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## **Analysis of Ecological Tradeoffs Between Congeneric Shrimp in Coastal Mississippi Waters**

Baylor K. Lynch

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Analysis of Ecological Tradeoffs Between Congeneric Shrimp in Coastal Mississippi  
Waters

by

Baylor K. Lynch

A Thesis  
Submitted to the Honors College of  
The University of Southern Mississippi  
in Partial Fulfillment  
of Honors Requirements

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## ABSTRACT

Palaemonidae is an ecologically important and abundant family of shrimp that link the benthos to many estuarine food webs. *Palaemon pugio* and *Palaemon vulgaris* regularly co-occur along estuarine edge habitats despite previous studies suggesting different preferred sediment types and salinity regimes. The objective was to determine if competition is occurring between the congeners by comparing their relative abundance and assessing isotope niche space along an estuarine gradient. I seasonally sampled various edge habitats at four sites throughout Biloxi Bay, MS, using fyke nets fished over a tidal cycle from November 2020 to November 2021. Collected organisms were identified to the species level, enumerated, relative abundance estimated using catch per unit effort (CPUE), and up to 20 individuals were measured for total length and weighed. Stable carbon and nitrogen isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of the subsampled shrimp from each sampling event were analyzed. *Palaemon pugio* was the more abundant congener based on relative abundance estimates, and *P. pugio* CPUE varied based on abiotic factors (salinity, season, estuary position). During the study period, Biloxi Bay experienced a prolonged, high freshwater discharge event that likely influenced the lower CPUE of *P. vulgaris* based on presumed physiological stress from this event. Stable isotope analyses suggest *P. pugio* and *P. vulgaris* are partitioning resources and occupying different niche spaces throughout the estuarine gradient. *Palaemon vulgaris* occupied a higher trophic position regardless of abundance, estuarine position, or if *P. pugio* co-occured. *Palaemon pugio* trophic position was influenced by *P. vulgaris* trophic position, *P. vulgaris* CPUE categories, and salinity regime. These observations were

attributed to exploitative competition between congeners, affecting ecological niche spaces and trophic positions.

**Keywords:** *Palaemon*, stable isotope analysis, estuary, living shoreline, competition

## **DEDICATION**

To my late grandfather, Michael “Hoot” Gibson. Thankfully, the mentoring you provided me throughout my life continues to pay off.

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# TABLE OF CONTENTS

LIST OF TABLES .....	x
LIST OF ILLUSTRATIONS .....	xi
LIST OF ABBREVIATIONS.....	xii
CHAPTER I: INTRODUCTION.....	1
CHAPTER II: METHODS .....	6
Study Location .....	6
Collections .....	7
Sample Processing for Stable Isotope Analysis.....	8
Data Analysis .....	9
Abundance Estimates.....	9
Stable Isotope Analysis.....	10
CHAPTER III: RESULTS.....	12
Abundance Estimates.....	12
Stable Isotope Analysis.....	12
CHAPTER IV: DISCUSSION .....	14
Abundance and Distribution of Palaemonid Shrimp .....	14
Stable Isotopes within Congeners .....	15
Limitations .....	17
Conclusion .....	18

APPENDIX A: Figures.....	20
APPENDIX B: Tables .....	29
REFERENCES .....	37

## LIST OF TABLES

Table 1. Two-way analysis of variance (ANOVA) results for mean catch per unit effort (CPUE).....	29
Table 2. Tukey’s HSD posthoc results for two-way analysis of variance results for catch per unit effort (CPUE) .....	30
Table 3. Generalized linear model output for <i>Palaemon pugio</i> catch per unit effort (CPUE).....	31
Table 4. Tukey’s HSD posthoc results for generalized linear model output for <i>Palaemon pugio</i> catch per unit effort (CPUE).....	32
Table 5. Two-way analysis of variance results for mean individual carbon isotope values ( $\delta^{13}\text{C}$ ).....	33
Table 6. Two-way analysis of variance results for mean individual nitrogen isotope values ( $\delta^{15}\text{N}$ ).....	33
Table 7. Tukey’s HSD posthoc results for individual carbon isotope values ( $\delta^{13}\text{C}$ ).....	34
Table 8. Tukey’s HSD posthoc results for two-way analysis of variance (ANOVA) results for individual nitrogen isotope values ( $\delta^{15}\text{N}$ ).....	34
Table 9. Generalized linear model output for trophic position of <i>Palaemon pugio</i> .....	35
Table 10. Tukey’s HSD posthoc results for <i>Palaemon pugio</i> trophic position generalized linear model .....	36

## LIST OF ILLUSTRATIONS

Figure 1: Map depicting the 18 sampling stations within Biloxi Bay, Mississippi. ....	20
Figure 2: Boxplots of the catch per unit effort (CPUE) of <i>Palaemon pugio</i> (purple) and <i>Palaemon vulgaris</i> (red) at each sampling site .....	21
Figure 3: Dual axes plot of mean catch per unit effort (CPUE) for <i>Palaemon pugio</i> (purple) and <i>Palaemon vulgaris</i> (red).....	22
Figure 4: Boxplot of $\delta^{13}\text{C}$ (right) and $\delta^{15}\text{N}$ (left) isotopic values for <i>Palaemon pugio</i> and <i>Palaemon vulgaris</i> at each sampling site.....	23
Figure 5: Isotopic composition ( $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ values) of <i>Palaemon pugio</i> (purple), <i>Palaemon vulgaris</i> (red), and potential carbon baseline sources.....	24
Figure 6: Boxplot of the trophic positions of <i>Palaemon pugio</i> (purple) and <i>Palaemon vulgaris</i> (red) at each site (1–4) .....	25
Figure 7: Boxplot of the trophic positions of <i>Palaemon pugio</i> (purple) and <i>Palaemon vulgaris</i> (red) by salinity regime.....	26
Figure 8: Boxplot of the trophic positions of <i>Palaemon pugio</i> (purple) and <i>Palaemon vulgaris</i> (red) by sampling event (1–5).....	27
Figure 9: Linear regression of <i>P. pugio</i> TP by <i>P. vulgaris</i> TP .....	28

## LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
BIC	Bayesian Information Criterion
CPUE	Catch per Unit Effort
DO	Dissolved Oxygen
GLM	Generalized Linear Model
GOM	Gulf of Mexico
HS	Hardened Shorelines
LS	Living Shorelines
MS	Mississippi
NS	Natural Shorelines
POM	Particulate Organic Matter
RR	Riprap
SIA	Stable Isotope Analysis
SIBER	Stable Isotope Bayesian Ellipses in R
TEF	Trophic Enrichment Factor
TP	Trophic Position
USA	United States of America
USM	The University of Southern Mississippi

## CHAPTER I: INTRODUCTION

Estuarine environments provide many important ecological functions in coastal waters, such as supporting high diversity and abundances of nekton in addition to serving as nursery habitats (Beck et al., 2001). Despite the high diversity of nekton that use estuaries, only a few abundant species dominate nekton community structure (Kneib & Knowlton, 1995; Barletta et al., 2005). These dominant fauna typically are seasonal residents such as Gulf Menhaden (*Brevoortia patronus*) and white shrimp (*Penaeus setiferus*) which use estuarine habitats at differing times throughout their life history (Peterson & Ross, 1991; Kneib & Knowlton, 1995). Many of the abundant and permanent inhabitants in estuarine ecosystems are saltmarsh residents, including palaemonid shrimp (Odum & Heald, 1972; Welsh, 1975; Anderson, 1985).

*Palaemon* is comprised of 86 species (Carvalho et al., 2017), several species of which are an important energy source for many fisheries species including white shrimp (*Penaeus setiferus*; Kneib & Knowlton, 1995), juvenile American alligators (*Alligator mississippiensis*; Platt et al., 1990), and Red Drum (*Sciaenops ocellatus*; Overstreet & Heard, 1978). Palaemonid shrimp are opportunistic omnivores that serve as an ecological link between the benthos and various coastal nekton species in estuarine food webs (Welsh, 1975; Bell & Coull, 1978). Many studies have shown that palaemonid shrimp consume various meiofauna, primary production sources, and detritus (Odum & Heald, 1972; Bell and Coull, 1978). The two most common species of palaemonid shrimps within the Mississippi Sound, *Palaemon pugio* and *Palaemon vulgaris* (Heard, 1982), regularly co-occur along the Atlantic and Gulf of Mexico coasts within estuarine

environments (Thorp, 1976; Anderson, 1985). Therefore, their combined morphological similarity coupled with regular co-occurrence has led to many palaemonid shrimp being misidentified or lumped together and labeled as a single species in larger ecosystem monitoring projects (Anderson, 1985).

