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Effects of Freshwater Inflow on Nekton Assemblages and Blue Crab Populations in Southeastern Louisiana

Caleb Benjamin Taylor

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EFFECTS OF FRESHWATER INFLOW ON NEKTON ASSEMBLAGES AND BLUE CRAB POPULATIONS IN SOUTHEASTERN LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College
In partial fulfillment of the requirements for the degree of Master of Science
in
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by
Caleb Benjamin Taylor
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ABSTRACT

Estuaries along the northern Gulf of Mexico represent some of the most productive ecosystems in the world, providing vital habitat for many recreationally and commercially valuable species, including the blue crab, *Callinectes sapidus*. The mixing of fresh river and saline ocean water in coastal estuaries contribute to this productivity. Dominated by large river influences and consisting of multiple estuaries, Louisiana contributes the largest commercial fishery in the Gulf of Mexico, and remains, on average, the largest supplier of blue crabs in the nation. However, across southeast Louisiana, freshwater flow is largely dependent on Mississippi River discharge, which is highly variable and changing rapidly due to multiple factors including river leveeing and changing precipitation patterns. As Louisiana is experiencing high rates of coastal land loss, large restoration projects diverting river sediment and water into adjacent estuaries further impact freshwater flow, yet the impacts on dependent nekton species, including the economically important blue crab, remain largely unknown. Managers lack basic data on population dynamics, habitat use and environmental factors influencing blue crabs in the region. For this study, we quantified nekton species assemblages and blue crab populations seasonally using throw traps (N=96) and bag seines (N=96) within an active delta characterized by high freshwater flow (Mississippi River Delta) and an inactive delta characterized by low freshwater flow (Terrebonne Basin). Nekton species composition differed between both deltas, though differences for crustacean and fish densities, nekton species richness, and blue crab densities were largely seasonally driven and reflected individual species life history. Both deltas supported similar densities of recently settled, juvenile blue crabs during fall when abundances were highest within both deltas. Panaeid shrimp were largely absent from active delta sites, though densities where consistently high in the inactive delta during summer and fall. The most
pronounced differences between the active and inactive deltas largely occurred in the spring during an extended period of flooding for the Mississippi River, which in 2019 exceeded previous river flows in both volume and length of time providing a stark contrast between the deltas. This unusually high riverine flow provides some indication of the impact that extended, high river flow may have on nekton assemblages and habitat availability within an estuary. As changes in freshwater flow are associated with numerous water quality and habitat availability effects, determining direct linkages to nekton and economically important species remains critical, and may be location and estuarine dependent.
1. INTRODUCTION

The history of the marshes of the Mississippi River Delta is inextricably intertwined with the history of the river itself. Like some ancient god, it broods over the coastal plain, implacable in its power, its purpose inscrutable. With its sediment it spawns the flat, verdant marshes of the delta, nourishes them with its nutrients, and finally abandons them to senesce slowly under the influence of time and subsidence, while it renewes the cycle elsewhere along the coast.

-- James Gosselink

The Ecology of Delta Marshes of Coastal Louisiana: A Community Profile

Most fishery production worldwide occurs within coastal regions, and is largely associated with coastal upwelling, tidal mixing, and land-based runoff including major river flow (Caddy & Bakun, 1994). Terrestrially enriched river discharge can positively influence biological processes (growth, survival, recruitment) that affect fisheries production (Grimes, 2001). Alterations in riverine outflow could potentially devastate coastal fishery landings, yet demand for freshwater resources has caused many rivers to run dry. For instance, the Colorado River historically flowed into the Gulf of California, yet has gradually been diverted for use by cities and agriculture since the completion of the Hoover Dam in 1935 (Lavín & Sánchez, 1999). Not only has decreased freshwater flow to the Gulf of California been shown to be a root cause of decreased growth and a confounding factor in the endangerment of a fish species (Totoaba macdonaldi), but it is also correlated with a decrease in shrimp total catch (Galindo-Bect et al., 2010). Within Apalachicola Bay, Florida, high river flow (> 30,000 cfs) for over 100 days was correlated with reduced oyster landings (Wilber, 1992). The balance of mixing fresh and salt water in estuaries is highly variable across systems and within systems; understanding how estuarine resources, fisheries and functions respond to changing flows remains critical to helping manage these systems and the fisheries that depend on them (Alber, 2002).

Within the United States, the Magnuson-Stevens Fisheries Conservation and Management Act of 1976 was enacted to ensure sustainability of fisheries. In 1996, this act was
amended to acknowledge the importance of essential fisheries habitat. The addition of essential fisheries habitat recommends fishery managers to include habitat – the basis of healthy fisheries – in their management regimes to ensure the long term sustainability of fisheries and fishing communities (Rosenberg et al., 2000). Since river flow has been shown to impact estuarine resources related to primary (habitat) and secondary production (fisheries), it is vital that we strive to understand the relationships between flow and habitat to sustain our fisheries (Alber, 2002). In particular, river effects are most noticeable in oligotrophic seas such as the Gulf of Mexico and the Mediterranean Sea where processes associated with river flow from the Mississippi and Rhone Rivers, the presence of a wide shelf, and mixing from winds create favorable reproductive conditions for many species (Lloret et al., 2004). Fishery landings from Louisiana waters surrounding the Mississippi River, the largest river system in North America, contribute some 70-80% annually to the total fishery landings of the Gulf of Mexico (Grimes, 2001). Similar to other estuarine regions, freshwater flow here is generally considered to be one of the most influential factors affecting biotic community structure and production for estuarine nekton communities (Piazza & La Peyre, 2011).

Estuarine dependent species comprise over 50% of U.S. commercial fisheries landings (Houde & Rutherford, 1993). Louisiana consistently leads Gulf landings due to catch of five major species: Gulf menhaden (*Brevoortia patronus*), brown shrimp (*Farfantepenaeus aztecs*), white shrimp (*Litopenaeus setiferus*), Eastern oysters (*Crassostrea virginica*), and blue crabs (*Callinectes sapidus*); all of which are estuarine dependent (Keithly & Roberts, 2017). This high production relates to generally enhanced nutrient cycling and land-based nutrients driving high primary production rates within estuaries (Jordan & Peterson, 2012). This impacts the fisheries
not just through impacts to water quality, but through impacts on habitat availability, food availability, and the interaction of fixed habitat availability with overlying water quality.

Freshwater flow can influence fishery production through transport of detritus and nutrients, as well as transport and deposition of sediments, reduction of salinity, and mixing and transport of water masses (Jordan & Peterson, 2012). Nutrient transport strongly influences productivity of wetland vegetation, phytoplankton, and seagrasses, which in turn influences distributions of many juvenile fish and shellfish either directly or through the food chain. For instance, increased nitrogen inputs into the Gulf of Mexico from the Mississippi River, alongside wetland loss, has caused increased eutrophication and hypoxia along coastal shelf waters (Mitsch et al., 2005). Nitrogen loads from the Mississippi River are partially denitrified by anaerobic bacteria and assimilated by wetland plants, yet algae (normally nutrient limited within estuarine systems) can bloom in warmer months with increased nitrogen loads derived from agricultural runoff and pollutants, which can lead to alterations in estuarine trophic structure and ultimately hypoxic conditions along coastal shelf waters (Mitsch et al., 2005).

Changes in freshwater flow have been directly linked to fisheries production. For example, in Matagorda Bay, Texas, quality of organic matter was found to be higher following low salinity events driven by freshwater flow, ultimately contributing to enhanced oyster production (Marshall et al., 2019). Within Louisiana, extended low salinities from flooding resulted in negative impacts on oyster survival, recruitment, and growth in Breton Sound (La Peyre et al., 2013). Similarly, another study concluded that lower estuarine salinities from diversions or increased freshwater flow during peak recruitment periods may reduce overall growth rates and productivity of white shrimp (*Litopenaeus setiferus*) and brown shrimp (*Farfantepenaeus aztecus*) in affected areas (Rozas & Minello, 2011). In contrast, *Gambusia*
*affinis* was found to have higher growth rates in response to increased freshwater flow derived from the Caernarvon diversion in Breton Sound, Louisiana (Piazza & La Peyre, 2010).

While changes in water quality may have direct effects on fisheries, they also indirectly influence them through impacts on habitat characteristics, and the interaction of available fixed habitat with overlying water quality. The Mississippi River’s immense fishery productivity is not only related to riverine processes, but also habitat those processes create. The Mississippi River delta is composed of vast wetlands and shallow water areas created through sediment deposition (mostly fine grained clays and silts) draining from an area of 3,344,560 km² over thousands of years (Coleman, 1988). The Mississippi River drainage basin covers a vast amount of the continent, stretching from the Rocky Mountains in the west, the Appalachians to the east, and the Precambrian shield in Canada on the northern boundary. Sediment from these regions continuously washes towards the Gulf of Mexico through the many tributaries leading into the Mississippi River channel, resulting in fluvial deltaic deposition (sedimentation and building of land) from the shoreline to the continental shelf edge at a faster rate than waves and tides can redistribute it. This process slowly built the entire southeast Louisiana region known as the Mississippi River Deltaic Plain from the Chandeleur Islands in the east to Vermilion Bay in the west. The system formed this region through successive switching of major deltaic lobe complexes involving the meandering, altering courses of the river channels filling in and changing over time, known as the deltaic lobe process (Frazier, 1967).
Figure 1.1. Past deltaic lobes of the Mississippi River in order from oldest to youngest, the lobes are (1) Maringouin, (2) Teche, (3) St. Bernard, (4) Lafourche, (5) modern (Plaquemines-Balize), and (6) Atchafalaya. Source: (National Research Council 2006)

Marshes still under the direct influence of riverine processes are considered active deltas, while marshes no longer under direct influence of riverine processes are referred to as inactive deltas. Inactive deltas depend largely on local rainfall for freshwater inputs and resuspension of sediments for inputs of mineral matter (Nyman et al., 1990). Currently only the Plaquemine-Balize or Mississippi River Delta at the mouth of the Mississippi River and the Wax Lake Outlet and Atchafalaya Delta at the mouth of the Atchafalaya River are active (Figure 1). While active deltaic processes slowly accrete new land, inactive deltas degrade, subside, and erode naturally over time due to the absence of riverine connectivity and subsequent domination of marine processes (Day et al., 2007).

