove production accounted for no more than 0.2 % to any species, well within the error associated with the mixing model, indicating it is not a contributor to the food web (Table 2).

Mullet showed the highest contribution from the *Spartina* channel (25 %) followed by spot (*Leiostomus xanthurus*) (20 %). With the exception of silversides, all other species received more than 40 % of their energy via the benthic algal pathway. When added to the detrital support provided by the *Spartina* pathway, the system overall is benthically-driven with all species, excluding silversides, receiving greater than 56 % of their production via benthic sources (Table 2). The calculated trophic levels ranged from 1.2 – 3.2, spanning just two trophic levels. Overall, silversides occupied the highest trophic position of the species sampled. However, there was substantial overlap among species, with most species feeding between trophic level one and two, indicating large amounts of trophic plasticity and/or omnivory.

3.3 Habitat Mapping

Habitat estimation revealed two general areas with different areas of mangrove cover. Barataria Bay had a significantly lower proportion of mangrove cover (ANOVA, F (1, 67) = 124.58, $p < 0.05$), and a significantly higher proportion of *Spartina* cover than Terrebonne Bay (ANOVA, F (1, 67) = 96.56, $p < 0.05$). No sites in Barataria Bay had mangrove cover greater than 30% and all sites in Terrebonne bay had mangrove cover greater than 20%. Overall, Barataria Bay had 194% less mangrove cover and 146% more marsh cover than Terrebonne Bay (Fig. 2).

3.4 White Shrimp Diet in Relation to Habitat

White shrimp trophic position significantly increased as mangrove cover increased in Terrebonne Bay ($R^2 = 0.33$, F (1, 34) = 18.369, $p < 0.05$, Fig. 4), but not in Barataria Bay. We found a significant correlation of higher contribution of particulate organic matter production (Terrebonne: correlation coefficient =0.71, $p < 0.05$, Barataria: correlation coefficient =0.66, $p < 0.05$, Fig. 5a), and a significantly lower contribution of algal production, as their trophic level increased (Terrebonne: correlation coefficient = -0.83, $p < 0.05$, Barataria: correlation coefficient = -0.71, $p < 0.05$, Fig. 5b).

3.5 White Shrimp Caloric Content

There was no difference in the caloric content between shrimp captured in Barataria and Terrebonne bay. White shrimp captured in Barataria had a mean caloric content of 3,961 ± 131 cal/g and white shrimp captured in Terrebonne had a mean caloric content of 3,966 ± 200 cal/g.

Discussion

At the time, of this study the transition of the primary foundation species coverage from *Spartina* to black mangrove does not appear to be altering primary sources to the food web. Overall, the food web is supported primarily via the “green” pathway with benthic microalgae production being the primary contributor (Table 2). The detrital pathway is currently dominated by *Spartina*-derived inputs and there is no indication that mangrove detritus is a source despite mangrove habitat present for decades. Studies of mangrove-dominated ecosystems in the tropics have shown that mangrove detritus can be a significant source of energy to the food web, particularly in more closed systems (Bouillon et al., 2008; Zieman et al., 1984). However, even in the tropics, the inputs of mangrove-derived organic matter were typically limited to detritivores, such as fiddler crabs and polychaete worms that live in the benthos underneath mangrove stands (Bouillon et al., 2008; Rodelli et al., 1984). Studies in nearby systems also experiencing mangrove expansion have observed no major changes in the rates of detrital accumulation or decomposition (Perry and Mendelssohn, 2009). Therefore, we conclude that the lack of mangrove derived energy in the food web is a result of either lower overall inputs into the detrital pool from mangroves caused by their relatively lower density or consumers that would feed preferentially on mangrove detrital inputs have not colonized the system yet in a substantial way. This may change as the system continues to shift toward a mangrove-dominated estuary.

As observed in previous studies in coastal ecosystems, the foundation species serves as substrate for the growth of epiphyte production that forms the base of the food web rather than directly contributing to secondary production (Bouillon et al., 2008; Nelson et al., 2015; Rodelli et al., 1984). Other studies suggest habitat structure provided by foundation species plays a critical non-trophic role in facilitating food web interactions and coupling food webs in space (Baiser et al., 2013; Gotelli and Ellison, 2006; Nelson et al., 2019). Our habitat analysis revealed that the marshes in the

Barataria basin had significantly more mangrove cover than marshes in the Terrebonne basin (Fig. 2). Individual mixing model results of white shrimp showed no real change in the primary sources to the food web in areas with higher mangrove cover indicating that, in terms of supporting the production of the benthic epiphytic algae that is the base of the food web, both mangrove and *Spartina* habitat function similarly.