The frequent misidentification and grouping of each species could potentially impact management decisions made within an ecological framework as previous studies have suggested the congeners have differing ecological preferences. Thorp (1976) suggested the congeners preferred different bottom types with *P. pugio* preferring soft (e.g., mud, sand) sediments and hard bottom (e.g., shell, wood), whereas *P. vulgaris* preferred hard bottom types only. Thorp (1976) advocated that interspecific competition for habitat causes *P. vulgaris* to displace *P. pugio* from preferred shell substrate. Additionally, a study off the coast of South Carolina demonstrated *Palaemon* species had strong (>90%) site fidelity, suggesting that the congeners are stationary (Allen et al., 2015). Thorp and Hoss (1975) found that temperature did not play a vital role in habitat partitioning between the congeners. Other field experiments suggested the congeners had differing salinity tolerances, with *P. pugio* tolerating a wide range of salinities (<1 to 35) whereas *P. vulgaris* being restricted to salinities <10 (Heard, 1982; Anderson, 1985). Previous studies of salinity tolerance of *P. pugio* and *P. vulgaris* showed considerable overlap in salinity tolerances between the congeners with a range of 0.5–44 and 0.8–51 for *P. pugio* and *P. vulgaris*, respectively (Knowlton and Kirby, 1984; Knowlton and Schoen, 1984). More recent studies showed that *P. pugio* exhibit lower energy expenditure when under low salinity conditions relative to *P. vulgaris* in laboratory experiments (Rowe, 2002). This finding suggests that differences in individual

maintenance-energy costs (e.g., metabolism) allows *P. pugio* to occur in environments that are too energy-demanding for *P. vulgaris* (e.g., freshwater) despite the overlap in salinity tolerance.

Niche theory is a fundamental concept in biology, describing the role an organism plays within an environment and the environmental factors that help define the space. Hutchinson determined that there were two distinct niches; the fundamental and the realized niche (Hutchinson, 1958; Mittelbach & McGill, 2019). The fundamental niche of an organism describes all parts of an environment that satisfy a species' needs, whereas the realized niche is the portion of the fundamental niche an organism occupies in nature due to the presence of other species (Mittelbach & McGill, 2019). Numerous studies have suggested that *P. pugio* and *P. vulgaris* population abundances are affected by various abiotic and biotic factors such as temperature, salinity, habitat, and predation (Thorp & Hoss, 1975; Thorp, 1976; Heard, 1982; Anderson, 1985; Kneib & Knowlton, 1995); however, there are few studies that have examined resource use between *P. pugio* and *P. vulgaris*. Gause's competitive exclusion principle states that two species cannot coexist if they occupy the same niche, i.e., they use the same space and resources (Mittelbach & McGill, 2019). Studies conducted on other co-occurring palaemonid species suggested that interference competition caused distribution and abundance differences between *P. floridanus* and *P. vulgaris* in seagrass meadows in Florida (Coen et al., 1981). Still, trophic structure has not been studied for *P. pugio* and *P. vulgaris*, other than traditional diet analyses of both species which show a wide overlap in prey items (Odum & Heald, 1972; Welsh, 1975; Bell and Coull, 1978; Anderson, 1985).



The feeding behavior of palaemonid shrimp (shredding of prey) makes traditional diet analysis difficult, which has contributed to insufficient trophic position (TP) and diet comparisons between species of *Palaemon*. Previous diet analyses have shown traditional stomach analysis to be unreliable in determining the trophic position of *Palaemon* species (Tiffan and Hurst, 2016) and emphasized the need for an alternative method. Kling et al. (1992) showed that stable isotope analysis (SIA) allows comparisons in trophic position (where the organism feeds in a food web) to be made between species which have difficult-to-distinguish physical diets. Stable isotope analysis has become a staple in determining resource use and trophic interactions within food webs (Minagawa and Wada, 1984; Fry, 1988; Post, 2002). Stable isotopes are atoms of the same element that contain an equal number of protons but differ in the number of neutrons. The most analyzed stable isotopes in ecological studies are carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ; Fry, 1988). When a predator consumes a prey item, that organism will assimilate the prey item's isotopic signature in a relatively predictable way. The enrichment factors for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are  $\sim 3.4\text{‰}$  and  $\sim 1\text{‰}$ , respectively, per each trophic position increase (Minagawa and Wada, 1984; Fry, 1988; Post 2002). Hence the stable isotope values in consumer tissues can be used to infer an organism's primary production source and trophic position, overcoming limitations associated with traditional stomach content analyses.

The goal of the research was to determine whether competition occurs between the co-occurring *P. pugio* and *P. vulgaris* along an estuarine positional gradient, using relative abundance estimates and stable isotope analysis. The null hypotheses were:

- I. There are no differences in congener abundance due to abiotic and biotic interactions along the estuarine gradient.
- II. Isotopic niche spaces and trophic position of *P. pugio* and *P. vulgaris* do not differ along the estuarine gradient and by environmental variables.

## CHAPTER II: METHODS

### Study Location

The study was conducted in Biloxi Bay (Figure 1), a coastal estuary in Mississippi, USA. Biloxi Bay is a diurnal microtidal estuary with freshwater inputs from the Biloxi River, Tchoutacabouffa River, and several small tributaries (Eleuterius and Christmas, 1973; Lowe and Petterson, 2014). Four sampling sites were positioned on an estuarine gradient from the mouth of the Biloxi River to the mouth of the Mississippi Sound, with site 1 near the mouth of the Biloxi River, progressing to site 4 at the mouth of the bay and the Mississippi Sound (Figure 1). Each site had three different shoreline types sampled (stations), i.e., Natural Shoreline (NS), Hardened Shoreline (HS), and Riprap (RR), with site 1 and 4 having a fourth shoreline type; Living Shoreline (LS). Various shoreline types were sampled to represent the most prevalent habitats in Biloxi Bay.

All natural shorelines were tidal marshes dominated by a mixture of *Juncus roemerianus* and *Spartina alterniflora*, with *S. alterniflora* being the dominant vegetation at the mouth of the Mississippi Sound and *J. roemerianus* becoming more dominant further up Biloxi Bay (Eleuterius and Christmas, 1973). All hardened shorelines were wooden bulkheads. Riprap sites were constructed with concrete rubble or cobblestone. Living shorelines were shorelines that had been planted with native vegetation and also possessed hard structures to help stabilize the shoreline (Bryars et al., 2016).

## Collections

Physical-chemical parameters at each site were measured before fyke nets were set and again before fyke nets were retrieved. Salinity, dissolved oxygen (mg/L), pH, and water temperature (°C) were measured with a YSI 6600 V2 sonde. Abiotic parameters were measured and water samples were collected from a boat before accessing the shoreline. Water collections were taken mid-depth with a 4 L beta sampler before net placement and processed in the lab for particulate organic matter (POM). Primary production sources were collected and identified for each site and station, including submerged aquatic vegetation and terrestrial sources. Benthic microalgae were collected using settlement plates. Plates were constructed using 152.4 mm<sup>2</sup> glass squares with a 3 mm gap and were set out during the September 2021 sampling event and recovered two weeks later. Water samples were filtered with Pall polycarbonate filter towers connected to a Millipore stainless steel filtration manifold. Known volumes of sample water (50 ml to 150 ml) were filtered through muffled (500 °C for 2 hours) GF/F filters (0.7 µm nominal pore size), then immediately frozen in Petri dishes after filtration. Prior to analysis, filters were oven dried (65 °C) and then fumed in a glass desiccator with concentrated HCl vapors to remove any inorganic carbon present. Filters were then analyzed using a Thermo Delta V Advantage stable isotope ratio mass spectrometer coupled with a Costech 4010 elemental analyzer via a Thermo Conflo IV interface for POM  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotope values.

