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Nekton community dynamics within active and inactive deltas in a major river estuary: potential implications for altered hydrology regimes

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ABSTRACT: High fisheries production within estuaries is associated with coastal upwelling, tidal mixing, and land-based runoff facing increasing impacts from climate and human activities. Active river deltas receive large riverine inflows compared to inactive river deltas, providing contrasting estuaries to compare impacts of river inflow on estuarine nekton. We quantified nekton assemblages and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) of commercially important blue crab *Callinectes sapidus* Rathbun, 1896 within an active and inactive delta in coastal Louisiana to explore the impacts of differing riverine inflow. Crustaceans dominated estuarine assemblages, differing only by season and not delta type, with summer and fall supporting highest densities. Fish density and assemblages differed by the interaction of season and delta due to differences during the 2019 record high spring river inflow. During this period, the active delta supported reduced fish densities and richness compared to the inactive delta. Nekton densities across deltas and seasons reflect a combination of species life history characteristics and habitat conditions. The high spring river discharge in 2019 impacted habitat availability (reduced presence of submerged aquatic vegetation), water conditions (decreased temperature and salinity), and potentially displaced nekton to unsampled habitat areas (i.e. interior marsh surface) within the active delta. While differences in nekton density and assemblages were only evident during the high spring river discharge, $\delta^{15}N$ values of blue crabs were approximately 1.5 times higher in the active delta, potentially indicating more terrestrial influence. Understanding how altered inflow impacts environmental variables supporting estuarine nekton production remains critical for supporting management within these hydrologically managed regions.

KEY WORDS: Habitat · Salinity · Blue crab · River discharge · Mississippi River

1. INTRODUCTION

Coastal upwelling, tidal mixing, and land-based freshwater runoff including river inflows drive fisheries production (Caddy & Bakun 1994). While terrestrially enriched river discharge can positively influence biological processes (growth, survival, recruitment) impacting fisheries production (Grimes 2001), the impacts of large fluctuations or decreasing river discharge on estuarine-dependent species are less well understood (Wilber 1992, Galindo-Bect et al. 2010, Tupitza & Glaspie 2020). This variation in riverine inflow and its impacts are due to both natural variability from differences in regional weather, climate, and basin geomorphology, as well as anthropogenic activities resulting in altered river flows, including leveeing of rivers and river diversions (Orlando et al. 1993, Allison et al. 2012, Hiatt et al.

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2019). With climate change, altered precipitation patterns may further impact river flows (Yang et al. 2015, Marshall et al. 2021). Understanding how estuarine resources, fisheries, and functions respond to changing riverine inflows remains critical to the management of these systems and the fisheries that depend on them (Alber 2002).

Within the northern Gulf of Mexico, the Mississippi River has formed vast coastal wetlands within past and present deltas, supporting over 60% of fishery landings in this region since 1950 (Chesney et al. 2000). However, this area is also experiencing one of the fastest rates of wetland loss in the world due to a combination of anthropogenic and natural factors (Couvillion et al. 2013). Levee construction along the Mississippi River in the early half of the 20th century disconnected many estuaries from riverine sources, interrupting the supply of nutrients and sediments provided during annual flooding. Salt water intrusion, subsidence, and subsequent marsh loss in areas separated from the river by the levees have been relatively rapid and widespread (Day et al. 2011). Marshes still under direct influence of riverine processes are considered active deltas, and 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 (Coleman et al. 2008). In Louisiana, only the Plaquemine-Balize Delta at the mouth of the Mississippi River and the Atchafalaya/Wax Lake Outlet at the mouth of the Atchafalaya River are active.

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). Specifically, freshwater flow can influence fishery production through transport of detritus and nutrients, 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 submerged aquatic vegetation, which in turn influences distributions of many juvenile fishes and shellfish, either directly or indirectly through the food web (Heck et al. 2003, Warry et al. 2016). However, impacts may vary depending on the extent of freshwater inflow and the initial conditions within an estuary. For example, in Matagorda Bay, Texas, quality of organic matter was found to be higher following low salinity events driven by high freshwater flow, ultimately contributing to enhanced oyster production (Marshall et al. 2019). In contrast, within Louisiana, extended low salinities from flooding resulted in negative impacts on oyster survival, recruitment, and growth (La Peyre et al. 2013). These contrasting findings extend to other species as well. 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* (Linnaeus, 1767) and brown shrimp *Farfantepenaeus aztecus* (Ives, 1891) in affected areas (Rozas & Minello 2011). In contrast, western mosquitofish *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).

Impacts on fisheries extend to other economically important species, such as blue crabs *Callinectes sapidus* Rathbun, 1896. Louisiana consistently supports the largest blue crab fishery in the nation, largely due to the vast mosaic of estuarine habitats created by the Mississippi River (Bourgeois et al. 2014). Despite this, juvenile blue crab abundance is in general decline in the region (West et al. 2018). While several studies have modeled the organismal response to changes in river flow (Wissel & Fry 2005, Wilkinson et al. 2006, Wang et al. 2017), 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 loss and alteration) on populations in the region. 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.

Beyond measuring direct impacts on nekton species, studies have examined how riverine inflow and changing connectivity between continental and coastal habitats may impact food resources or food quality. Stable isotope composition analyses can provide information on the origin and composition of organic matter available between water bodies (Riera & Richard 1997) and have been used previously to examine impacts of differing inflow into estuaries on organic matter quality. Marshall et al. (2021) compared 5 northwestern Gulf of Mexico estuaries based on stable isotope analyses to assess how food quality may differ according to freshwater inflow. They found a general trend of decreasing connectivity between continental and coastal habitats with decreasing inflow, resulting in lower quality organic matter, potentially impacting estuarine function and health.

Despite the uncertainty of the association between fisheries production and freshwater inflow, large rivers continue to be manipulated, impacting their inflow into estuaries. In coastal Louisiana, a region dominated by the Mississippi River, a multi-billion dollar restoration plan dedicates significant resources to diverting Mississippi River flow in order to reinitiate natural land-building processes and reconnect coastal estuaries to terrestrial inputs (Coastal Protection and Restoration Authority of Louisiana; CPRA 2017). While these changes in river inflow may directly impact water quality, they may also indirectly influence fisheries through impacts on habitat characteristics and the interaction of available fixed habitat with overlying water quality. As large river systems continue to be manipulated, better understanding of how nekton assemblages respond and of how economically important species, such as the blue crab, adapt to changed inflow remains critical.

We explore differences in estuarine nekton assemblages, blue crab abundance, and stable isotope compositions of blue crabs and several primary producers between active (open) and inactive (closed) deltaic systems. Specifically, we explore whether there are differences in fish and crustacean densities and assemblages between active and inactive deltas, quantifying environmental variables potentially impacted by different river inflows (i.e. salinity, temperature, water depth, submerged aquatic vegetation). Specific hypotheses are as follows: (1) fish and crustacean densities and assemblages differ between delta types; and (2) environmental variables follow seasonal patterns, and differ between delta types. As many restoration and management actions are driven by commercial fisheries production specifically, this study also explored juvenile blue crab densities and stable isotope compositions ($\delta^{13}C$ and $\delta^{15}N$) between an inactive and an active delta, examining environmental variables, as above. Specific hypotheses are as follows: (1) blue crab densities differ between delta types; and (2) $\delta^{13}C$ and $\delta^{15}N$ stable isotopes from blue crabs and some primary producers differ between active and inactive deltas with greater $\delta^{15}N$ in active deltas, reflecting greater continental influence.

2. MATERIALS AND METHODS

2.1. Study area

Two delta systems were identified for sampling for this project, an active delta site (Plaquemine-Balize Delta), located at the mouth of the Mississippi River, and an inactive delta site (Lake Mechant and Mud Lake), located in Terrebonne Basin (Fig. 1).