Historically, subsidence and accretion offset one another in the region. However, since the early 1900s, a myriad of anthropogenic and natural processes have caused land loss in coastal Louisiana to far exceed land gain (Day et al., 2000). Levee construction along the Mississippi
River in the early half of the century disconnected many estuaries from riverine sources and the nutrient and sediment deposition provided from them during annual flooding; thus salt water intrusion, subsidence and subsequent marsh loss have been relatively rapid and widespread (Wissel & Fry, 2005). Other research has identified dredging of canals through coastal marshes in the area to contribute a large percentage to subsequent erosion (Turner, 1997). The introduction and invasion of nutria, a semi-aquatic rodent hailing from South America, is also attributed to be a contributing factor in facilitating marsh conversion to open water through herbivory on wetland vegetation (Scarborough & Mouton, 2007). Coastal wetland loss in Louisiana is currently greater than all other states in the continuous United States combined, and in the 1960’s was recognized as one of the most rapidly changing coastlines on the planet (Day et al., 2000). From 1932 to 2016, Louisiana has lost approximately 4,833 km$^2$ representing close to 25% of the 1932 land area. Wetland change in the region has slowed since peaking in 1970 with a further reduction in rate of loss since 2010. However, projected increases in relative sea level rise as well as major storms could alter this trajectory in the future (Couvillon et al., 2017). Over the last few decades, significant focus and investment seek to combat land loss and protect coastal communities in Louisiana.

One noteworthy strategy has been to partially divert Mississippi River flow into subsiding, inactive deltas in order to reinitiate natural land building processes that created the Mississippi River deltaic plain. The most recent coastal master plan has assigned $5 billion dollars towards future diversion projects (LACPRA, 2017). Initially, these river diversions (Caernarvon and Davis Pond) were built to mediate salinities, and have been implicated in causing negative impacts on wetland ecosystem function and structure due to increased nutrient loads and insufficient sediment delivery (Poormahdi et al., 2018). Future planned diversions, or
“sediment” diversions, are being designed as larger, deeper structures engineered to transport greater quantities of sediment and river water to subsiding marshes to develop land more resilient to hurricane damage and erosion (Amer et al., 2017). Current working diversions along the Mississippi River include the Davis Pond Freshwater Diversion, Caernarvon Diversion, Fort St. Phillip Diversion, West Bay Sediment Diversion and the Channel Armor Gap Crevasse. Future planned restoration projects such as the mid-Barataria Bay diversion may further impact estuarine organisms along the Louisiana coastline.

Changes in riverine flow, from altered precipitation and river management (i.e., diversions, dams) alter dynamics of estuarine environments and have been shown to affect the abundance and distribution of nekton within estuaries (Rozas et al., 2005). Caernarvon Freshwater Diversion began reintroducing Mississippi river water into the Breton Sound, Louisiana in 1991, and was found by two studies to have either no effect or an increase in general biomass and densities for nekton assemblages including some ecologically and economically important estuarine species (de Mutsert & Cowan, 2012; Piazza & La Peyre, 2011). Other studies have linked oyster growth and mortality to flow (La Peyre et al., 2003, 2013, 2014), and white and brown shrimp growth and production (Rozas & Minello, 2011) to river flow, and the consequent effects on water quality and fixed habitat locations. In general, the relationships are often species-dependent, and time-dependent. In Louisiana, Guillory (2000) noted an association of commercial blue crab harvest with high Mississippi River discharge, but suggested this does not necessarily imply causality. Limited work has been done to explicitly examine how freshwater flow may impact blue crabs (West, 2016).

The blue crab is a common portunid (swimming crab) inhabiting nearshore coastal and estuarine environments from Nova Scotia to northern Argentina, and supports the most
prodigious commercial crab fishery in the United States (Perry & VanderKooy 2015; National Marine Fisheries Service, 2017). Nationally, landings for the species have valued over $150 million dollars per year since 2008, with value generally increasing annually. Total landings have been reported as high as 117,000 metric tons in 1993, and has remained above 60,000 metric tons every year since with the exception of 59,797 metric tons in 2013 (National Marine Fisheries Service 2017). The Gulf States Marine Fisheries Commission recommends management action for blue crabs for the five states along the Gulf of Mexico (Perry & VanderKooy 2015). Of the Gulf States, Louisiana contributes over half of total blue crab landings with over 18,143 metric tons reported annually. Furthermore, Louisiana is consistently the largest domestic supplier of blue crabs in the nation (Bourgeois et al., 2014). Despite this, the blue crab fishery within the state was overfished in 1995, 2013, and 2015, and assessment models show that juvenile abundance is in a general decline (West et al., 2016). While significant work has examined and attempted to model organism response to changes in river flow (Wilkinson et al., 2006; Wang et al., 2017; Wissel & Fry, 2005), we lack explicit data on potential impacts of river flow on blue crabs, including direct impacts (i.e., density, size class distribution), and indirect impacts (i.e., diets, habitat) on populations in the region. Research focused on understanding influential environmental conditions coupled with food web analyses may lead to a better understanding of the blue crab stock and its habitat in Louisiana (West et al., 2018).

The link between habitat and riverine influence on blue crab abundance has been explored in other regions, such as along the Atlantic coast (Hines et al., 1987; Ma et al., 2010; Posey et al., 2005). Within the Chesapeake Bay, juvenile blue crabs grew faster in submerged aquatic vegetation habitat than unvegetated habitat, implying that conditions favoring submerged
aquatic vegetation growth could provide better food availability for early stage blue crabs (Perkins-Visser et al., 1996). However, this study focused on one submerged aquatic vegetation species (*Zostera marina*), and did not specify substrate type. Another study within the same system analyzed outputs from a Chesapeake Bay Ecosystem Model to assess water quality and submerged aquatic vegetation impacts on blue crabs, suggesting that reduced nutrient input could enhance blue crab biomass (Ma et al., 2010). Within North Carolina, lower salinities within a small river dominated estuary were associated with greater survivorship, more rapid molting, and greater crab dry weight when compared to higher salinity areas (Posey et al., 2005). In Texas, reduced freshwater flow (alongside overfishing, shrimp trawl bycatch, and habitat loss or degradation) were suggested to be largely responsible for declines in abundance and commercial harvest of blue crabs (Sutton & Wagner, 2007). This study did not address impacts on different blue crab size classes and occurred largely within an environment with limited freshwater influence. While informative, many of these studies may not be applicable to the larger river dominated estuaries in the Gulf of Mexico with generally higher rates of flow, non-point source nutrient inputs, high turbidity and extensive marsh landscape.

Freshwater flow may also influence blue crab populations through impacts on their food resources (Wissel & Fry 2005; Hoeinghaus & Davis, 2007). Food availability has been found to influence young juveniles in seagrass beds, and may be similarly important in defining the distribution of juvenile and adult blue crabs in other habitats, which can be determined through use of stable isotope analyses within animal and plant tissue (Perkins-Visser et al., 1996). Animals acquire stable isotope δ¹³C and δ¹⁵N compositions from diets that are often habitat specific; therefore recording changes in stable isotopes provides a means to quantify the diet of organisms in the field while giving insight into habitat use (Fry et al., 2003). Stable isotopes have
proven useful to determine food sources and trophic levels of blue crabs in response to restoration (Llewellyn & LaPeyre, 2010), and may prove useful in identifying impacts of altered flow on changes in habitat and dietary subsidies, which could indirectly impact overall population densities. Increased inputs of nitrates to estuarine systems can influence primary producer uptake, which may increase phytoplankton productivity and alter the quality and quantity of food sources (Bucci et al., 2007). Consumers retain the δ^{13}C signatures of foods they ingest and when analyzed in combination with δ^{15}N from aquatic plant and animal tissues, a consistent separation between trophic levels is reflected (Deniro & Epstein, 1981).

The Louisiana coastal zone encompasses approximately 37,780 km² of lowland plains, inactive and active deltaic lobes and open water. Although approximately a quarter of these wetlands have been lost in the past 84 years, the area continues to support 30% of the total commercial fisheries in the United States, largely due to dynamics associated with the Mississippi River. Anthropogenic controls (levees and dams) throughout the drainage basin have contributed to reduced capacity for sediment accretion along the Louisiana coastal zone, allowing for subsidence and relative sea level rise to outpace sediment accretion throughout the Mississippi River deltaic plain (Couvillion et al., 2017). Restoration efforts in Louisiana reintroducing freshwater flow to subsiding, inactive deltas may further alter biotic community structure and production for estuarine nekton communities (Piazza & La Peyre, 2011).

Considering the continuous change occurring within Louisiana’s estuaries, understanding how these complex processes and alterations will impact estuarine ecosystems as a whole, as well as with economically important species, such as the blue crab would be helpful in managing our fisheries and habitats. More explicit information about riverine influence on blue crab habitat, diet and abundance in the region would help to better understand and manage this species in
Louisiana and the Gulf of Mexico in the face of continuous habitat degradation (West et al., 2016). This study has three objectives aimed at understanding how freshwater flow affects estuarine nekton communities, blue crab abundance and trophic characteristics. Specifically, the project goals are (1) to compare nekton communities in an active and an inactive delta (2) to compare juvenile blue crab densities and abundance between an inactive and an active delta; and (3) to compare $\delta^{13}$C and $\delta^{15}$N stable isotopes from blue crabs, primary producers and potential blue crab prey within an active and inactive delta.
2. METHODS

2.1. STUDY SITES

Two delta systems were identified for sampling for this project. We selected an active delta site, the Mississippi River Delta, and an inactive delta site, Lake Mechant and Mud Lake, located in Terrebonne Basin (Figure 2.1).