*Palaemon pugio* and *P. vulgaris* were sampled using fyke nets fished over an entire tidal cycle (~24 hours) at 18 stations throughout Biloxi Bay. Water depth (m) at the

mouth of the fyke net was noted after net placement and again before net retrieval. Prior to fyke retrieval, abiotic data (salinity, pH, and DO) were measured using the aforementioned procedure. Fyke net construction and dimensions are outlined in Schumacher (2022). Fyke nets were fished with the center lead as near to the landward edge as possible, and wings were placed about 1 m from shore. Seasonality was captured by sampling in November 2020, April 2021, July 2021, September 2021, and November 2021. All sites were sampled consecutively over six days during spring tide. The contents of each net were euthanized by placing them on ice, then transported back to the lab to be frozen until processed. Shrimp were identified to the species level as described by Heard (1982) and enumerated. Up to 20 individuals were weighed (nearest 0.001 g) and measured (nearest 1 mm) for total length (from rostrum tip to telson). Subsampled individuals were then placed in whirl-paks and frozen for stable isotope analysis.

### **Sample Processing for Stable Isotope Analysis**

To compare trophic structure between congener shrimp species,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotope values were analyzed from specimens collected during November 2020, April 2021, July 2021, September 2021, and November 2021 sampling events. For each station and sampling event, the subsamples weighed and measured from the collections noted above were analyzed for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values. In the laboratory, individual shrimp and primary production sources were frozen at  $-80\text{ }^{\circ}\text{C}$  for 0.5 h, then freeze-dried for 48 h. After freeze-drying, the samples were homogenized into a fine powder using mortar and pestles, followed by weighing (0.300-0.700 mg) and packing into tin capsules for analysis in a Thermo Delta V stable isotope ratio mass spectrometer coupled with a

Costech 4010 elemental analyzer. Stable Isotope analysis was conducted at the Marine Environmental Research Laboratory (Department of Coastal Sciences, The University of Southern Mississippi, Ocean Springs, Mississippi, USA). Stable isotope ratios were referenced to known certified standards and expressed in per mil (‰) delta ( $\delta$ ) notation where:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\text{‰}) = \left( \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} \right] - 1 \right) * 1000$$

where R is  $^{13}\text{C}:^{12}\text{C}$  or  $^{15}\text{N}:^{14}\text{N}$  heavy to light isotopic ratio (Peterson and Fry, 1987; Vander Zanden and Rasmussen, 1999; McCarthy et al., 2012). The internationally agreed upon standards for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were atmospheric di-nitrogen gas and PeeDee beliminite, respectively, to which all certified standards were referenced.

## **Data Analysis**

### ***Abundance Estimates***

Catch per unit effort (CPUE) was calculated using the equation:  $\frac{\# \text{ of shrimp}}{\text{net night}}$ . The

CPUE data was analyzed using analyses of variance (ANOVA) and generalized linear models (GLM). Catches per unit effort for both congeners were analyzed using ANOVAs for each location to determine the competitive dominant congener (by abundance) along the estuarine gradient. To assess biotic and abiotic variables affecting CPUE, the most abundant congener's CPUE (*P. pugio*) was used as the response variable within GLMs. By using the most abundant congener's CPUE, it was possible to compare congener CPUEs to each other and interactions with environmental factors. The variables used to create an extensive suite of models were salinity, length (mm), weight (g), salinity regime

(pooled in Venice system categories commonly used in previous studies (Odum, 1988)), sampling event (1-5), season, *P. vulgaris* CPUE, *P. vulgaris* CPUE categories, site, DO (mg/L), and temperature (°C). Salinity, length, weight, temperature, *P. vulgaris* CPUE, and DO were all continuous variables. Seasons were categorized based on northern hemisphere astronomical season categories (Trenberth 1983). Lastly, mean *P. vulgaris* CPUE was pooled into three categories: 0-10 CPUE, 11-50 CPUE, and 50+ CPUE. Initial exploratory models also included shoreline type as a factor, but shoreline type had no statistical significance for any analyses and was not used for further analysis. The best-fit model was chosen by comparing Bayesian information criterion (BIC) for each candidate model. Tukey's honest significant differences (HSD) posthoc was used to examine for significant differences ( $p < 0.05$ ) of dominant species CPUE between factor levels of categorical variables included in best-fit GLMs.

### ***Stable Isotope Analysis***

Congener stable isotopic niche differences were analyzed using ANOVA, stable isotope Bayesian ellipses in R (SIBER) analysis, and GLMs. To standardize niche differences along the estuarine gradient and between seasons, trophic position was measured and compared. Trophic position was calculated using the equation:

$$TP = a + (\delta^{15}N_{Secondary\ Consumer} - \delta^{15}N_{Baseline\ Consumer})/TEF$$

(Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002). Where  $a$  is the trophic position of the baseline, and  $TEF$  is the trophic enrichment factor for the consumer. The  $\delta^{15}N$  TEF used within this study is 3.4 ‰. The baseline consumer used for trophic

position calculations was the nerite snail *Vitta usnea* (TP = 2), which were sampled simultaneously with the palaemonid shrimp during each sampling event. Mean trophic position of *V. usnea* at each site was used to standardize trophic position across the estuary due to variable basal  $\delta^{15}\text{N}$  values of primary producers between sites and seasons.

Mean stable isotope values between species at each site were assessed for significance between congeners using ANOVAs with factors of site and species. SIBER analysis plots were constructed using 40% ellipses to determine isotopic niche size, position and overlap in isotopic space bipolts ( $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$ ). Trophic positions were compared using GLMs using abiotic data, trophic position and CPUE of congeners to determine potential drivers of differences in trophic position. The most abundant congener's (*P. pugio*) trophic position was used as the response variable to assess both environmental and biotic interactions between congeners. Abiotic and biotic variables used to create an extensive suite of models were salinity, length (mm), weight (g), salinity regime, sampling event (1-5), season, *P. vulgaris* CPUE, *P. vulgaris* CPUE categories, site, DO (mg/L), temperature ( $^{\circ}\text{C}$ ), and mean *P. vulgaris* trophic position. All variables followed groupings from the CPUE models, with the addition of *P. vulgaris* trophic position as a continuous variable. The best-fit model was chosen by comparing BIC for each candidate model. To determine correlation between congener trophic positions, regression analysis was conducted between *P. vulgaris* and *P. pugio* trophic positions, in addition to performing Tukey's HSD posthoc to look at significance between factor levels within the best-fit GLMs.



## CHAPTER III: RESULTS

### Abundance Estimates

*Palaemon pugio* was the most abundant congener at each site across all sampling events in the study (Figure 2). Analysis of variance (Table 1) showed no difference between *P. pugio* and *P. vulgaris* CPUE at each site. The best-fit modeled GLM had the factors of sampling event, site, salinity, and season with no interaction terms, all factors being significant to the intercept (Table 2). Tukey's HSD posthoc showed no statistical significance between sampling events and sites on the abundance of *P. pugio*, but there were differences in *P. pugio* CPUE from autumn and spring (Table 3). During the sampling period persistent rains resulted in decreased salinity throughout Biloxi Bay during the course of the study (Figure 3). *Palaemon pugio* CPUE had an initial increase at the beginning of the salinity decline followed by a subsequent decline, while *P. vulgaris* CPUE largely decreased. During the last sampling event salinity had risen to higher levels; however, both congener shrimp CPUE remained low.

### Stable Isotope Analysis

Mean  $\delta^{13}\text{C}$  values for both congeners followed the gradual enrichment in  $\delta^{13}\text{C}$  along the estuarine positional gradient from sites 1 to 4 (Figure 4). *Palaemon vulgaris* had consistently higher  $\delta^{15}\text{N}$  values than *P. pugio* at each site (Figure 4 & Table 8). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values differed by site and species, except for the interaction of site and species for  $\delta^{15}\text{N}$  values (Tables 5–6). However,  $\delta^{13}\text{C}$  values of *P. pugio* and *P. vulgaris* differed at sites 2 and 3 (Table 7). At each site sampled *P. vulgaris* had higher mean  $\delta^{15}\text{N}$

values than *P. pugio* (Table 8). Congeners at sites 1 and 4 had little isotopic niche overlap while those at sites 2 and 3 showed no overlap (Figure 5).