We also examined food web metrics and habitat parameters to determine if habitat structure was indirectly influencing how energy was moving through food webs. We observed that white shrimp captured in sites with greater than 20 % mangrove cover had a higher trophic level with increasing mangrove cover, but there was no such relationship with *Spartina* cover (Fig. 4). Previous studies on fish have shown that the physical structure of habitats can influence trophic position by allowing for increased access to prey or by providing refugia for prey (Nelson et al., 2015). While further study is needed, perhaps mangrove structure alters white shrimp's ability to forage. Regardless of habitat cover, we detected a significant increase in trophic position of white shrimp with increasing reliance on POM (Figure 5). Because shrimp are benthic feeders, this increase is likely due to a decrease in trophic path efficiency when water column production settles out and is reprocessed in the benthos via benthic pelagic coupling.

While our results clearly show no substantial inputs from mangrove derived production to the animals sampled in this study there are some limitations to our interpretations. First, isotope values of animals and producers will turnover and change at different rates and are limited to the relevant turnover time of the consumer or producer sampled during the study. For example, all our samples were collected in the early fall and would likely represent only the production assimilated during the summer for most of the consumers in the study. The primary producers used in this study represent our best determination of the dominant potential sources we could sample. In some soft bottom system microphytobenthos can be a substantial contributor to the food web (Nelson et al. 2015).

Although we sampled the benthos to collect this potential producer we did not observe any substantial accumulation of benthic microalga biomass. Our system is quite turbid with light typically only penetrating a few centimeters below the water surface perhaps limiting benthic algal production. Finally, stable isotope mixing models are sensitive to the trophic enrichment factors and concentration corrections used to set the mixing space for the model. Our inputs were in keeping with the best practices outlined by Phillips et al. (2014), but there are other valid configurations that would alter our interpretation, particularly with regard to trophic level assignments.

Conclusion

Climate change is driving unprecedented ecological change that is rapidly altering species distributions, interactions, and ultimately ecosystem function (Osland et al., 2013). The effects of these climate driven changes are intensified when foundation species alter their distributions because of the outsized role they play in structuring entire communities and influencing ecosystem function (Ellison et al., 2005; Yando et al., 2016). However, as we demonstrate here and others have recently, determining how food webs will respond to changing foundation species distributions may not be directly linked to the foundation species' role in providing energy but, perhaps other factors such as altered geomorphologies or ecosystem structure (Nelson et al. 2019).

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Declarations of interest

None.

Conflict of interest

There are no conflicts of interest concerning our article.

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Tables

Table 1: Mean and standard deviations (s.d.) of source stable isotopes and elemental concentrations.

Source	$\delta^{13}C$	s.d.	[C]	$\delta^{15}N$	s.d.	[N]	$\delta^{34}S$	s.d.	[S]
POM	-22.1	0.8	48.0	6.7	0.8	8.0	18.7	3.0	0.60
S. alterniflora	-14.5	0.3	42.6	6.6	0.6	1.2	-5.9	2.0	0.53
A. germinans	-26.3	1.1	46.8	4.9	0.1	1.9	-8.9	2.8	0.64
epiphytes	-20.5	1.8	6.3	5.4	1.0	8.0	4.1	3.0	0.50