2.1.1. Mississippi River Delta “active delta”

The largest active delta system within Louisiana, the modern day Plaquemine-Balize Delta (also called “Bird’s foot Delta”), lies at the southern end of Plaquemines Parish, south of Venice, Louisiana, within the northern Gulf of Mexico. The Mississippi River began its current course through the Balize delta around 800 to 1,000 years ago (Coleman, 1988). Average monthly salinities within this active delta ranged from 0.1 to 6.44, with a mean of 0.8 ± 0.1 (Jan 2010-Oct 2019, Coastwide Reference Monitoring System site 0159; Figure 3.1). Average water temperature for the same time period ranged from 5.2°C to 31.5°C with a mean of 19.6 ± 0.8°C. Natural and man-made passes meander through the marsh and are characterized by deep channels and shallow sand bars scoured by high flows. The area’s marshes are dominated by Roseau cane, *Phragmites australis*, alongside emergent stands of *Zizaniopsis miliacea* (cut grass), *Salix nigra* (black willow), *Salix exigua* (sandbar willow), *Lantana camara* (lantana), *Sambucus canadensis* (elderberry), *Myriophyllum spicatum* (Eurasian water milfoil), *Potamogetun* spp. (pond weed), *Colocasia esculenta* (elephant ears), and *Sagittaria platyphylla* (duck potato). Diurnal tides here are largely influenced by wind speed and direction (Rabalais et al., 1995) with water levels largely influenced by wind speed and direction.
2.1.2. Terrebonne Basin “inactive delta”

Terrebonne basin occupies the abandoned deltaic lobes of the Teche and Lafourche, within the Mississippi River deltaic plain. Lake Mechant and Mud Lakes in Terrebonne basin (inactive deltaic complex) are the locations of our low flow sites (Figure 2.1). Average monthly salinities ranged from 1.1 to 18.6 with a mean of 8.1 (0.4) (January 2010 to October 2019; Coastwide Reference Monitoring System site 4455; Figure 3.1). Average monthly water temperature from the same time period ranged from 11.5°C to 31.6°C with a mean of 23.4 (0.5)°C. The surrounding marsh is dominated by *Spartina patens* (saltmeadow cordgrass), alongside many other species including but not limited to: *Spartina alterniflora* (smooth cordgrass), *Juncus roemereanus* (black rush), and *Phragmites australis* (Roseau cane). In contrast to the active sites, inactive delta sites represent an area with rapidly eroding and subsiding marsh due to lack of access to alluvial sedimentation and little restoration impacts. Similar to active delta sites, tides here are diurnal and water levels are largely dependent on wind speed and direction.
Figure 2.1 Field study site locations within A) Terrebonne Basin and B) Mississippi River Delta, Louisiana, USA. Colored dots indicate selected study sites for sampling in spring, summer, fall and winter; black dots indicate CRMS site locations used for continuous environmental data.
2.2. SAMPLING DESIGN & DATA COLLECTION

Within each selected delta, six sites were haphazardly selected using a stratified random sampling design. Each site consisted of a GPS location with a 100 m radius circle, where two sampling stations were selected within shallow water of depths less than 2 m. The two sampling stations within each site included one haphazardly placed along marsh edge (<1 m from marsh edge in open water) and one within open water (>3 m from marsh edge). Sites were sampled seasonally (May and June: summer 2018, September and October: fall 2018, December: winter 2018, and March: spring 2019; 2 deltas X 2 sample areas X 3 sites X 2 habitats X 4 dates = 96 samples).

2.2.1. Environmental

Upon approaching each site, water quality data were collected using a YSI model 556 multiprobe (Yellow Springs Instruments, Yellow Springs, OH) to determine water temperature (°C), salinity, dissolved oxygen (mg l⁻¹), and conductivity (S/m). A secchi disk was used to determine water clarity (cm). Data were also downloaded from the closest Coast wide Reference Monitoring System (CRMS) continuous data recorders to the study sites (inactive delta, CRMS 4455; active delta, CRMS 0159).

2.2.2. Nekton

To characterize nekton assemblages, each site was sampled using two gear types: a 1-m² throw trap and 5-m long by 2-m deep bag seine with a 3-mm square mesh. The throw trap consisted of a 1-m x 1-m x 0.66-m (height) aluminum frame with 1.6-mm knotless nylon mesh sides. To facilitate sampling in water greater than 0.66-m deep the nylon mesh was extended above the frame to a total height of 1.25 m. A 1-m² PVC square was integrated into the top of the
extended netting and buoyed by net floats. For throw trap deployment, a 22 ft. Boston whaler research skiff was slowly idled to the sample area before tossing the gear from the vessel’s bow. Water depth for throw trap samples was determined by calculating the mean of five depth measurements (cm) within the trap; with one measurement at each corner and one in the center. Bottom type was recorded as either mud bottom, hard bottom, or submerged aquatic vegetation. For throw trap samples, percent cover of submerged aquatic vegetation was estimated. If submerged aquatic vegetation was present, all aboveground biomass was collected. Submerged aquatic vegetation was placed into labeled bags and on ice for transport to the laboratory at Louisiana State University Agricultural Center. Once in the lab, submerged aquatic vegetation samples were sorted according to species, dried in a forced air drying oven at 60°C to a constant weight and weighed to the nearest 0.001-g dry weight to determine submerged aquatic vegetation biomass (g m\(^{-2}\)). Nekton within throw trap samples were cleared with a 1-m bar seine with 3-mm square mesh until the seine was empty of nekton for three consecutive clearings. All nekton from throw trap samples were placed into a labeled bag and onto ice for transport to the laboratory at LSU AgCenter.

Upon completion of throw trap sampling, the 5x2-m bag seine was pulled adjacent to the area previously sampled for 10 m. Bag seines are commonly used for sampling fishes in shallow water and have been shown to capture a greater number of species than other gears within these habitats (Crane & Kapuscinski, 2018). Water depth was determined by a single measurement using a depth pole just before pulling the net. All seine samples were collected, bagged, labeled and placed on ice for transportation to the laboratory at LSU AgCenter.

All nekton were returned to the laboratory for identification to species or lowest feasible taxon. Individuals of each species were then counted, measured to the nearest 0.1-mm total
length for fishes and shrimps and nearest 0.1-mm carapace width for crabs. Organisms were then weighed to the nearest 0.001-g wet-weight to determine blotted wet biomass (g) using an Ohaus Adventurer model top-loading laboratory balance (Ohaus Corp., Pinebrook, NJ, U.S.A.). Twenty five individuals were randomly chosen and subsampled from each species numbering over 25 individuals per sample. Blue crabs sex was also recorded.

2.2.3. Stable Isotope

2.2.3.1. Field sampling

Adult and juvenile blue crabs, primary producers, and potential blue crab prey species were collected from all sites to compare diets and trophic characteristics of blue crabs between the two deltas (active and inactive) in summer 2018 through the use of stable isotopes (δ\(^{13}\)C, δ\(^{15}\)N). The most abundant nekton species common between both deltas were collected (\textit{Menidia beryllina}, \textit{Anchoa mitchilli}, \textit{Palaemonetes spp.}) from throw trap and bag seine samples post laboratory analysis. At all sampling sites, crab traps and dip nets were used to sample for two size classes of blue crabs (juvenile < 90-cm, adult > 90-cm). Crab traps were deployed for 24 hours. Bait within traps was securely bound and closed off from consumption using fine wire mesh as to not be ingested and influence isotope values within blue crabs. A minimum of 3 crabs were collected for each sample site within deltas. Only male adult blue crabs were analyzed due to higher site fecundity compared to females. A minimum of three stems were collected from dominant primary producers from adjacent marsh or waters within the 100 m radius of sample sites. \textit{Phragmites australis}, a dominant emergent plant located within both deltas represented the C3 carbon pathway, primary producer samples. \textit{Spartina alterniflora} was the dominant C4 plant collected on adjacent marsh within inactive sites, while active sites were dominated by \textit{P}. 
*australis*. Submerged aquatic vegetation was sampled when present, with *Myriophyllum spicatum* used for analysis due to occurrence within both deltas. Particulate organic matter (POM) Water samples were collected by filling two dark brown 200ml bottles with water on site at 50-cm depth below water surface and placed on ice before being returned to the laboratory. Benthic macro – algae (*Cladophora* spp.) were also collected from sites when present. All samples collected were placed in separate sterile bags, labeled and frozen for transport to the lab at LSU AgCenter.

2.2.4. Laboratory methods

In the lab, plant tissue and muscle tissue samples were rinsed with distilled water, cleaned, and dried (Hoeinghaus & Davis, 2007). Muscle tissue was used for all animals except adult blue crabs, where hepatopancreas tissue was used. Blue crab hepatopancreas tissue was extracted, and frozen in the lab. Hepatopancreas tissue was used since isotope values in this tissue reflect the short term diet of the blue crab (~ 3 weeks; Llewellyn & La Peyre 2011). Hepatopancreas tissue underwent hexane decantations before being dried at 60°C to constant weight. Potential blue crab prey were dried at 60°C in a drying oven until constant weight. Plant samples were rinsed with deionized water and new growth clipped before drying at 60°C in a drying oven until weight was constant. Dried material was then ground into powder using mortar and pestle (WiglBug for plant tissue; Dentsply Rinn, Elgin, Illinois, U.S.A.) before weighing and loading samples. Water samples were filtered using 2 micron thick, pre-burned glass filters using suction. Filters were dried at 60°C in a drying oven until weight was constant upon subsequent measurements. All dried powder sample weights within tins was calculated depending on carbon/nitrogen ratios of tissue used, using the online tool provided by University of California
Davis Isotope Analysis Facility (https://stableisotopofacility.ucdavis.edu/), where the samples were shipped for analyses.

2.3. DATA ANALYSES

For all analyses, a significance level of alpha of $p < 0.05$ was used. Data residuals were tested for normality using Shapiro-Wilks test. Unless otherwise indicated, mean (standard error) are presented.

2.3.1. Environmental

Discrete salinity, water temperature, water depth and dissolved oxygen ranges are listed in results. Summary statistics (means, standard error) were calculated for environmental variables.

2.3.2. Nekton

Species richness was determined for all samples. Shannon-Weiner diversity index ($H'$) and Pielou’s Evenness Index ($J'$) were calculated for each throw trap and bag seine sample. Shannon diversity index was calculated as:

$$H' = -\sum p_i \ln p_i$$

where $p_i$ is the proportion of individuals found in the $i$th species. Using the Shannon-Weiner index, Pielou’s evenness index was calculated as:

$$J' = H'/\ln(S)$$

Evenness ranges from 1-0 with higher numbers being more even and lower numbers reflecting communities that are more skewed.
All data were analyzed using the R programming language R version 3.5.3 (2019-03-11) - "Great Truth" - ©2019, RStudio, inc. Generalized linear models with negative binomial distributions (glm.nb()) and a log link were performed on nekton crustacean or fish abundance (seine) and densities (throw trap), and young of the year blue crab abundance and densities. Linear models (lm()) were performed on J’ evenness and blue crab biomass. Generalized linear models (glm()) with Poisson distribution and log link was performed on nekton species richness. All response variables were tested separately by gear type (throw trap, seine) and habitat (marsh edge and open water) by deltas (inactive, active), season, and the interaction of delta and season as fixed effects. Blue crab biomass was log transformed log(x +1) to meet assumptions of homogeneity of variance. All final model residuals met assumptions of normality and homogeneity of variance or was determined accurate due to fit statistics.

