

THE RELATIONSHIP BETWEEN MACROFAUNA DIVERSITY, FUNCTIONAL
DIVERSITY, AND SECONDARY PRODUCTION

A Thesis

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This thesis meets the standards for scope and quality of
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ABSTRACT

The relationship between functional diversity and secondary production are known to influence ecosystem stability and can be used to measure the functioning of an ecosystem. Functional diversity is a component of biodiversity that classifies organisms by what they do (i.e., functional types) in a community or ecosystem, or more specifically by how certain traits effect the functioning of the environment. Secondary production occurs when biomass is generated by heterotrophic organisms when they consume organic material or primary producers. The research objective is to determine the relationship between secondary production and the connection between functional diversity and species diversity in estuary systems. The goal is to test the hypothesis that there is a positive relationship between functional diversity and secondary benthic productivity among bays within four mid-coastal Texas estuaries: Nueces Estuary, Laguna Madre Estuary, Guadalupe Estuary, and Lavaca-Colorado Estuary. Freshwater inflow differences among these estuaries can affect biodiversity, productivity, and habitat. Thus, changes of freshwater inflow could lead to variability in functional diversity and secondary productivity. Functional diversity was calculated based on seven classifiers: feeding strategy, habitat, mobility, lifespan, reproduction, sediment depth, and body size. There was a positive correlation between benthic production and diversity for species richness, species diversity, and species evenness and secondary production. Most functional diversity indices did not show any significance; however, functional dispersion was shown to explain >77% of variation for secondary production. Apart from functional originality, there did not appear to be a significant relationship between indicators of freshwater inflow influence (i.e., increase in nutrients and decrease in salinity) and the diversity metrics. In general, the response in primary and secondary

bays is different, except for the lower part of San Antonio Bay. Overall, classical measures of macrofauna species diversity have a strong relationship with secondary production, while functional diversity does not appear to have any relationship. Thus, for Texas estuaries, it appears that functional diversity metrics do not explain or drive benthic ecosystem processes.

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1. INTRODUCTION

1.1 Background

The relationship between functional diversity (FD) and secondary production has been shown to influence ecosystem stability and can be used to measure the functioning of an ecosystem (Dolbeth et al., 2015). FD is a component of biodiversity that separates/classifies organisms by what they do (i.e., functional types) in a community or ecosystem, or more specifically by how certain traits effect the functioning of the environment. It is of ecological importance because it is the component of diversity that influences ecosystem dynamics, stability, productivity, nutrient balance, as well as other aspects of ecosystem functioning (Tilman, 2001; Dolbeth et al., 2015). Ecosystem processes and resilience to environmental change rely on FD within a community. The concept of FD is founded on the idea than an ecosystem's capacity to function and maintain itself is more closely related to species-specific traits than to diversity itself (Hooper et al., 2005; Hewitt et al., 2008; Shojaei et al, 2021). Research in this area has revealed that the strength and nature of the relationship between species diversity and FD may differ (Shojaei et al., 2021). Scientists can generalize the functional contributions of species to ecosystem functions and anticipate the ecological effects of species loss by measuring FD (Weigel et al., 2016; Teichert et al., 2017). However, the assessment of the functional organization of communities requires the use of a multifaceted approach rather than a single measure (Ricotta et al., 2014). Because marine benthic invertebrates are taxonomically and functionally diverse and support important ecological processes, the marine benthos is a promising system for investigating the connection between species diversity and FD (Brey, 2012). Due to their restricted mobility, benthic organisms are particularly vulnerable to environmental disturbances (Shojaei et al., 2016). The focus on functional traits highlights the

importance of integrating natural history into ecology (Hewitt et al., 2008). Secondary production occurs when biomass is generated by heterotrophic organisms when they consume organic material or primary producers. Benthic secondary production is important to understand ecosystem dynamics as it represents the formation of community biomass by growth (Dolbeth et al., 2005). It is a process that links population characteristics (such as biomass, growth rate, development time) to other ecosystem-level processes (Dolbeth et al., 2015). Studying FD and its relationship with secondary production will improve our understanding of ecosystem function.

Estuaries are coastal bodies of water where fresh water from land mixes with saltwater from the ocean. They can vary in terms of climate, geology, and tidal regime (Montagna et al., 2013). Texas estuaries are similar in terms of geomorphology. They consist of lagoons that open to a primary bay and a smaller secondary bay with barrier islands located parallel to the mainland (Montagna et al., 2018). Secondary bays have greater freshwater influence because one or two rivers generally flow into them. Since the primary bays provide the connection with the Gulf of Mexico, they have greater marine influence. However, Texas estuaries lie in a climatic gradient with decreasing rainfall from the northeast to the southwest (Montagna et al., 2018). Along the gradient, the freshwater inflow balance changes from positive to negative. Consequently, nutrient loading decreases. Variability of precipitation along the Texas coast is caused by El Niño Southern Oscillation (ENSO) events. During the El Niño phase, salinity decreases within the estuaries due to increase in precipitation and freshwater inflows (Tolan, 2007; Kim and Montagna, 2012; Murgulet et al., 2017). Conversely, freshwater inflows are reduced during La Niña periods due to lower amounts of precipitation, causing increases in salinity. There is also a salinity gradient within the estuaries (Montagna et al., 2013). The quantity, timing, and

frequency of freshwater inflow effects estuarine conditions and in turn drives biological resources such as diversity and secondary production (Montagna et al., 2013).

Salinity variability caused by freshwater inflow changes can affect biodiversity (Van Diggelen and Montagna 2016), primary productivity (Montagna and Li 2010), and habitat (Montagna et al., 2007). Because benthic organisms are widely distributed and typically immobile, they are usually susceptible to changes in their environment (Montagna et al., 2013). Salinity gradients drive differences in community structure and diversity of benthic organisms (Remane and Schlieper, 1971). Higher variability in salinity drives decreases in benthic infauna diversity (Van Diggelen and Montagna, 2016). For instance, a study by Kim and Montagna (2012) found that when salinity increases with decreasing nutrient concentrations, deposit feeder biomass will increase while suspension feeder biomass will decrease. As a result, there should be a decrease in FD when salinity is increased due to the loss of a trophic guild (Kim and Montagna 2012). It has also been observed that the upstream benthic community is reduced by reduced inflow while the downstream community increases with higher salinities (Kim and Montagna 2012). FD has been connected to promoting production levels as well. How organisms and their traits respond to their environment implies that it will have an impact on production levels (Dolbeth et al., 2015). A study by Dolbeth et al. (2015) found that production levels seemed to be dependent on the biomass from a particular group of functional characteristics. Therefore, changes in salinity could also lead to changes in FD and secondary productivity.

Because inflow arrives in pulses, it can be viewed as a disturbance (Attrill et al., 1996; Gillanders and Kingsford 2002). The health or stability of a community can be studied based on its ability to resist or recover from a disturbance. Freshwater- related disturbances can cause changes in salinity and impact benthic diversity (Van Diggelen and Montagna 2016). Disturbed

systems are characterized by a reduced FD and, in turn, elevated redundancy (Micheli and Halpern, 2005). A system can be more resistant with increasing diversity because there are more species to offset the stress (Whitford et al., 1999). A systems ability to resist and recover is a contributing factor to ecosystem health and stability (Van Diggelen and Montagna 2016). Indicators of freshwater inflow influence, such as an increase in nutrients and decrease in salinity, may have an affect on secondary production and diversity. Overall, these studies have shown that freshwater inflow maintains secondary production and FD which is important for a healthy and sustainable estuary. The data from this project can be used to assess ecosystem health as it relates to salinity changes from freshwater inflow. There is an increasing need to determine the implications of these events on community dynamics. Therefore, the present study can connect the relationship between changes in salinity, diversity, and production.

Functional traits are morphological, physiological, and phenological characteristics that affect an individual's fitness by influencing growth, reproduction, and survival (Ricotta et al., 2014). As a result, functional diversity measurements tend to correlate more strongly with ecosystem functioning than standard species diversity measures. Functional traits have been shown to be an important factor when considering environmental assessments. For example, polychaetes' trophic structure and feeding modes were examined to assess the effect of aquaculture activity in coastal marine ecosystems (Sanchis et al. 2021). Each species was divided into five feeding modes. The researchers concluded that the analysis of structure and function of polychaete assemblages did show the impact of aquaculture activity and the functional traits approach revealed the environmental condition of the benthos (Sanchis et al., 2021). Ultimately, the researchers suggested that functional trait studies on benthic communities must be considered when performing environmental assessments.

A study by Henriques et al. (2017) assessed the trait-environment relationship of fishes in estuaries. Researchers collected a global database of fish assemblages in estuaries as well as the functional traits of fishes and ecosystem features. The scientists quantified the relative importance of ecosystem features as drivers of patterns of fish functional traits (i.e., drivers of the proportions of fish traits) (Henriques et al., 2017). The study concluded that trait patterns and trait-environment relationships indicate that assemblage composition is determined by the functional role of species within ecosystems (Henriques et al., 2017). Similarly, Silvia-Junior et al. (2017) investigated the FD among estuaries with different levels of impacts and environmental features using a fish functional trait-based approach. Food acquisition and locomotion were the two key functions used to develop twelve ecomorphological traits. The researchers combined fish abundance and functional dissimilarities into a multivariate analysis. Overall, combining diversity indices and functional topology through a multivariate analysis allowed the researchers to create a more in-depth diversity assessment of the functional patterns of assemblages for estuarine fishes (Silvia-Junior et al., 2017).

Shojaei et al. (2021) investigated how changes in species alters the functional properties of benthic communities using a functional trait-based approach. Traits were selected to describe the life history, behavioral, and morphological characteristics of the benthic communities in study. Finally, one study by Dolbeth et al. (2015) investigated the relationship between secondary production and FD in a disturbed estuary. The researchers chose six traits that are likely to have an influence on production levels: life span, mean body mass, feeding guilds, depth position, mobility, and reproduction frequency (Dolbeth et al., 2015). Scientists found that FD explained a major part of the secondary production variation (74%) in an estuarine system

(Dolbeth et al., 2015). Because there is currently no accepted consensus regarding the selection of traits, the final selection is guided by the trait information available for benthic communities.

1.2 Questions and Approach

The relationship between FD and biodiversity in the marine benthos has recently piqued scientific interest (Danovaro, 2012; Clare et al., 2015; Van der Linden et al., 2016; Weigel et al., 2016; Pandey et al., 2022). In most studies, there was a strong relationship between the two indices however, Weigel et al. (2016) found that FD seemed to stabilize with increasing numbers of species (Shojaei et al., 2021). Pandey et al. (2022) used biological trait analysis (BTA) to assess the functional response of macrobenthos with stressors and found a division between smaller, short-lived, deposit feeding fauna in disturbed areas and larger, long-lived, and highly motile fauna in undisturbed areas. A study by Clare et al. (2015) demonstrated that even when the benthic fauna community experienced temporal changes, FD remained stable over time, but with temporary disruptions. A study by Van der Linden et al. (2016) found a positive linear relationship between species diversity and FD. Species with little trait overlap are complementary and support a high level of FD (Teichert et al., 2017). The sensitivity of ecological functioning to the loss of species diversity is determined by the degree of trait overlap (Shojaei et al., 2021). A loss of species diversity in a highly redundant community causes only minor loss in ecosystem functioning, whereas in a non-redundant community, the loss of any taxon may have a significant impact on ecosystem functioning (Naeem, 1998).

The overall goal of this study is to determine if species diversity is connected to FD, and either diversity measure is connected to secondary productivity and how it is affected by changes in salinity. The hypothesis is that environments with higher macrofauna diversity will have more FD and will have higher secondary production. Measurements of benthos production and

community structure have been performed in four estuaries: Laguna Madre Estuary (LM), Nueces Estuary (NC), Guadalupe Estuary (GE), and Lavaca-Colorado Estuary (LC). Each estuary has different amounts of inflow entering resulting in various salinity levels and nutrient concentrations. The FD and secondary production of benthic communities was compared across the four estuaries and within the estuaries along salinity gradients. Traits were classified based on existing literature. The hypothesis will be tested using linear and non-linear regression models. A multivariate analysis will be performed to relate the three metrics (productivity, species diversity, and functional diversity) to one another and to salinity over space and time. A principal component analysis was performed to relate water quality variables and inorganic nutrients to each of the bays.

2. METHODS

2.1 Study Sites

The Lavaca-Colorado Estuary, Guadalupe Estuary, Nueces Estuary, and Laguna Madre Estuary lie in the Coastal Bend region of south Texas (Figure 2). The estuaries are hydrologically diverse due to the climatic gradient along the Texas coast. Rainfall decreases by a factor of two along the gradient resulting in increased salinities from the northeast to the southwest (Montagna et al., 2013). The estuaries share similar geomorphological features (Van Diggelen and Montagna, 2016). The secondary bays are closer to the mouth of a river and connect to the primary bays, which are open to the Gulf of Mexico (Van Diggelen and Montagna, 2016). The salinity gradients within the estuaries vary from year to year due to flood events and droughts. Benthic data was collected from 6 sites in the Lavaca Colorado Estuary, the largest among the four Texas estuaries. The six stations are positioned along the salinity gradient from the Lavaca River to Matagorda Bay. The density of the benthos community in this estuary is lower than all other estuaries (Montagna and Li, 1996). The phytoplankton abundance is less than the Guadalupe Estuary however, it is 4 times higher than in the Nueces and Laguna Madre estuaries (Montagna and Li, 1996). The Lavaca Colorado Estuary and the Guadalupe Estuary have an average inflow rate of about $10^9 \text{ m}^3 \text{ yr}^{-1}$ (Montagna et al., 2013). In the Guadalupe Estuary, 4 stations were set up to collect benthic data. The estuary receives freshwater inflow from the San Antonio and Guadalupe Rivers (Arismendez et al., 2009). The salinity gradient within the estuary is from the west to east direction. Benthos abundance is 3-30 times higher in this estuary than in any of the others and the average density is 4-20 times higher (Montagna and Li, 1996). The Nueces Estuary has 5 stations positioned along the salinity gradient that begin by the Nueces River and end in Corpus Christi Bay. This estuary has an average inflow rate of about $10^8 \text{ m}^3 \text{ yr}^{-1}$

(Montagna et al., 2013). Because the estuary receives inflow from creeks and rivers, it has a higher level of oxygen storage, kinetic storage, and nutrient storage than the Laguna Madre Estuary (Montagna and Li, 1996; 2010). The southernmost estuary to be sampled was the Laguna Madre Estuary. Data was collected from 3 stations within the estuary and two of the sites are located in Baffin Bay. The Laguna Madre is considered a negative estuary because evaporation exceeds inputs and has an average negative inflow rate of approximately $10^8 \text{ m}^3 \text{ yr}^{-1}$ (Montagna et al., 2013). This estuary is also considered to be a reverse estuary where the secondary bay has a higher salinity than the primary bay (Van Diggelen and Montagna, 2016). Laguna Madre has high primary production due to an extensive seagrass habitat and the consumer subsystem is dominated by deposit feeding benthos (Montagna and Li 2010). All of the sampling locations are located in muddy bottoms of the open bays. However, Station 189 in Laguna Madre is in a seagrass habitat. There are two paired stations, 189G and 189S, where G is within seagrass habitat and S is in the unvegetated sand patch. Diversity and richness are greater in the seagrass habitat than in the unvegetated area (Montagna et al., 2010; Van Diggelen and Montagna, 2016). The differences in FD and secondary production within the vegetated and non-vegetated areas can be compared to examine effects of seagrass, but these stations will not be used to identify inflow effects on the diversity-productivity relationship.