The largest active delta system within Louisiana, the modern Plaquemine-Balize Delta (also called 'Bird's Foot Delta'), lies at the southern end of the Mississippi River, Louisiana, with an estimated two-thirds of the Mississippi River flow discharged at or slightly north of there. Over the last 10 yr, average monthly salinities ranged from 0.1 to 6.4, with an overall mean ± SE of 0.8 ± 0.1 (January 2010 to October 2019, CRMS 0159; www.lacoast.gov/crms2; Fig. 2). During the same time period, average daily water temperature ranged from 5.2 to 31.5ºC with a mean of 19.6 ± 0.8ºC. Natural and man-made channels meander through the marshes and are characterized by deep channels and shallow sand bars scoured by high flows. The marshes in the area are dominated by common reed *Phragmites australis*, alongside other emergent species including giant cutgrass *Zizaniopsis miliacea* and black willow *Salix nigra*. Diurnal tides and water levels are largely influenced by river flow, and wind speed and direction (Hiatt et al. 2019).

Terrebonne Basin occupies the abandoned deltaic lobes of the extinct Teche and Lafourche distributaries. Lake Mechant and Mud Lake in Terrebonne Basin (inactive deltaic complex) are the locations of our low flow sites (Fig. 1). Average monthly salinities ranged from 1.1 to 18.6 with a mean of 8.1 ± 0.4 (January 2010 to October 2019; CRMS 4455; www.lacoast.gov/crms2; Fig. 2). During the same time period, average monthly water temperature ranged from 11.5 to 31.6ºC with a mean of 23.4 ± 0.5ºC. When this lobe was active 2500 to 800 yr ago (Coleman 1988), the surrounding marshes were characterized as fresh. Now, the surrounding marsh reflects a more mesohaline environment and is dominated by smooth cordgrass *Spartina alterniflora*, alongside other species including black needlerush *Juncus roemerianus* and common reed. 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. Diurnal tides and water levels here are also largely influenced by wind speed and direction.

2.2. Sampling design

Within both deltas, 6 sites were haphazardly selected. Each site consisted of a GPS location with a 100 m radius circle, where 2 sampling stations were

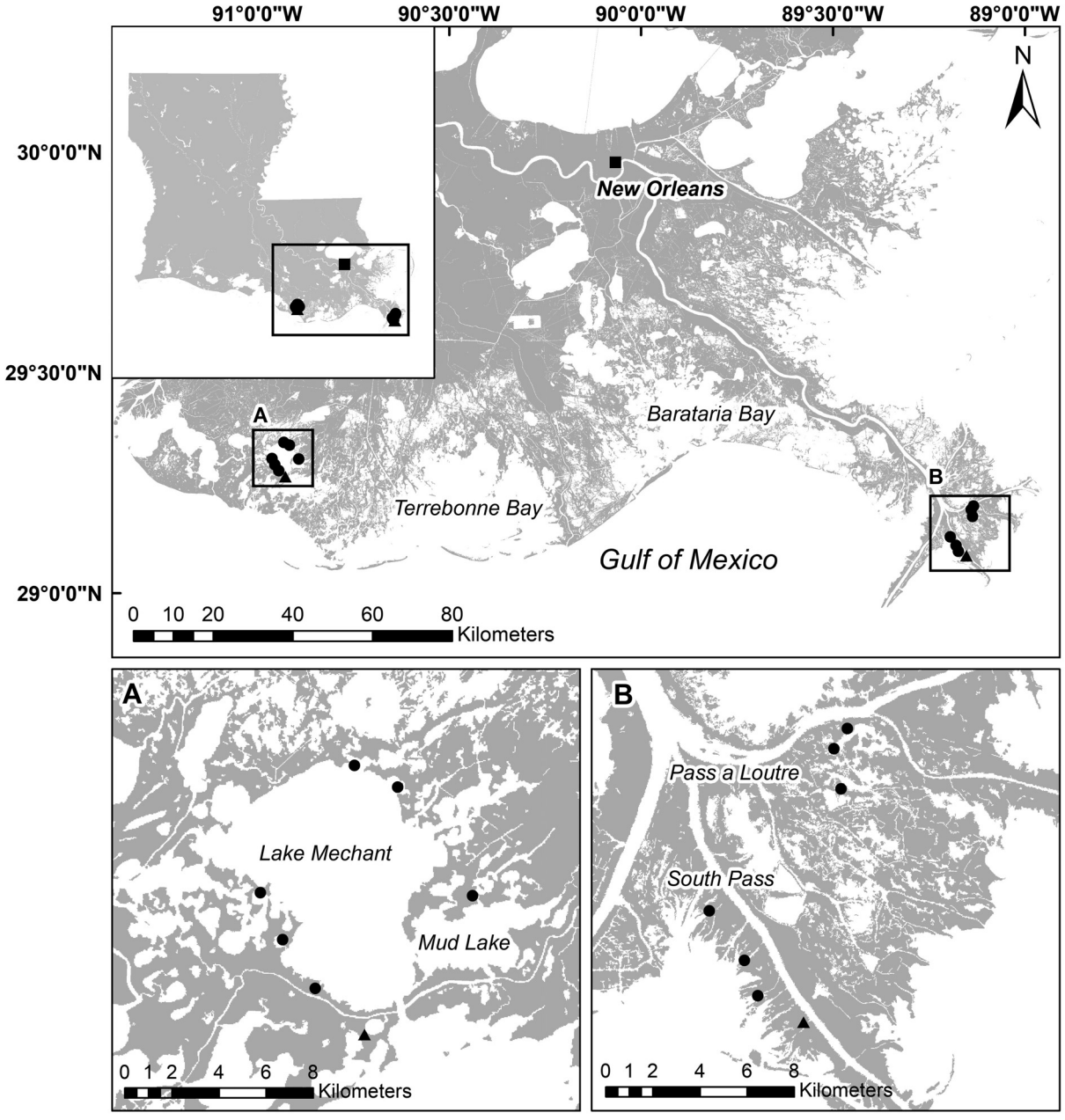

Fig. 1. Field study site locations within (A) Terrebonne Basin (inactive delta) and (B) Mississippi River Delta (active delta), Louisiana, USA. (●) Selected study sites for sampling in spring, summer, fall, and winter; (▲) Coastwide Reference Monitoring System (CRMS) site locations used for continuous environmental data provided in Fig. 2

selected within shallow water of depths less than 2 m. The 2 sampling stations within each site included one haphazardly placed along emergent marsh edge (<1 m from marsh edge in open water) and one haphazardly placed within open water (>3 m from marsh edge). Sites were sampled in summer (May and June 2018), fall (September and October 2018), winter (December 2018) and spring (March 2019) for a total of 96 samples (2 deltas × 2 sample areas × 3 sites × 2 habitats × 4 dates).

2.3. Field sampling

2.3.1. Environmental conditions and nekton assemblages

Upon approaching each site, water quality data were measured using a YSI model 556 multiprobe (Yellow Springs Instruments) to determine water temperature (ºC), salinity, and dissolved oxygen (mg l^{-1}). A Secchi disk was used to determine water