A post-hoc pairwise Tukey test with significant interaction was used on all models to determine significant differences between the interaction of delta and season with adjusted p values through the emmeans() function in R. The effect of delta on nekton community structure was analyzed by season and habitat using a two-way analysis of similarity (ANOSIM) (anosim(), R package ‘Vegan’; Oksanen et al., 2013). ANOSIM tests for differences between groups based on the relative abundance of species. A Bray – Curtis dissimilarity matrix was created using raw nekton abundance data from throw trap samples. ANOSIM was performed on the Bray-Curtis dissimilarity matrix of nekton community species to determine similarities or differences based on the test statistic R, ranging from -1 to 1, where positive values indicate differences among groups. If differences were found (R > 0.30), an analysis of similarity of percentages (SIMPER, R Package ‘Vegan’; Oksanen et al., 2013) procedure was performed on nekton community abundance data using delta as a factor to determine species responsible for assemblage
differences between deltas. The effect of delta on nekton communities was further visualized using a non-metric multidimensional scaling plot (NMDS, package ‘Vegan’; Oksanen et al., 2013) to display relative association among species assemblages for each delta. Plots used have a stress (measure of distortion of ordination of multidimensional species data) of less than 0.20.

2.3.3. Isotope

Only sites containing over three adult blue crabs and three juvenile blue crabs were used for final analyses, and both size classes were analyzed separately. T-tests were used to compare differences of mean δ¹³C and δ¹⁵N values between delta s by individual species.
3. RESULTS

3.1. ENVIRONMENTAL

Discrete environmental variables measured are reported below (Table 3.1). Active and inactive deltas differed greatly in salinity and submerged aquatic vegetation, but only slightly in temperature and dissolved oxygen. Water temperature ranged between 8°C and 29°C with a mean of 19.0 ± 1.2 °C for active sites, while inactive sites temperature ranged slightly higher from 11°C to 32°C with a mean of 21.4 ± 1.1 °C. Highest temperatures were recorded in summer and lowest in winter across both deltas. Salinity ranged from 0.1 during spring sampling to 0.2 for all other sampling events with a mean of 0.18 ± 0.01 within active delta sites. Salinity for inactive delta sites ranged from 0.2 during winter sampling to 7 during fall sampling with a mean of 2.6 ± 0.2. Dissolved oxygen ranged from 4 mg l⁻¹ during fall sampling to 11.3 during summer sampling for active delta sites, with a mean of 8.1 ± 0.4 mg l⁻¹. Dissolved oxygen recorded for inactive delta sites ranged from 4.9 mg l⁻¹ during fall sampling to 10.8 mg l⁻¹ for winter sampling with a mean of 8.3 ± 0.2 mg l⁻¹. Mean overall submerged aquatic vegetation biomass for active sites was over two times as high as inactive delta sites (active: 51.8 ± 9.6, inactive: 20.9 ± 6.0; F₁=9.5, p < 0.01; Table 3.1).
Figure 3.1 Continuous hydrologic data (water temperature (˚C) and salinity) from CRMS sites nearest sample sites. Dotted lines indicate CRMS site 0159 from the active delta, while solid lines indicate CRMS site 4455 within the inactive delta. Vertical blue lines denote sampling dates.

Table 3.1. Discrete hydrological and environmental variables (mean ± 1 SE) collected quarterly for summer, fall, winter 2018, and spring 2019 within Mississippi River Delta (active delta) and Terrebonne Basin (inactive delta) concurrent with nekton sampling. Mean depth (cm) for throw trap (TT) and bag seine (BS) samples, salinity, water temperature (˚C), dissolved oxygen (mg l\(^{-1}\)) were recorded using a YSI Model 556 multiprobe. Submerged aquatic vegetation (SAV) dried biomass (g m\(^{-2}\)) was recorded for TT samples.

<table>
<thead>
<tr>
<th></th>
<th>summer</th>
<th>fall</th>
<th>winter</th>
<th>spring</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Active</td>
<td>Inactive</td>
<td>Active</td>
<td>Inactive</td>
</tr>
<tr>
<td>depth (TT) (cm)</td>
<td>37.2(3.1)</td>
<td>57.6(3.5)</td>
<td>39.8(5.7)</td>
<td>47.3(3.0)</td>
</tr>
<tr>
<td>depth (BS) (cm)</td>
<td>36.8(2.6)</td>
<td>56.8(2.6)</td>
<td>40.7(3.8)</td>
<td>47.3(2.1)</td>
</tr>
<tr>
<td>salinity</td>
<td>0.2(0)</td>
<td>2.5(0.4)</td>
<td>0.2(0)</td>
<td>5.1(0.6)</td>
</tr>
<tr>
<td>temperature (˚C)</td>
<td>28.2(0.2)</td>
<td>30.0(0.4)</td>
<td>26.6(0.2)</td>
<td>27.2(0.2)</td>
</tr>
<tr>
<td>DO(mg l(^{-1}))</td>
<td>7.0(0.6)</td>
<td>7.5(0.5)</td>
<td>5.0(0.1)</td>
<td>6.9(4.3)</td>
</tr>
<tr>
<td>SAV biomass (TT) (g m(^{-2}))</td>
<td>101.5(24.6)</td>
<td>36.0(18.5)</td>
<td>77.2(18.5)</td>
<td>33.1(13.6)</td>
</tr>
</tbody>
</table>
3.2. NEKTON

A total of 34,215 individuals from 46 species were collected in 96 throw trap throws and 96 bag seine hauls. Throw traps collected 5,135 individuals (active: 2,102, inactive: 3,033) from 41 species (Table 3.2), while bag seines collected 29,079 total individuals (active: 6,411, inactive: 22,668) from 43 species (Table 3.3).
Table 3.2. Crustacean and fish species listed separately in order of numerical abundance from 96 throw trap samples by habitat (marsh edge, ME; open water, OW). Total catch % corresponds to the percentage of individuals caught relative to the total individuals within each delta.

<table>
<thead>
<tr>
<th>Species</th>
<th>Active Delta</th>
<th>Inactive Delta</th>
<th>Both Deltas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ME</td>
<td>OW</td>
<td>Total</td>
</tr>
<tr>
<td><strong>CRUSTACEANS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pugio</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>M. ohione</em></td>
<td>522</td>
<td>594</td>
<td>1116</td>
</tr>
<tr>
<td><em>C. sapidus</em></td>
<td>113</td>
<td>151</td>
<td>264</td>
</tr>
<tr>
<td><em>F. aztecus</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Panopaeidae spp.</td>
<td>3</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td><em>R. harrisi</em></td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><em>L. setiferus</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>FISH</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. patronus</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>L. parva</em></td>
<td>102</td>
<td>101</td>
<td>203</td>
</tr>
<tr>
<td><em>C. shufeldti</em></td>
<td>63</td>
<td>81</td>
<td>144</td>
</tr>
<tr>
<td><em>A. mitchilli</em></td>
<td>3</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td><em>M. cephalus</em></td>
<td>83</td>
<td>0</td>
<td>83</td>
</tr>
<tr>
<td><em>P. latipinna</em></td>
<td>4</td>
<td>62</td>
<td>66</td>
</tr>
<tr>
<td><em>M. undulatus</em></td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>M. beryllina</em></td>
<td>19</td>
<td>18</td>
<td>37</td>
</tr>
<tr>
<td><em>G. affinis</em></td>
<td>10</td>
<td>32</td>
<td>42</td>
</tr>
<tr>
<td><em>Lepomis spp.</em></td>
<td>13</td>
<td>13</td>
<td>26</td>
</tr>
<tr>
<td><em>E. lyricus</em></td>
<td>8</td>
<td>11</td>
<td>19</td>
</tr>
<tr>
<td><em>S. scovelli</em></td>
<td>7</td>
<td>7</td>
<td>14</td>
</tr>
<tr>
<td><em>D. maculatus</em></td>
<td>9</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td>Fundulidae spp.</td>
<td>2</td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td><em>G. bosc</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>L. miniatus</em></td>
<td>6</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td><em>E. pisonis</em></td>
<td>2</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td><em>H. formosa</em></td>
<td>0</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td><em>A. spatula</em></td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><em>G. oceanicus</em></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><em>M. punctatus</em></td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><em>L. microlophus</em></td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><em>F. grandis</em></td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>L. rhomboides</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>M. gulosus</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>L. griseus</em></td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

Table 3.2 continued.
## Table 3.3

### Crustacean and Fish Species Listed Separately in Order of Numerical Abundance from 96 Bag Seine Samples by Habitat Type (Marsh Edge, ME; Open Water, OW). Total % Corresponds to the Percentage of Individuals Caught Relative to the Total Individuals within Each Delta.

<table>
<thead>
<tr>
<th>Species</th>
<th>ME</th>
<th>OW</th>
<th>Total</th>
<th>%</th>
<th>ME</th>
<th>OW</th>
<th>Total</th>
<th>%</th>
<th>Total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. arenarius</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>C. nebulosus</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>F. jenkensi</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>A. xenica</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. spilopterus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. variegatus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Gobiidae spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>L. xanthurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>S. plagiusa</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total Abundance</strong></td>
<td><strong>982</strong></td>
<td><strong>1120</strong></td>
<td><strong>2102</strong></td>
<td></td>
<td><strong>1369</strong></td>
<td><strong>1664</strong></td>
<td><strong>3033</strong></td>
<td></td>
<td><strong>5135</strong></td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.3 continued.**
For both gear types, abundance and biomass were highly correlated, so only abundance data results are presented \((r = 0.76, p < 0.0001)\). Nekton abundance was also highly correlated with crustacean abundance for each gear type, so crustacean and fish abundance are presented.
separately only (TT: \( r = 0.88, \ p < 0.001 \); BS: \( r = 0.96, \ p < 0.001 \)). Crustacean and fish species richness were highly correlated for bag seines (\( r = 0.73, \ p < 0.0001 \)) and throw traps (\( r = 0.91, \ p < 0.0001 \)), thus only total nekton species richness was analyzed for throw traps and bag seines. Total nekton species richness was also correlated with \( H' \) diversity index (\( r = 0.77, \ p < 0.001 \)), and thus \( H' \) is not reported in results.

3.2.1. Crustacean Abundance

Throw trap crustacean densities within active sites ranged from 0 to 134 ind. m\(^{-2}\), with a mean of 29 ± 5.3 ind. m\(^{-2}\). Densities within the inactive delta ranged from 0 to 341 ind. m\(^{-2}\) with a mean of 46 ± 10.3 ind. m\(^{-2}\). Crustacean densities for marsh edge and open water varied significantly by season (ME: \( F_3=9.9, \ p<0.0001 \); OW: \( F_3=3.7, \ p<0.009 \)), with no significant difference by delta or the interaction of delta by season (Figure 3.2). Marsh edge differences are largely explained by fall crustacean densities being significantly higher than spring and summer sampling. Open water differences are largely explained by summer densities being higher than spring and winter (Figure 3.2).