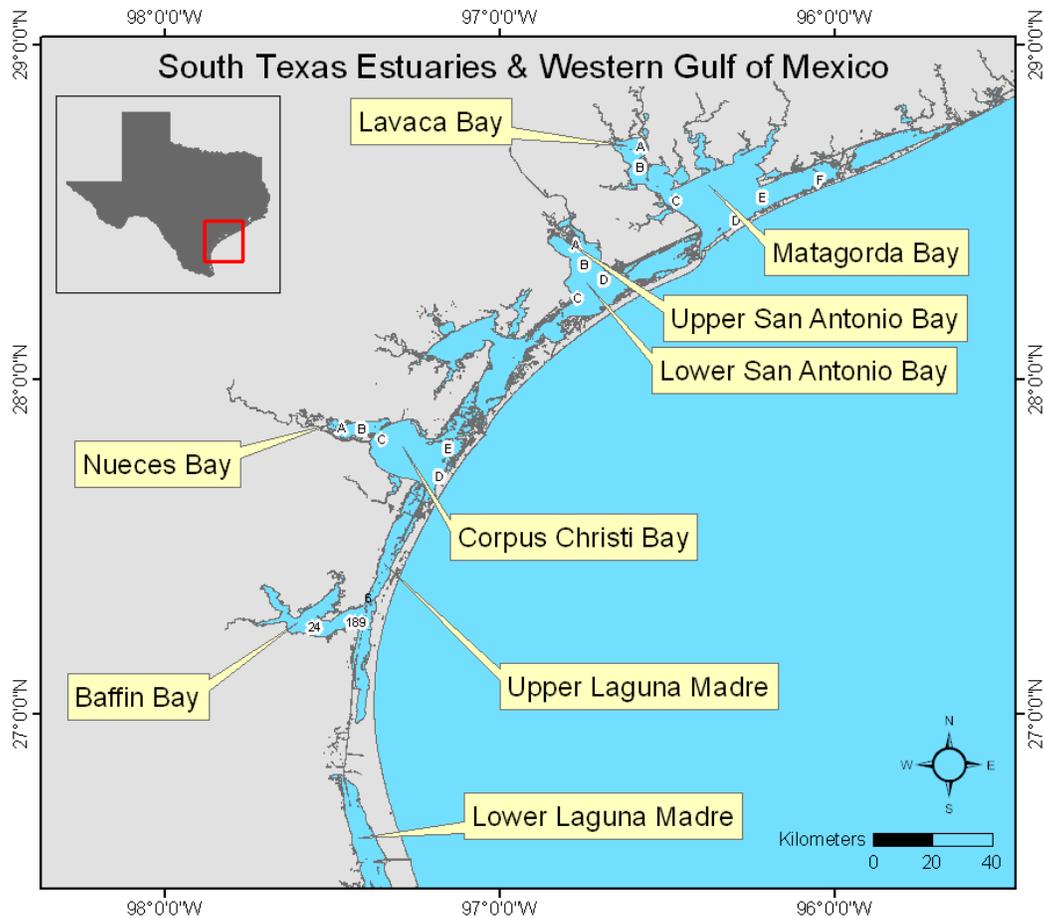


Figure 1. Sampling locations along the Texas Coast where there is infauna secondary production and diversity data.

2.2 Data Sources

2.2.1 Secondary Production

Secondary production has been calculated by Kim and Montagna (2012). The calculations are based on biomass changes over time using a bioenergetic model. Productivity was calculated for the eight bays by averaging the biomass from stations within the bay for each time period. Most of the calculations were based on 22 years of data (Table 1).

Table 1. Sampling stations, locations and periods for the continuous long-term monitoring database in the eight Texas bays. Environmental and biological variables (temperature, salinity, nutrients, predator density and benthos biomass) used in the model were selected from the same database. Abbreviations: LC = Lavaca-Colorado Estuary, GE = Guadalupe Estuary, NE = Nueces Estuary, LM = Laguna Madre Estuary, LB = Lavaca Bay, MB = Matagorda Bay, USB = upper San Antonio Bay, LSB = lower San Antonio Bay, NB = Nueces Bay, CCB = Corpus Christi Bay, BB = Baffin Bay, ULM = upper Laguna Madre.

Estuary	Bay Name	Station	Location	Sampling Period	Analysis Period (years sampled)
Lavaca-Colorado Estuary	Lavaca	A	28° 40' 12" N, 96° 34' 48" W	1984 – 2009	1988 – 2008 (21)
		B	28° 38' 24" N, 96° 34' 48" W	1988 – 2009	1988 – 2008 (21)
	Matagorda	C	28° 32' 24" N, 96° 28' 12" W	1988 – 2009	1988 – 2008 (21)
		D	28° 28' 48" N, 96° 17' 24" W	1988 – 2009	1988 – 2008 (21)
		E	28° 33' 0" N, 96° 12' 36" W	1993 – 1995 2004 – 2007	1993 – 1995 (3) 2004 – 2007 (4)
		F	28° 36' 0" N, 96° 02' 24" W	1993 – 1995 2004 – 2007	1993 – 1995 (3) 2004 – 2007 (4)
Guadalupe Estuary	Upper San Antonio	A	28° 23' 37" N, 96° 46' 20" W	1987 – 2009	1989 – 2000 (12)
		B	28° 20' 52" N, 96° 44' 45" W	1987 – 2009	1989 – 2000 (12)
	Lower San Antonio	C	28° 14' 46" N, 96° 45' 54" W	1987 – 2009	1989 – 2000 (12)
		D	28° 18' 8" N, 96° 41' 4" W	1987 – 2009	1989 – 2000 (12)
Nueces Estuary	Nueces	A	27° 51' 39" N, 97° 28' 25" W	1987 – 2009	1988 – 2002 (15)
		B	27° 51' 26" N, 97° 24' 37" W	1987 – 2009	1988 – 2002 (15)
	Corpus Christi	C	27° 49' 31" N, 97° 21' 8" W	1987 – 2009	1988 – 2002 (15)
		D	27° 42' 46" N, 97° 10' 43" W	1987 – 2009	1988 – 2002 (15)
		E	27° 47' 50" N, 97° 9' 3" W	1987 – 2009	1988 – 2002 (15)
Laguna Madre Estuary	Baffin	6	27° 16' 37" N, 97° 25' 37" W	1988 – 2000	1988 – 2000 (13)
		24	27° 15' 50" N, 97° 33' 5" W	1988 – 2000	1988 – 2000 (13)
	Laguna Madre	189G 189S	27° 20' 60" N, 97° 23' 33" W	1988 – 2000	1988 – 2000 (13)

2.2.2 Diversity

Benthic community structure data already exists (Montagna and Kalke 1992; 1995; Van Diggelen and Montagna 2016). Benthic abundance, biomass, and community structure was measured along salinity gradients within each Texas estuary (Figure 1; Montagna and Kalke 1992; 1995). Samples for the benthos were collected quarterly each year from 1987 to 2013. The sediment cores were taken by hand by divers within a 2 m radius. The cores are 6.715 cm diameter, covering an area of 35.4 cm². The cores are sectioned (at 0-3 cm, and 3-10 cm) to examine the vertical distribution of macrofauna. Animals were then extracted using a 0.5 mm mesh sieve. In the laboratory, animals are enumerated, identified, and dried at 50 °C for 24 hours and weighed. Mollusk shells are removed by an acidic vaporization technique (Hedges and Stern, 1984). A study by Van Diggelen and Montagna (2016), used the community structure data to compare salinity average and variance with benthic community diversity, evenness, and species richness. Numerous studies (Kalke and Montagna 1991; Montagna 2000; Palmer et al., 2011; Kim and Montagna 2012) have proven the efficiency of quarterly sampling for capturing temporal benthic dynamics in estuaries. For the current study, only data from four of the estuaries sampled over the time periods in Table 1 will be used for analysis.

2.3 Trait Classifications

2.3.1 Trait Selection

The functioning and stability of communities and ecosystems are determined by traits and their interactions (Loreau et al., 2001). Therefore, BTA should be integrated with taxonomic analysis to provide a comprehensive description of communities and ecosystems (Paganelli et al., 2012; Villegar et al., 2010; Pandey et al., 2022). For this present study, traits suggested by existing literature (Dolbeth et al., 2015; Silvia-Junior et al., 2016; Henriques et al., 2017; Hewitt

et al., 2008; Ranasinghe et al. 1994; Munari, 2013; Sanchis et al., 2021; Shojaei et al., 2021; Weigal et al., 2016; Pilo et al., 2016; Van der Linden et al., 2017) were selected including: feeding strategy, habitat, mobility, lifespan, depth, reproduction, and size (Table 2). Feeding strategy indicates food source availability, habitat, and trophic structure (Dolbeth et al., 2015; Van der Linden et al., 2017) (Table 3). Due to the strong link between habitat and species diversity, habitat variability is likely to be of importance (Hewitt et al., 2008). Mobility relates to resource dynamics (i.e., nutrients, sediment, space) (Dolbeth et al., 2015). Living depth shows what species are more or less vulnerable to impacts related to hydrodynamics, predation, and temperature. Studies have shown that during a disturbance there is a shift from large slow-growing species with longer life spans to less vulnerable faster growing species (Roads et al. 1978; Pearson and Rosenberg 1978; Diaz et al., 2006; Dolbeth et al., 2015). The same may be true for species of various sizes facing disturbances from freshwater inflow (Van Diggelen and Montagna 2016). Reproduction frequency reflects a species chance of survival in an unstable environment and may indicate disturbance. Size correlates with other life history traits and structuring interactions.

Table 2. Traits selected for this study based off existing literature.

Traits	Sources
Feeding Strategy	Van der Linden et al., 2017; Dolbeth et al, 2015; Shojaei et al., 2021; Munari, 2013; Sanchis et al., 2021; Pilo et al., 2016; Sanchis et al 2021; Hewitt et al., 2008; Pandey et al., 2022
Habitat	Van der Linden et al., 2017; Shojaei et al., 2021; Hewitt et al., 2008; Pandey et al., 2022
Mobility	Paganelli et al., 2012; Dolbeth et al., 2015; Shojaei et al., 2021; Munari, 2013; Pilo et al., 2016; Hewitt et al., 2008; Pandey et al., 2022
Lifespan	Paganelli et al., 2012; Van der Linden et al., 2017; Dolbeth et al., 2015; Munari, 2013; Pilo et al., 2016; Weigal et al., 2016; Pandey et al., 2022
Reproduction	Paganelli et al., 2012; Dolbeth et al., 2015; Munari, 2013
Depth	Hewitt et al., 2008; Dolbeth et al., 2015
Size	Dolbeth et al, 2015; Munari, 2013; Pilo et al., 2016; Weigal et al., 2016; Hewitt et al., 2008; Pandey et al., 2022

2.3.2 Classification Approach

In various animal and plant species, the concept of a guild has shown to be a useful tool for both generalizations and ongoing investigations of ecosystem functioning (Fauchald, 1979). For the present study, each of the organisms are grouped into feeding guilds based on a research paper by Ranasinghe et al. (1994). The functional groups are as follows: Browser (B), Conveyer Belt (C), Interface (I), Predator/Omnivore (P), Subsurface (S), Water Column (W), and Unknown (U) (Table 3). Browsers are classified as organisms that move around or scavenge on the soft sediment to capture food. This guild encompassed surface deposit feeders who mainly feed on detritus. Interface suspension feeders consist of organisms that use their tentacles or modified legs to capture food off the sandy bottom. Water Column feeders are organisms that siphon suspended matter and food particles from the water. Many of these organisms are filter or suspension feeders. Subsurface deposit feeders are comprised of organisms that ingest sediment to satisfy their nutritional requirements. These organisms bury themselves in the substrate. Similarly, Conveyer Belt deposit feeders were classified as organisms that absorb sediments at various depths and deposit stomach contents from protruding tails above the sediment surface.

(Robbins, 1986). Predators and Omnivores are grouped into one guild which encompassed organisms that feed on other living things. Organisms with limited information are labeled as Unknown. Another functional characterization used was habitat which was separated into Tube (HT), Burrow (HB), Free Living (HF), or Attached (HA). This trait was highly dependent on the food source availability for each of the organisms. Lifespan was categorized by Short (LS), less than 1 year, Medium (LM), between 1 and 3 years, and Long (LL), greater than 3 years. Mobility was characterized by fixed (MF) in space, minimal movement (MM), and free living (MFR). All organisms were classified as either semelparous or iteroparous depending on their reproductive strategy. Classifications for Depth and Size were suggested by previous studies.

An aggregation table was assembled using trait classifications and the Linnaean system. Finding literature material on a variety of traits of numerous species is difficult and time consuming. In the case of extensive taxonomic lists, gaps in knowledge of species biology make impossible to complete the coding of some traits for all taxa (Munari, 2013). Therefore, when an attribute for a specific species was not found, the next higher level in the taxonomic classification was used.

Table 3. Traits, trait modalities, and labels used for functional characterization of benthic species, with indication of the importance for the selection.