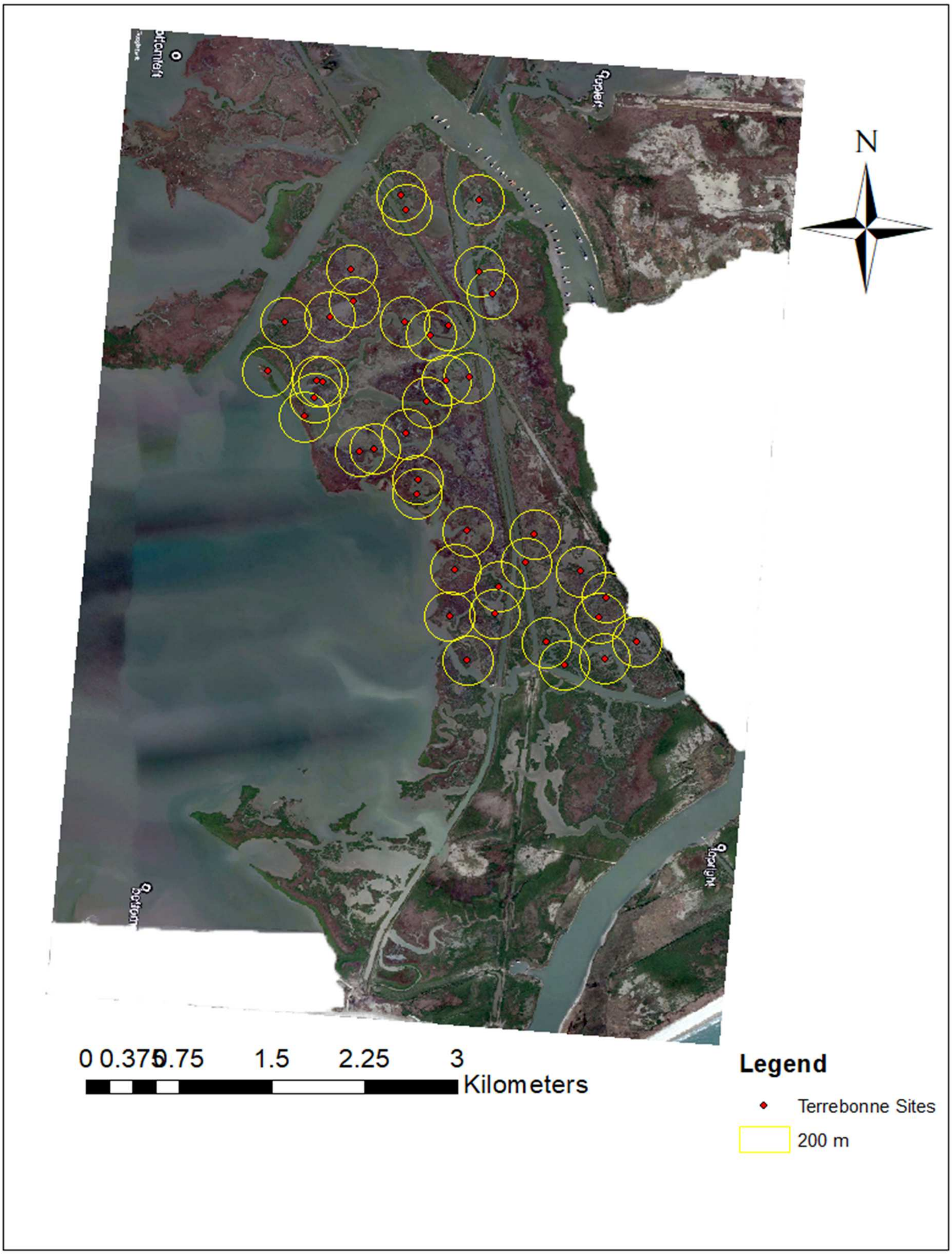
Common Name	**Species Name**	**$\delta^{13}C$**	**s.d.**	**$\delta^{15}N$**	**s.d.**	**$\delta^{34}S$**	**s.d.**	**Number**
blue crab	*Callinectes sapidus*	-17.87	1.85	7.93	0.38	10.95	1.40	10
brown shrimp	*Farfantepenaeus aztecus*	-20.17	0.70	8.80	0.56	10.26	1.66	8
grass shrimp	*Palaemonetes pugio*	-18.24	0.68	8.49	1.13	11.17	1.62	13
gulf killifish	*Fundulus grandis*	-18.28	1.30	9.00	1.38	7.62	2.63	11
silverside	*Menidia menidia*	-19.61	1.01	11.38	1.38	13.57	1.08	7
mojarra	*Eucinostomus sp.*	-19.53	0.92	9.66	1.03	6.30	2.78	4
mullet	*Mugil cephalus*	-15.87	0.59	8.28	1.67	7.07	2.27	4
spot	*Leiostomus xanthurus*	-17.84	1.29	10.78	0.47	7.13	1.51	5
white shrimp	*Litopenaeus setiferus*	-19.27	0.97	8.25	0.78	8.10	1.67	70

Table 2: Mean and standard deviation (s.d.) of all species sampled for C, N, and S stable isotopes.