Bag seine crustacean catch per unit effort within the active delta ranged from 0 to 423 with a mean of 70 ± 13.3, while inactive delta crustacean catch per unit effort ranged from 0 to 3,555 with a mean of 357 ± 86. Crustacean catch per unit effort for marsh edge differed significantly between deltas (\( F_1=9.5, \ p<0.002 \)), with no significant difference by season or the interaction of delta by season (Figure 3.2). Marsh edge crustacean catch within the active delta was significantly lower than within the inactive delta (contrast estimate = -1.28). Open water crustacean catch per unit effort differed significantly by season and delta (\( F_3 = 2.7, \ p<0.04; \ F_1 = 21.4, \ p < 0.0001 \)), but not for the interaction of season by delta (Figure 3.2). Open water crustacean catch per unit effort for inactive sites was significantly higher than active sites. Open
water crustacean catch per unit effort for summer, fall, and winter samples were significantly higher than spring.

Figure 3.2. Total crustacean abundance reported by gear type and habitat. A.) Throw trap, marsh edge (ME); B.) Throw trap, open water (OW); C.) Bag seine, marsh edge (ME); D.) Bag seine, open water (OW). Letters above bars denote significant statistical differences (p<0.05).

3.2.2. Fish Abundance

Throw trap fish densities within the active delta ranged from 0 to 147 ind. m\(^{-2}\) with a mean of 14.8 ± 3.6 ind. m\(^{-2}\), while inactive delta fish densities ranged from 0 to 188 ind. m\(^{-2}\) with a mean of 18.2 ± 5.2 ind. m\(^{-2}\). Densities of fish for marsh edge and open water varied significantly by the delta and season interaction (ME: F\(_{1,3}\) = 8.3, p < 0.0001; OW: F\(_{1,3}\) = 16.2, p < 0.0001), but not by individual season or delta (Figure 3.3). The significant interaction for marsh edge samples was largely explained by fish densities for the active delta spring being significantly lower than all other season and delta combinations, with the exception of fall within
the inactive delta, which did not differ from any other season by delta combination. Open water fish densities were significantly greater in fall within the active delta compared to all other delta and season combinations which were similar, with the exception of spring active delta samples which were significantly lower (Figure 3.3).

Bag seine fish catch per unit effort within active sites ranged from 0 to 385, and had a mean of 64 ±12.8. Fish catch per unit effort within inactive sites ranged from 0 to 1151, with a mean of 115 ± 25.7. Fish catch per unit effort within marsh edge and open water bag seine samples varied significantly by the delta and season interaction (ME: F1,3 =5.4, p<0.0009; OW: F1,3 = 18.7, p < 0.0001; Figure 3.3). The interaction for marsh edge samples is largely explained by low catch per unit effort for spring active delta sites being significantly lower than summer within the same delta, as well as fall and spring catch per unit effort within the inactive delta (Figure 3.3). Catch per unit effort during winter in active delta sites were also significantly lower than spring in the inactive delta. The interaction for open water samples can largely be explained due to spring active delta fish catch per unit effort being significantly lower than all other seasons within the active delta and all seasons within the inactive delta. Furthermore, within active delta open water samples, fall catch per unit effort was significantly higher than winter. Inactive delta spring open water fish catch per unit effort were significantly higher than summer and winter active delta and fall and summer within the inactive delta. Fall fish catch per unit effort within the active delta open water samples were significantly higher than winter samples within the same delta.
Figure 3.3. Total fish abundance reported by gear type and habitat. A.) Throw trap, marsh edge (ME); B.) Throw trap, open water (OW); C.) Bag seine, marsh edge (ME); D.) Bag seine, open water (OW). Letters above bars denote statistically significant differences (p<0.05).

3.2.3. Species Richness

Throw trap nekton species richness for the active delta ranged from 0 to 11 species m$^{-2}$ with a mean of 4.5 ± 0.4 species m$^{-2}$, while nekton species richness for inactive throw trap samples ranged from 0 to 9 species m$^{-2}$ with a mean of 4.4 ± 0.3 species m$^{-2}$. Density of species richness for marsh edge differed significantly by season ($F_{1,3}=6.6$, p<0.001; Figure 3.4), with spring richness being significantly lower than fall and summer. Open water species richness densities differed significantly by the interaction of delta and season ($F_{1,3}=6.6$, p<0.001; Figure 3.4) with active delta richness densities for spring significantly lower than summer and winter richness for the active delta, as well as fall, spring, and summer for the inactive delta.
Bag seine nekton species richness for the active delta ranged from 1 to 15 species with a mean of $7 \pm 0.5$ species catch per unit effort, while inactive samples ranged from 3 to 14 species with a mean of $7.2 \pm 0.3$ species catch per unit effort. Nekton species richness for marsh edge and open water seine samples differed significantly by season (ME:$F_{1,3}=5.6$, $p<0.01$; OW:$F_{1,3}=6.9$, $p<0.005$), but not for delta or by the interaction between delta and season (Figure 3.4). Marsh edge differences are largely explained by spring richness being significantly lower than summer and fall while open water samples are due to spring samples being significantly lower than all seasons.

Figure 3.4 Nekton Species richness reported by gear type and habitat. A.) throw trap, marsh edge (ME); B.) throw trap, open water (OW); C.) bag seine, open water (OW); D.) bag seine, marsh edge (ME). Letters above bars, beside seasons, and beside deltas denote statistically significant differences ($p<0.05$).
3.2.4. J’ evenness index

Pielou’s Evenness index J’ (calculated for total nekton) from throw trap samples within active and inactive deltas ranged from 0 to 1 per m\(^2\), with active sites having a mean of 0.6 ± 0.05 per m\(^2\) and inactive having a mean of 0.6 ± 0.04 per m\(^2\). J’ differed significantly for open water by the season and delta interaction (F\(_{1,3}\) = 7.2, p < 0.0006; Figure 3.5), with marsh edge differences between delta, season, and the interaction between delta and season not statistically significant (Figure 3.5). The significant differences for the open water season and delta interaction is largely explained by spring active delta sites’ J’ being significantly lower than all other seasons within the same delta, as well as all seasons except for summer in the inactive delta.

Bag seine J’ for the active delta ranged from 0 to 0.98 with a mean of 0.6 ± 0.04, while inactive J’ ranged from 0.06 to 0.97 with a mean of 0.47 ± 0.03. J’ for seine marsh edge samples differed significantly only by delta (ME: F\(_1\) = 8.1, p < 0.006; Figure 3.5), but not by season or by the interaction of delta and season. The marsh edge significant variance is largely explained by summer active delta sites’ J’ being significantly higher than spring in the inactive delta. J’ for open water samples differed by seasons (OW: F\(_3\) =3.0, p<0.007; Figure 3.5), but not by delta or by the interaction between delta and seasons. Open water samples variance is largely explained by J’ within spring samples being significantly lower than J’ within summer and fall samples.
3.2.5. Species Composition

ANOSIM of Bray-Curtis dissimilarity matrix results demonstrated significant differences in nekton species composition between deltas for marsh edge and open water throw trap samples for all seasons (Table 3.4). SIMPER analysis further demonstrated individual species most responsible for these differences (Table 3.4). NMDS of Bray-Curtis dissimilarity matrix of species between deltas were also plotted for visualization, with NMDS permutations reaching a solution in 2 dimensions with stress < 0.15 for each analysis (Figure 3.6). Fall NMDS may have insufficient data for accurate NMDS plotting as indicated by low stress (2d, stress = 0.0008).
Figure 3.6 Non-metric multidimensional scaling ordination 2-D bi plots of Bray-Curtis dissimilarity indexes of nekton species composition by season and basin. Denoted are Summer (marsh edge:A, open water:B), Fall(marsh edge:C, open water:D), Winter(marsh edge:E, open water: F), and Spring(marsh edge:G, open water:H) throw trap samples by habitat (marsh edge, open water) for active (red) and inactive deltas (blue).
Table 3.4 ANOSIM and SIMPER results for comparison of nekton densities by habitat type (marsh edge, ME; open water, OW) and season within throw trap samples. Presented are the Global R for significant ANOSIM tests (p < 0.01), along with the top five dominant species and SIMPER results for percentage distribution of dominant specie showing dissimilarity in species composition between deltas.

<table>
<thead>
<tr>
<th></th>
<th>Summer ME</th>
<th>Summer OW</th>
<th>Fall ME</th>
<th>Fall OW</th>
<th>Winter ME</th>
<th>Winter OW</th>
<th>Spring ME</th>
<th>Spring OW</th>
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<tbody>
<tr>
<td><strong>Global R</strong></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. pugio</td>
<td>0.75</td>
<td>0.92</td>
<td>0.62</td>
<td>0.59</td>
<td>0.61</td>
<td>0.78</td>
<td>0.70</td>
<td>0.92</td>
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<tr>
<td>M. ohione</td>
<td>7.9</td>
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<td>27.4</td>
<td>20.0</td>
<td>16.6</td>
<td>18.0</td>
<td></td>
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<tr>
<td>B. patronus</td>
<td>15.1</td>
<td>9.8</td>
<td>8.6</td>
<td>31.0</td>
<td>19.9</td>
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<tr>
<td>C. sapidus</td>
<td>10.8</td>
<td>3.5</td>
<td>4.6</td>
<td>6.3</td>
<td>6.8</td>
<td></td>
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<td></td>
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<tr>
<td>C. shufeldti</td>
<td>8.7</td>
<td>4.4</td>
<td>13.5</td>
<td></td>
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<td></td>
<td></td>
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<td>F. aztecus</td>
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<td></td>
<td>8.9</td>
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<td>L. parva</td>
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<td></td>
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<td>A. mitchilli</td>
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<td>5.6</td>
<td>5.9</td>
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<td>M. cephalus</td>
<td>10.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Cumulative percentage</strong></td>
<td>52.8</td>
<td>48.5</td>
<td>69.7</td>
<td>57.9</td>
<td>81.2</td>
<td>75.5</td>
<td>87.6</td>
<td>86.2</td>
</tr>
</tbody>
</table>

3.2.6. Blue Crab Young of the Year

Blue crab young of the year densities from throw traps for the active delta ranged from 0 to 22 ind. m$^{-2}$ with a mean of 5 ± 0.9 ind. m$^{-2}$, while young of the year for inactive sites ranged from 0 to 33 ind. m$^{-2}$ with a mean of 4.9 ± 0.9 ind. m$^{-2}$. Blue crab young of the year densities for marsh edge and open water throw trap samples differed significantly by the delta and season interaction (ME: $F_{1,3}$=7.3, p<0.0001; OW: $F_{1,3}$=4.7, p<0.002). The marsh edge significant interaction derives from fall densities from both deltas, and winter inactive densities being significantly higher than all summer, and active delta winter and spring densities. The significant interaction for young of the year blue crab densities within open water throw trap samples can be largely explained by active delta fall young of the year blue crab densities being significantly higher than spring and summer within the same delta, as well as summer inactive...
delta samples. Fall young of the year blue crab densities within inactive samples were also significantly higher than inactive summer and active delta spring samples.