Traits	Modalities	Labels	Importance
Feeding Strategy	Browser	B	Reflects trophic structure, indicates food source availability, may indicate disturbance
	Conveyer Belt	C	
	Interface	I	
	Predator/Omnivore	P	
	Subsurface	S	
	Unknown	U	
	Water Column	W	
Habitat	Tube	HT	Food source availability and indication of disturbance
	Burrow	HB	
	Free Living	HF	
	Attached	HA	
Lifespan	Short (<1 year)	LS	Differences have been documented in large slow-growing species with long life spans versus less vulnerable fast-growing species
	Medium (1-3 years)	LM	
	Long (>3 years)	LL	
Mobility	Fixed	MF	Relates to resource dynamics
	Minimal	MM	
	Free	MFR	
Reproduction	Semelparous	RS	Reflects the investment in reproduction
	Iteroparous	RI	
Depth	Epifauna	D0	Determines vulnerability to stress, susceptibility to predation
	0-2 cm	D2	
	2-5 cm	D5	
	>5 cm	DG5	
Size	1-5 mm	SS	Correlates with other life history traits and structuring interactions
	6-30 mm	SM	
	>30 mm	SL	

2.4 Species Diversity Formulas

Diversity is calculated using Hill's diversity number one (N1) (Hill, 1973). It is a measure of the effective number of species in a sample and indicates the number of abundant species. It is calculated as the exponentiated form of the Shannon diversity index:

$$N1 = e^{H'} \quad (1)$$

As diversity decreases N1 will tend toward 1. The Shannon index (H') is the average uncertainty per species in an infinite community made up of species with known proportional abundances (Shannon and Weaver, 1949). The Shannon index is calculated by:

$$H' = -\sum [(n_i/n) \ln(n_i/n)] \quad (2)$$

Where n_i is the number of individuals belonging to the i th of S species in the sample and n is the total number of individuals in the sample.

Richness (R) is an index of the number of species present. The obvious richness index is simply the total number of all species found in a sample regardless of their abundances. Hill (1973) named this index N_0 . Another well-known index of species richness is the Margalef (1958) index (R1). R1 is based on the relationship between the number of species (S) and the total number of individuals (n) observed:

$$R1 = (S - 1) / \ln(n) \quad (3)$$

Although common, this relationship presupposes that there is a functional relationship between S and n . This assumption may not be justified in all cases.

Evenness (E) is an index that expresses that all species in a sample are equally abundant. Evenness is a component of diversity. Two evenness indices, E1 and E5, have been calculated. E1 is probably the most common, it is the familiar J' of Pielou (1975). It expresses H' relative to the maximum value of H' :

$$E1 = \ln(N1) / \ln(R0) \quad (4)$$

E1 is sensitive to species richness. E5 is an index that is not sensitive to species richness. E5 is a modified Hill's ratio (Alatalo, 1981):

$$E5 = (1/\lambda)^{-1} / (N1-1) \quad (5)$$

$$\lambda = \sum [n_i(n_i-1) / n(n-1)] \quad (6)$$

λ is the Simpson (1949) diversity index. E5 approaches zero as a single species becomes more and more dominant.

2.5 Statistical Techniques

The mFD (multifaceted functional diversity) package in R Programming Software was used to compute FD indices in a principal components analysis (PCA)-based multidimensional space. A species by trait data frame and a species by bay data frame were used as the foundation to compute most FD indices (Magneville et al., 2021). The assigned nominal traits are guild, habitat, mobility, reproduction, and lifespan. The ordinal traits are depth and size range. The functional traits-based distances between species were calculated (Magneville et al., 2021). This required the application of Gower distance as this method combines the use of various types of traits. Because the functional distance between some species is equal to zero, the species with similar trait values were used to create functional entities. The entities were named after their decreasing rank in terms of number of species (e.g., fe_1 has the most species). To build a functional space, a PCA was performed using the trait-based distances (Mouillot et al., 2013). After assessing the quality of the multidimensional spaces, PC1-PC6 were chosen as they had the lowest deviations between trait-based distances and distances in the functional space (Maire et al., 2015). The procedure outlined by Magneville et al. (2021) was used to compute the FD indices and plot them. FD Hill indices were computed as suggested by Chao et al. (2019). The

mFD package was used to calculate functional beta diversity indices using the Jaccard index following Villeger et al. (2013) and Baselga et al. (2021).

The indices calculated to test our hypothesis were functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), functional identity (FId), functional originality (FOri), functional specialization (FSpe), functional mean pairwise distance (FMPD), functional mean nearest neighbor distance (FNND), and functional beta diversity (FBD). FRic represents the amount of niche space inhabited by the species in a community (Mason et al., 2005). It is independent of species abundances, and it has no upper limit (Villeger et al., 2008). FEve is the regularity of the species abundance in the functional trait space and FDiv measures the degree to which abundance distribution in the niche space maximizes divergence in functional characters within the community (Mason et al., 2005). Both FEve and FDiv are scaled between 0 and 1. FDis measures the abundance-weighted mean distance to the abundance-weighted mean trait values of the assemblage and has no upper limit (Laliberté & Legendre 2010; Mouillot et al., 2013). FId is the weighted average position of species of the assemblage along each axis (Garnier et al., 2004; Mouillot et al., 2013). FOri is the weighted mean distance to the nearest species from the global species pool (Mouillot et al., 2013). FSpe is the weighted mean distance to the center of the functional space (Bellwood et al., 2005; Mouillot et al., 2013). FMPD is the mean weighted distance between all species pairs (Mouillot et al., 2013). FNND is the weighted distance to the nearest neighbor within the assemblage (Weiher et al., 1998). FBD computes the overlap between convex hulls for a pair of assemblages (Villeger et al., 2013; Magneville et al., 2021).

The Spearman Correlation and a simple linear regression was used to measure the relationship between productivity and diversity for each of the bays. A PCA was performed to

analyze the relationship between inorganic nutrients, water quality variables, and each of the bay systems.

3. RESULTS

3.1 Functional Diversity Indices

Functional beta diversity calculations only consider the presence and absence of traits. A dissimilarity matrix was generated to visualize the pairwise relations between the bays (Table 4). The turnover component is the highest if no shared traits combination exists between the two assemblages (Table 6). The nestedness component is the highest when one assemblage hosts a small subset of the functional strategies found in the other (Table 5) (Magneville, 2021). The bays with the highest functional similarities are BB and CC, CC and US, MB and BB, and BB and NB. The bays with the lowest functional similarities are BB and US, LM and LS, LB and LM, and LB and BB.

3.2 Production and Functional Diversity Models

Species richness increased with increasing benthic production and has a statistically significant linear relationship that explains ~ 58% of variability (Richness: $P \leq 0.0276$, $R^2 = 0.583$) (Table 7). The bays with low productivity and richness are BB, LB, and LS and the bays with high productivity and richness are LM, CC, and MB. NB appears to be neutral (Figure 2). The US bay is shown to have low richness and high productivity. H' and $N1$ also have a significant linear relationship with production and yielded similar results to richness. H' explained > 62% of variation indicating a substantial relationship with productivity (H' : $P \leq 0.0200$, $R^2 = 0.622$; $N1$: $P \leq 0.0340$, $R^2 = 0.555$). Evenness increased with productivity as well however, the trend was not linear ($P \leq 0.0949$, $R^2 = 0.396$). The relationship between FDis and production is linear and statistically significant with > 77% of variation explained ($P \leq 0.0040$, $R^2 = 0.774$). FDis increased with increasing production. LB, LS, and BB are shown to have low FDis while US, CC, MB, and LM have high FDis. All FDis values were lower than 0.6. FMPD

increased with decreasing production though, it was not a significant predictor ($P \leq 0.2910$, $R^2 = 0.183$). FNND and FEve increased with decreasing production as well. FNND has a significant relationship with productivity ($P \leq 0.1319$, $R^2 = 0.336$) and all values were all lower than 0.6. FEve has a statistically significant relationship with production as well with $> 55\%$ of the variance explained ($P \leq 0.0338$, $R^2 = 0.556$). All FEve values were lower than 0.6. LB, LS, and BB all have low productivity and high FEve while CC, LM, and MB have high productivity and low FEve. These functional diversity results are consistent with the macrofauna diversity. FRic increased with increasing production however, the relationship was not linear nor was it significant ($P \leq 0.332$, $R^2 = 0.157$). An increase in FDiv was related with decreasing production however, it was not significant ($P \leq 0.2665$, $R^2 = 0.200$). FOr has no significant relation to productivity and only explained $\sim 6\%$ of variation ($P \leq 0.5543$, $R^2 = 0.061$). FSpe had no significant relationship to production as well ($P \leq 0.3851$, $R^2 = 0.243$). FIde for PC2 and PC4 showed the strongest relationship with productivity out of the four different PCs. FIde increased as production decreased. FIde for PC4 has a more statistically significant relationship with production with over 67% of variance explained ($P \leq 0.0124$, $R^2 = 0.675$) while FIde for PC2 only explains 26% of variance ($P \leq 0.1967$, $R^2 = 0.260$). The bays that exhibited the lowest diversity were BB, LB, and LS while the highest were LM, CC, and MB.

Table 4. A dissimilarity index decomposed by turnover and nestedness-resultant.

Beta Dissimilarity matrix								
	BB	CC	LB	LM	LS	MB	NB	US
BB	0	0.45	0.30	0.28	0.39	0.39	0.36	0.28
CC	0.45	0	0.32	0.27	0.17	0.15	0.19	0.43
LB	0.30	0.32	0	0.27	0.23	0.23	0.23	0.23
LM	0.28	0.27	0.27	0	0.25	0.22	0.16	0.33
LS	0.39	0.17	0.23	0.25	0	0.16	0.17	0.34
MB	0.39	0.15	0.23	0.22	0.16	0	0.13	0.36
NB	0.36	0.19	0.23	0.16	0.17	0.13	0	0.33
US	0.28	0.43	0.23	0.33	0.34	0.36	0.33	0

Table 5. The nestedness component is the highest if one assemblage hosts a small subset of the functional strategies present in the other.

Beta Nestedness matrix								
	BB	CC	LB	LM	LS	MB	NB	US
BB	0	0.43	0.14	0.28	0.29	0.34	0.33	0.02
CC	0.43	0	0.32	0.20	0.17	0.11	0.14	0.41
LB	0.14	0.32	0	0.10	0.17	0.22	0.18	0.13
LM	0.28	0.20	0.10	0	0.05	0.10	0.07	0.22
LS	0.29	0.17	0.17	0.05	0	0.05	0.01	0.28
MB	0.34	0.11	0.22	0.10	0.05	0	0.03	0.33
NB	0.33	0.14	0.18	0.07	0.01	0.03	0	0.31
US	0.02	0.41	0.13	0.22	0.28	0.33	0.31	0

Table 6. The turnover component is the highest if there is no shared traits combination between the two assemblages.

Beta Turnover matrix								
	BB	CC	LB	LM	LS	MB	NB	US
BB	0	0.01	0.16	0.00	0.10	0.05	0.03	0.26
CC	0.01	0	2E-15	0.07	0.00	0.04	0.05	0.01
LB	0.16	2E-15	0	0.18	0.06	0.01	0.05	0.10
LM	0.00	0.07	0.18	0	0.20	0.13	0.09	0.11
LS	0.10	0.00	0.06	0.20	0	0.11	0.16	0.06
MB	0.05	0.04	0.01	0.13	0.11	0	0.09	0.03
NB	0.03	0.05	0.05	0.09	0.16	0.09	0	0.02
US	0.26	0.01	0.10	0.11	0.06	0.03	0.02	0

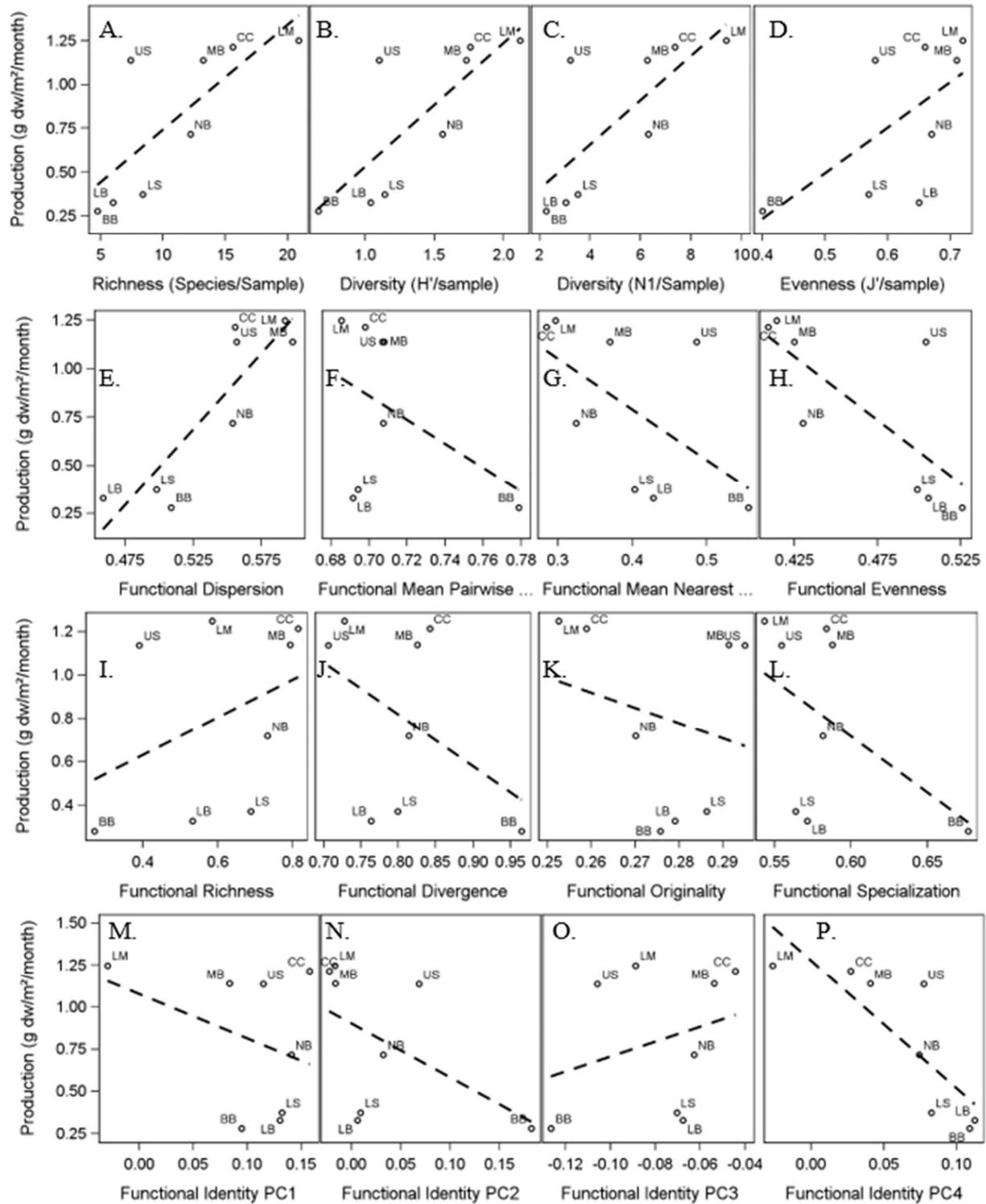


Figure 2. Production versus diversity metrics in bays (symbols), and linear regression (dotted lines).

Table 7. Spearman correlation and linear regression results of production and diversity. Highlighted values are < 0.05.