Table 3:

Common Name	**Species Name**	**% Spartina**	**s.d.**	**% Mangrove**	**s.d.**	**% Algae**	**s.d.**	**% POM**	**s.d.**
blue crab	*Callinectes sapidus*	15.1	5.8	0.2	0.0	57.2	5.8	27.5	9.4
brown shrimp	*Farfantepenaeus aztecus*	9.2	2.5	0.2	0.1	45.9	3.2	44.7	5.3
grass shrimp	*Palaemonetes pugio*	14.1	3.4	0.2	0.0	54.2	9.5	31.5	11.6
gulf killifish	*Fundulus grandis*	17.1	7.8	0.3	0.0	48.7	10.4	33.9	13.2
silverside	*Menidia menidia*	8.3	3.1	0.2	0.0	30.9	12.9	60.6	16.0
mojarra	*Eucinostomus sp.*	12.1	4.4	0.3	0.1	44.1	9.6	43.6	13.7
mullet	*Mugil cephalus*	25.8	7.8	0.3	0.1	56.1	9.4	17.9	6.8
spot	*Leiostomus xanthurus*	20.9	9.2	0.3	0.1	41.2	4.1	37.6	12.4
white shrimp	*Litopenaeus setiferus*	12.5	3.6	0.3	0.0	49.2	3.7	38.1	6.8

Figures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Legend
Terrebonne Sites
200 m