*Palaemon vulgaris* occupied a higher trophic position at each site during the study (Figure 6). This trend was consistent among oligohaline, mesohaline, and polyhaline salinity regimes and during sampling events 1, 2, 4, and 5 throughout the study (Figures 7–8). *Palaemon vulgaris* occupied a similar trophic position as *P. pugio* within fresh salinity regimes and during sampling event 3. Congener trophic position separation increased from fresh to polyhaline salinity regimes. The best-fit trophic position model found that *P. vulgaris* trophic position, *P. vulgaris* CPUE categories, and salinity regime affected *P. pugio* trophic position values (Table 9), with no pairwise difference between the 50+ *P. vulgaris* CPUE category, fresh-oligohaline, and fresh-mesohaline salinity regimes (Table 10). A linear regression model showed mean trophic position of both congeners were correlated and increased with one another (Figure 9). However, the  $R^2$  value was 0.47, suggesting a weak but positive correlation between the trophic positions of both congeners.

## CHAPTER IV: DISCUSSION

The null hypotheses for this experiment were both rejected. *Palaemon pugio* and *P. vulgaris* abundances were both affected by abiotic data (Hypothesis I), and the stable isotopic niche space and trophic positions of the congeners differed (Hypothesis II). The current study found that *P. pugio* was the most abundant congener, and *P. vulgaris* consistently occupied a higher trophic position than *P. pugio* throughout the study.

### **Abundance and Distribution of Palaemonid Shrimp**

General trends in CPUE showed one congener, *P. pugio*, constituting most of the catch (Figure 2). McCarthy et al. (2012) found that palaemonid shrimp assemblages along estuarine gradients are generally composed of two co-occurring species, with one species constituting most of the catch. Low CPUE values for *P. pugio* at site 1 and *P. vulgaris* at sites 1–3 are attributed to salinity preferences of the two congeners. The high freshwater discharge event that occurred during the 2021 sampling periods of April, July, and September lowered salinity to a level that *P. pugio* could not tolerate at the sampled estuary position closest to the Biloxi River (site 1) and to a level throughout the bay system that *P. vulgaris* could not physiologically tolerate either, resulting in low abundances for both species. Previous field observations showed similar trends in *P. pugio* and *P. vulgaris* distributions, where *P. pugio* occurred more frequently in lower salinity waters while *P. vulgaris* did not (Heard, 1982; Anderson, 1985; Pinto, 2019; McCarthy et al., 2012). However, observations did show *P. vulgaris* occurring within salinities <10, suggesting that multiple factors affect distribution. Gallin (2002)

previously suggested that salinity was not the sole driver of species field distributions and that no single factor could explain *P. pugio* and *P. vulgaris* distributions.

By examining multiple factors that could affect species abundances and distribution, the best-fit GLM for the CPUE of *P. pugio* was determined to consist of abiotic variables of sampling event, site, salinity, and season. This model suggested that biotic interactions among the two congeners, did not affect abundance and distribution. The posthoc for the CPUE GLM showed no significant differences within factors for *P. pugio* CPUE, with the exception of differences between the autumn and spring seasons; this finding is contrary to Pinto's (2019) suggestion that differences in abundances of co-occurring palaemonid shrimp was not due to season. Seasonal differences observed within the study were related to salinity differences in that, three of five sampling events took place during increased rainfall events which caused exceptionally low salinity throughout Biloxi Bay. The unforeseeable influence of seasonality (coinciding with salinity) and correlation between sampling events and salinity may have similarly reduced statistical power within candidate models. Overall, the current and previous studies have shown that a variety of abiotic variables influence species specific field distributions. Still, within this study no evidence suggested that abundances of one congener affected the other.

### **Stable Isotopes within Congeners**

To assess competition beyond relative abundances, stable isotope analysis was used to examine differences in stable isotope niche space of *P. pugio* and *P. vulgaris*. Niche separation between congeners was small with most separation occurring in  $\delta^{15}\text{N}$

values (those of *P. vulgaris* being higher than those of *P. pugio*), suggesting a separation in trophic position throughout Biloxi Bay. There have been previous studies that examined palaemonid prey sources, showing palaemonid shrimp consume small grazing invertebrates (e.g., amphipods, copepods, mysid shrimp) and meiofauna (Odum & Heald, 1972; Bell & Coull, 1978; Tiffan and Hurst, 2016). This study suggests that *P. vulgaris* was consuming trophically higher prey items than *P. pugio*, and these increased  $\delta^{15}\text{N}$  values suggest that some resource partitioning exists between these species. *Palaemon vulgaris* was most likely consuming a higher proportion of grazing invertebrates and/or meiofauna than *P. pugio*. Odum and Heald (1972) suggested that most *Palaemon* shrimp share the same prey sources; however, the authors used traditional stomach content analysis that gives only a snapshot of what an organism consumes and did not allow calculation of the proportion of these prey items consumed over time.

The study results suggest that estuarine position (site) had no effect on the trophic position of either *P. pugio* and *P. vulgaris*. These results were surprising, considering potential carbon baseline sources are expected to change down an estuarine gradient, further suggesting the congeners occupied slightly different ecological niches regardless of carbon sources. Trophic position remained higher for *P. vulgaris* regardless of the predominant salinity regime at which the congeners were sampled, with slight differences occurring when samples were obtained during conditions closest to freshwater. However, the low statistical significance for freshwater salinity regimes on trophic position is likely due to low observations, with only two *P. vulgaris* included for stable isotope analyses in this salinity regime. Lastly, the trophic position of *P. vulgaris* was also higher than that of *P. pugio* during each sampling event, except for sampling event 3. However, Biloxi Bay

was experiencing the lowest mean salinity values during this sampling event, which may have altered the abundance of potential prey or altered feeding behaviors due to increased physiological stress.

The best-fit GLM for trophic position revealed that trophic positions of the two congeners are correlated with each other. Additionally, the CPUE of *P. vulgaris* influenced the trophic position of *P. pugio* possibly due to exploitative competition from one congener better utilizing prey sources than the other. Contrary to previous literature suggesting that interference competition allowed *P. pugio* and *P. vulgaris* to co-occur, this study found that trophic position differed between congeners throughout the study, suggesting resource partitioning (Thorp, 1976). Results from Tukey's HSD posthoc on the trophic position GLM suggest that *P. vulgaris* CPUE below 50 and salinity regimes other than freshwater all influenced *P. pugio* trophic position. The low abundance of *P. vulgaris* within freshwater salinity regimes may have caused difficulty in detecting significant effects of estuary position on trophic position of *P. pugio* using GLMs. The increased separation of trophic position between congeners from fresh to polyhaline salinity regimes is likely due to exploitative competition for prey sources as congener abundances fluctuate. For example, when *P. vulgaris* occurred in high abundance they most likely consumed more meiofauna, resulting in lower meiofauna foraging opportunity for *P. pugio*.

### **Limitations**

Palaemonid shrimp were obtained as a portion of another study aimed at assessing nekton community use of various habitat types, so the use of fyke nets may not be the

most efficient capture method for assessing palaemonid shrimp assemblages as fyke nets are a passive gear and may select for more mobile individuals. Previous studies have used dip nets, minnow traps, epibenthic sleds, beam trawls, and seine nets for palaemonid shrimp sampling; however, standardization of some of those methods is difficult, particularly when physical habitat structure varies greatly as in the current study (Odum & Heald, 1972; Thorp, 1976; McCarthy et al., 2012; Tiffan and Hurst, 2016; Pinto, 2019). Secondly, sampling was restricted to five events within a single year and not over multiple years. Additional sampling events would have given more robust data and have provided models that can be used to assess palaemonid CPUE and trophic position over periods without high freshwater discharge. Finally, a third isotopic tracer was not examined that could distinguish between carbon baseline sources that share similar  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic signatures (Peterson & Fry, 1987). This ability would have been beneficial to distinguishing which primary production sources contributed most to congener food webs.