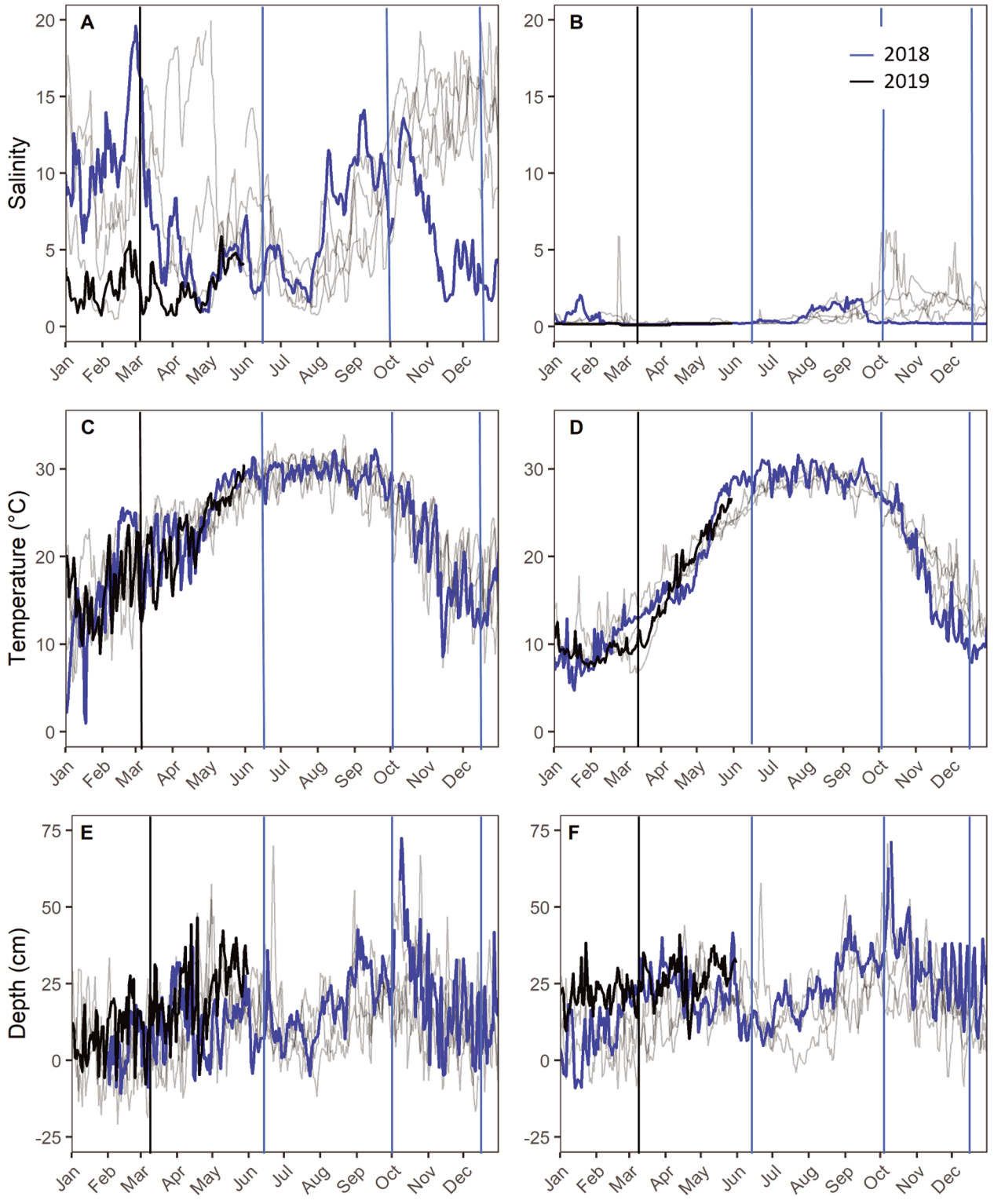

Fig. 2. Downloaded daily environmental variables from (A,C,E) the inactive delta (CRMS4455; www.lacoast.gov/crms2) and (B,D,F) the active delta (CRMS0159; www.lacoast.gov/crms2) from May 2014 through June 2019. Thin light grey line: mean daily values for 2014 through 2017; dark thick blue line: 2018; black line: 2019. Data presented include (A,B) salinity, (C,D) temperature, and (E,F) water depth. Vertical lines indicate sampling dates for this study, with line color indicating calendar year (dark thick blue line: 2018; black line: 2019). These data are not sampling site specific but provide a general overview of delta-specific variation

clarity (cm). Data were also downloaded from the Coastwide Reference Monitoring System (CRMS) continuous data recorders closest to the study sites (inactive delta, CRMS 4455; active delta, CRMS 0159; www.lacoast.gov/crms2).

Nekton were sampled using a 1 m^2 throw trap. The throw trap consisted of a 1 × 1 × 0.66 m 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 m^2 PVC square was integrated into the top of the extended netting buoyed by net floats. For throw trap deployment, a skiff was idled to the sample area before tossing the gear from the bow of the vessel. Immediately upon securing the throw trap in the mud, water depth was measured at each corner and in the center of the trap, and the mean of these 5 depth measurements (cm) was used. Bottom type was recorded as either mud, sand bottom, or submerged aquatic vegetation (SAV). If SAV was present, all aboveground SAV within throw trap samples was clipped at the sediment surface, placed into labeled bags, and transported to the laboratory at Louisiana State University Agricultural Center (LSU AgCenter) for processing to determine above-ground biomass. Nekton were then cleared with a 1 m^2 net with 3 mm square mesh until no nekton were collected in 3 consecutive sweeps. Samples were placed into a labeled bag and onto ice for transport to the laboratory at LSU AgCenter.

2.3.2. Stable isotope field samples

Blue crabs, primary producers, and common nekton species were collected from all nekton sampling sites to compare $\delta^{13}C$ and $\delta^{15}N$ values between the 2 deltas (active and inactive) in summer 2018. The most abundant shared nekton species between both deltas were collected from throw trap samples: inland silverside *Menidia beryllina* (Cope, 1867), bay anchovy *Anchoa mitchilli* (Cuvier & Valencieenes, 1848), and grass shrimp *Palaemonetes* spp. Crab traps and dip nets were used to sample 2 size classes of blue crab (juvenile 30–90 mm, adult >90 mm). Crab traps were deployed for 24 h. Bait within traps was securely bound and closed off from consumption using fine wire mesh so as to not be ingested and influence isotope values within blue crabs. A minimum of 3 crabs were collected for each sample site. Only male adult blue crabs were analyzed for stable isotopes, as they have greater site fidelity compared to females. A minimum of 3 stems were collected from representatives of C3 and C4 carbon pathway, dominant primary producers from adjacent marsh or waters. Common reed, a dominant emergent plant within both deltas, represented the C3 carbon pathway, primary producer samples. *S. alterniflora* was the dominant C4 plant collected within inactive sites, while active sites lacked *S. alterniflora*. Submerged aquatic vegetation was sampled when present, with Eurasian watermilfoil *Myriophyllum spicatum* used for analysis due to occurrence within both deltas. Benthic macroalgae (*Cladophora* spp.) were also collected from sites when present. All samples collected were placed in separate sterile bags, labeled, and transported for processing to the laboratory at LSU AgCenter.

2.4. Laboratory processing

2.4.1. Environmental conditions and nekton assemblages

Within 1 wk of sampling, SAV were sorted according to species, dried in a forced air-drying oven at 60ºC to a constant weight, weighed to the nearest 0.001 g dry weight, and recorded (g m^{-2}).

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 carapace width for crabs. Organisms were then weighed to the nearest 0.001 g to determine blotted wet biomass (g) (Ohaus Explorer Precision Balance). Subsamples of 25 individuals were randomly chosen from each species numbering over 25 individuals per sample. Blue crab sex was recorded and individuals were measured by carapace width and grouped according to size class (young-of-the-year <30 mm, juveniles, adults).

2.4.2. Stable isotopes

In the laboratory, 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 as isotope values in this tissue reflect the short-term diet of the blue crab (~3 wk; Llewellyn & La Peyre 2011). Blue crab hepatopancreas tissue was extracted and frozen in the laboratory. Hepatopancreas tissue underwent hexane decantations before being dried at 60ºC to

constant weight. Remaining nekton species muscle tissue was dried at 60ºC until constant weight. Plant samples were rinsed with deionized water and new growth clipped before drying at 60ºC in a drying oven until weight was constant. Dried material was then ground into powder using a mortar and pestle (Wig-L-Bug for plant tissue; Dentsply Rinn) before weighing and loading samples into tins. All dried powder sample weights within tins were calculated depending on carbon/nitrogen ratios of tissue used, using the online tool provided by University of California Davis Isotope Analysis Facility (https://stableisotopefacility.ucdavis.edu/), where the samples were shipped for analyses.

2.5. Statistical analyses

For all analyses, a significance level of alpha < 0.05 was used. Data residuals were tested for normality using the Shapiro-Wilks test. Unless otherwise indicated, mean ± SE values are presented.