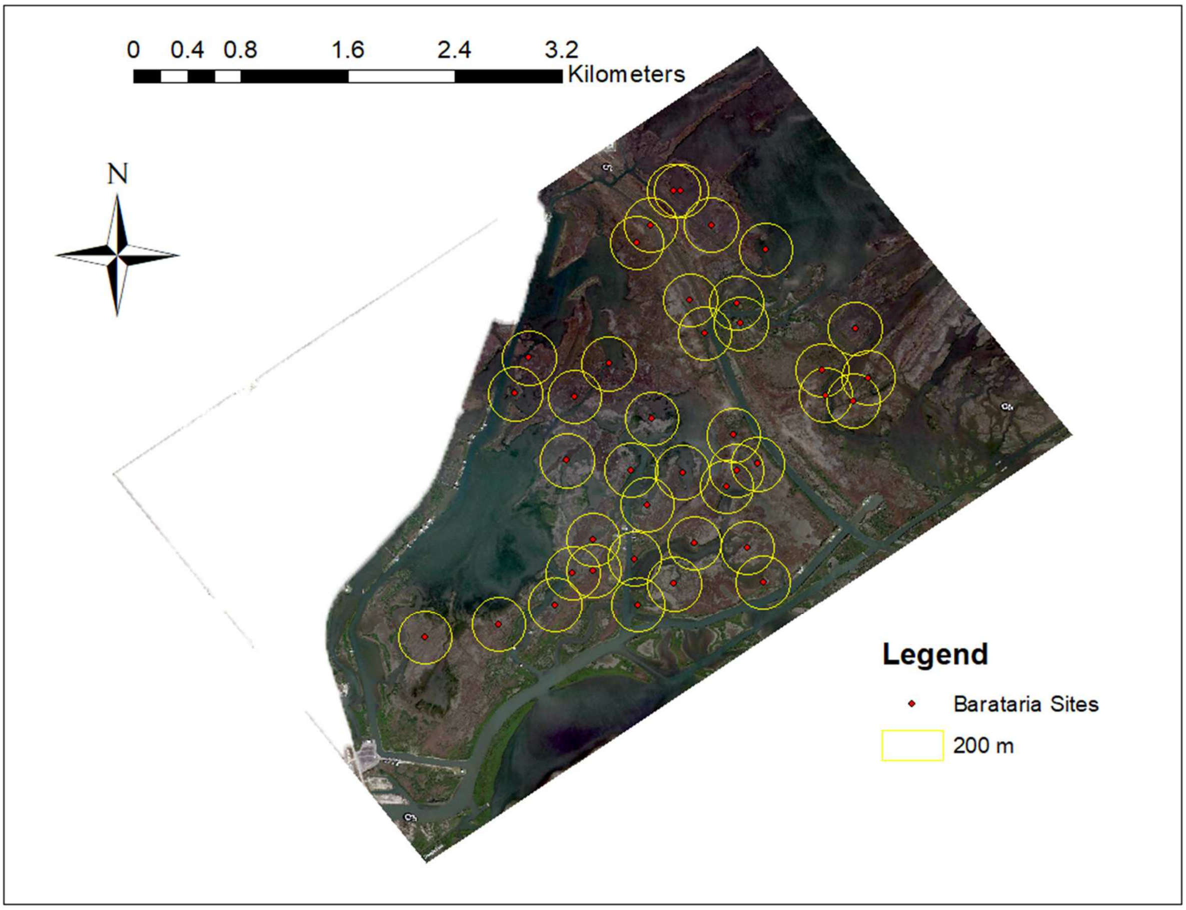
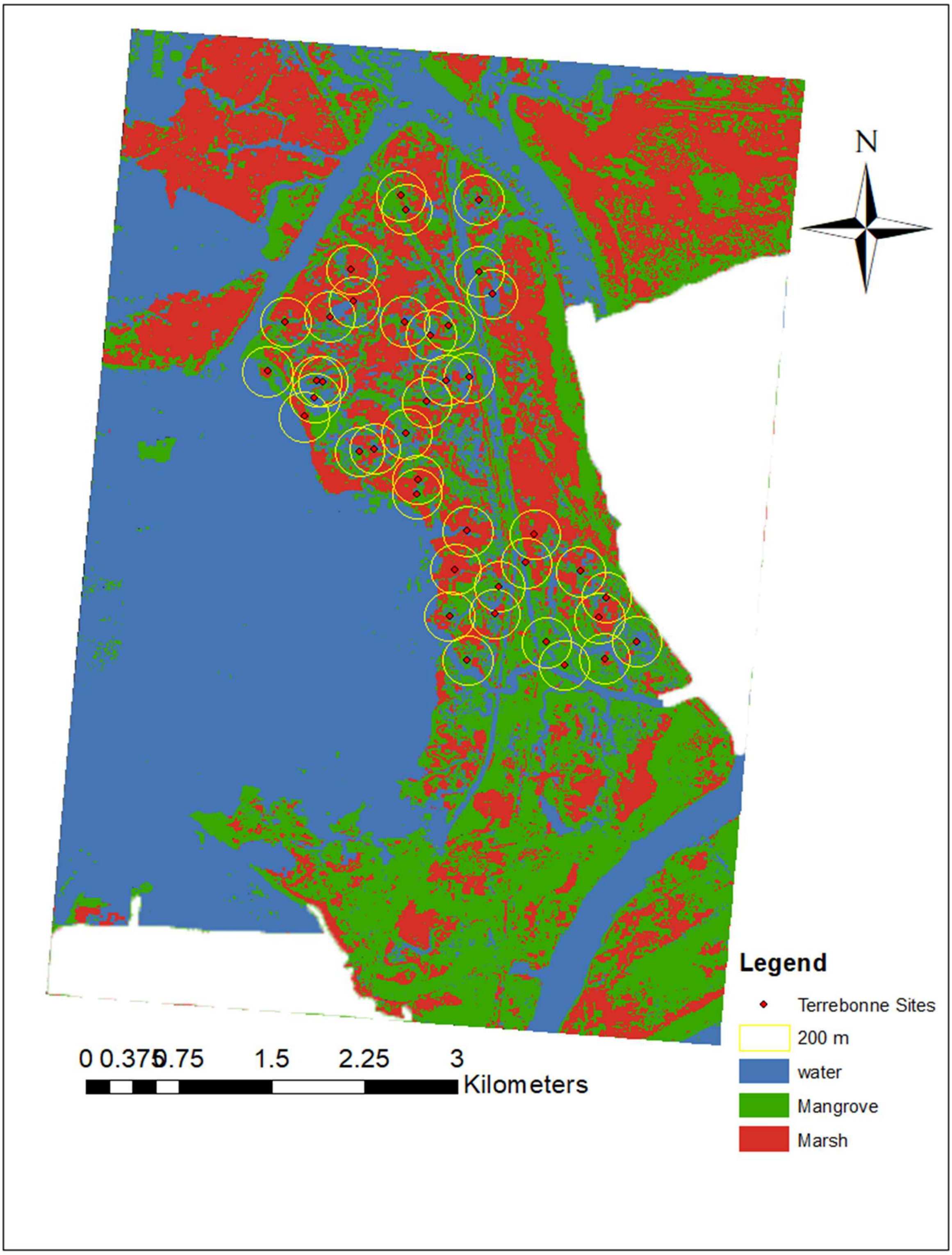