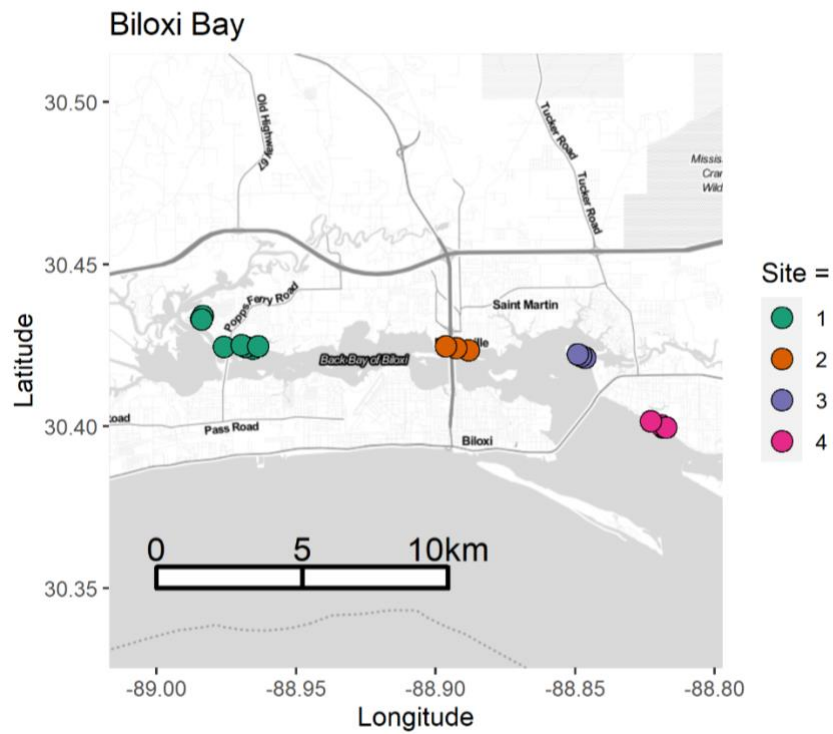
## **Conclusion**

The results of this study provide new insight into the ecology and competition of two co-occurring palaemonid shrimp species within coastal Mississippi waters. The present study suggests that multiple abiotic factors (salinity, season, estuary position) influence the distribution and abundance of *P. pugio* and *P. vulgaris* within Biloxi Bay. Furthermore, this study demonstrated that *P. pugio* and *P. vulgaris* occupy different ecological niche spaces, independent to the abundance of its congener or abiotic factors, and that these congeners follow a predictable separation in trophic position. This study is the first to suggest that exploitative competition and environmental preferences both

allow co-occurrence between congener palaemonid species, limiting competition within heterogeneous environments.



## APPENDIX A: FIGURES



*Figure 1: Map depicting the 18 sampling stations within Biloxi Bay, Mississippi. Color denotes study site, with Site 1 having the most freshwater influence based on its proximity to the Biloxi and Tchoutacabouffa Rivers, and Site 4 having the most marine influence being closer to the Mississippi Sound.*

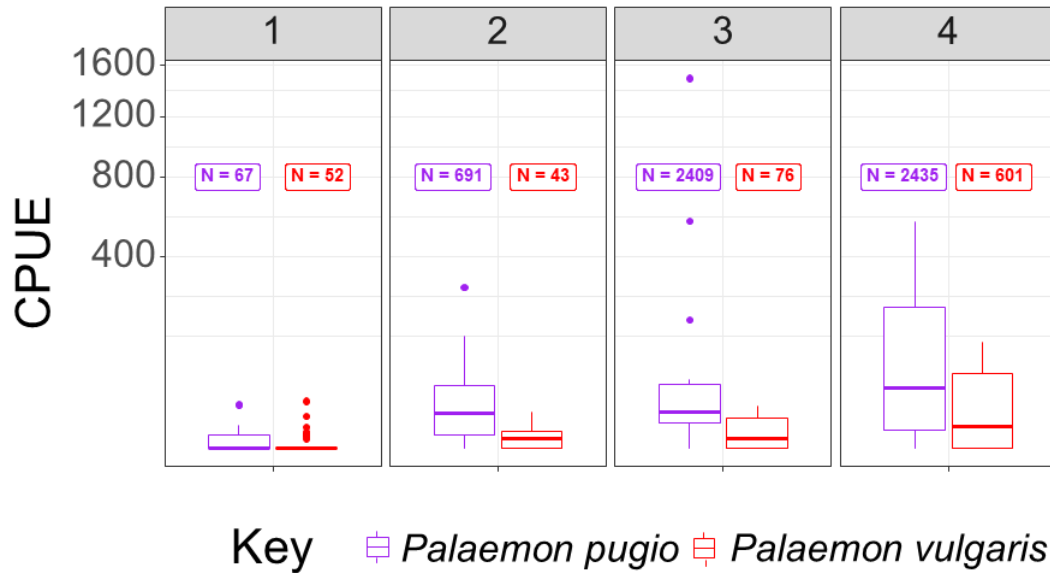


Figure 2: Boxplots of the catch per unit effort (CPUE) of *Palaemon pugio* (purple) and *Palaemon vulgaris* (red) at each sampling site. Site 1 represents the highest estuary position whereas site 4 represents the lowest (see Figure 1). N = the total number of each species collected at each sampling site throughout the entire project.

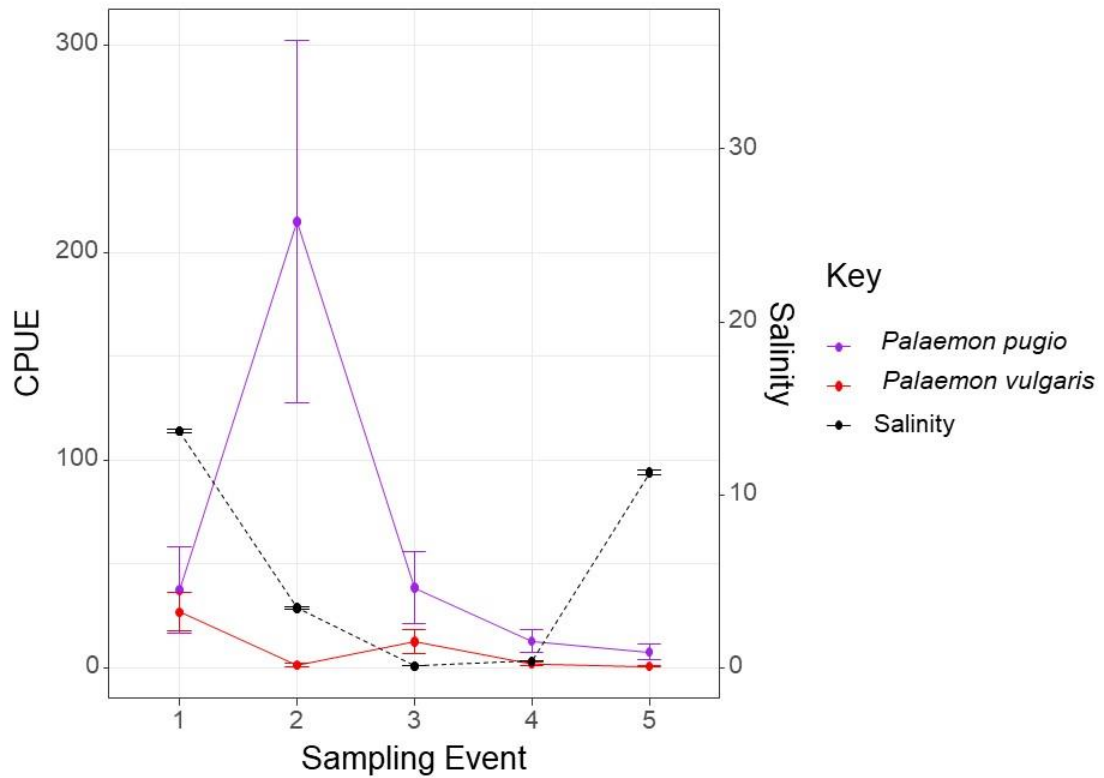


Figure 3: Dual axes plot of mean catch per unit effort (CPUE) for *Palaemon pugio* (purple) and *Palaemon vulgaris* (red) on the left y-axis and mean salinity per sampling event (black) on the right y-axis. Sampling event 1= November 2020, Sampling event 2= April 2021, Sampling event 3= July 2021, Sampling event 4= September 2021, and Sampling event 5= November 2021, Error bars= standard error.