Diversity Metrics	Spearman Correlation		Linear Regression			
	r	P	Intercept	Slope	P Slope=0	R ²
Richness (Species/Sample)	0.93	0.0009	0.1429	0.0599	0.0276	0.5825
Diversity (N1/Sample)	0.88	0.0039	0.1515	0.1262	0.0340	0.5547
Diversity (H'/sample)	0.93	0.0009	-0.1719	0.7030	0.0200	0.6220
Evenness (J'/sample)	0.79	0.0208	-0.8026	2.5920	0.0949	0.3955
Richness (Species/Bay)	0.57	0.1390	0.1952	0.0058	0.2348	0.2252
Functional Dispersion	0.81	0.0149	-3.4371	7.8521	0.0040	0.7739
Functional Mean Pairwise Distance	-0.38	0.3518	5.2141	-6.2209	0.2910	0.1825
Functional Mean Nearest Neighbor Distance	-0.79	0.0208	1.8385	-2.6261	0.1319	0.3362
Functional Evenness	-0.9	0.0020	3.8559	-6.5746	0.0338	0.5555
Functional Richness	0.57	0.1390	0.2816	0.8704	0.3316	0.1568
Functional Divergence	-0.24	0.5702	2.7296	-2.3902	0.2665	0.2001
Functional Originality	-0.33	0.4198	2.7546	-7.0620	0.5543	0.0613
Functional Specialization	-0.36	0.3851	3.8238	-5.1792	0.2149	0.2427
Functional Identity PC1	-0.17	0.6932	1.0762	-2.6344	0.3785	0.1309
Functional Identity PC2	-0.74	0.0366	0.9021	-3.2021	0.1967	0.2600
Functional Identity PC3	0.40	0.3199	1.1468	4.4180	0.4922	0.0818
Functional Identity PC4	-0.95	0.0003	1.2776	-7.6031	0.0124	0.6748
Functional Identity PC5	-0.24	0.5702	0.7988	1.3213	0.6201	0.0435
Functional Identity PC6	0.00	1.0000	0.8313	-0.3803	0.9217	0.0017

Production and diversity data were fitted to a logistic growth model to explain variance (Figure 3). Richness met the convergence criterion and appeared to have a significant relationship with production ($P > 0.0033$). The diversity samples H' ($P > 0.0030$) and $N1$ ($P > 0.0044$) also met the convergence criterion. The sigmoid shape was most apparent in functional dispersion ($P > 0.0005$), the only functional diversity metric to fit the model.

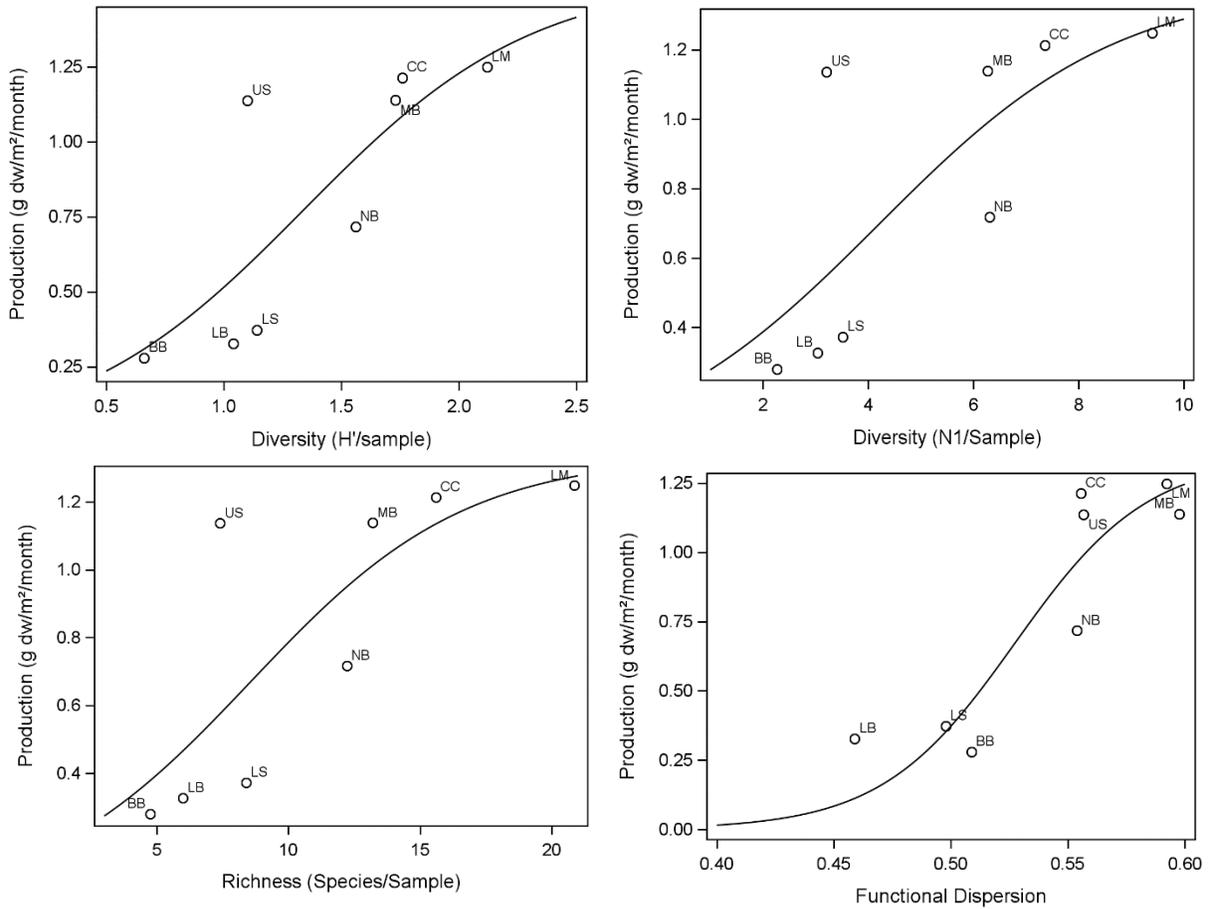


Figure 3. Production versus diversity logistic growth models.

3.3 Inflow Effects on Diversity

Bays with low salinity and high nutrients are represented by positive PC1 values, whereas bays with high salinity and low nutrients are represented by negative PC1 values (Figure 4). PC1 is thus an inflow indicator. Positive PC2 readings indicate bays with high ammonium and

chlorophyll levels. The bays with the highest PC1 scores are US, LB, and LS. NB is neutral and MB, CC, LM, and BB are negative. There is a division between the primary and secondary bays with the exception of LS which is the lower part of San Antonio Bay. The only bay located on PC2 is BB. It appears that BB has high salinity, low nutrients, and high ammonium and chlorophyll levels.

The spearman correlation results do not indicate significant relationships between PC1 and the diversity metrics. The only metric with any significance is functional originality ($P \leq 0.0208$, $r = 0.79$) (Table 8). The spearman correlation results between PC2 and the diversity metrics appear to show a significant relationship between species richness (species/bay) ($P \leq 0.003$, $r = -0.95$), functional richness ($P \leq 0.003$, $r = -0.95$), and FIde PC3; however, these are negative correlations.

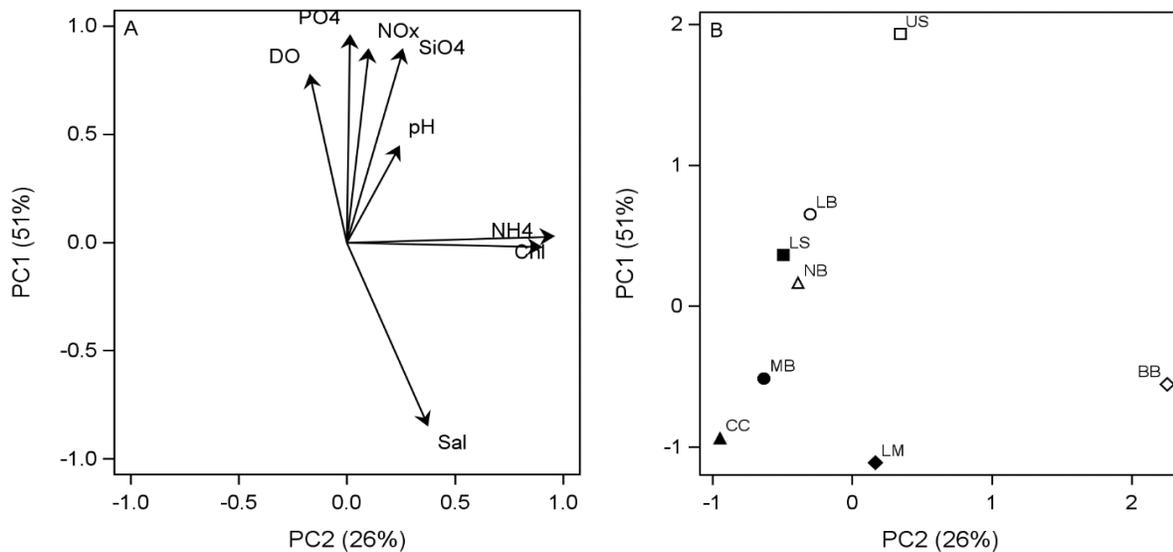


Figure 4. Principal components (PC) analysis of water quality variables averaged by bay. A) Variable loads. Abbreviations: Chl = chlorophyll-a, DO = dissolved oxygen, NH4 = ammonium, NOx = nitrite+nitrate, PO4 = phosphate, Sal = salinity, and SiO4 = silicate. B) Bay sample scores with symbols representing estuaries, open symbols are primary bays, and filled symbols are secondary bays.

Table 8. Spearman correlation (r) and significance (P) between water quality PCA and diversity metrics. Highlighted values are < 0.05.

Diversity Metrics	PC1		PC2	
	r	P	r	P
Abundance(n/m ²)	-0.50	0.2070	0.29	0.4927
Biomass(g/m ²)	-0.33	0.4198	-0.02	0.9554
Production (g dw/m ² /month)	-0.50	0.2070	-0.40	0.3199
Richness (Species/Sample)	-0.62	0.1017	-0.57	0.1390
Diversity (N1/Sample)	-0.60	0.1195	-0.52	0.1827
Diversity (H'/sample)	-0.62	0.1017	-0.57	0.1390
Evenness (J'/sample)	-0.45	0.2604	-0.38	0.3518
Richness (Species/Bay)	-0.33	0.4198	-0.95	0.0003
Functional Dispersion	-0.40	0.3199	-0.14	0.7358
Functional Mean Pairwise Distance	0.21	0.6103	0.33	0.4198
Functional Mean Nearest Neighbor Distance	0.60	0.1195	0.69	0.0580
Functional Evenness	0.60	0.1195	0.69	0.0580
Functional Richness	-0.33	0.4198	-0.95	0.0003
Functional Divergence	-0.48	0.2329	-0.31	0.4556
Functional Originality	0.79	0.0208	0.07	0.8665
Functional Specialization	-0.24	0.5702	-0.21	0.6103
Functional Identity PC1	0.24	0.5702	-0.50	0.2070
Functional Identity PC2	0.52	0.1827	0.69	0.0580
Functional Identity PC3	-0.17	0.6932	-0.93	0.0009
Functional Identity PC4	0.67	0.0710	0.40	0.3199
Functional Identity PC5	0.50	0.2070	-0.55	0.1600
Functional Identity PC6	0.24	0.5702	-0.69	0.0580

4. DISCUSSION

4.1 Functional Diversity Trends

Matagorda Bay and Laguna Madre have the highest functional dispersion values. Larger functional dispersion values indicate a more functionally diverse community in the multivariate trait space. Ecosystems with high functional dispersion are thought to display broader ecosystem functioning (Clark et al., 2012; Weigel et al., 2016). Because Laguna Madre has a seagrass habitat, it hosts a different species assemblage than bays with muddy bottoms (Montagna and Kalke, 1995; Montagna et al., 2010), which can explain its high functional dispersion value. The inflow of freshwater into Matagorda Bay combined with its connection to the sea may also influence functional dispersion in the bay system. Lavaca Bay has the lowest functional dispersion value. This may be because there is less variety of functions and biomass in Lavaca Bay resulting in low dispersion (Dolbeth et al., 2015). Previous research has indicated that benthic macrofauna biomass, abundance, and diversity was significantly positively correlated with salinity in the Lavaca-Colorado Estuary (Pollack et al., 2011). Therefore, functional dispersion may be influenced by Lavaca Bay's low salinity environment. Pawluk et al. (2022) investigated functional diversity indices across eight major bays along the Texas Coast and found a clear trend of higher functional dispersion in the north compared to the south, indicating that bays in the south were more strongly dominated by fewer trait types. Pawluk's study also noted that functional dispersion was relatively low for all of the bays. Functional evenness represents the degree to which a community's biomass is distributed to allow effective utilization of all the resources available to it (Mason et al. 2005). The bays with the lowest functional evenness were Corpus Christi, Laguna Madre, and Matagorda Bays. This indicates that these bays contain areas that are underutilized. Also, the functional traits within these bays are at risk

of being diluted from the environment if they are not evenly distributed since existing traits will face intense competition (Goswami et al., 2017). Baffin Bay and Lavaca Bay appear to have the highest functional evenness implying that the functional traits are spread evenly throughout the ecosystem. So, if some individuals in these ecosystems with a certain characteristic are lost due to disturbances, the existing member with a comparable trait may substitute the lost trait (Goswami et al., 2017). However, a recent study by Ricotta et al. (2022) revealed that the regularity of species abundances in a functional space is usually inadequately captured by measurements of functional evenness. It is suggested that functional imbalance, an indicator of the strength of interaction between species abundances and their functional dissimilarities, would be a more appropriate indicator of community structure because functional diversity always increases with functional imbalance (Ricotta et al., 2022). Corpus Christi and Matagorda Bays have the highest functional richness values and Baffin Bay has the lowest. Higher functional richness indicates more diverse trait types within the bays (Villéger et al., 2008). Pawluk et al. (2002) found significant differences in functional richness among the bays, but no apparent spatial pattern was evident. Functional richness and functional evenness are orthogonal to each other (Mason et al., 2005). Baffin Bay appears to have the highest functional divergence value indicating that there is a high degree of niche differentiation and low resource competition (Mason et al., 2005). Upper San Antonio has the lowest functional divergence between all the bays which may indicate high resource competition. Upper San Antonio and Matagorda Bay have the highest functional originality indicating functionally unique species. Laguna Madre has the lowest functional originality value which implies high functional redundancy. If high functional redundancy exists within Laguna Madre, the loss of functionally redundant species is anticipated to improve functional originality (as surviving species become more unique) (Brandl

et al., 2016). This may occur during periods of increased freshwater inflow or other disturbances. Overall, functional redundancy has been shown to increase ecosystem stability and resilience (Biggs et al., 2020; Pawluk et al., 2022). Functional specialization is highest in Baffin Bay and lowest in Laguna Madre. Since specialist species (i.e., having extreme trait combinations, narrow niches) are relatively less abundant than generalist species (i.e., broad niches), functional specialization may decrease after a disturbance (Mouillot et al., 2013). Baffin Bay receives significantly less inflow than the other bays and thus less disturbance, which may explain the abundant specialist species.