Bag seine blue crab young of the year catch per unit effort for the active delta ranged from 0 to 126 with a mean of 10 ± 3.6, while inactive delta blue crab young of the year catch per unit effort ranged from 0 to 71 with a mean of 8 ± 1.9. Blue crab young of the year catch per unit effort for marsh edge and open water seine samples differed significantly by the delta and season interaction (ME: F$_{1,3}$=8.4, p<0.0001; OW: F$_{1,3}$=3.3, p<0.02). The marsh edge significant interaction is largely explained by fall catch per unit effort for both habitats, and winter inactive delta catch per unit effort being significantly higher than all summer, and active delta winter and spring catch per unit effort. Open water significant interaction can be largely explained by fall catch per unit effort for both deltas, and winter inactive being significantly higher than summer and spring for both deltas.

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Figure 3.7. Blue crab, young of the year (YOY) (<30mm carapace width) reported by gear type and habitat for each delta. A.) throw trap, marsh edge (ME); B.) throw trap, open water (OW); C.) bag seine, marsh edge (ME); D.) bag seine, open water (OW). Letters above bars denote statistically significant differences (p<0.05). Figure 3.7 continued.
3.2.7. Blue Crab Biomass

Throw trap blue crab biomass for the active delta ranged from 0 to 68 g m$^{-2}$ with a mean of 18.8 ± 5.4 g m$^{-2}$, while biomass for throw trap within inactive sites ranged from 0 to 9.4 g m$^{-2}$ with a mean of 1.3 ± 0.3 g m$^{-2}$. Blue crab biomass for marsh edge throw trap samples differed significantly by the interaction between delta and season ($F_{1,3} = 4.3$, p < 0.04; Figure 3.8), while open water biomass differed by delta, but not by season or by the interaction between season and delta ($F_{1}=9.2$, p < 0.002; Figure 3.8). The marsh edge significant interaction is largely explained by mean fall active delta biomass being higher than all other seasons within the same delta, as well as all seasons within the inactive delta. Throw trap open water blue crab biomass significant differences can be explained by the active delta having significantly higher biomass than inactive, mostly due to samples from fall (Figure 3.8).

Blue crab biomass for bag seines within the active delta ranged from 0 to 156.2 g with a mean of 18.8 ± 5.5 g, while blue crab biomass for inactive delta bag seines ranged from 0 to 176.1 g with a mean of 11.2 ± 4.7 g. Blue crab biomass for seine marsh edge samples differed significantly by the interaction of season and delta ($F_{1,3}=3.5$, p<0.05; Figure 3.8). The marsh edge significant interaction is largely explained by fall active delta biomass means being significantly higher than winter within the same delta (Figure 3.8). The open water seine blue
crab biomass means differed significantly by season ($F_3=7.9$, $p<0.0002$), but not between delta or by the interaction between season and delta. The significance was largely due to higher biomass within fall for both deltas when compared to all other seasons (Figure 3.8).

Figure 3.8. Blue crab biomass reported by gear type and habitat for each delta. A.) throw trap, marsh edge (ME); B.) throw trap, open water (OW); C.) bag seine, marsh edge (ME); D.) bag seine, open water (OW). Letters above bars denote statistically significant differences ($p<0.05$).

### 3.2.8. Species – Environment Relationships

Regression models of throw trap catch for nekton species richness individuals $m^2$, nekton biomass $g m^2$, young of the year blue crab densities individuals $m^2$, and blue crab biomass $g m^2$ against submerged aquatic vegetation biomass $g m^2$ were all statistically significant, but had low $R^2$ values(Figure 3.9). CCA models examining species-environment relationships (salinity,
temperature, water depth, turbidity, submerged aquatic vegetation) on throw trap assemblages were not significant.

Figure 3.9. Regression of A) nekton species richness, B) log transformed nekton biomass (g m$^{-2}$), C) Young of the year blue crab densities, and D) blue crab biomass (g m$^{-2}$) against submerged aquatic vegetation (SAV) biomass (g m$^{-2}$). Grey area represents 95% confidence intervals.

3.3. ISOTOPE

Mean $\delta^{13}$C values did not vary significantly between deltas for any species. *Phragmites australis* tissue, benthic macro algae (benthic macro algae, BMA) tissue, and grass shrimp muscle tissue mean $\delta^{15}$N values were also similar for both deltas. *Myriophyllum spicatum*
(submerged aquatic vegetation) samples mean $\delta^{15}N$ values varied by delta, with active delta submerged aquatic vegetation means being two times higher than inactive sites. Adult and juvenile *Callinectes sapidus* mean $\delta^{15}N$ values varied between deltas, with active delta values 1.6 times higher than inactive sites for adult blue crabs, and 1.5 times for juvenile blue crabs (Table 3).

Table 3.5. Mean (SE) $\delta^{13}$C and $\delta^{15}$N stable isotope values by delta and species. n= sample size, primary producers were pooled using triplicate samples at three sites.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>n</th>
<th>$\delta^{13}$C (%)</th>
<th>$\delta^{15}$N (%)</th>
<th>$\delta^{13}$C (%)</th>
<th>$\delta^{15}$N (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Active Delta</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult <em>Callinectes sapidus</em></td>
<td>9</td>
<td>-23.9 (0.5)</td>
<td>13.2 (0.2)</td>
<td>-25.5 (1.0)</td>
<td>8.2 (0.4)</td>
</tr>
<tr>
<td>Palaemonidae spp.</td>
<td>9</td>
<td>-22.1 (0.5)</td>
<td>12.2 (1.0)</td>
<td>-22.3 (0.1)</td>
<td>11.2 (0.8)</td>
</tr>
<tr>
<td>Juvenile <em>Callinectes sapidus</em></td>
<td>9</td>
<td>-22.5 (0.3)</td>
<td>12.7 (0.1)</td>
<td>-21.9 (1.4)</td>
<td>8.3 (0.4)</td>
</tr>
<tr>
<td><em>Menidia beryllina</em></td>
<td>9</td>
<td>-24.5 (0.1)</td>
<td>15.9 (0.1)</td>
<td>-23.5 (0.6)</td>
<td>11 (0.6)</td>
</tr>
<tr>
<td><em>Phragmites australis</em></td>
<td>3</td>
<td>-26.8 (0.2)</td>
<td>2.4 (1.5)</td>
<td>-27.9 (0.3)</td>
<td>4.8 (0.3)</td>
</tr>
<tr>
<td><em>Myriophyllum spicatum</em></td>
<td>3</td>
<td>-21.5 (1.8)</td>
<td>8.9 (0.7)</td>
<td>-15.9 (0.2)</td>
<td>4.4 (0.3)</td>
</tr>
<tr>
<td>Cladophora spp.</td>
<td>3</td>
<td>-21.8 (0.3)</td>
<td>7.9 (2.1)</td>
<td>-22.3 (1.5)</td>
<td>5.3 (1.1)</td>
</tr>
<tr>
<td><em>Spartina alterniflora</em></td>
<td>4</td>
<td></td>
<td>-13.5 (0.2)</td>
<td>4.9 (0.3)</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.10. Bi-plot of Mean ±SE $\delta^{13}$C and $\delta^{15}$N stable isotope values for nekton and dominant vegetation species within active and inactive deltas.
4. DISCUSSION

Nekton, blue crab abundance and nekton species richness differences were seasonally driven, reflecting individual species life history, with most pronounced differences occurring within and between deltas during the winter and spring when river flow was highest within the active delta. This high river flow was associated with reduced salinity, temperature, and submerged aquatic vegetation habitat within active delta sites compared to warmer seasons within the same delta. During this time, decreased densities of nekton species and species richness were evident in comparison to the inactive delta which did not experience these altered water quality or habitat conditions during spring. Differences between the active and inactive delta largely occurred during the extended period of high riverine flow, which in 2019, exceeded previous river flows in both volume and duration providing a stark contrast between the deltas. This unusually high riverine flow, however, provides some indication of the impact that extended, high river flow may have on nekton assemblages and habitat availability within an estuary. What is not clear, is whether the lower abundances of nekton were due to displacement or increased habitat availability through flooding of often inaccessible marsh surfaces. Mean Gulf menhaden and shrimp landings in Louisiana have been found to positively correlate with sea level anomalies; thus variation in sea level could also play a role in nekton distribution (Morris et al., 1990). As changes in freshwater flow are associated with numerous water quality and habitat availability effects, determining direct linkages to nekton and economically important species remains critical, and may be location and estuarine dependent.

Despite an increasing number of studies examining nekton assemblages in estuarine shallow water environments, differences in habitats sampled, gear types used, and sample size result in variable results. In particular, comparisons of “marsh edge” and “open water” habitat
sampling highlights significant differences depending on distance from edges, and bottom type for “open water”, and whether marsh edge is within the emergent vegetation or within the water of shallow water areas. Differences have been previously identified when moving from within the marsh surface, across the marsh/water interface, and away from the marsh into open water habitat (i.e., Baltz et al., 1993, Peterson & Turner, 1994, Raposa & Oviatt, 2000, Kanouse et al., 2006). Furthermore, studies have shown that variables, such as shoreline morphology landscape location, and bottom characteristics (i.e., submerged aquatic vegetation or bare substrate) are often associated with different nekton assemblages, but difficult to control for (La Peyre & Birdsong 2008; Castellanos & Rozas, 2001; Fry et al., 2003, Jerabeck et al., 2017; Kanouse et al., 2006; Raposa & Roman, 2001). Additionally, differences in gear types limit the ability to compare actual numbers as opposed to just trends. For example, Louisiana Department of Wildlife and Fisheries uses seine nets for nekton sampling, however comparison with this study’s data remains difficult due to differences in mesh size, and sampling technique (LDWF, 2002). Despite this variation in descriptions of habitat, this and past studies support the overwhelming consensus that nekton in general, assemble in habitats providing structure; although the composition of the assemblages may vary.