Figure 1: Maps depicting the marsh areas surrounding Port Fourchon, LA used in this study. Top, sites in Terrebone Bay, and Bottom, sites in Barataria Bay. Each red point represents a drop sample location; yellow circle surrounding each point is a 400 m diameter representing the home range of species samples there. Maps taken from Google Earth Imagery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Kilometers
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Mangrove
Marsh

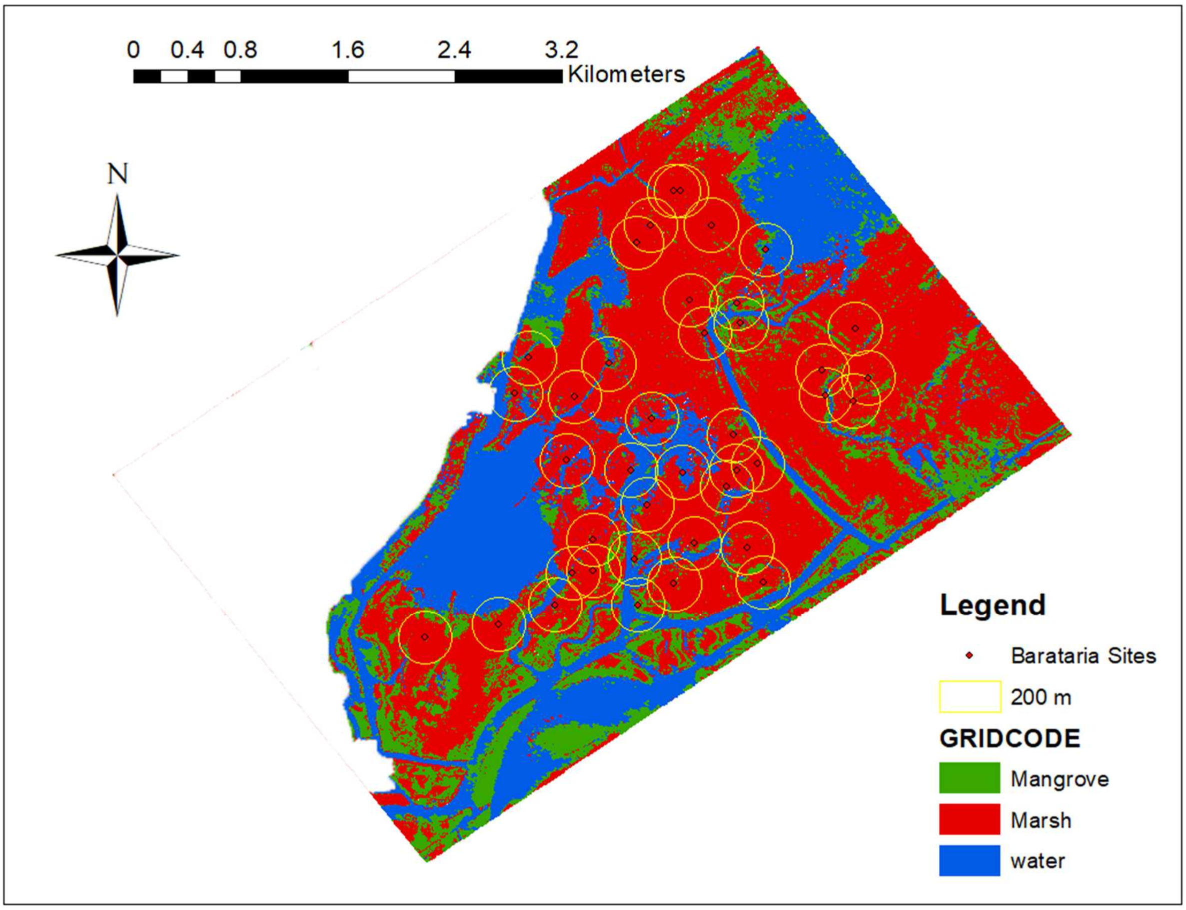


Figure 2: Habitat cover maps of Terrebonne Bay (Top) and Barataria Bay (Bottom).