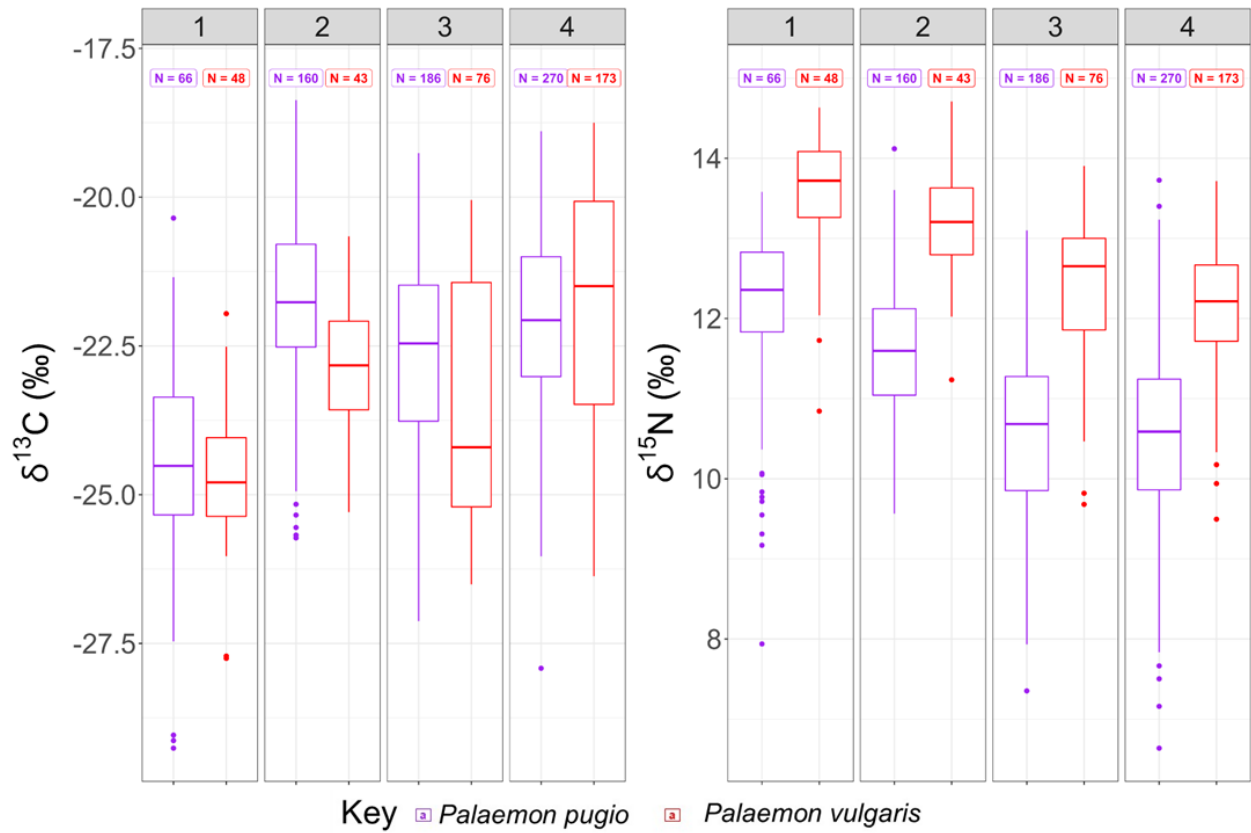


Figure 4: Boxplot of  $\delta^{13}\text{C}$  (right) and  $\delta^{15}\text{N}$  (left) isotopic values for *Palaemon pugio* and *Palaemon vulgaris* at each sampling site. Site 1 represents the highest estuary position whereas site 4 represents the lowest (see Figure 1). N = total number of each species analyzed for stable isotopes at each site throughout the length of the project.

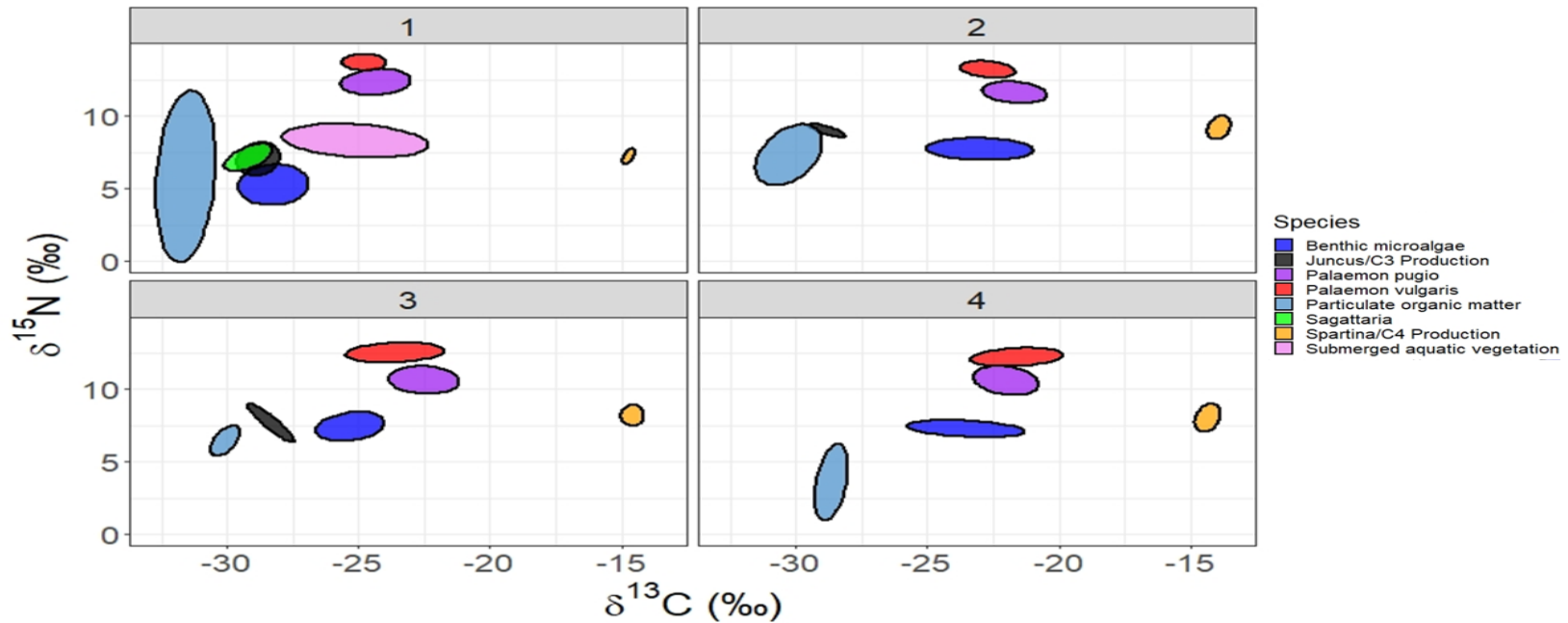


Figure 5: Isotopic composition ( $\Delta^{13}C$  and  $\Delta^{15}N$  values) of *Palaemon pugio* (purple), *Palaemon vulgaris* (red), and potential carbon baseline sources. Ellipses represent 40% of the isotopic composition data calculated using Stable Isotope Bayesian Ellipses in R (SIBER). Carbon baseline sources: benthic microalgae (blue), *Juncus roemerianus*/C3 primary production sources (black), particulate organic matter (light blue), *Sagattaria* sp. (green), *Spartina alterniflora*/C4 primary production sources (yellow), submerged aquatic vegetation (pink). Grouped by Site (1–4), where Site 1 represents the highest estuary position whereas site 4 represents the lowest (see Figure 1).

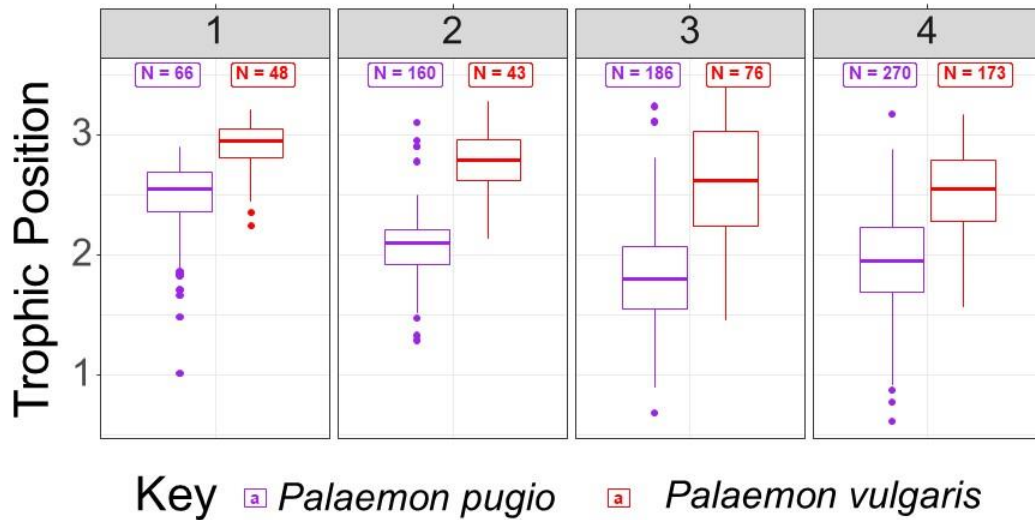


Figure 6: Boxplot of the trophic positions of *Palaemon pugio* (purple) and *Palaemon vulgaris* (red) at each site (1–4), where Site 1 represents the highest estuary position whereas site 4 represents the lowest (see Figure 1). N = total number of each species analyzed for trophic position at each site throughout the study period.