Nekton species densities (throw trap) and abundance (bag seines) measured in this study fall within the wide range of previously reported values within similar shallow water, estuarine habitats in Louisiana; though studies within tidally influenced, active deltas in the region are lacking. For this study, mean nekton densities for the active delta were 44 ± 7.9 ind. m⁻², while inactive delta densities were 63.9 ± 10.8 ind. m⁻². Previous studies within estuaries in Louisiana have reported nekton densities ranging from 4 to 485 ind. m⁻² (Thom et al., 2004, Jerabeck et al., 2017; Kanouse et al., 2006, Piazza & La Peyre, 2007). Within the active Atchafalaya River
Delta, one study reported nekton densities of 22 ind. m$^{-2}$ within several shallow water habitats, slightly lower than densities within active sites (Castellanos and Rozas, 2001). For this study, mean nekton catch per unit effort for seine hauls was 88.9 ± 12.2 catch per unit effort for active delta sites and 268 ± 49.7 catch per unit effort for the inactive delta. Previous studies using seines within Louisiana estuaries have reported nekton catch ranging from 69 to 227 catch per unit effort (Thom et al., 2004; La Peyre & Birdsong, 2008). Active delta nekton assemblages were comparable to other studies within tidal freshwater marsh. Nekton species composition for inactive and active deltas were largely dominated by crustaceans, with Palaemonid species (grass and river shrimp) comprising from 44 % to 65% of total catch for both gear types for both deltas. The dominance of crustaceans (predominately grass and river shrimp) alongside blue crabs within tidal freshwater and oligohaline marshes has been reported in previous studies in Louisiana, Texas, and Virginia similar to our results (Castellanos & Rozas, 2001; Rozas & Odum, 1987; Zimmerman et al., 1990). Panaeid shrimp contributed a large percentage to inactive delta samples, similar to other studies within brackish and salt marshes, (Hettler Jr., 1989; Rozas & Minello, 2015; Jerabeck et al., 2017; Kanouse, et al., 2006) though these species were absent from fresher waters within active delta sites. Other studies within tidally influenced freshwater marshes also report few Panaeid shrimp, though within both the Atchafalaya River and the diversion influenced upper Breton Sound, studies have reported higher densities of *C. variegatus*, sheepshead minnow (Piazza & La Peyre, 2007; Castellanos & Rozas, 2001). Castellanos & Rozas also reported a higher percentage of fish within Atchafalaya River Delta samples (> 65%) than ours (44% for both gears within active sites), which could be due to sampling different habitats during fewer seasons.
Though differences between deltas were evident during winter and spring, season was found to be the most influential factor in determining nekton community characteristics within both deltas. Seasonality and life history traits of individual species may be a large driver of differences between nekton communities within both deltas, with the exception of spring sampling, when there were large increases in discharge from historic flooding of the Mississippi River for active delta sites. Temperature and salinity are generally held as key environmental variables that drive estuarine organisms life history (Neuparth et al., 2002). For example, both deltas experienced higher densities of blue crabs during fall sampling than any other season, similar to previous research looking at blue crab larval dispersion within the northern Gulf of Mexico which reports high numbers of blue crab megalopae settlement to occur in the fall (between August and September within the Mississippi bight, just east of the Mississippi River delta (Perry et al., 2003).

While suitable habitat is important for settling blue crab megalopae, many other factors can influence larval dispersal including currents, winds, and timing of recruitment (Etherington & Eggleston, 2000). Another estuarine dependent decapod crustacean, brown shrimp (*F. aztecus*), has been found to be most abundant in estuaries in the northern Gulf of Mexico from February to March, followed by a peak from August to September (Rogers et al., 1993). Estuarine recruitment of brown shrimp post larvae occurs when the strongest atmospheric cold fronts pass through which result in significant shelf-estuarine exchanges and organismal transport (Rogers et al., 1993). These seasonal (winter) events often dominate and override astronomically driven tides in the northern Gulf (Denes & Caffrey, 1988). Brown shrimp was most abundant during fall sampling within the inactive delta, and absent here during winter sampling. Estuarine densities of another commercially important species, the gulf menhaden (*Brevoortia patronus*) is largely
dependent on life history. A similar seasonal peak can be explained for gulf menhaden (*Brevoortia patronus*). *B. patronus* spawns offshore in fall through winter, and larvae are carried into estuaries where they metamorphose into juveniles. Juveniles then spend spring and their first summer in estuaries before migrating offshore by fall (Vaughan et al., 2007). This study found highest numbers of *B. patronus* occurred in both deltas during spring sampling as would be predicted based on their life history.

Seasonal variation in environmental and water quality variables may impact nekton assemblages directly, through impacts on salinity and temperature, and indirectly, through salinity and temperature impacts on submerged aquatic vegetation. Submerged aquatic vegetation seasonal growth patterns can influence availability of structured habitat for nekton within upper estuaries. While greatest submerged aquatic vegetation biomass was recorded during early fall sampling for this study, studies focused explicitly on submerged aquatic vegetation indicate peak biomass during summer months, though this may vary depending on water clarity, temperature, or even nutrient concentrations (Hillmann et al., 2019; Cho & Poirrier, 2005; Orth et al., 2010). Greater submerged aquatic vegetation biomass and diversity were also found with lower salinity environments across coastal Louisiana (Hillmann et al., 2019).

Changes in submerged aquatic vegetation biomass impact structural habitat available to nekton, and, in this study, partially explained nekton richness, density and blue crab densities specifically. These findings are similar to findings from Aransas Bay, Texas, as well as in the Atchafalaya Delta, Louisiana, which found highest abundance of nekton species within structured habitat (submerged aquatic vegetation or emergent marsh) when compared with unvegetated mud bottom (Castellanos & Rozas, 2001; Kanouse et al., 2006; Rozas & Minello,
Another study across coastal Louisiana found five times higher nekton densities in submerged aquatic vegetation when compared with marsh edge or mud bottom (La Peyre & Gordon, 2012). These findings are important when examining effects of flow as submerged aquatic vegetation prevalence and biomass has been found to be impacted by amount of freshwater flow. Previous research shows that flow and lower salinities from Carnaervon diversion coincided with increased growth of submerged aquatic vegetation within flow areas compared to a more saline reference area, suggesting that higher flow could benefit nekton community diversity through increased habitat (Rozas et al., 2005). However, within this study lowest submerged aquatic vegetation biomass occurred from sampling during periods of highest river discharge, implicating a possible lagged effect relating higher flow and increased submerged aquatic vegetation biomass.

Density estimates for many species among different habitats could further be influenced through other hydrodynamic processes such as tidal movement (Rozas & Minello, 1997) or sea level anomalies (Morris et al., 1990). Water depths within samples were consistently lower for active sites, and shallowest depths were reported for both sites during winter sampling. One study along the Connecticut coast found flooding depth, duration, and frequency within *Phragmites australis* marshes were significantly reduced compared with *Spartina alterniflora* marshes, meaning nekton could not use *P. australis* marsh interior as much as *S. alterniflora* interior (Osgood et al., 2003). However, these findings may not be applicable to Louisiana coastal marshes due largely to spatial and temporal differences. Active delta marshes are dominated by *P. australis*, while the inactive delta marshes are more variable, though dominated by *S. alterniflora*. These differences in emergent vegetation species alone could alter availability of flooded marsh habitat for nekton usage. Another study found *Spartina* production to be highly
correlated with mean monthly sea level anomalies during the summer growing period, and that Gulf menhaden (*Brevoortia patronus*) and Panaeid shrimp landings in Louisiana were positively correlated with lagged (to account for life cycle) mean sea level anomalies (Morris et al., 1990). Thus, primary and secondary production can increase with increased but intermittent marsh inundation depending on sea level anomalies.

Water levels vary temporally and spatially for each delta, and freshwater flow from the Mississippi River is generally highest during winter and spring. Lower numbers reported during these seasons could be due to not sampling interior marsh surface. Research in Florida actually noted an increase in species richness with decreasing flows due to invasion by marine species, and suggested other metrics be analyzed as well as diversity to set flow criteria (Palmer et al., 2015). Physical characteristics of marsh edge such as slope is also a factor in determining nekton community structure. One study found that shallower slopes support more organisms and resident species than steeper slopes, though marsh edges with steeper slopes support more diverse and species rich assemblages (La Peyre & Birdsong, 2008). Though marsh edge type and slope was not accounted for in this study, variation in these factors between sites and deltas could impact nekton assemblages and blue crab population dynamics.

High freshwater flow for winter and spring in the active delta created more variation throughout the sampling period when compared to the inactive delta, which is reflected in higher variation of nekton assemblage characteristics in the active delta sites. Variation from flow can influence nekton through altering salinity, temperature, and water depth. Magnitude of freshwater flow has been shown to influence nekton along other estuaries, and extreme flow where frequency or severity becomes too great can lower species diversity and abundance, possibly explaining differences within spring samples (Olin et al., 2015). Furthermore,
temperature has been shown to be a contributing factor to the distributions of marine organisms, and lower temperatures within active sites during winter and spring associated with high flow may not only lower submerged aquatic vegetation biomass, but also alter nekton densities (Leffler, 1972). Thus, timing of flows could negatively or positively influence estuarine nekton; possibly depending on water temperature. Contrary to active delta sites, inactive delta sites’ temperature was less variable, and nekton communities were generally less so as well.

Studies have demonstrated the importance of freshwater flow to estuarine systems in determining estuarine function and ecosystem health, though freshwater flow is difficult to quantify within the Louisiana coastal region (Benson, 1981). Differences among nekton species assemblages between deltas can be further attributed to variations in salinity by delta. Salinity has been shown to be an important factor structuring nekton communities within estuaries, and to be highly negatively correlated to riverine freshwater flow (Greenwood et al., 2007; Piazza & La Peyre, 2011). Panaeid shrimp were largely absent from active delta sites, yet densities were consistently high in the inactive delta during summer and fall. Brown (F. aztecs) and white shrimp (L. setiferus) use estuaries as nurseries, though the role of salinity in their production is complex (Doeru et al., 2016). Our results are similar to previous research in that these species had higher densities associated with higher salinities (Zimmerman et al., 1990).

Selected gear types had different patterns when compared with each other, though richness was similar between both. Total nekton densities for the inactive delta were 1.5 times greater than the active delta for throw trap samples, while bag seine differences were greatly exaggerated with the inactive delta abundance being 3.5 times greater within inactive than active. Throw traps were adequate in effectively sampling both areas, yet bag seine effort varied due to extremely soft, mud bottom within active sites most notably during winter and spring. Catch
efficiencies for bag seines have been shown to be highly variable due to environmental characteristics, which is problematic when environmental characteristics are related to the treatment (Rozas & Minello, 1997). For instance, seining over soft substrate within different sites may have altered catch efficiencies, which could have confounded nekton abundance numbers. Specifically within active delta sites, soft bottom and steep drop offs at several sites made effective seining almost impossible, while inactive sites where characterized by firmer substrate and more consistent depths gently sloping away from the marsh edge, making sampling with bag seines here more effective. Furthermore, previous research suggests abundances cannot be accurately measured using seines in submerged aquatic vegetation or emergent marsh, further impeding results (Orth & Vanmontfrans, 1987). Gear types could further impact nekton results through species selectivity. Juvenile Penaeid shrimp have been found to avoid seines by burrowing into the substrate, and small, epibenthic species are more difficult to remove from throw traps than pelagic or semi-pelagic organisms (Rozas & Minello, 1997).