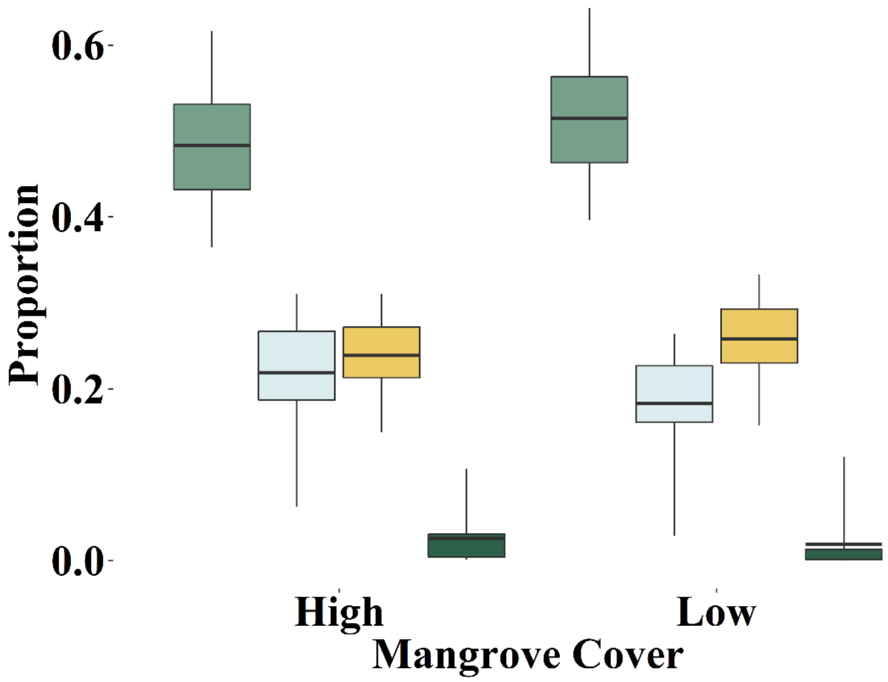


Figure 3: Source contributions for individual white shrimp by mangrove cover. The high mangrove cover area is Terrebonne bay and the low mangrove cover area is Barataria bay. Light green = benthic epiphytic algae, light blue = POM, yellow = *Spartina*, dark green = mangrove.