4.2 Benthic Production versus Functional Diversity

Corpus Christi Bay, Laguna Madre, and Matagorda Bay have high productivity and are consistently grouped together. Baffin Bay, Lavaca Bay, and Lower San Antonio have low productivity. There is a division between the primary and secondary bays with the exception of Upper and Lower San Antonio Bay. The spearman correlation results between benthic production and diversity reveals that the species diversity metrics, richness, the diversity samples H' and $N1$, and evenness, all appear to have a significant relationship with production (Table 7). These results are consistent with Cardinale et al. (2013) who found that biodiversity enhances the production and stability of community biomass. When taking the linear regression results into consideration, evenness is not deemed to be significant, indicating that the relationship between evenness and production may be weak. Results from the logistic growth model for productivity and diversity are parallel to the linear regression results. When referring to the logistic growth model, it is apparent that the sigmoid curve would be more prominent if not for Upper San Antonio Bay. Benthic production does not appear to have a significant relationship to the functional diversity indices. Community functional dispersion is the only functional diversity

metric that is significant and positively increased with productivity, indicating that more variety of functionally different species are beneficial to production. However, Dolbeth et al. (2015) investigated the relationship between secondary production and functional diversity in a disturbed estuary and found that the relationship between functional dispersion and secondary production appeared to be weak and negative. Although, the Dolbeth study took place primarily in seagrass habitat. Functional evenness appears to have a significant negative relationship with productivity. Lower functional evenness indicates that some niche spaces are underutilized thus reducing productivity (Mason et al., 2005). Conversely, Dolbeth et al. (2015) found a positive relation between functional evenness and production. Goswami et al. (2017) indicates that reduced functional richness and evenness reduces ecosystem productivity and stability, resulting in a reduction in functional diversity within the same ecosystem. However, for the present study, the opposite appears to be true in the diversity and linear regression models. Bays with low functional evenness had the highest productivity values. Low functional richness reduces ecosystem production since it indicates that some of the potentially available resources are being underutilized. This is likely because the variation of species inhabiting a given niche is lower, and so the ecosystem is unable to utilize all of the available resources (Goswami et al., 2017).

According to Griffin et al. (2009), functional diversity alone cannot predict the total magnitude of ecosystem process; however, it may be used as a supplementary tool to explain the effects in ecosystem functioning once the effect of species identity has been taken into consideration. Most studies involving the relationship between functional diversity and productivity are based on terrestrial systems (Garnier et al., 2004; Griffin et al., 2005; Hooper et al., 2005; Clark et al., 2012; Roscher et al., 2012; Bongers et al., 2021). Hooper et al. (2005) found that species' functional characteristics and the distribution and abundance of those species

strongly influence ecosystem properties. A study by Roscher et al. (2012) found that the identification of relevant traits and functional diversity are essential for understanding drivers of different ecosystem processes such as biomass production. In contrast, Staples et al. (2019) investigated the relationship between productivity and functional diversity in reforestation plantings and found no correlation. However, it was noted that diversity may play a more critical role in ecosystem resilience than in production. According to van der Plas (2019), biodiversity and ecosystem functioning studies have primarily focused on terrestrial plants (74% of studies).

The functional diversity versus production results for the present study were not consistent with other marine studies. Functional diversity and productivity in fish assemblages has been widely studied (Gifford et al., 2009; Leduc et al., 2015; Henriques et al., 2017; Silvia-Junior et al., 2017; Teichert et al., 2017). Leduc et al. (2015) studied a fish assemblage in a tropical stream and found that functional diversity rather than species diversity had the greatest impact on macroconsumer production. Henriques et al. (2017) and Silvia-Junior et al. (2017) studied the trait-environment relationships in fish assemblages as well and concluded that the functional role of species drives assemblage composition. In coral reef communities, it was found that functional diversity and fish species richness were among the strongest predictors of fish biomass (Duffy et al., 2016). However, 64.5% of all coral reef studies are focused on fishes while only 12.8% focused on sessile invertebrates and 7.3% on mobile invertebrates (Brandl et al., 2019). Overall, more research on the relationship between diversity and productivity is needed specifically in marine benthic communities.

While the results of this present study indicate a strong positive relationship between species diversity and secondary production, it is not yet clear whether diversity drives production or vice versa. The historical view is that productivity drives diversity (Abrams, 1995; Warwick,

1995; Waide et al., 1999). According to this viewpoint, the productivity of ecosystems is thought to be what limits the variation in the number of species within communities (Cardinale et al., 2009). However, more recent biological reviews have assessed the relationship between biodiversity and ecosystem functioning in both terrestrial and aquatic ecosystems (Hooper et al., 2005; Humbert and Dorigo 2005; Gamfeldt et al., 2014; Song et al 2014; van der Plas, 2019); and the majority of studies have demonstrated that species diversity drives or controls biomass production instead of just responding to it. The question of whether diversity is the cause or the consequence of biological productivity has been debated due to the divergence between the historical notion that diversity drives productivity and the more recent perspective that diversity drives production (Cardinale et al., 2009).

4.3 Functional Beta Diversity

The dissimilarities in the composition of benthic communities at various locations are primarily a result of niches or environmental aspects and factors related to geographic distances (Medeiros et al., 2016). Lavaca Bay and Laguna Madre are on opposite ends of the climate and salinity gradient along the Texas Coast, which explains the lack of functionally similar traits. The same is true for Lower San Antonio and Lavaca Bay. While Baffin Bay, Lavaca Bay, and Upper San Antonio are secondary bays, there are low functional similarities between them. This can also be explained by the salinity gradient. In comparison to Lavaca Bay and Upper San Antonio, Baffin Bay receives less inflow. Baffin Bay appears to have some of the highest functional similarities with two primary bays, Corpus Christi Bay and Matagorda Bay. It also has similarities with Nueces Bay. While Baffin Bay is a secondary bay, it appears that is more functionally similar to bays with high salinities (primary bays). This could be explained by the fact that Laguna Madre is a negative estuary, with an average negative inflow rate of

approximately $10^8 \text{ m}^3 \text{ yr}^{-1}$ (Montagna et al., 2013). Interestingly, Upper San Antonio and Corpus Christi Bay appear to have high functional similarities. This is somewhat unusual considering that rainfall decreases by a factor of two along the Texas Coast and one is a primary bay while the other is a secondary bay. The results are consistent with Medeiros et al. (2016) who found that the spatial organization of the benthic macroinvertebrate communities in two tropical estuaries was strongly influenced by differences in salinity. Overall, environmental conditions such as salinity and geographical distances seemed to influence the factors that generate dissimilarity in the composition of communities.

4.4 Inflow Relation to Diversity and Productivity

When considering water quality parameters, salinity is inversely related to dissolved oxygen (DO), pH, nutrient concentrations of dissolved inorganic nitrogen (NO_x : sum of nitrate and nitrite), dissolved orthophosphate (PO_4), and silicate (SiO_4), and salinity is inversely related to inflow (Kim and Montagna, 2009; Pollack et al., 2009). Freshwater inflow variations drive the inverse relationship between nutrients and salinity. Thus, PC1 is an inflow indicator and lines up the bays to the freshwater inflow index. The Lavaca-Colorado Estuary and the Guadalupe Estuary receive more freshwater inflow than the Nueces and Laguna Madre Estuaries. The Colorado and Tres Palacios Rivers provide the majority of freshwater inflow to Matagorda Bay, whereas the freshwater inflow to Lavaca Bay is primarily from the Lavaca River (Montagna et al., 2007). The Guadalupe Estuary receives inflow from the San Antonio River and Guadalupe Rivers. Because the Lavaca-Colorado Estuary and the Guadalupe Estuary have an average inflow rate of about $10^9 \text{ m}^3 \text{ yr}^{-1}$, Lavaca Bay and Upper San Antonio have the highest PC1 scores. While Lower San Antonio is considered a primary bay (connected to the Gulf of Mexico), its high PC1 score may be explained by its position on the northern end of the Texas

Coast where rainfall is more prevalent. Nueces Bay receives freshwater inflow from the Nueces River and Rincon Bayou. In 1958 and 1982, the Nueces River was dammed reducing average annual inflow by 99% (Palmer et al., 2002). Due to this circumstance, Nueces Bay has higher salinity than the other secondary bays resulting in a neutral PC1 score. Baffin Bay is unique because it is the only bay system explained by PC2. The bay's positive PC2 score indicates high levels of ammonium and chlorophyll. Ammonium (NH₄) is the only nutrient on the freshwater inflow index that is a reduced form. High ammonium concentrations have been observed at tributary sites in Baffin Bay (Montagna and Palmer 2012; Wetz, 2018). Chlorophyll levels have also been observed to be considerably high in Baffin Bay exceeding TCEQ screening levels. There was a seasonal pattern of high chlorophyll in the spring and summer and low chlorophyll in the winter (Montagna and Palmer 2012; Wetz, 2018). Very high and increasing levels of chlorophyll have been found in Petronilla Creek indicating that chlorophyll may be flushed downstream into Baffin Bay (Wetz, 2018). Corpus Christi Bay, Matagorda Bay, and Laguna Madre are all primary bays with higher salinity and lower nutrient concentrations, which can explain their negative PC1 scores.

Previous research has shown a significant relationship between diversity, productivity, and freshwater inflow. Montagna and Kalke (1992) investigated the relationship between benthic infauna and freshwater inflow in the Guadalupe and Nueces Estuaries. It was found that macrofauna diversity decreased with lower salinities both within the bays and between the estuaries. Macrofauna productivity appeared to enhance in zones of high freshwater inflow while meiofauna was inhibited. Palmer et al. (2002) researched the effects of freshwater inflow in the Nueces Estuary and found that macrofauna blooms are related to inflow events. An overflow channel was dug in 1995 after the Nueces River was dammed. It was discovered that freshwater

inflow pulses increased benthic productivity because salinity patterns were restored by the overflow channel. Similarly, Drake et al. (2002) found that salinity had a considerable effect on nekton and macroinvertebrate abundance, biomass, and species richness. Pollack et al. (2009) investigated the Lavaca-Colorado Estuary to see if there was a relationship between benthic macrofauna community structure and hydraulic parameters. It was found that inflow regimes significantly correlated with macrobenthic diversity and evenness. Comparably, Pollack et al. (2011) found that salinity was significantly correlated with total biomass, abundance, and diversity in the Lavaca-Colorado Estuary. Generally, the abundance, biomass, and diversity of benthic macrofauna were all higher in marine influenced stations. Inflow variability has been continuously proven to effect diversity and productivity (Kim and Montagna, 2009; Kim and Montagna, 2012; Van Diggelen and Montagna, 2016).

According to the spearman correlation and significance between water quality PCA and the diversity metrics (Table 8), there is no relationship between the species diversity and functional diversity metrics and PC1 (the inflow indicator). These results are consistent with Van Diggelen and Montagna (2016) which found that diversity is driven by salinity variance rather than salinity average.

4.5 Why Didn't Functional Diversity Relate to Production in Texas Estuaries?

The results from the current study indicate that functional diversity does not explain or drive secondary production (Figure 2). The overall consensus in the science community is that functional diversity has a strong and positive relationship with productivity. From these assumptions, suggestions for conservation and restorations management efforts have been made in various studies regarding terrestrial organisms and fish assemblages. Functional diversity works in these systems because actual measurements of functional differences are being made on

fish or plants. In contrast, the present study used categorical data that was transferred to numerical values in order to conduct the PCA, which was then used to create the functional diversity index. There are weaknesses in this calculation method. First, it is difficult to know the exact functions of every species. In the case of extensive taxonomic lists, gaps in knowledge of species biology make it impossible to complete the coding of some traits for all taxa (Munari, 2013). Therefore, for this present study, when an attribute for a specific species was not found, the same or the next higher level in the taxonomic classification was used. Second, these are categorical classifications that are artificially assigned numeric values. A PCA is then used to classify these and come up with a PCA score. The issue with this method is that PCA scores range from -1 to +1. However, there are no inverse relationships among the traits. This is also a small range, and all the variable loads will end up on the positive side because we are not setting up inverse correlations. PCA does not work well when there are no inverse relationships among the factors. Overall, these functional diversity calculations of community structure data are not easy to interpret.

There is a long history of using higher taxonomic levels, such as the family level rather than the species level, in community structure and environmental assessment studies. Using the family level was first proposed at the IOC/GEEP workshop (Bayne et al. 1988). It was discovered that aggregating species abundance data at the family level did not lose information on environmental processes (Heip et al. 1988, Herman and Heip 1988, Warwick 1988a, Warwick 1988b, Warwick et al. 1988). This is largely because of the hierarchical nature of taxonomy and that the family level typically separates organisms at functional levels. Aggregating species at higher levels is beneficial because it increases the speed at which the analyses can be performed and reduces the noise in community data introduced by rare species (Somerfield and Clark

1995). There have been numerous studies on this topic since 1988 because a Google Scholar search for “taxonomic levels analysis” returned 1.1 million results. However, it has been noted that phylogeny alone does not predict ecological differences and there are many studies that (mostly terrestrial) that find no relationships between phylogenetic distance and ecological differences, and this is where traits can be informative (Cadotte et al. 2017). Functional diversity metrics are simply another approach to aggregating species data to simplify analyses.

5. CONCLUSIONS

While species diversity, community structure, and productivity of benthic macrofauna have been extensively studied in Texas estuaries, this is not the case for functional diversity. The mFD package in R was used to compute functional diversity indices in a PCA based multidimensional space. Results reveal that functional diversity does not have a statistically significant relationship with productivity. Implying, that functional diversity does not drive productivity. However, community functional dispersion is the only functional diversity metric with a positive and significant relationship to production; indicating that more variety of functionally different species is beneficial to production. Richness, H', and N1 all appear to have a statistically significant relationship to production as well. These relationships can be clearly seen in the linear regression models as well as the logistic growth models. While previous studies have shown a clear relationship between inflow and diversity, the spearman correlation results between PC1 (the inflow indicator), and the diversity metrics do not show such results. In general, the response in primary and secondary bays is different with the exception of the lower part of San Antonio Bay. Richness and functional richness appear to be significantly correlated with PC2 (high ammonium and chlorophyll levels); however, the only bay located on PC2 is Baffin Bay. Overall, results reveal that macrofauna species diversity metrics and secondary production have a strong positive relationship to one another while functional diversity does not appear to drive production in Texas Estuaries. This can be attributed to weaknesses in the functional diversity calculation methods. Most functional diversity research involving its relationship to production indicates that species' functional characteristics strongly influence ecosystem properties; however, this has been primarily investigated in terrestrial ecosystems or fish assemblages. Further research of the relationship between functional diversity and

ecosystem processes such as secondary production is necessary for marine benthic communities. This present study has further advanced the understanding of long-term dynamics of benthic ecosystems by providing insight into the relationship of functional diversity and ecosystem functioning as well as explanations as to why functional diversity measurements may not work. Ultimately, this research will contribute to the understanding of estuarine community dynamics and ecosystem health.