2.5.1. Environmental conditions and nekton assemblages

Discrete salinity, water temperature, water depth and dissolved oxygen ranges are listed in Section 3.1. Summary statistics (means, SE) were calculated for environmental variables.

All nekton and habitat data were analyzed using R version 3.5.3 (2019-03-11 'Great Truth' ©2019, RStudio). Generalized linear models with negative binomial distributions (glm.nb) and a log link were performed on nekton crustacean or fish densities (throw trap) and young-of-the-year blue crab densities. Linear models (lm) were performed on 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 habitat (marsh edge and open water) with delta (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 the model was deemed accurate due to fit statistics. A post-hoc pairwise Tukey's 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. Linear regression was used to examine the potential relationship between SAV biomass (independent predictor variable) and nekton density, richness, and blue crab densities and biomass (dependent response variables).

The effect of delta on nekton community structure was analyzed by season and habitat using a 2-way analysis of similarity (ANOSIM) (anosim, R package 'Vegan'; Oksanen et al. 2019). 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. 2019) procedure was performed on nekton community abundance data using delta as a factor to determine species responsible for assemblage differences between deltas.

2.5.2. Stable isotope analyses

Only sites where a minimum of 3 adult male blue crabs and 3 juvenile male blue crabs were captured were used for final analyses to ensure adequate sample sizes. Size classes were analyzed separately. A *t*-test was used to compare differences in mean $\delta^{13}C$ and $\delta^{15}N$ values between deltas by individual species.

3. RESULTS

3.1. Environmental conditions and nekton assemblages

Discrete environmental variables varied by season and delta (Table 1). Water temperature ranged between 8 and 29ºC with a mean of 19.0 ± 1.2ºC for active sites, while inactive sites temperature ranged slightly higher from 11 to 32ºC with a mean of 21.4 ± 1.1ºC. 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 sam-

Table 1. Mean (SE) hydrological and environmental variables collected in summer, fall, and winter 2018, and spring 2019 within Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana concurrent with nekton sampling. Mean salinity, water temperature, and dissolved oxygen (DO) were recorded using a YSI Model 556 multiprobe. Mean water depth and submerged aquatic vegetation (SAV) percent presence and biomass are also reported

	Summer		Fall		Winter		Spring	
	Active	Inactive	Active	Inactive	Active	Inactive	Active	Inactive
Depth (cm)	37.2 (3.1)	57.6 (3.5)	39.8 (5.7)	47.3 (3.0)	30.4 (2.9)	39.8 (3.5)	43.8 (3.7)	49.2 (3.6)
Salinity	0.2 (0)	2.5 (0.4)	0.2 (0)	5.1 (0.6)	0.2 (0)	1.3 (0.3)	0.1 (0)	1.6 (0.4)
Temperature (ºC)	28.2 (0.2)	30.0 (0.4)	26.6 (0.2)	27.2 (0.2)	9.9 (0.3)	12.6 (0.2)	11.2 (0.1)	15.8 (0.4)
DO (mg l^{-1})	7.0 (0.6)	7.5 (0.5)	5.0 (0.1)	6.9 (4.3)	10.6 (0.1)	10.3 (0.1)	9.9 (0.1)	8.5 (0.2)
SAV (% presence)	75	33	92	75	58	58	75	83
SAV (g m^{-2})	101.5 (24.6)	36.0 (18.5)	77.2 (18.5)	33.1 (13.6)	9.9 (3.9)	8.2 (3.4)	18.7 (9.1)	6.7 (4.1)

pling to 11.3 mg l^{-1} 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}.

SAV was present at 98% of sampling sites during at least 1 sample period. Overall, SAV occurred in 75% of active delta samples, and 63% of inactive samples, with presence at open water sites greater than 80% regardless of delta, and ranging from 46% (inactive delta), to 67% (active delta) at marsh edge sites (Table 1). In general, SAV biomass for active sites was more than twice that of inactive delta sites (active: 51.8 ± 9.6 g m^{-2}, inactive: 20.9 ± 6.0 g m^{-2}; Table 1). Five species of SAV were collected at both active and inactive delta sites (*Ruppia maritima*, *Hydrilla verticillata*, *Potamogeton pusillus*, *Ceratophyllum demersum*, *Myriophyllum spicatum*), and composed more than 75% of total biomass. Additionally, 1 other species was only collected within the inactive delta (*Vallisneria americana*), while 6 other species were collected only in active delta sites (*Najas guadalupensis*, *P. crispus*, *Heteranthera dubia*, *Stuckenia pectinata*, *Egeria densa*, *P. nodosus*).

A total of 5135 individuals representing 41 species of nekton were collected (Table 2). Nekton density and biomass were highly correlated, so only abundance data results are presented ($r = 0.76$, $p < 0.0001$). Crustacean and fish density were analyzed separately; however, crustacean and fish species richness were highly correlated ($r = 0.91$, $p < 0.0001$); thus, only total nekton species richness was analyzed.

Crustacean densities within active sites ranged from 0 to 134 individuals (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 (ME) and open water (OW) varied significantly by season (ME: $F_{3,47} = 9.9$, $p < 0.0001$; OW: $F_{3,47} = 3.7$, $p < 0.009$), with no significant difference between deltas or with the interaction of delta by season (Fig. 3). Marsh edge differences were largely explained by fall crustacean densities being significantly higher than during spring and summer sampling. Open water differences were largely explained by summer densities being higher than in spring and winter.

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 fishes for marsh edge and open water varied significantly by the delta and season interaction (ME: $F_{3,47} = 8.3$, $p < 0.0001$; OW: $F_{3,47} = 16.2$, $p < 0.0001$; Fig. 3). During spring, fish density was lower at active delta sites than at inactive delta sites at edge sites as well as at open water sites. During summer, fall and winter, there was no difference between the deltas in fish density at edge sites or at open water sites.

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}. Species richness for marsh edge differed significantly by season only ($F_{3,47} = 6.6$, $p < 0.001$; Fig. 4A). At open water sites, species richness was lower at active delta sites than at inactive delta sites during spring ($F_{3,47} = 5.3$, $p < 0.001$, Fig. 4B). During summer, fall, and winter, there was no difference between deltas in species richness at open water sites.

Blue crab young-of-the-year (9–30 mm carapace width) densities for the active delta ranged from 0 to 22 ind. m^{-2} with a mean of 5 ± 0.9 ind. m^{-2}, and from 0 to 33 ind. m^{-2} with a mean of 4.9 ± 0.9 ind. m^{-2} for the inactive delta, with a significant delta and season interaction (ME: $F_{3,47} = 7.3$, $p < 0.0001$; OW: $F_{3,47} = 4.7$, $p < 0.002$). Edge sites at both deltas supported similar densities of crabs during spring, summer, and fall, but

Table 2. Crustacean and fish species listed separately in order of numerical abundance from 96 throw trap samples by habitat in 2018–2019 within the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. ME: marsh edge; OW: open water; %: percentage of individuals caught relative to the total individuals collected