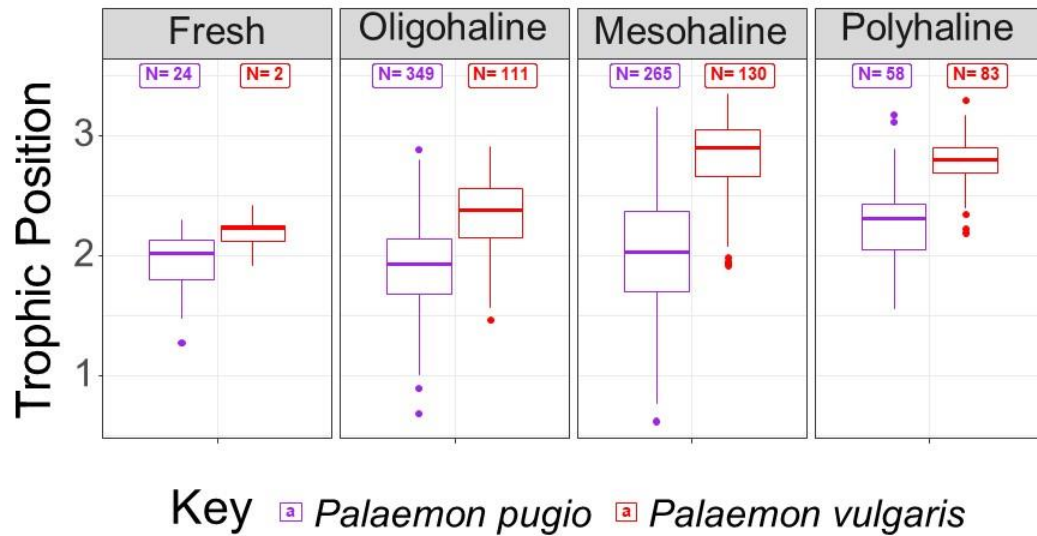
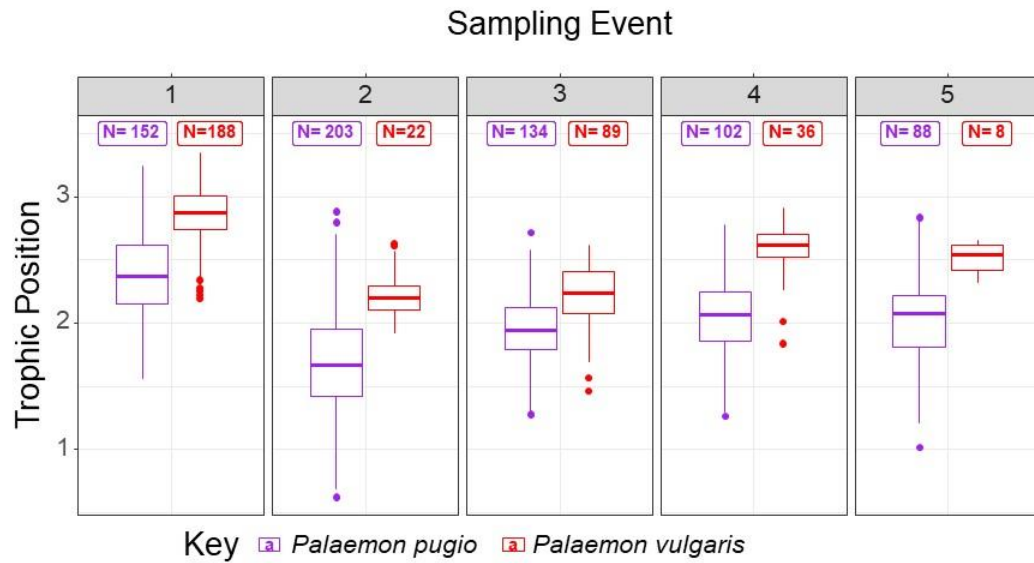
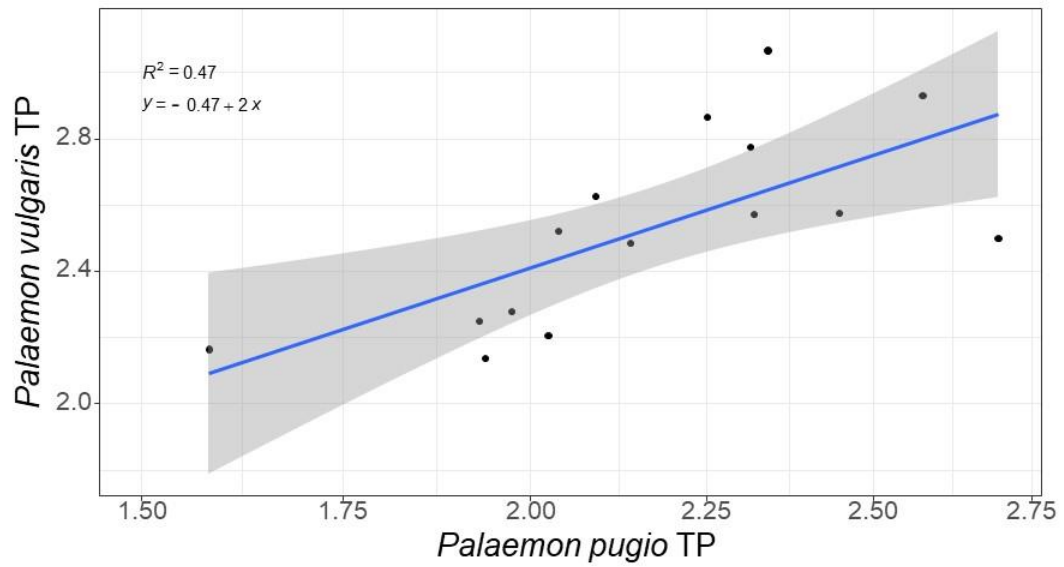


Figure 7: Boxplot of the trophic positions of *Palaemon pugio* (purple) and *Palaemon vulgaris* (red) by salinity regime. Salinity regimes are representative of the conditions during sampling: fresh (0.0-0.5), oligohaline (0.5-5.0), mesohaline (5.0-18.0), polyhaline (18.0-30.0). N = total number of each species analyzed for trophic position within each salinity regime throughout the study period; note low sample sizes encountered in the fresh salinity regime.