Past research has suggested that riverine flow quantity and timing affect nekton species abundance and recruitment of resident consumers, thus understanding this relationship is of utmost importance in regards to river management and biological resources (Piazza & La Peyre, 2007; Piazza & La Peyre, 2011). Previous studies have reported positive relationships between freshwater flow and blue crab landings in Texas, Florida, and Louisiana (Doering & Wan, 2018; Guillory, 2000; Powell et al., 2002; Wilber, 1994). However, these studies are limited in that they do not explain the mechanisms that drive these trends, hypothesizing possible causes such as increased juvenile habitat or increased nutrient and detrital flow indirectly enhancing food supply from increased flows. Guillory (2000) analyzed Louisiana Department of Wildlife and Fisheries blue crab commercial landings from 1960 to 1997 with corresponding annual discharge.
in cubic feet per second from the Mississippi River gauge at Tarbert’s Landing, reporting increased commercial landings associated with increased discharge. Using the same gauge and Louisiana Department of Wildlife and Fisheries commercial blue crab landing data from 1999 to 2016, a negative correlation between landings from the active Mississippi River Delta and discharge is evident ($r = -0.56$, $p = 0.02$; Figure B.1). However, data on effort were not available to validate this finding.

Enriched $\delta^{15}$N values from primary producers, nekton species, and blue crabs suggest that trophic webs within the active delta are supported through riverine influence - freshwater flows have been shown to carry distinct stable isotope values that can be traced through the estuarine food web, providing a tool for examining connections between freshwater flows and estuarine consumers (Fry, 2002). Stable isotope analysis within this study was useful to confirm allochtonous support of the trophic system within the active delta, but not relative contributions of primary producers towards blue crab diets. Future research aimed at better understanding blue crab dietary contributions and trophic support from freshwater flow should address these shortcomings by including analyses of more potential sources, including samples of particulate organic matter (POM) and detritus.

Diversions may provide increased production due to increased nutrient input. Our study complements other research in that the active delta contained higher biomass of submerged aquatic vegetation (Hillmann et al., 2019), though not during winter and early spring. Regardless, blue crab densities were comparable to inactive delta sites with less flow and less submerged aquatic vegetation, and overall nekton abundance – contrary to other research – was not strongly correlated with higher submerged aquatic vegetation biomass. Species richness, nekton biomass, young of the year blue crab abundance, and blue crab biomass regressions against submerged
aquatic vegetation biomass were significant, however r squared was very low for all analyses. Furthermore, Louisiana Department of Wildlife and Fisheries fisheries independent seine data from 2013 to 2018 show a mean catch per unit effort of 4.2 for blue crabs for active sites, while mean seine catch per unit effort within the inactive delta was reported to be over twice as high at 8.5 crabs per seine.

Gear efficiency differences may also be responsible for the different catch per unit effort patterns between deltas. For our study, blue crab densities within throw traps for both deltas were similar, with the exception of winter and early spring sampling; thus variation in gear capture efficiency between areas could also explain differences in catch per unit effort for Louisiana Department of Wildlife and Fisheries data. Louisiana Department of Wildlife and Fisheries commercial blue crab landings for both regions from 1999 to 2016 show landings to also be higher in the inactive delta than active delta, though this area is more accessible with a higher amount of crabbers. Highest densities of recently settled blue crabs were found during fall months within our study, similar to others (Aguilar et al., 2005; Rabalais et al., 1995; Sutton & Wagner, 2007; Thomas et al., 1990). This may suggest flow effects from sediment diversions are likely most important to consider during this period of settlement for blue crab populations in Louisiana. This complements previous research which has suggested operating river diversions to minimize effects to mating females during spring, as well as the spawning period in the fall (Peyronnin et al., 2017).

Overall, both deltas supported similar densities of nekton species, though assemblages differed. There was a distinct seasonal trend within both deltas, reflecting individual species life histories as well as temperature driven submerged aquatic vegetation cycles and salinities. Seasonal variation was most pronounced within the active delta during winter and spring, the
periods of highest flow resulting in low salinity, temperatures, and reduced submerged aquatic vegetation alongside increased variation in nekton communities in the active delta than the inactive delta. Flow can affect water quality and habitat, and the timing and quantity is likely important in determining nekton community structure and habitat availability. As changes in freshwater flow are associated with numerous water quality and habitat availability effects, determining direct linkages to estuarine nekton and economically important species remains critical, and may be location and estuarine dependent.
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APPENDIX A. BLUE CRAB LIFE CYCLE DESCRIPTION

The blue crab life cycle involves planktonic, nektonic, and benthic stages that are dependent on the different salinity gradients and habitats within entire estuaries and coastal marine waters, thus it is vital to understand the complex life cycle of the species to understand potential vulnerabilities (Perry & VanderKooy, 2015) (Figure 2). Females migrate to brackish waters of the upper estuary to mate, timing the event to the female’s pubertal (or final) molt. Mating involves intricate interactions between males and females, as well as other competing males, throughout the process (Jivoff & Hines, 1998). Courtship behavior in males is elicited by release of a pheromone in the urine of receptive pubertal molt females. Males then guard the females up to seven days post copulation until her shell has hardened (Jivoff, 1997).

Contrary to most estuarine species, mating and spawning occur at different times for the blue crab, with spawning usually occurring within two months of mating in spring, summer, and fall. Females migrate from lower salinities in upper estuaries to higher salinities along the coast.
and offshore before spawning. Spawning tends to occur in waters when temperatures and salinities are favorable for hatching of eggs and growth of larvae (over 19˚C, 21 ppt) and females having mated in the fall may delay spawning until the following spring brings improved conditions (Perry & VanderKooy, 2015). Most females spawn more than once and have the potential to spawn up to 18 times throughout a lifetime (which lasts around 3 years in the Gulf of Mexico) (Hines et al., 2003). Eggs develop within “sponges” along the underside of the apron, are small, and occur in large numbers per brood (upwards of 2.8 x 10^6) (Graham et al., 2012). However, little is known about the relationship between spawning stock and recruitment (Perry & VanderKooy, 2015).

Larvae develop in the offshore waters above the continental shelf, and release of larvae is dependent on many variables associated with tides, light, and salinities (Tankersley et al., 1998). Larvae ontogeny includes seven (occasionally eight) zoeal stages and a megalopal stage before tides and winds transport megalopae larvae back within estuaries where settlement and further development occurs. Settlement of postlarvae, recruitment of young juveniles, and postsettlement processes including dispersal comprise a critical period in the life history of blue crabs that can determine the abundance and distribution of young juveniles (Caley et al., 1996). These processes can be strongly influenced by food access and the availability of structured habitat including submerged aquatic vegetation, course woody debris, oyster reef, and salt marshes (Heck et al., 2003). Furthermore, Increased coastal erosion leading to barrier island loss could reduce landward current strength and tidal pull (not as strong as when concentrated through inlets) thus decreasing chances that drifting larval crabs would reach essential inshore habitats (O’Connell et al., 2005).
Figure B.1. Regression of commercial blue crab landings within the Mississippi River Delta plotted against Mississippi River mean annual discharge for years 1999 – 2016. Grey area represents 95% confidence intervals.

Figure B.2. Mississippi River water gauge height at Baton Rouge, LA, from daily means from April, 2018, to April, 2019. Vertical, green lines indicate sampling dates.
Figure B.3. Mississippi River delta commercial blue crab landings and Mississippi River mean yearly discharge from 2000 to 2016.
APPENDIX C. COASTWIDE REFERENCE MONITORING SYSTEM
CONTINUOUS ENVIRONMENTAL DATA GRAPHS

Figure C.4. Continuous daily mean salinity by year from CRMS site 4455 near Terrebonne Basin sites from May 2014 to June 2019. Red vertical lines indicate sampling dates during 2018, while blue horizontal lines indicate sampling dates for 2019.

Figure C.5. Continuous daily mean salinity by year from CRMS site 0159 near Mississippi River delta sites from May 2014 to June 2019. Red vertical lines indicate sampling dates during 2018, while blue horizontal lines indicate sampling dates for 2019.
Figure C.6. Continuous daily mean water temperature by year from CRMS site 4455 near Terrebonne Basin sites from May 2014 to June 2019. Red vertical lines indicate sampling dates during 2018, while blue horizontal lines indicate sampling dates for 2019.

Figure C.7. Continuous daily mean water temperature by year from CRMS site 0159 near Mississippi River delta sites from May 2014 to June 2019. Red vertical lines indicate sampling dates during 2018, while blue horizontal lines indicate sampling dates for 2019.
Figure C.8. Continuous daily mean water temperature by year from CRMS site 4455 near Terrebonne Basin sites from May 2014 to June 2019. Red vertical lines indicate sampling dates during 2018, while blue horizontal lines indicate sampling dates for 2019.

Figure C.9. Continuous daily mean water temperature by year from CRMS site 0159 near Mississippi River delta sites from May 2014 to June 2019. Red vertical lines indicate sampling dates during 2018, while blue horizontal lines indicate sampling dates for 2019.
VITA

Caleb Taylor was born in 1992 in McComb, Mississippi. Growing up, he witnessed coastal erosion, hurricanes, and an oil spill diminish and degrade the Louisiana coast over years of family fishing trips out of Grand Isle, Port Fourchon, and Leeville, and was driven to a profession of protecting fragile coastal ecosystems and the people that rely on them. After graduating from Parklane Academy in 2011, he attended the University of Southern Mississippi, finding employment as a student worker in the evolutionary ecology lab and teaching introductory biology as a teaching assistant. In May 2015, after graduating with honors, he interned with the Center for Research and Development within the Gulf Coast Research Lab in Ocean Springs, Mississippi. Since then, he has lived in Alaska, Texas, and Louisiana, working in one aspect or another of coastal fisheries management. Caleb joined the coastal restoration ecology lab within the department of Renewable Natural Resources at Louisiana State University in early January, 2018, to learn how estuarine species relate to their changing habitats and environments. He has since kept busy working to better the graduate student experience at LSU and within his department through student government, while continuing to focus on research and academics. Caleb anticipates graduating in May, 2020, and plans to continue working towards protecting and sustaining coastal and marine ecosystems.