Species	Active delta				Inactive delta			
	ME	OW	Total	%	ME	OW	Total	%
Crustaceans								
Palaemonetes pugio	0	0	0	0	523	1196	1719	56.7
Macrobrachium ohione	522	594	1116	53.1	0	0	0	0
Callinectes sapidus	113	151	264	12.6	136	118	254	8.4
Farfantepenaeus aztecus	0	0	0	0	134	54	188	6.2
Panopeidae	3	5	8	0.4	12	15	27	0.9
Rhithropanopeus harrisii	2	0	2	0.1	9	3	12	0.4
Litopenaeus setiferus	0	0	0	0	2	2	4	0.1
Fish								
Brevoortia patronus	0	0	0	0	347	118	465	15.3
Lucania parva	102	101	203	9.7	22	51	73	2.4
Ctenogobius shufeldti	63	81	144	6.9	1	20	21	0.7
Anchoa mitchilli	3	4	7	0.3	83	32	115	3.8
Mugil cephalus	83	0	83	3.9	5	2	7	0.2
Poecilia latipinna	4	62	66	3.1	0	1	1	0
Micropogonias undulatus	1	0	1	0	44	23	67	2.2
Menidia beryllina	19	18	37	1.8	17	4	21	0.7
Gambusia affinis	10	32	42	2	0	0	0	0
Lepomis spp.	13	13	26	1.2	0	0	0	0
Evorthodus lyricus	8	11	19	0.9	0	0	0	0
Syngnathus scovelli	7	7	14	0.7	2	7	9	0.3
Dormitator maculatus	9	8	17	0.8	0	0	0	0
Fundulidae	2	14	16	0.8	0	0	0	0
Gobioscoma bosc	0	0	0	0	13	4	17	0.6
Lepomis miniatus	6	4	10	0.5	0	0	0	0
Eleotris pisonis	2	4	6	0.3	0	0	0	0
Heterandria formosa	0	4	4	0.2	1	0	1	0
Atractosteus spatula	2	1	3	0.1	0	0	0	0
Gobionellus oceanicus	1	2	3	0.1	0	0	0	0
Micropterus punctatus	2	1	3	0.1	1	0	1	0
Lepomis microlophus	2	0	2	0.1	0	5	5	0.2
Fundulus grandis	0	1	1	0	3	0	3	0.1
Lagodon rhomboides	0	0	0	0	1	5	6	0.2
Microgobius gulosus	0	0	0	0	7	0	7	0.2
Lutjanus griseus	2	0	2	0.1	0	0	0	0
Cynoscion arenarius	0	1	1	0	1	0	1	0
Cynoscion nebulosus	0	1	1	0	0	0	0	0
Fundulus jenkensi	1	0	1	0	1	0	1	0
Adenia xenica	0	0	0	0	2	0	2	0.1
Citharichthys spilopterus	0	0	0	0	0	2	2	0.1
Cyprinodon variegatus	0	0	0	0	1	0	1	0
Gobiidae	0	0	0	0	0	0	0	0
Leiostomus xanthurus	0	0	0	0	0	1	1	0
Symphurus plagiusa	0	0	0	0	1	1	2	0.1
Total abundance	982	1120	2102		1369	1664	3033	

during winter densities were higher at inactive delta sites (Fig. 5A). The significant interaction for young-of-the-year blue crab densities within open water throw trap samples can be largely explained by active delta blue crab densities being significantly higher in fall than spring and summer within the same delta, as well as summer inactive delta samples (Fig. 5B).

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 traps within inactive delta 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 samples differed significantly by the interaction between delta and season ($F_{3,47}$ = 4.3, $p < 0.04$; Fig. 6), while open water biomass differed by delta, but not by season or by the interaction between season and delta ($F_{1,47}$ = 5.6, $p < 0.03$). At edge sites, the interaction was explained by higher biomass in fall samples at active delta sites than at inactive delta sites. Open water sites had greater biomass at active versus inactive delta sites.

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). SIMPER analysis identified individual species most responsible for these differences. Daggerblade grass shrimp *Palaemonetes pugio* and Ohio river shrimp *Macrobrachium ohione* accounted for the largest percentage of differences between deltas, accounting for approximately 10 to 70% of the differences within any given season and habitat type. These differences reflect large numbers of *P. pugio* within the inactive delta, and large numbers of *M. ohione* within the active delta. Gulf menhaden *Brevoortia patronus*, *Callinectes sapidus*, and freshwater goby *Ctenogobius shufeldti* accounted for another 5 to 40% of differences between deltas within each season and habitat. *B. patronus* was more abundant within inactive sites for summer, winter, and spring.

Regression models of nekton species richness (ind. m^{-2}), nekton biomass (g m^{-2}), young-of-the-year blue crab (ind. m^{-2}), and blue crab biomass (g m^{-2}) against SAV (g m^{-2}) were all statistically significant, but had low R^2 values (Fig. 7).

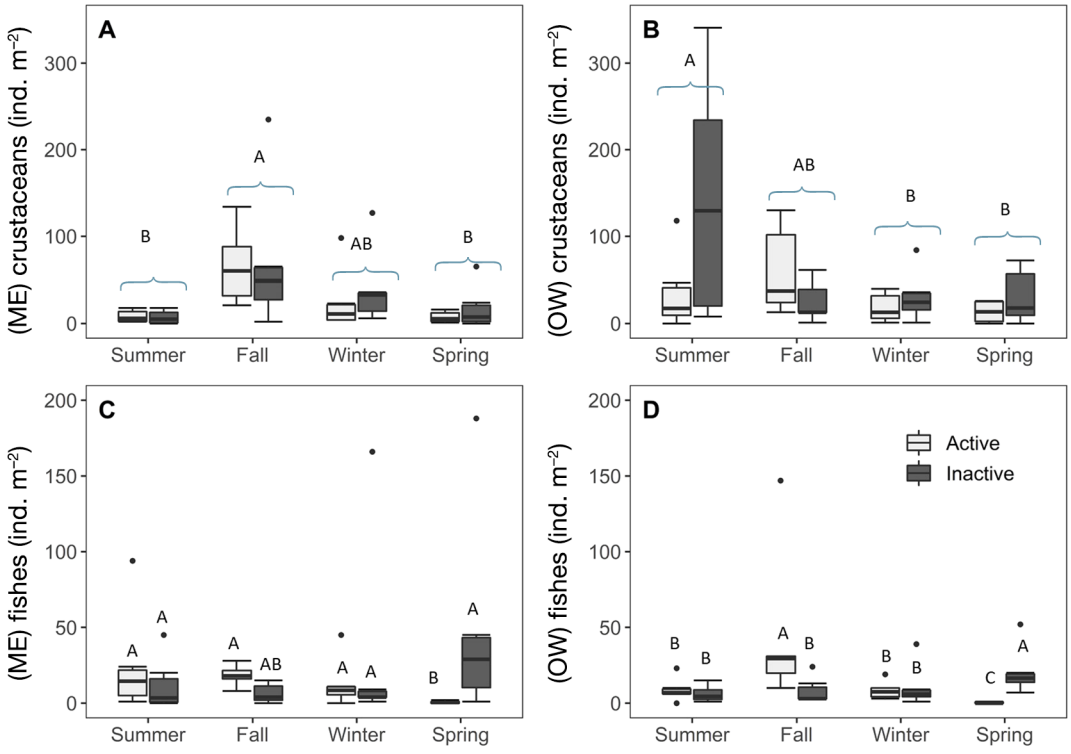

Fig. 3. Total (A,B) crustacean and (C,D) fish density for (A,C) marsh edge (ME) and (B,D) open water (OW) by season and delta for the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. Boxplot parameters: middle line denotes the median; boxes represent the first, and third quantiles; whiskers represent 1.5 times the interquartile range (IQR). Outliers greater or less than 1.5 × IQR are indicated. Letters above bars denote significant statistical differences between seasons and deltas ($p < 0.05$)

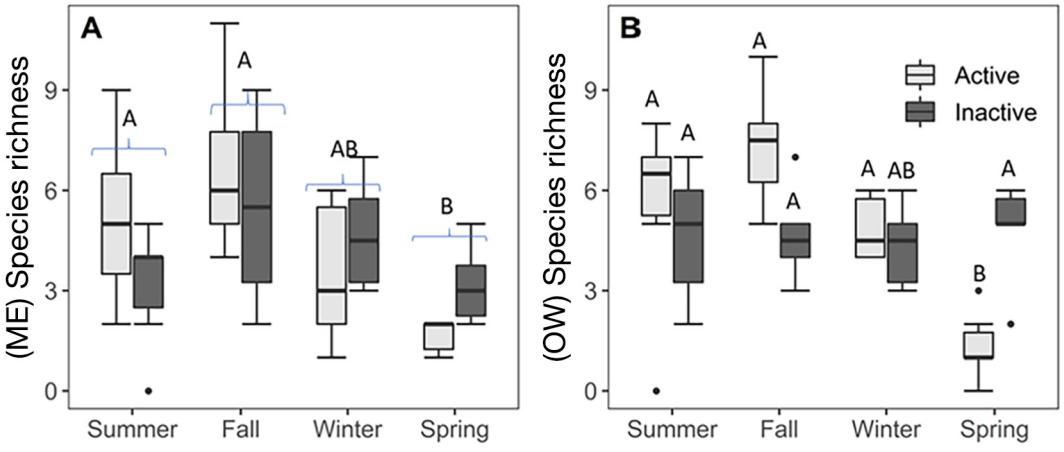

Fig. 4. Nekton species richness (ind. m^{-2}) for (A) marsh edge (ME) and (B) open water (OW) by season and delta for the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. See Fig. 3 for other details