*Figure 8: Boxplot of the trophic positions of Palaemon pugio (purple) and Palaemon vulgaris (red) by sampling event (1–5). Sampling event 1= November 2020, Sampling event 2= April 2021, Sampling event 3= July 2021, Sampling event 4= September 2021, and Sampling event 5= November 2021, N = total number of each species analyzed for trophic position during each sampling events.*





*Figure 9: Linear regression of *P. pugio* TP by *P. vulgaris* TP. Linear regression plotted over a scatterplot of mean congener trophic positions when species co-occur. Blue line represents the linear regression line with the equation of  $y = -0.47 + 2X$  ( $R^2=0.47$ ). Shaded region represents pointwise 95% confidence interval on the fitted values.*

## APPENDIX B: TABLES

**Table 1. Two-way analysis of variance (ANOVA) results for mean catch per unit effort (CPUE) by the factors of species (*P. pugio* and *P. vulgaris*), site (1–4), and the interaction of species and site. Df= degree of freedom, F= F value (variation among samples), P= p-value, \*\*\* = statistically significant (p-value = <0.05).**

	Df	F	P
Species	1	3.65	0.065
Site	3	1.19	0.328
Species*Site	3	0.71	0.553

**Table 2. Tukey's HSD posthoc results for two-way analysis of variance results for catch per unit effort (CPUE) by the the interaction of species and site. diff= differences in observed means, P adj= adjusted p-value, \*\*\* = statistically significant (p-value = <0.05), PLV= *Palaemon vulgaris*, PLP= *Palaemon pugio* and site (1-4).**

	diff	P adj
PLV:1-PLP:1	-3.0	1.000
PLP:2-PLP:1	124.8	1.000
PLV:2-PLP:1	-4.8	1.000
PLP:3-PLP:1	468.4	0.595
PLV:3-PLP:1	-1.0	1.000
PLP:4-PLP:1	473.6	0.582
PLV:4-PLP:1	106.8	1.000
PLP:2-PLV:1	127.8	1.000
PLV:2-PLV:1	-1.8	1.000
PLP:3-PLV:1	471.4	0.587
PLV:3-PLV:1	2.0	1.000
PLP:4-PLV:1	476.6	0.574
PLP:4-PLV:1	109.8	1.000
PLV:2-PLP:2	-129.6	1.000
PLP:3-PLP:2	343.6	0.870
PLV:3-PLP:2	-125.8	1.000
PLP:4-PLP:2	348.8	0.862
PLV:4-PLP:2	-18.0	1.000
PLP:3-PLV:2	473.2	0.583
PLV:3-PLV:2	3.8	1.000
PLP:4-PLV:2	478.4	0.570
PLV:4-PLV:2	111.6	1.000
PLV:3-PLP:3	-469.4	0.593
PLP:4-PLP:3	5.2	1.000
PLV:4-PLP:3	-361.6	0.839
PLP:4-PLV:3	474.6	0.579
PLV:4-PLV:3	107.8	1.000
PLV:4-PLP:4	-366.8	0.829

**Table 3. Generalized linear model output for *Palaemon pugio* catch per unit effort (CPUE) by the factors of sampling event (1–5), site (1–4), season (autumn, spring, summer), and salinity. Estimate= estimate, Std. Error= standard error, Z value= Z value, P= p-value, \*\*\* = statistically significant (p-value = <0.05).**

	Estimate	Std. Error	Z value	P
Intercept	4.85	0.09	53.19	< 0.001 ***
Sampling Event	-1.20	0.04	-30.53	< 0.001 ***
Site	1.45	0.03	48.37	< 0.001 ***
Salinity	-0.17	0.01	-31.81	< 0.001 ***
Season: Spring	1.09	0.05	23.76	< 0.001 ***
Season: Summer	-0.74	0.07	-11.33	< 0.001 ***

**Table 4. Tukey’s HSD posthoc results for generalized linear model output for *Palaemon pugio* catch per unit effort (CPUE) by the factors of sampling event, site, season, and salinity. SE= sampling event (1–5), Site (1–4), season (autumn, spring, summer), diff= differences in observed means, P adj= adjusted p-value, \*\*\* = statistically significant (p-value = <0.05).**

	diff	P adj
SE 2-1	800.00	0.184
SE 3-1	5.25	1.000
SE 4-1	-110.50	0.997
SE 5-1	-134.25	0.994
SE 3-2	-794.75	0.188
SE 4-2	-910.50	0.106
SE 5-2	-934.25	0.094
SE 4-3	-115.75	0.997
SE 5-3	-139.50	0.993
SE 5-4	-23.75	1.000
Site 2-1	124.80	0.985
Site 3-1	468.40	0.564
Site 4-1	473.60	0.556
Site 3-2	343.60	0.769
Site 4-2	348.80	0.761
Site 4-3	5.20	1.000
Spring-Autumn	881.58	0.010 ***
Summer-Autumn	86.83	0.942
Summer-Spring	-794.75	0.060

**Table 5. Two-way analysis of variance results for mean individual carbon isotope values ( $\delta^{13}\text{C}$ ) by the factors of species (*P. pugio* and *P. vulgaris*), site (1–4), and the interaction between species and site. Df= degree of freedom, F= F value (variation among samples), P= p-value, \*\*\* = statistically significant (p-value = <0.05).**

	Df	F	P
Species	1	9.81	< 0.001 ***
Site	3	99.32	< 0.001 ***
Species*Site	3	10.56	< 0.001 ***

**Table 6. Two-way analysis of variance results for mean individual nitrogen isotope values ( $\delta^{15}\text{N}$ ) by the factors of species (*P. pugio* and *P. vulgaris*), site (1–4), and the interaction between species and site. Df= degree of freedom, F= F value (variation among samples), P= p-value, \*\*\* = statistically significant (p-value = <0.05).**

	Df	F	P
Species	1	596.01	< 0.001 ***
Site	3	103.11	< 0.001 ***
Species*Site	3	0.93	0.424

**Table 7. Tukey's HSD posthoc results for individual carbon isotope values ( $\delta^{13}\text{C}$ )**

and the interaction of species and site. diff= differences in observed means, P adj= adjusted p-value, \*\*\* = statistically significant (p-value = <0.05), PLV= *Palaemon vulgaris*, PLP= *Palaemon pugio*, and site (1–4).

	diff	P adj
PLV:1-PLP:1	-0.24	0.991
PLV:2-PLP:2	-0.99	0.006 ***
PLV:3-PLP:3	-0.93	< 0.001 ***
PLV:4-PLP:4	0.31	0.448

**Table 8. Tukey's HSD posthoc results for two-way analysis of variance (ANOVA)**

**results for individual nitrogen isotope values ( $\delta^{15}\text{N}$ )** and the interaction of species and site. diff= differences in observed means, P adj= adjusted p-value, \*\*\* = statistically significant (p-value = <0.05), PLV= *Palaemon vulgaris*, PLP= *Palaemon pugio* and site (1-4).

	diff	P adj
PLV:1-PLP:1	1.51	< 0.001 ***
PLV:2-PLP:2	1.58	< 0.001 ***
PLV:3-PLP:3	1.82	< 0.001 ***
PLV:4-PLP:4	1.59	< 0.001 ***

**Table 9. Generalized linear model output for trophic position of *Palaemon pugio* by the factors of *Palaemon vulgaris* trophic position, *Palaemon vulgaris* catch per unit effort categories (VCPUE; 0-10, 11-50, 50+), and salinity regime (fresh, mesohaline, oligohaline, polyhaline; see Figure 7 for salinity regime details). Estimate= estimate, Std. Error= standard error, Z value= Z value, P= p-value, \*\*\* = statistically significant (p-value = <0.05).**

	Estimate	Std. Error	Z value	P
(Intercept)	4.22	0.03	144.08	< 0.001 ***
<i>P. vulgaris</i> Trophic Position	0.51	0.01	39.91	< 0.001 ***
11-50 VCPUE	-0.12	0.01	-14.90	< 0.001 ***
50+ VCPUE	-0.04	0.01	-3.84	< 0.001 ***
Mesohaline	-0.11	0.01	-7.88	< 0.001 ***
Oligohaline	-0.06	0.01	-4.26	< 0.001 ***
Polyhaline	-0.14	0.02	-8.54	< 0.001 ***



**Table 10. Tukey’s HSD posthoc results for *Palaemon pugio* trophic position generalized linear model** by the factors of *Palaemon vulgaris* trophic position, *Palaemon vulgaris* catch per unit effort categories (VCPUE; 0-10, 11-50, 50+), and salinity regime (fresh, mesohaline, oligohaline, polyhaline; see Figure 7 for salinity regime details). Estimate= estimate, Std. Error= standard error, Z value= Z value, P= p-value, \*\*\* = statistically significant (p-value = <0.05).

	diff	p adj
11-50 VCPUE - 0-10 VCPUE	0.14	< 0.001 ***
50+ VCPUE - 0-10 VCPUE	0.20	< 0.001 ***
50+ VCPUE - 11-50 VCPUE	0.06	0.456
Mesohaline-Fresh	0.07	0.770
Oligohaline-Fresh	-0.05	0.887
Polyhaline-Fresh	0.35	< 0.001 ***
Oligohaline-Mesohaline	-0.12	0.004 ***
Polyhaline-Mesohaline	0.28	< 0.001 ***
Polyhaline-Oligohaline	0.40	< 0.001 ***

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