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APPENDIX: SPECIES CLASSIFICATION

Trait Keys

Guild	Code	n
WaterColumn	W	1
Browser	B	2
Interface	I	3
ConveyorBelt	C	4
Subsurface	S	5
Predator/Omnivore	P	6
Unknown	U	0

Depth	Code	n
Epifauna	D0	1
Up to 2 cm	D2	2
2 to 5 cm	D5	3
>5 cm	DG5	4
unknown	U	0

Habitat	Code	n
Free	HF	1
Burrow	HB	2
Tube	HT	3
Attached	HA	4
unknown	U	0

Mobility	Code	n
Free	MFR	1
Minimal	MM	2
Fixed	MF	3
unknown	U	0

Lifespan	Code	n
>1 year	LS	1
1-3 years	LM	2
>3 years	LL	3
unknown	U	0

SizeRange	Code	n
1 to 5 mm	SS	1
6 to 30 mm	SM	2
>30 mm	SL	3
unknown	U	0

Reproduction	Code	n
Semelparous	RS	1
Iteroparous	RI	2
unknown	U	0

Size (mm)

Functional Trait Table

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
<i>Abra aequalis</i>	I	DG5	HB	MM	LM	SS	RI	3
<i>Acetes americanus</i>	W	D0	HF	MFR	LM	SM	RI	10
<i>Acteocina canaliculata</i>	P	D2	HB	MFR	LM	SS	RI	5
<i>Aglaophamus verrilli</i>	P	DG5	HB	MFR	LL	SL	RI	60
<i>Agriopoma texasianum</i>	I	D5	HB	MM	LL	SL	RI	57
<i>Aligena texasiana</i>	S	DG5	HF	MF	LL	SS	RI	2
<i>Alitta succinea</i>	P	D2	HB	MFR	LM	SL	RS	190
<i>Allothyone mexicana</i>	I	D0	HF	MM	LL	SM	RI	20
<i>Alpheus heterochaelis</i>	P	D0	HF	MFR	LM	SM	RI	30
<i>Alteutha depressa</i>	B	D0	HF	MFR	LS	SS	RI	1
<i>Amaeana trilobata</i>	C	DG5	HT	MF	LM	SM	RI	30
<i>Americamysis almyra</i>	P	D0	HF	MFR	LM	SM	RI	10
<i>Americamysis bahia</i>	P	D0	HF	MFR	LM	SM	RI	10
<i>Americamysis bigelowi</i>	P	D0	HF	MFR	LM	SM	RI	7
<i>Americhelidium americanum</i>	I	D0	HF	MFR	LM	SM	RI	10
<i>Ampelisca abdita</i>	I	D0	HF	MF	LM	SS	RS	5
<i>Ampelisca sp.</i>	I	D0	HF	MF	LM	SS	RS	5
<i>Ampelisca sp. B</i>	I	D0	HF	MF	LM	SS	RS	5
<i>Ampelisca verrilli</i>	I	D0	HF	MF	LM	SS	RS	5
<i>Ampharetidae (unidentified)</i>	I	DG5	HT	MF	LL	SL	RI	50
<i>Amphilochus sp.</i>	I	D0	HB	MFR	LM	SS	RI	5
<i>Amphinomidae (unidentified)</i>	P	DG5	HB	MFR	LL	SL	RI	75
<i>Amphipoda (unidentified)</i>	I	D0	HF	MFR	LM	SS	U	.
<i>Amygdalum papyrium</i>	I	D0	HF	MF	LL	SS	RI	5
<i>Anachis obesa</i>	P	D0	HF	MFR	LL	SM	RI	6
<i>Anachis semiplicata</i>	P	D0	HF	MFR	LL	SM	RI	15
<i>Anadara ovalis</i>	W	D2	HB	MM	LL	SM	RI	21

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Anadara sp.	I	D2	HB	MM	LL	SS	RI	4
Anadara transversa	I	D2	HB	MM	LL	SS	RI	4
Ancistrosyllis falcata	P	DG5	HB	MFR	LM	SM	RI	15
Ancistrosyllis groenlandica	P	DG5	HB	MFR	LM	SM	RI	15
Ancistrosyllis jonesi	P	DG5	HB	MFR	LM	SM	RI	10
Ancistrosyllis papillosa	P	DG5	HB	MFR	LM	SM	RI	16
Ancistrosyllis sp.	P	DG5	HB	MFR	LM	SM	RI	15
Anomalocardia auberiana	I	D5	HB	MM	LL	SS	RI	3
Anomia simplex	I	D0	HA	MF	LM	SM	RS	9
Anthozoa (unidentified)	P	D0	HA	MF	LL	SS	U	.
Apomatus sp.	W	D0	HT	MF	LM	SM	RI	6
Apseudes sp. A	I	D0	HF	MFR	LM	SM	RS	7
Arenicola cristata	C	DG5	HB	MM	LL	SL	RI	100
Argopecten irradians amplicostatus	W	D0	HA	MF	LM	SM	RS	9
Aricidea (Acmira) catharinae	S	DG5	HB	MFR	LM	SM	RI	20
Aricidea (Acmira) jeffreysii	S	DG5	HB	MFR	LM	SM	RI	20
Aricidea bryani	S	DG5	HB	MFR	LM	SM	RI	30
Aricidea fragilis	S	DG5	HB	MFR	LM	SL	RI	70
Aricidea sp.	S	DG5	HB	MFR	LM	SL	RI	100
Aricidea taylori	S	DG5	HB	MFR	LM	SM	RI	20
Armandia agilis	S	DG5	HB	MM	LL	SM	RI	11
Armandia maculata	S	DG5	HB	MM	LL	SM	RI	11
Armandia sp.	S	DG5	HB	MM	LL	SM	RI	20
Asciacea (unidentified)	W	D0	HA	MF	LL	SM	U	.
Assiminea succinea	B	D2	HF	MFR	LM	SS	RI	4
Asychis sp.	S	D5	HB	MM	LM	SL	RI	40
Austinixa chacei	I	D0	HF	MFR	LM	SM	RI	10
Austinixa cristata	I	D0	HF	MFR	LM	SM	RI	10
Autolytus sp.	B	D2	HB	MFR	LM	SM	RI	8
Axiothella sp. A	S	D5	HB	MM	LM	SL	RI	100
Balanus eburneus	W	D0	HA	MF	LL	SL	RI	50
Balanus trigonus	W	D0	HA	MF	LL	SM	RI	14
Batea catharinensis	B	D0	HF	MFR	LM	SS	RI	5
Bispira melanostigma	W	D0	HA	MF	LL	SL	RI	50
Bivalvia (juvenile)	I	DG5	HB	MM	LL	SL	RI	100
Bivalvia (unidentified)	I	DG5	HB	MM	LL	SL	RI	100
Boccardia sp.	I	DG5	HB	MFR	LM	SL	RI	35
Boonea impressa	P	D2	HA	MM	LM	SM	RS	6
Bowmaniella sp.	P	D0	HF	MFR	LM	SM	RI	10
Brachidontes exustus	W	D0	HA	MF	LL	SS	RI	4
Brachyuran zoea	W	D0	HF	MFR	LM	SS	RI	2

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
<i>Brada villosa capensis</i>	I	DG5	HT	MM	LL	SM	RI	10
<i>Brada</i> sp.	I	DG5	HT	MM	LL	SM	RI	30
<i>Brania furcelligera</i>	B	D2	HB	MM	LM	SS	RI	5
<i>Bulla striata</i>	P	D2	HB	MFR	LM	SL	RI	44
<i>Busycon contrarium</i>	P	D0	HF	MFR	LL	SL	RI	120
<i>Cabira incerta</i>	P	DG5	HB	MFR	LM	SM	RI	16
<i>Caecum glabrum</i>	B	D0	HT	MM	LL	SS	RI	5
<i>Caecum johnsoni</i>	B	D0	HT	MM	LL	SS	RI	5
<i>Caecum pulchellum</i>	B	D0	HT	MM	LL	SS	RI	2
<i>Callianassa</i> sp.	S	D0	HF	MFR	LM	SL	RI	40
<i>Callinectes sapidus</i>	P	D0	HF	MFR	LM	SL	RI	100
<i>Callinectes similis</i>	P	D0	HF	MFR	LM	SL	RI	100
<i>Callinectes</i> sp.	P	D0	HF	MFR	LM	SL	RI	100
<i>Cantharus cancellarius</i>	P	D0	HF	MFR	LL	SM	RI	24
<i>Capitella capitata</i>	S	D2	HB	MF	LS	SM	RI	10
Capitellidae (unidentified)	S	D5	HB	MF	LS	SM	RI	10
<i>Capitellides jonesi</i>	S	DG5	HB	MF	LS	SM	RI	10
Caprellidae sp.(unidentified)	P	D0	HF	MFR	LM	SS	U	.
<i>Cassidinidea lunifrons</i>	B	D0	HF	MFR	LS	SS	RS	3
<i>Caulleriella</i> sp. B	I	DG5	HB	MM	LL	SM	RI	7
<i>Cerapus tubularis</i>	B	D0	HF	MFR	LM	SM	RS	20
<i>Ceratonereis irritabilis</i>	P	D2	HF	MFR	LM	SL	RS	100
<i>Ceratonereis mirabilis</i>	P	D2	HF	MFR	LM	SL	RS	100
<i>Ceriantharia</i> (unidentified)	P	D0	HA	MF	LL	SM	U	.
<i>Cerithium lutosum</i>	B	D0	HA	MFR	LM	SM	RI	13
<i>Chaetopterus variopedatus</i>	C	DG5	HT	MF	LM	SL	RI	500
<i>Chaetozone setosa</i>	I	D2	HB	MM	LL	SM	RI	20
<i>Chione cancellata</i>	I	D5	HB	MM	LL	SM	RI	11
<i>Chione</i> sp.	I	D5	HB	MM	LL	SM	RI	11
Chironomidae (larvae)	B	D0	HF	MM	LS	SS	RS	5
Chironomidae (pupae)	B	D0	HF	MFR	LS	SM	RS	10
<i>Chlamydoleon dissimile</i>	P	D0	HF	MFR	LM	SM	RI	10
<i>Chloeia viridis</i>	P	DG5	HB	MFR	LL	SL	RI	95
<i>Chone</i> sp.	W	D0	HT	MF	LM	SL	RI	40
Cirratulidae (unidentified)	I	DG5	HB	MM	LL	SM	U	.
<i>Cirripedia cypris</i> larvae	W	D0	HA	MF	LL	SS	RI	1
<i>Clibanarius vittatus</i>	P	D0	HF	MFR	LL	SM	RI	20
<i>Clymenella mucosa</i>	C	DG5	HB	MM	LM	SL	RI	50
<i>Clymenella torquata</i>	C	DG5	HB	MM	LM	SL	RI	50
<i>Corbula contracta</i>	W	D0	HA	MF	LL	SM	RI	6
<i>Corbula dietziana</i>	I	DG5	HB	MF	LL	SM	RI	5
<i>Corophium louisianae</i>	B	D0	HF	MFR	LM	SM	RI	10

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Corophium sp.	B	D0	HF	MFR	LM	SM	RI	11
Cossura delta	S	DG5	HB	MM	LS	SM	RI	11
Crassinella lunulata	I	D0	HF	MM	LL	SS	RI	3
Crassostrea virginica	I	D0	HA	MF	LL	SM	RI	13
Crepidula fornicata	W	D0	HF	MM	LL	SL	RI	34
Crepidula plana	W	D0	HF	MM	LL	SM	RI	25
Crepidula sp.	W	D0	HF	MM	LL	SM	RI	28
Cyclaspis sp.	I	D0	HF	MFR	LS	SM	RI	10
Cyclaspis varians	I	D0	HF	MFR	LS	SM	RI	10
Cyclinella tenuis	I	D5	HB	MM	LL	SM	RI	6
Cyclopoida (commensal)	P	D0	HF	MFR	LS	SS	RI	1
Cyrtopleura costata	I	D2	HB	MF	LL	SL	RI	140
Dawsonius latispinus	I	D0	HF	MFR	LM	SL	RI	40
Decapoda (larvae)	P	D0	HF	MFR	LM	SS	RI	2
Dentalium sp.	I	D2	HB	MM	LM	SL	RI	59
Dentalium texasianum	I	D2	HB	MM	LM	SL	RI	59
Diastoma varium	B	D0	HF	MFR	LM	SL	RI	34
Diastylis sp.	I	D0	HF	MFR	LS	SM	RI	9
Diopatra cuprea	P	D2	HT	MM	LL	SL	RI	300
Dipolydora caulleryi	I	DG5	HB	MM	LM	SL	RI	50
Dipolydora socialis	I	DG5	HB	MM	LM	SL	RI	55
Diptera (unidentified)	B	D0	HF	MFR	LS	SS	U	.
Dispio uncinata	I	DG5	HB	MM	LM	SM	RI	20
Doridella obscura	B	D0	HF	MFR	LS	SS	RI	3
Dorvillea rubra	P	D0	HF	MFR	LM	SL	RS	40
Dorvilleidae (unidentified)	P	D0	HF	MFR	LM	SL	RS	40
Dosinia discus	I	D5	HB	MM	LL	SM	RI	15
Dosinia elegans	I	D5	HB	MM	LL	SL	RI	9
Dosinia sp.	I	D5	HB	MM	LL	SL	RI	6
Drilonereis magna	P	D0	HF	MFR	LM	SL	RS	240
Dyspanopeus texanus	P	D0	HF	MFR	LM	SL	RI	100
Echiuridae (unidentified)	I	D0	HB	MM	LM	SM	U	.
Eclysippe eliasoni	I	DG5	HT	MF	LL	SM	RI	10
Edotia montosa	P	D0	HB	MFR	LS	SS	RS	4
Elasmopus sp.	B	D0	HB	MFR	LM	SM	RI	6
Ensis minor	W	DG5	HB	MM	LL	SM	RI	13
Episiphon sowerbyi	S	D2	HB	MM	LM	SM	RI	10
Epitonium rupicola	P	D0	HB	MFR	LS	SM	RS	19
Epitonium sp.	P	D0	HB	MM	LS	SM	RI	19
Erichsonella attenuata	P	D0	HF	MFR	LS	SM	RS	10
Erichthonius brasiliensis	B	D0	HF	MFR	LM	SM	RS	10
Erichthonius punctatus	B	D0	HF	MFR	LM	SM	RS	10