3.2. Stable isotopes

Mean $\delta^{13}C$ values did not vary significantly between deltas for any species. Common reed *Phragmites australis*, benthic macroalgae, and grass shrimp mean $\delta^{15}N$ values were also similar for both deltas. Mean $\delta^{15}N$ values for *Myriophyllum spicatum* samples varied by delta, with active delta means approximately 2 times greater than those for inactive sites. Adult and juvenile *Callinectes sapidus* mean $\delta^{15}N$ values varied between deltas, with active delta values 1.5 times greater than those for inactive delta values (Table 4).

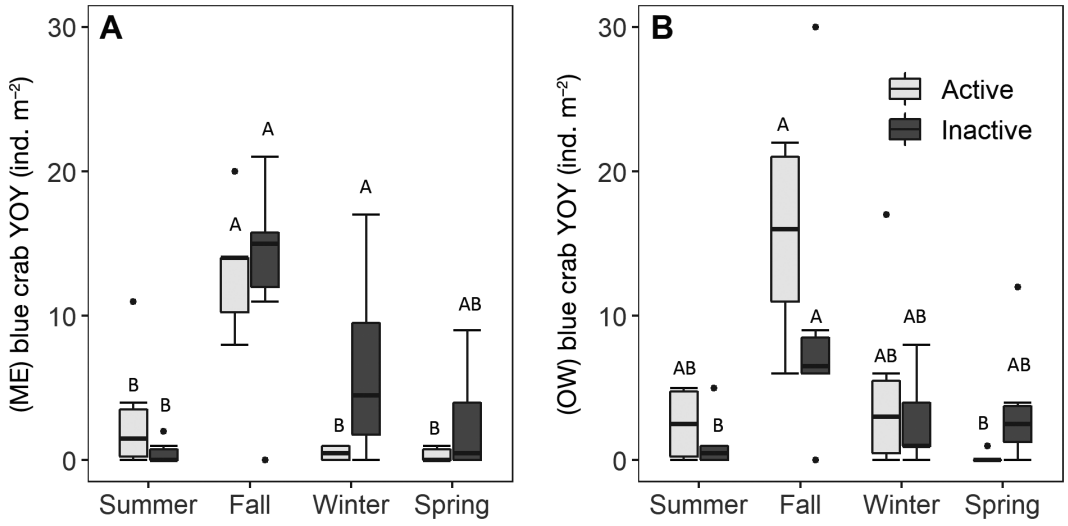

Fig. 5. Blue crab young-of-the-year (YOY) (<30 mm carapace width) for (A) marsh edge (ME) and (B) open water (OW) habitat by season and delta for the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. See Fig. 3 for other details

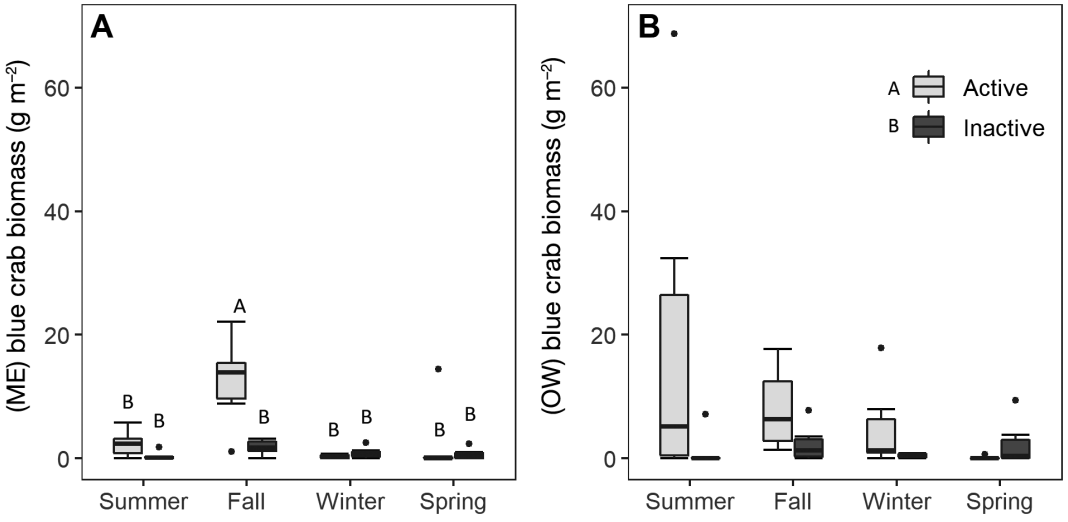

Fig. 6. Blue crab biomass (>30 mm carapace width) for (A) marsh edge (ME) and (B) open water (OW) habitat by season and delta for the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. See Fig. 3 for other details. Letters above bars and beside legend denote significant statistical differences for the season by delta interaction (A), and delta only (B) ($p < 0.05$)

4. DISCUSSION

In 2019, the Mississippi River exceeded flood stage water height for a record-breaking 5 months from early spring through late summer, with the region experiencing one of the wettest years in recorded history (https://rivergages.mvr.usace.army.mil/WaterControl/stationinfo2.cfm?dt=S&sid=01300, Gledhill et al. 2020). This unprecedented freshwater coming down the Mississippi River consequently provided a stark contrast in inflow between the active and inactive deltas compared in the present study. The high spring river flow was associated with reduced salinity, temperature, and submerged aquatic vegetation biomass and presence within active delta sites. During this time, lower nekton density and species richness were observed at active delta sites compared to inactive delta sites; this is in contrast to other sample dates in this study where minimal differences in densities and richness were detected between deltas. This provides some indication of the impact that extended, high flow may have on nekton assemblages within an estuary. What is not clear is what mechanism drove these observed differences. The lower abundances of fishes may be due to displacement caused by increased habitat availability through

Table 3. ANOSIM and SIMPER results for comparison of nekton densities by delta, analyzed by habitat type and season in the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. Global R values for significant ANOSIM tests ($p < 0.01$) are shown, along with the dominant species. SIMPER results provide the relative contribution of dominant species explaining dissimilarity in species between deltas. ME: marsh edge; OW: open water. Blank cells indicate when species were not dominant for a specific season by habitat type combination

	Summer		Fall		Winter		Spring	
Habitat:	ME	OW	ME	OW	ME	OW	ME	OW
Global R:	0.75	0.92	0.62	0.59	0.61	0.78	0.70	0.92
Palaemonetes pugio		50.3	12.7	4.2	36.8	35.7	26.0	23.8
Macrobrachium ohione	7.9	23.1	33.4	27.4	20.0	16.6	18.0	
Brevoortia patronus	15.1				9.8	8.6	31.0	19.9
Callinectes sapidus		3.2	5.5	11.1	6.7	7.8	7.4	5.4
Ctenogobius shufeldti	10.8	3.5	4.6	6.3		6.8		
Farfantepenaeus aztecus	8.7	4.4	13.5					
Lucania parva				8.9	7.9			
Anchoa mitchilli							5.6	5.9
Mugil cephalus	10.3							
Cumulative percentage	52.8	48.5	69.7	57.9	81.2	75.5	87.6	86.2

flooding of otherwise inaccessible marsh surfaces. Alternatively, as changes in freshwater flow are associated with numerous effects on water quality and habitat availability, which in turn may impact fish physiology, reproduction, or behavior, the impacts of this high inflow may involve multiple direct and indirect effects, and may be location and estuary dependent.