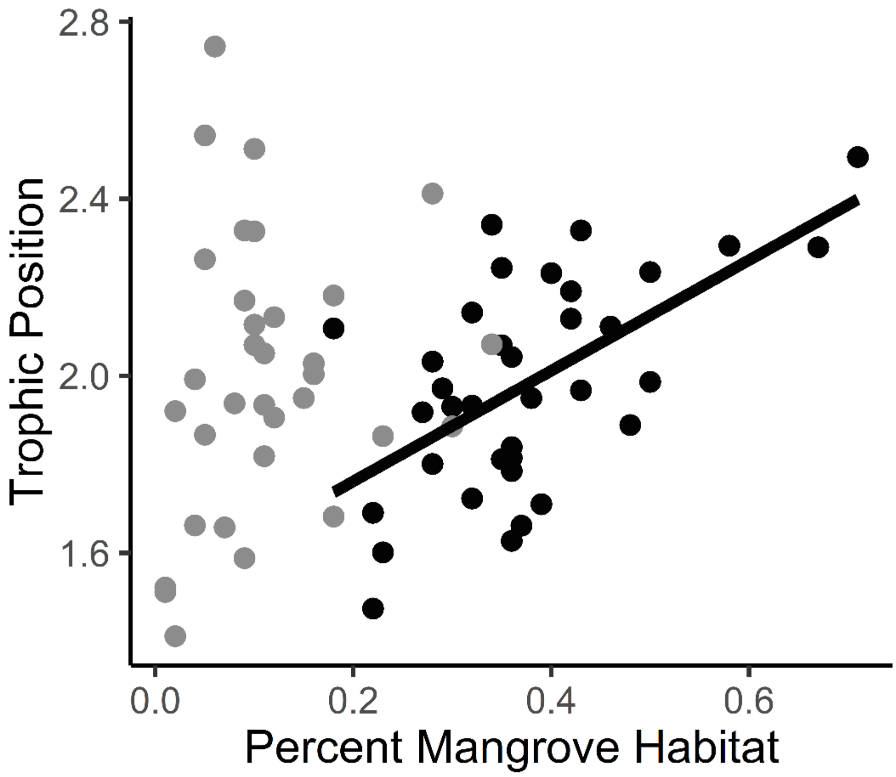
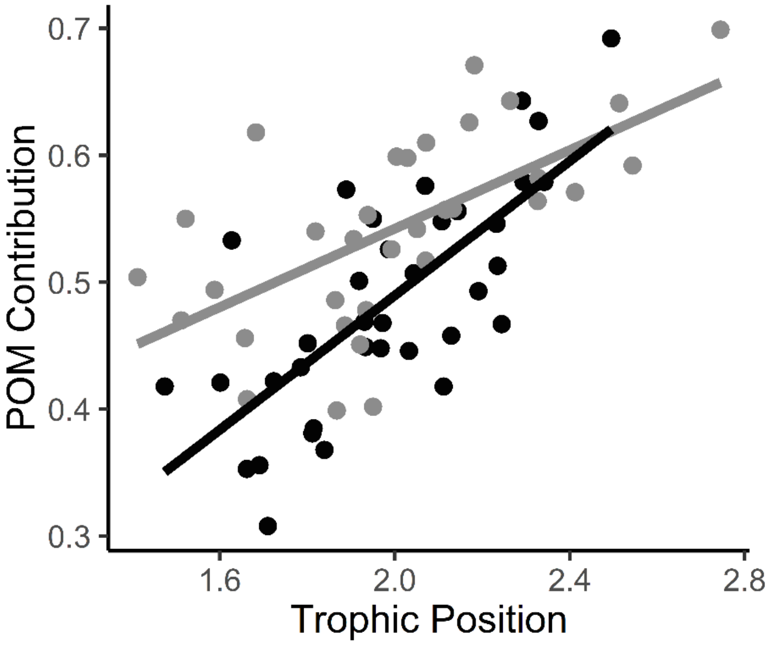


Figure 4: White shrimp trophic position as a function of mangrove cover in Terrebonne Bay (black) but not in Barataria Bay (gray).

A)



B)

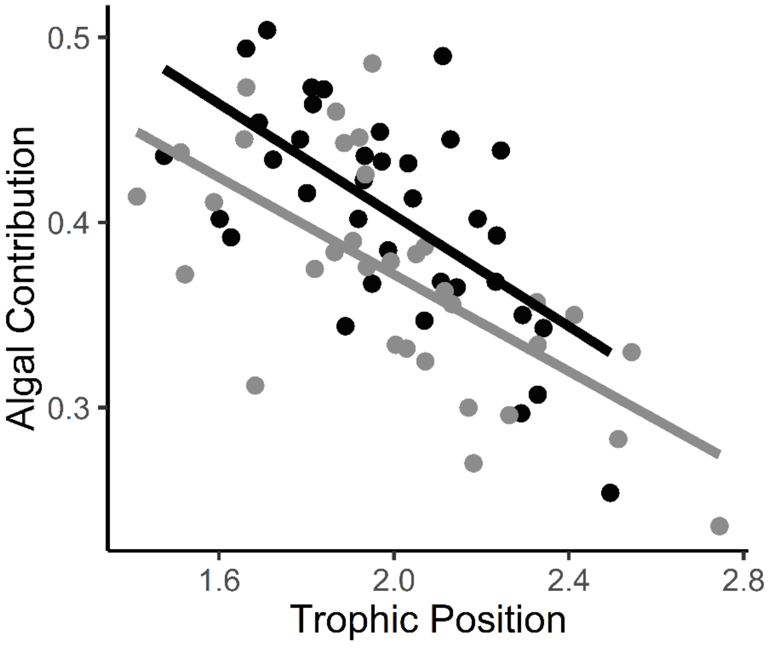


Figure 5: White shrimp POM contribution (A,top) and algal contribution (B, bottom) is significantly correlated with trophic position in Terrebonne Bay (black) and Barataria Bay (gray).