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
<i>Erinaceusyllis erinaceus</i>	B	D2	HB	MFR	LM	SS	RI	2
<i>Eteone lactea</i>	P	D2	HF	MFR	LL	SL	RI	60
<i>Euceramus praelongus</i>	P	D0	HF	MFR	LM	SL	RI	40
<i>Euclymene</i> sp. A	C	DG5	HB	MM	LM	SL	RI	100
<i>Euclymene</i> sp. B	C	DG5	HB	MM	LM	SL	RI	100
<i>Eudorella monodon</i>	I	D0	HF	MFR	LS	SS	RI	5
<i>Eudorella</i> sp.	I	D0	HF	MFR	LS	SM	RI	10
<i>Eulimastoma teres</i>	P	D0	HA	MM	LM	SS	RI	5
<i>Eulimastoma teres</i>	W	DG5	HB	MM	LL	SM	RI	25
<i>Eulimastoma</i> sp.	P	D2	HA	MM	LM	SS	RI	3
<i>Eumida sanguinea</i>	P	D2	HF	MFR	LL	SL	RI	90
<i>Eunoe nodulosa</i>	P	D0	HF	MFR	LL	SL	RI	50
<i>Eupolymnia</i> sp.	I	D5	HT	MM	LM	SL	RI	.
<i>Eurythoe</i> sp.	P	DG5	HB	MFR	LL	SL	RI	33
<i>Eusarsiella Sarsiella zostericola</i>	P	D0	HF	MFR	LM	SM	RI	30
<i>Eusarsiella spinosa</i>	P	D0	HF	MM	LM	SM	RI	30
<i>Eusarsiella texana</i>	P	D0	HF	MM	LM	SM	RI	30
<i>Exogone dispar</i>	B	D2	HB	MFR	LM	SS	RI	5
<i>Exogone</i> sp.	B	D2	HB	MFR	LM	SM	RI	6
<i>Fabricia</i> sp. A	W	D0	HT	MF	LM	SS	RI	4
<i>Fabricinuda trilobata</i>	W	D0	HT	MF	LM	SM	RI	10
<i>Farfantepenaeus aztecus</i>	P	D0	HF	MFR	LM	SL	RI	100
<i>Fargoa gibbosa</i>	P	D0	HA	MM	LM	SS	RI	5
Flabelligeridae (unidentified)	I	DG5	HB	MM	LL	SS	U	.
<i>Gammarus mucronatus</i>	I	D0	HF	MFR	LS	SS	RS	5
Gastropoda (unidentified)	B	D2	HA	MFR	LM	SS	U	.
<i>Glycera americana</i>	P	DG5	HB	MFR	LL	SL	RS	150
<i>Glycera capitata</i>	P	DG5	HB	MM	LL	SL	RS	150
Glyceridae (unidentified)	P	DG5	HB	MFR	LL	SL	RS	100
<i>Glycinde nordmanni</i>	P	DG5	HB	MM	LL	SM	U	30
<i>Glycinde solitaria</i>	P	DG5	HB	MFR	LL	SM	U	10
<i>Glyphohesione klatti</i>	P	DG5	HB	MFR	LM	SM	RI	15
Goniadidae (unidentified)	P	DG5	HB	MFR	LL	SM	U	30
<i>Grandierella bonnieroides</i>	B	D0	HF	MFR	LM	SM	RS	18
<i>Gyptis brevipalpa</i>	B	DG5	HB	MFR	LL	SM	RI	15
<i>Gyptis vittata</i>	P	DG5	HB	MFR	LL	SM	RI	9
Halocaridae (unidentified)	B	D0	HF	MFR	LS	SS	RI	1
<i>Haminoea antillarum</i>	P	D0	HF	MFR	LL	SM	RI	18
<i>Haminoea succinea</i>	P	D0	HF	MFR	LL	SM	RI	12
<i>Haploscoloplos foliosus</i>	S	DG5	HB	MM	LL	SL	RI	150
<i>Haploscoloplos fragilis</i>	S	DG5	HB	MM	LL	SL	RI	100
<i>Haploscoloplos robustus</i>	S	DG5	HB	MM	LL	SL	RI	100

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Haploscoloplos sp.	S	DG5	HB	MM	LL	SL	RI	100
Harrieta faxoni	B	D0	HF	MFR	LS	SM	RS	10
Hauchiella sp.	I	D5	HT	MF	LM	SM	RI	20
Hemicyclops sp.	I	D0	HF	MFR	LS	SS	RI	1
Henrya goldmani	B	D0	HB	MFR	LL	SS	RI	2
Hermundura ocularis	P	D5	HB	MFR	LM	SM	RI	25
Hesione picta	P	DG5	HB	MFR	LL	SM	RI	15
Hesionidae (unidentified)	B	DG5	HB	MFR	LL	SL	RI	50
Heteromastus filiformis	C	DG5	HB	MM	LM	SL	RS	100
Hiatella arctica	I	D2	HB	MF	LL	SM	RI	25
Hippolyte zostericola	B	D0	HF	MFR	LM	SM	RI	10
Hirudinea (unidentified)	P	D0	HF	MFR	LM	SS	U	.
Hobsonia florida	I	DG5	HT	MF	LL	SM	RI	10
Holothuroidea (unidentified)	I	D0	HF	MM	LL	SM	U	20
Hydroides dianthus	W	D0	HT	MF	LM	SM	RI	15
Hydroides protulicola	W	D0	HT	MF	LM	SM	RI	23
Hydrozoa (unidentified)	W	D0	HF	MFR	LS	SS	U	.
Hypereteone heteropoda	P	D2	HB	MFR	LL	SL	Ri	100
Insecta (unidentified)	B	D0	HF	MFR	LS	SS	U	.
Ischadium recurvum	I	D0	HA	MF	LL	SS	RI	4
Isolda pulchella	I	DG5	HT	MF	LL	SM	RI	17
Labidocera aestiva	P	D0	HF	MFR	LS	SS	RI	2
Laeonereis culveri	P	D2	HF	MFR	LM	SL	RS	50
Laevicardium mortoni	W	D2	HB	MM	LL	SS	RI	3
Laonome sp.	W	D0	HT	MF	LM	SL	RI	100
Lembos sp.	B	D0	HB	MFR	LM	SM	RS	10
Lepidasthenia maculata	P	D0	HF	MFR	LL	SL	RI	60
Lepidasthenia sp.	P	D0	HF	MFR	LL	SL	RI	60
Lepidonotus sp.	P	D0	HF	MFR	LL	SL	RI	100
Lepidophthalmus louisianensis	I	D0	HF	MFR	LM	SL	RI	40
Leptocheilia rapax	I	D0	HF	MFR	LM	SS	RS	5
Leptocuma sp.	I	D0	HF	MFR	LS	SS	RI	5
Lepton sp.	I	D0	HF	MFR	LL	SS	RI	2
Leptostylis sp.	I	D0	HF	MFR	LS	SS	RI	5
Leucon sp.	I	D0	HF	MFR	LS	SS	RI	5
Libinia dubia	P	D0	HF	MFR	LL	SL	RI	60
Lima pellucida	I	D0	HF	MM	LL	SM	RI	8
Linopherus sp.	P	DG5	HB	MFR	LL	SL	RI	100
Lioberus castaneus	I	D0	HA	MF	LL	SM	RI	13
Listriella barnardi	I	D0	HF	MFR	LM	SS	RI	4
Listriella clymenellae	I	D0	HF	MFR	LM	SS	RI	4
Listriella sp.	I	D0	HF	MFR	LM	SS	RI	4

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
<i>Litocorsa stremma</i>	P	DG5	HB	MFR	LM	SM	RI	25
<i>Littorina ziczac</i>	B	D0	HF	MFR	LM	SM	RI	17
<i>Loimia medusa</i>	I	D5	HB	MF	LM	SL	RI	84
<i>Lucifer faxoni</i>	W	D0	HF	MFR	LM	SM	RI	10
<i>Lucina amianta</i>	I	DG5	HB	MM	LL	SS	RI	5
Lumbrineridae (unidentified)	P	D2	HB	MM	LL	SM	RS	.
<i>Lumbrineris branchiata</i>	P	D2	HB	MM	LL	SL	RS	60
<i>Lumbrineris latreilli</i>	P	D2	HB	MM	LL	SL	RS	34
<i>Lumbrineris parvapedata</i>	P	D2	HB	MM	LL	SL	RS	60
<i>Lyonsia hyalina floridana</i>	I	DG5	HB	MM	LL	SM	RI	18
<i>Lysidice ninetta</i>	P	D2	HF	MFR	LL	SM	RI	30
<i>Lysilla</i> sp.	I	DG5	HT	MM	LM	SL	RI	80
<i>Macoma brevifrons</i>	I	D2	HB	MM	LL	SM	RI	7
<i>Macoma mitchelli</i>	I	D2	HB	MM	LL	SS	RI	5
<i>Macoma</i> sp.	I	D2	HB	MM	LL	SS	RI	5
<i>Macoma tenta</i>	I	D2	HB	MM	LL	SS	RI	5
<i>Macroclymene</i> sp. A	S	DG5	HB	MM	LM	SL	RI	100
<i>Mactra fragilis</i>	W	D5	HB	MM	LL	SM	RI	10
<i>Magelona pettiboneae</i>	I	DG5	HB	MF	LM	SM	RS	25
<i>Magelona phyllisae</i>	I	DG5	HB	MF	LM	SM	RS	12
<i>Magelona rosea</i>	I	DG5	HB	MF	LM	SL	RS	50
Magelonidae (unidentified)	I	DG5	HB	MF	LM	SM	RS	.
<i>Maldane sarsi</i>	S	DG5	HB	MM	LM	SL	RI	100
Maldanidae (unidentified)	C	DG5	HB	MF	LM	SL	U	.
<i>Malmgreniella</i> sp.	P	D0	HF	MFR	LL	SM	RI	11
<i>Malmgreniella taylori</i>	P	D0	HF	MFR	LL	SL	RI	100
<i>Marphysa sanguinea</i>	P	D2	HB	MM	LL	SL	RI	40
<i>Martesia</i> sp.	I	D2	HB	MF	LL	SM	RI	15
<i>Mediomastus ambiseta</i>	C	D2	HB	MM	LS	SM	RI	20
<i>Mediomastus californiensis</i>	S	D2	HB	MM	LS	SL	RI	50
<i>Megalomma bioculatum</i>	W	D0	HT	MF	LM	SL	RI	74
<i>Megalomma lobiferum</i>	W	D0	HT	MF	LM	SL	RI	70
<i>Megalopa</i> larvae	P	D0	HF	MFR	LM	SS	RI	5
<i>Melinna maculata</i>	I	DG5	HT	MF	LL	SM	RI	19
<i>Melita nitida</i>	B	D0	HF	MFR	LM	SM	RI	10
<i>Mercenaria campechiensis</i>	W	D2	HB	MM	LL	SM	RI	7
<i>Micronephtys</i> sp.	P	D2	HB	MFR	LL	SM	RI	.
<i>Microphiopholis atra</i>	I	D0	HF	MM	LL	SM	RI	10
<i>Microphthalmus aberrans</i>	P	DG5	HB	MFR	LL	SM	RI	9
<i>Microprotopus</i> sp.	B	D0	HB	MFR	LS	SM	RI	10
<i>Mitrella lunata</i>	I	D0	HF	MFR	LL	SM	RI	6
<i>Molgula manhattensis</i>	W	D0	HA	MF	LL	SM	RI	10

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Mollusca (unidentified)	P	D2	HB	MM	LM	SM	U	.
Monocorophium acherusicum	B	D0	HB	MFR	LS	SS	RI	5
Monoculodes sp.	I	D0	HF	MFR	LM	SM	RI	10
Mulinia lateralis	I	D5	HB	MM	LL	SS	RI	3
Munnidae (unidentified)	I	D0	HF	MFR	LS	SS	RS	2
Mysella planulata	I	D2	HB	MF	LL	SS	RI	2
Mysidopsis sp.	P	D0	HF	MFR	LM	SM	RI	10
Mytilidae (unidentified)	I	D0	HF	MF	LL	SS	RI	1
Naineris bicornis	S	DG5	HB	MM	LL	SM	RI	20
Naineris laevigata	C	DG5	HB	MM	LL	SM	RI	20
Nassarius acutus	P	D2	HB	MM	LM	SM	RI	15
Nassarius sp.	P	D2	HB	MM	LM	SM	RI	9
Nassarius vibex	P	D2	HB	MM	LM	SM	RI	20
Natica pusilla	P	D2	HB	MM	LL	SM	RI	7
Nematonereis hebes	P	D2	HB	MM	LL	SM	RI	8
Nemertea (unidentified)	P	D0	HF	MFR	LM	SM	RI	.
Neopanope texana	P	D0	HF	MFR	LM	SM	RI	30
Neosamytha gracilis	I	DG5	HT	MM	LL	SL	RI	50
Nephtys incisa	P	D2	HB	MFR	LM	SL	RI	150
Nephtys magellanica	P	D2	HB	MFR	LM	SL	RI	100
Nephtys picta	P	D2	HB	MFR	LM	SL	RI	80
Nephtys sp.	P	D2	HB	MFR	LL	SL	RI	115
Nereididae (unidentified)	P	D2	HB	MFR	LM	SL	RS	100
Nereis lamellosa	P	D2	HF	MFR	LM	SL	RS	60
Nereis pelagica occidentalis	P	D2	HB	MFR	LM	SL	RS	60
Nereis sp. A	P	D2	HB	MFR	LM	SL	RS	60
Ninoe nigripes	P	DG5	HB	MM	LL	SL	RS	100
Nothria geophiliformis	P	D2	HB	MM	LL	SL	RI	200
Notomastus latericeus	S	DG5	HB	MM	LS	SM	RI	20
Notomastus latericeus	S	DG5	HB	MM	LS	SM	RI	20
Notomastus sp.	S	Dg5	HB	MM	LS	SM	RI	20
Nuculana acuta	I	DG5	HB	MM	LL	SM	RI	8
Nuculana concentrica	I	DG5	HB	MM	LL	SS	RI	3
Nudibranchia (unidentified)	P	D0	HF	MFR	LS	SM	U	.
Odostomia canaliculata	P	D0	HA	MM	LM	SS	RI	3
Odostomia sp.	P	D0	HA	MM	LM	SS	RI	3
Oenone fulgida	P	D0	HF	MFR	LM	SL	RS	100
Ogyrides alphaerostris	B	D0	HF	MFR	LM	SM	RI	30
Oligochaeta (unidentified)	S	D0	HF	MFR	LM	SL	RI	100
Onuphidae (unidentified)	P	D2	HT	MM	LL	SL	U	.
Onuphis eremita	B	D2	HB	MM	LL	SL	RI	40
Onuphis sp.	B	D2	HB	MM	LL	SL	RI	40