Nekton species densities observed in this study fall within the wide range of previously reported values within similar shallow water, estuarine habitats in Louisiana. 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, Kanouse et al. 2006, Piazza & La Peyre 2007, Jerabek et al. 2017). 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 our active delta sites (Castellanos & Rozas 2001). Differences in densities may reflect sampling season, as significant seasonal patterns were evident for both density and species assemblages.

Nekton species assemblages for inactive and active deltas were largely dominated by crustaceans, with Palaemonid species (grass and river shrimp) comprising 44 to 65% of total catch 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 (Rozas & Odum, 1987, Zimmerman et al. 1990, Castellanos & Rozas 2001). Penaeid shrimp contributed a large percentage to inactive delta samples, similar to other studies within oligohaline and mesohaline marshes, (Hettler 1989, Kanouse et al. 2006, Rozas & Minello 2015, Jerabek et al. 2017) though these species were absent within active delta sites. Other studies within tidally influenced freshwater marshes also report few penaeid shrimp, though within both the Atchafalaya River and the diversion influenced upper Breton Sound, studies have reported higher densities of sheepshead minnow *Cyprinodon variegatus* (Castellanos & Rozas 2001, Piazza & La Peyre 2007).

Differences in fish assemblages between deltas can at least be partially attributed to differences in abiotic factors such as salinity. 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). Several species, including *Brevoortia patronnus*, *Anchoa mitchilli*, and Atlantic croaker *Micropogonias undulatus*, were generally absent from the fresher active delta sites, but abundant at saltier inactive delta sites. Species more associated with freshwater systems, including sailfin molly *Poecillia latipinna*, *Gambusia affinis*, and redspotted sunfish *Lepomis miniatis*, were more abundant at active delta sites than at inactive delta sites. Penaeid shrimp were largely absent from the fresher active delta sites, yet densities were consistently high in the inactive delta during summer and fall, when salinity was elevated.

Similar observed patterns in nekton assemblages between the active and inactive delta suggest that seasonality and life history traits of individual species may be a large driver of differences between nekton assemblages within both deltas. 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 occurring in the fall (between August and September within the Mississippi Bight, just east of the Mississippi River delta; Perry & VanderKooy 2015). Post larvae of another estuarine-dependent decapod crustacean, brown shrimp *Farfantepenaeus aztecus*,

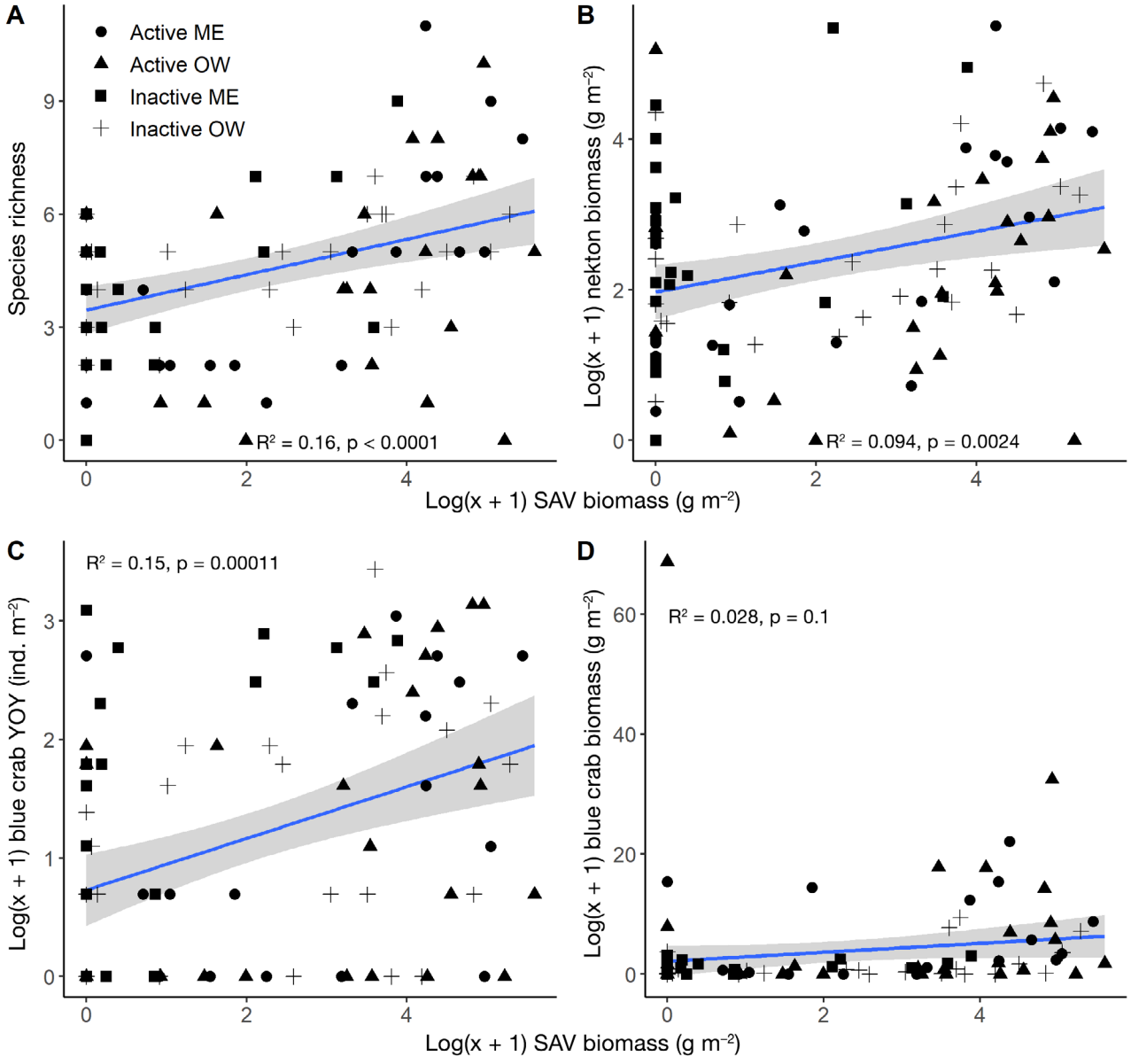

Fig. 7. Regression of (A) nekton species richness, (B) log-transformed nekton biomass, (C) young-of-the-year (YOY) blue crab densities, and (D) blue crab biomass against submerged aquatic vegetation (SAV) biomass for 2 deltas, the Mississippi River Delta (active) and the Terrebonne Basin (inactive), in Louisiana. Pearson's R^2 and p-values are reported. Grey areas represent 95% confidence intervals. ME: marsh edge; OW: open water

have been found to enter estuaries in the northern Gulf of Mexico from late winter to early spring and spend 3 to 4 months in estuarine nursery grounds before migrating offshore during summer months (Rogers et al. 1993). Zimmerman & Minello (1984) found this species and another penaeid shrimp, *F. setiferus*, to be most abundant in marsh edge and non-vegetated habitats during warmer months (late spring to late summer), similar to this study. Similarly, *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 its life history.

Seasonal variation in environmental and water quality variables may also impact nekton assemblages indirectly, through salinity, temperature, and water level impacts on structural habitat availability, such as SAV presence or availability of interior marsh surfaces. For

Table 4. Mean (SE) $\delta^{13}C$ and $\delta^{15}N$ stable isotope values by delta and species in the Mississippi River Delta (active) and Terrebonne Basin (inactive) in Louisiana. n = sample size, primary producers were pooled using triplicate samples at each site. *Spartina alterniflora* did not occur in the active delta sites. Isotope values in **bold** indicate significant differences between deltas

Species	n	Active delta		Inactive delta	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Adult *Callinectes sapidus*	9	−23.9 (0.5)	**13.2 (0.2)**	−25.5 (1.0)	**8.2 (0.4)**
Palaemonidae spp.	9	−22.1 (0.5)	12.2 (1.0)	−22.3 (0.1)	11.2 (0.8)
Juvenile *Callinectes sapidus*	9	−22.5 (0.3)	**12.7 (0.1)**	−21.9 (1.4)	**8.3 (0.4)**
Menidia beryllina	9	−24.5 (0.1)	15.9 (0.1)	−23.5 (0.6)	11 (0.6)
Phragmites australis	3	−26.8 (0.2)	2.4 (1.5)	−27.9 (0.3)	4.8 (0.3)
Myriophyllum spicatum	3	−21.5 (1.8)	**8.9 (0.7)**	−15.9 (0.2)	**4.4 (0.3)**
Cladophora spp.	3	−21.8 (0.3)	7.9 (2.1)	−22.3 (1.5)	5.3 (1.1)
Spartina alterniflora	4			−13.5 (0.2)	4.9 (0.3)

example, lower temperatures within active delta sites during winter and spring associated with high riverine flow bringing cooler waters may not only impact nekton use of the estuary directly but may also impact SAV habitat availability. SAV abundance or biomass may vary depending on water clarity, salinity, temperature, exposure, or even nutrient concentrations (Cho & Poirrier 2005, DeMarco et al. 2018, Hillmann et al. 2019). Higher river inflow likely impacts these variables and alters structural habitat available to nekton. Although nekton densities were only minimally related to SAV biomass (Fig. 7), this may be due to the availability of emergent vegetation habitat. Other studies in Aransas Bay, Texas, and the Atchafalaya Delta, Louisiana, found highest abundance of nekton species within structured habitat (SAV or emergent marsh) when compared with unvegetated mud bottom (Rozas & Minello 1998, Castellanos & Rozas 2001, Kanouse et al. 2006). Another study across coastal Louisiana found 5 times higher nekton densities in habitat with SAV present 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 presence and biomass have been found to be impacted not just by salinity and temperature but also by water level or exposure (DeMarco et al. 2018). Freshwater flow to estuarine systems defines estuarine function and ecosystem health; but the need to understand the complex relationships between inflow, and individual estuary morphology, weather and climate remains.

Young-of-the-year blue crab densities were similar between deltas and comparable to densities reported from previous studies across the Gulf coast (Williams et al. 1990, Zimmerman et al. 1990, Castellanos & Rozas 2001, Shakeri et al. 2020). Recent work in the inactive delta basin used in this study found higher blue crab densities associated with vegetated (marsh, SAV) habitats although the association was with presence of vegetation, rather than percentage plant cover (Shakeri et al. 2020). This is similar to our findings, which failed to find significant blue crab relationships with SAV biomass but noted a similar trend with higher presence of SAV (percentage of sites with presence) associated with higher blue crab densities (i.e. fall sampling season).

Highest densities of recently settled blue crabs occurred during fall months within our study, comparable to previous studies in the northern Gulf of Mexico (Thomas et al. 1990, Rabalais et al. 1995, Aguilar et al. 2005, Sutton & Wagner 2007). These findings that densities were similar within active and inactive deltas, regardless of freshwater inflow, are in contrast to previous work reporting positive relationships between freshwater flow and blue crab landings (Wilber 1994, Guillory 2000, Powell et al. 2002, Doering & Wan 2018). These past analyses, however, relied on fishery monitoring data, including commercial landings data (i.e. Guillory 2000), and results may have been confounded by fishing effort or capacity across estuaries. For example, Guillory (2000) found a positive relationship between blue crab commercial landings in Louisiana and Mississippi River discharge during the years 1960 through 1997 using water flow data from Tarbert's Landing (NOAA 2020a,b). However, a negative relationship between commercial blue crab landings within the Mississippi River Delta (Louisiana Department of Wildlife and Fisheries trip ticket data) plotted against Mississippi River mean annual discharge (NOAA 2020a,b) is evident for the years 1999 to 2016 (Fig. A1 in the Appendix). Data on fishing effort as a covariable would help us better understand relationships between landings and discharge.

Understanding how freshwater inflow impacts key environmental drivers within estuarine systems remains critical to understanding food availability and quality, and their trophic impacts (Layman et al. 2015, Lebreton et al. 2016). In this study, enriched $\delta^{15}N$ values from blue crabs occurred in the active delta, suggesting that trophic webs within the active delta are supported through more riverine influence and continentally derived organic matter (Fry 2002, Lebreton et al. 2016). While increased inflow may result in greater habitat availability or increased nutrients and food quality, existing research provides

conflicting results. For example, increased freshwater inflow has been associated with higher quality food or increased freshwater-derived organic matter in several studies (i.e. Garcia et al. 2017, Marshall et al. 2019, 2021), while other studies have found increased or altered food resources (phytoplankton) with increasing marine influences, but no clear trend related to food quality (i.e. Rishworth et al. 2017, Bargu et al. 2019, Possamai et al. 2020). A recent study examining stable isotope compositions of oysters, suspended particulate organic matter, and surface sediment organic matter from 5 estuaries in Louisiana and Texas indicated that food webs in lower salinity (generally higher freshwater inflow) estuaries tended to be more influenced by continental organic matter than higher salinity (generally lower freshwater inflow) estuaries (Marshall et al. 2021). This work suggested that decreased connectivity between continental and coastal habitats (i.e. in lower inflow estuaries) may impact organic matter flows, estuarine function, and health.

Riverine flow quantity and timing affect nekton density and species assemblages, but the actual mechanisms, and in some cases, the direction of impact remain elusive. Within this study, both active and inactive deltas supported generally similar nekton densities, but variable assemblages. Many possible mechanisms may have contributed to these results. Lower salinity, combined with lowered temperatures during this time may have directly contributed to a reduction in marine organisms entering the estuary. Decreased temperatures, combined with high flow rates may have reduced SAV production and presence, and increased water levels may have increased interior marsh surface habitat availability. As changes in freshwater flow are associated with numerous effects on water quality and habitat availability, determining the actual mechanisms or drivers impacting nekton use of affected estuaries remains critical and may be location and estuarine dependent.

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Appendix.

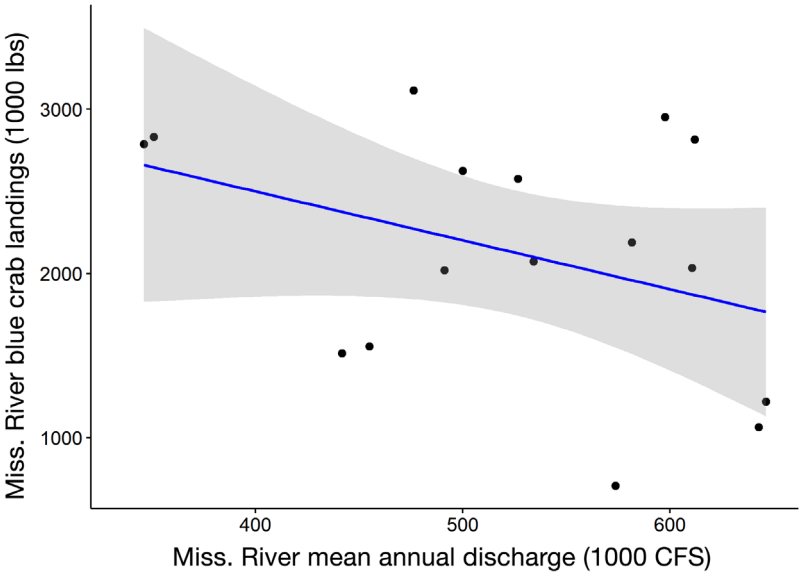

Fig. A1. Regression of commercial blue crab landings within the Mississippi River Delta (NOAA 2020a) plotted against Mississippi River mean annual discharge (NOAA 2020b) for the years 1999–2016. Grey area represents 95% confidence intervals

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