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Opheliidae (unidentified)	S	DG5	HB	MFR	LL	SL	RI	80
Ophiuroidea (unidentified)	B	D0	HF	MM	LL	SL	U	.
Ophryotrocha sp. (unidentified)	P	D0	HF	MFR	LM	SS	RS	1
Opisthosyllis sp.	B	D2	HB	MFR	LM	SM	RI	22
Orbiniidae (unidentified)	S	DG5	HB	MFR	LL	SL	RI	100
Ostracoda (unidentified)	P	D0	HF	MFR	LM	SS	U	.
Owenia fusiformis	I	DG5	HT	MF	LL	SM	RI	30
Oweniidae (unidentified)	I	DG5	HT	MF	LL	SM	U	.
Oxydromus obscurus	P	DG5	HB	MFR	LL	SL	RI	50
Oxyurostylis salinoi	I	D0	HF	MFR	LS	SS	RI	5
Oxyurostylis smithi	I	D0	HF	MFR	LS	SS	RI	5
Oxyurostylis sp.	I	D0	HF	MFR	LS	SS	RI	5
Paguridae (juvenile)	P	D0	HF	MFR	LL	SM	RI	20
Pagurus annulipes	P	D0	HF	MFR	LL	SL	RI	50
Pagurus longicarpus	P	D0	HF	MFR	LL	SM	RI	20
Paleanotus heteroseta	P	D2	HB	MFR	LM	SS	U	4
Pandora trilineata	W	D2	HB	MM	LL	SM	RI	22
Paradoneis lyra	S	DG5	HB	MM	LM	SM	RI	11
Parahesione luteola	B	DG5	HB	MFR	LL	SL	RI	50
Parametopella sp.	I	D0	HB	MFR	LM	SS	RI	3
Paramphinome jeffreysii	P	DG5	HB	MFR	LL	SM	RI	15
Paramphinome pulchella	P	DG5	HB	MFR	LL	SM	RI	15
Paramya subovata	I	DG5	HB	MM	LL	SM	RI	8
Paranaitis polynoides	B	D0	HF	MFR	LL	SL	RI	63
Paranaitis speciosa	P	D2	HB	MFR	LL	SS	RI	4
Parandalia sp.	P	DG5	HB	MFR	LM	SM	RI	12
Paraonidae Grp. A	S	DG5	HB	MFR	LM	SS	RI	3
Paraonidae Grp. B	S	DG5	HB	MFR	LM	SS	RI	3
Paraonides lyra	S	DG5	HB	MM	LM	SM	RI	10
Paraonis fulgens	S	DG5	HB	MM	LM	SL	RI	50
Paraonis gracilis	S	DG5	HB	MM	LM	SL	RI	50
Parapionosyllis sp.	B	D2	HB	MFR	LM	SS	RI	5
Paraprionospio pinnata	I	DG5	HT	MM	LM	SL	RI	65
Parasabella microphthalma	W	D0	HT	MF	LM	SM	RI	10
Parasterope sp.	W	D0	HF	MFR	LM	SM	RI	30
Parhyale sp.	B	D0	HB	MFR	LM	SM	RI	10
Pectinaria gouldii	I	DG5	HT	MM	LL	SM	RI	20
Pectinariidae (unidentified)	I	DG5	HT	MM	LL	SL	RI	60
Periploma margaritaceum	W	DG5	HB	MM	LL	SS	RI	2
Petricolaria pholadiformes	I	D2	HB	MM	LL	SM	RI	2
Phascolion strombus	S	D0	HB	MM	LM	SM	U	.
Phoronis architecta	W	D0	HT	MF	LS	SM	RI	20

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Photis sp.	B	D0	HB	MfR	LS	SS	RI	5
Phyllodoce erythrophyllus	P	D2	HB	MFR	LL	SL	RI	77
Phyllodoce longipes	P	D2	HB	MFR	LL	SM	RI	17
Phyllodocidae (unidentified)	P	D2	HB	MFR	LL	SM	RI	20
Phylo felix	S	DG5	HB	MM	LL	SL	RI	150
Pilargiidae (unidentified)	P	DG5	HB	MFR	LM	SL	RI	100
Pilargis berkeleyae	P	DG5	HB	MFR	LM	SL	RI	170
Pilargis sp.	P	DG5	HB	MFR	LM	SM	RI	.
Pinnixa retinens	I	D0	HF	MFR	LM	SM	RI	10
Pinnixa sp.	I	D0	HF	MFR	LM	SM	RI	10
Pinnotheres sp.	I	D0	HF	MFR	LM	SM	RI	10
Pinnotheridae (unidentified)	I	D0	HF	MFR	LM	SM	RI	10
Pionosyllis sp.	B	D2	HB	MFR	LM	SS	RI	5
Piromis arenosus	I	D5	HT	MM	LL	SL	RI	50
Pista cristata	I	DG5	HT	MM	LM	SL	RI	44
Pista palmata	I	DG5	HT	MM	LM	SM	RI	21
Placostegus sp.	W	D0	HT	MF	LM	SS	RI	.
Platyischnopus sp.	I	D0	HF	MFR	LM	SS	RI	5
Platynereis dumerilii	P	D2	HB	MFR	LM	SS	RS	3
Podocopida (unidentified)	I	D0	HF	MFR	LM	SS	RI	1
Polinices duplicatus	P	D2	HF	MM	LL	SL	RI	44
Polychaeta (unidentified)	P	D2	HB	MFR	LM	SS	U	.
Polychaeta juv. (unidentified)	P	D2	HB	MFR	LM	SS	U	.
Polydora cornuta	I	D0	HT	MFR	LM	SM	RI	12
Polydora sp.	I	D0	HT	MFR	LM	SM	RI	30
Polydora websteri	I	D0	HA	MM	LM	SM	RI	20
Polynoidae (unidentified)	P	D0	HF	MFR	LL	SM	RI	.
Polyonyx gibbesi	P	D0	HF	MFR	LM	SL	RI	40
Porcellanid juv.	P	D0	HF	MFR	LL	SM	RI	30
Potamanthidae (unidentified)	B	D0	HF	MM	LS	SS	RS	1
Potamethus spathiferus	W	D0	HT	MF	LM	SL	RI	100
Prionospio cirrifera	I	DG5	HB	MM	LM	SM	RI	30
Prionospio cristata	I	DG5	HB	MM	LM	SM	RI	10
Prionospio heterobranchia	I	DG5	HB	MM	LM	SM	RI	10
Prionospio pygmaeus	I	DG5	HB	MM	LM	SM	RI	10
Prionospio treadwelli	I	DG5	HB	MM	LM	SM	RI	15
Processa hemphilli	I	D0	HF	MFR	LM	SM	RI	10
Pseudodiaptomus pelagicus	W	D0	HF	MFR	LS	SS	RI	1
Pseudomystides rarica	P	D2	HB	MFR	LL	SL	RI	100
Pseudopotamilla reniformis	W	D0	HT	MF	LM	SL	RI	60
Pycnogonida (unidentified)	P	D0	HF	MFR	LM	SS	U	.
Pyramidella crenulata	P	D0	HA	MM	LM	SM	RI	8

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
Pyramidella sp.	P	D0	HA	MM	LM	SM	RI	8
Rangia cuneata	I	D5	HB	MM	LL	SM	RI	13
Rictaxis punctostriatus	P	D0	HB	MFR	LL	SS	RI	5
Rithropanopeus compta	I	D0	HB	MFR	LM	SM	RI	8
Rithropanopeus harrisi	P	D0	HF	MFR	LM	SM	RI	20
Sabaco elongatus	S	DG5	HB	MM	LM	SL	RI	100
Sabellastarte magnificia	W	D0	HT	MF	LM	SL	RI	130
Sabellidae (unidentified)	W	D0	HA	MF	LL	SM	RI	.
Salvatoria clavata	B	D2	HB	MFR	LM	SS	RI	3
Sarsiella capsula	P	D0	HF	MFR	LM	SS	RI	1
Sarsiella disparalis	P	D0	HF	MFR	LM	SS	RI	1
Sarsiella sp.	P	D0	HF	MFR	LM	SS	RI	1
Sayella crosseana	P	D0	HA	MM	LM	SS	RI	5
Schistomeringos rudolphi	P	D0	HF	MFR	LM	SM	RS	16
Schistomeringos sp. A	P	D0	HF	MFR	LM	SM	RS	6
Schizocardium sp.	S	DG5	HB	MM	LL	SL	RI	100
Scolecipis squamata	I	DG5	HB	MM	LM	SM	RI	9
Scolecipis texana	I	DG5	HB	MM	LM	SS	RI	5
Scoletoma tenuis	P	DG5	HB	MM	LL	SL	RS	100
Scoloplos rubra	C	DG5	HB	MM	LM	SL	RI	70
Scoloplos texana	C	DG5	HB	MM	LM	SM	RI	10
Serpulidae (unidentified)	W	D0	HT	MF	LM	SS	U	.
Serpulidae Serpulidae A	W	D0	HT	MF	LM	SL	RI	50
Sigalionidae (unidentified)	P	D2	HB	MFR	LL	SS	U	.
Sigambra bassi	P	DG5	HB	MFR	LM	SM	RI	40
Sigambra wassi	P	DG5	HB	MFR	LM	SL	RI	100
Sigambra sp.	P	DG5	HB	MFR	LM	SM	RI	10
Sigambra tentaculata	P	DG5	HB	MFR	LM	SL	RI	100
Sipuncula (unidentified)	S	DG5	HB	MFR	LM	SM	U	.
Solen viridis	W	DG5	HB	MM	LL	SS	RI	5
Sphaerosyllis sublaevis	B	<u>D2</u>	HB	MFR	LM	SS	RI	3
Sphaerosyllis sp. A	B	D2	HB	MFR	LM	SS	RI	3
Spio pettiboneae	I	DG5	HB	MM	LM	SM	RI	10
Spio setosa	I	DG5	HB	MM	LM	SM	RI	20
Spio sp.	I	DG5	HB	MM	LM	SM	RI	30
Spiochaetopterus costarum	I	DG5	HT	MF	LM	SL	RI	80
Spionidae (unidentified)	C	DG5	HB	MFR	LM	SM	RI	30
Spiophanes bombyx	I	DG5	HB	MM	LM	SL	RI	50
Spirobranchus americanus	W	D0	HT	MF	LM	SM	RI	20
Spirobranchus kraussi	W	D0	HT	MF	LM	SM	RI	15
Spirobranchus kraussii	B	D2	HT	MFR	LM	SM	RI	15
Spirorbis sp.	W	D0	HT	MF	LM	SS	RI	4

Species	Guild	Depth	Habitat	Mobility	Lifespan	SizeRange	Reproduction	Size
<i>Sthenelais boa</i>	P	D2	HB	MFR	LL	SL	RI	200
<i>Sthenelais</i> sp.	P	D2	HB	MFR	LL	SL	RI	200
<i>Streblosoma</i> sp.	I	DG5	HT	MM	LM	SL	RI	50
<i>Streblospio benedicti</i>	I	DG5	HT	MF	LM	SM	RI	20
<i>Stylochus ellipticus</i>	P	D0	HF	MFR	LS	SS	U	15
Syllidae (unidentified)	B	D2	HB	MFR	LM	SM	RI	10
<i>Syllis cornuta</i>	B	D2	HB	MFR	LM	SM	RI	21
<i>Syllis falgens</i>	B	D2	HB	MFR	LM	SM	RI	20
<i>Syllis</i> sp.	B	D2	HB	MFR	LM	SM	RI	15
<i>Synelmis albini</i>	P	DG5	HB	MFR	LM	SL	RI	50
<i>Synsyllis longigularis</i>	B	D2	HB	MFR	LM	SM	RI	30
<i>Tagelus divisus</i>	I	DG5	HB	MM	LM	SM	RI	12
<i>Tagelus plebeius</i>	W	DG5	HB	MM	LM	SM	RI	13
Tanaidacea (unidentified)	I	D0	HF	MFR	LM	SS	U	.
<i>Teinostoma biscaynense</i>	B	D0	HF	MFR	LS	SS	RI	2
<i>Tellidora cristata</i>	I	D2	HB	MM	LL	SM	RI	6
<i>Tellina</i> sp.	I	D5	HB	MM	LL	SS	RI	12
<i>Tellina tampaensis</i>	I	D5	HB	MM	LL	SS	RI	5
<i>Tellina texana</i>	I	D5	HB	MM	LL	SS	RI	3
<i>Tellina versicolor</i>	I	D5	HB	MM	LL	SM	RI	6
<i>Terebella Terebella</i>	I	D0	HT	MFR	LM	SM	RI	10
Terebellidae (unidentified)	I	DG5	HT	MM	LM	SL	RI	100
<i>Texadina barretti</i>	I	D2	HB	MFR	LL	SS	RI	2
<i>Texadina sphinctostoma</i>	I	D2	HB	MFR	LL	SS	RI	3
<i>Tharyx setigera</i>	I	D2	HB	MM	LL	SM	RI	20
<i>Tharyx</i> sp.	I	D2	HB	MM	LL	SM	RI	20
<i>Thompsonula</i> sp.	B	D0	HF	MFR	LS	SS	RI	1
<i>Trachypenaeus constrictus</i>	P	D0	HF	MFR	LM	SL	RI	100
<i>Truncatella caribaeensis</i>	B	D2	HB	MFR	LS	SM	RI	7
<i>Trypanosyllis aeolis</i>	B	D2	HB	MFR	LM	SL	RI	81
Turbellaria (unidentified)	B	D0	HF	MFR	LS	SS	U	.
<i>Turbonilla portoricana</i>	P	D0	HA	MM	LS	SS	RI	5
<i>Turbonilla</i> sp.	P	D0	HA	MM	LS	SS	RI	5
Unidentified	U	U	U	U	U	SS	U	.
<i>Upogebia affinis</i>	I	D0	HB	MFR	LM	SL	RI	50
<i>Uromunna hayesi</i>	I	D0	HB	MFR	LS	SS	RS	2
Veneridae juvenile	I	D5	HB	MM	LL	SM	RI	6
<i>Vitrinella floridana</i>	B	D0	HF	MFR	LS	SS	RI	2
Vitrinellidae (unidentified)	B	D0	HF	MFR	LS	SS	RI	2
Xanthidae (unidentified)	P	D0	HF	MFR	LM	SL	RI	100
<i>Xenanthura brevitelson</i>	I	D0	HB	MFR	LS	SM	RS	10