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The Functional Response of Estuarine Fish Communities to Hydrologic Change in a Semi-Arid Ecosystem

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Abstract: Functional assessment approaches were used to identify the responses of fish to environmental change in the San Antonio Bay System (Texas, USA). Using a 26-year coastal fisheries dataset (1993–2018), multivariate analyses revealed relationships between functional group abundance and freshwater inflows in the upper segments (Hynes Bay and Guadalupe Bay), but the patterns were decoupled from inflows in the lower bay segments (San Antonio Bay, Ayres Bay and Espiritu Santo Bay). In Hynes and Guadalupe Bays, freshwater migrant carnivores accounted for a significant fraction of the community irrespective of the gear, year or flow. Freshwater stragglers (omnivores and carnivores) were often present in the upper reaches of the bay. In the lower reaches, marine migrant omnivores were present during high and low flows in Espiritu Santos Bay, but only during low flows in Ayres Bay. Marine migrant carnivores were more important in gill nets irrespective of the flow conditions. The five most abundant fish were estuarine resident carnivores and omnivores, accounting for 53.5% of the community. Declines in the abundance of functional groups occurred during the 2011–2014 drought, with rebounds in 2015–2018. Functional methodologies provide insights into estuarine ecosystems and can serve as management tools to assess changes in fish assemblages.

Keywords: functional assessment; Guadalupe Estuary; San Antonio Bay; freshwater inflows; fisheries; ecosystem-based management

Key Contribution: This paper provides the first functional assessment of fishes in the San Antonio Bay System (Texas, USA). The findings compliment studies conducted in nearby estuaries and help us to understand the current fish community dynamics in the face of future climate change and sea level rises.

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1. Introduction

The "Estuarine Quality Paradox" identifies that biota are highly adapted to the variability in estuarine environments, such that effects of anthropogenic stressors may be difficult to distinguish from natural variability [1,2]. The paradox relies on two main facets—What constitutes stress? Is the stress measurable? [1]. Stress can be regarded as a perturbation with a negative effect on an area and thus a pressure that will reduce the ability of a level of biological organization (individual, community, or functional group) to survive and function. In areas that are inherently variable (e.g., estuaries and transition zones), detecting a change due to stress can be difficult because of a low signal to noise ratio [1]. Periodic pulses of freshwater inflows (river discharge) into estuaries influence the primary productivity, biodiversity, and energy transfer between trophic levels [3–6]. Freshwater inflows (magnitude, duration, timing, quality), the lack thereof, or an excess thereof may be considered a stressor of estuarine communities (e.g., [4,6–12]). In the coming decades, freshwater inflows are projected to decrease worldwide as the result of diversions upstream to support human population growth and shifts in land use patterns [6,13]. Decreased freshwater inflows reduce flushing rates, increase salinity, and protract the water residence time in estuaries, thereby affecting the distribution and abundance of organisms, including fish [6,7,14]. As anthropogenic pressures on freshwater resources continue, a balance must be achieved to ensure estuaries receive sufficient riverine inputs to sustain healthy ecosystems [6,8,12,15]. Distinguishing between natural and anthropogenic estuarine biological characteristics relies on the availability of multi-decadal datasets in which biological and water quality parameters are collected concurrently. This is particularly critical when an estuary is also impacted by intermittent extreme events such as hurricanes, droughts, and/or floods.

Of the underlying mechanisms driving the distribution of fishes, salinity and temperature have been identified as the primary explanatory factors [10,14,16–21]. Ichthyofaunal surveys are generally lists of species and their relative abundances, but these have limited value [22]. Some studies have considered that estuarine teleosts may be used as bioindicators of altered freshwater inflows [11]. A method of condensing all these data into a more practical format was developed by Elliott et al. [2] and Franco et al. [23], and later updated by Potter et al. [24], which applies a functional group approach to better understand the relationships between community organization and structure compared with abiotic factors in estuaries. Hence, the functional assessment approach endeavors to strike a balance between the conceptual and qualitative, to provide a quantitative understanding of changes within estuarine fish assemblages [22,23,25,26]. This documentation of the natural variation in fish communities is key to comparing changes across estuaries and has been applied worldwide. There are some challenges with this approach, particularly in defining which fish are £estuarine dependent"; however, Whitfield et al. [27] recently reviewed this concept to further explore the life-history guilds of fishes. In a global analysis, they found that most marine fish species found in estuaries are not estuary-dependent but estuarine opportunists. Clearly, more studies are required to better understand species populations as climate change and sea level rises alter historical estuarine hydrological patterns.

In this study, fish assemblages from the San Antonio Bay System (SABS), Texas (USA), were classified across functional groups based on the estuarine use (e.g., estuarine, marine, freshwater, stragglers, and migrants) and trophic guild (e.g., carnivore, omnivore) to gain insights into how freshwater inflows influence their ecological structure using a 26-year (1993–2018) coastal fisheries dataset (otter trawls and gill net). This ecosystem was chosen for three reasons. First, a recent analysis by West et al. [28] scored the SABS as vulnerable as it has experienced a net loss of wetlands since 2001, mostly due to sea level rises, and populations of the Eastern oyster (*Crassostrea virginica*, Gmelin, 1791), Southern flounder (*Paralichthys lethostigma*, Jordan and Gilbert, 1884), and Blue crab (*Callinectes sapidus*, Rathbun, 1896) are in decline, prompting questions about the longevity of these resources and the health of the SABS ecosystem. Second, in an examination of climate-related factors causing changes in the diversity of fish in the subtropical coast of the Gulf of Mexico, Fujiwara et al. [18] found that there has been an increasing trend in the Shannon diversity index in the San Antonio Bay over the last 35 years (1982–2016), which reflects a range expansion of some fishes northward as the availability of suitable environmental conditions shifts. Third, a functional assessment of estuarine fish communities in response to freshwater inflows in the nearby subtropical Galveston Bay (Texas, USA) was completed by Gonzalez et al. [12]. They found relationships between inflows, salinity, and functional group abundance in the upper segments of the bay, but these diminished with increasing distance from major freshwater sources. In the lower parts of the bay, functional abundance was decoupled from inflows and salinity changes.

Herein, we tested two hypotheses: (1) the distribution of functional groups of fish present in the SABS is influenced by high and low freshwater inflows on the system components, and (2) the prevalence of fish species varies with high and low freshwater inflow conditions; some of these fish may be useful as bioindicator species. Once the fish species were categorized into eleven groups and guilds (Table 1; Table S1), we examined the abundance patterns to assess the relationships to changes in freshwater inflows across broad spatial and temporal scales using a variety of statistical tests. This approach has successfully provided insights into how specific components of the fish community respond to hydrologic change elsewhere [2,23,29]. We also examined which fish species may be suitable bioindicators for freshwater inflows and the health of the SABS. Estuarine-dependent teleost fish species may be considered appropriate bioindicators of abiotic stressors and/or changing estuarine conditions [10,11,13]. Periodic pulses of freshwater can enhance primary productivity and support energy transfer to higher trophic levels [5,11]. Given that the SABS receives less freshwater inflows than Galveston Bay [12], and it is significantly less impacted by urban and industrial influences [3,13,20], this study may also provide management insights for fish assemblages, which reflect the unique hydrologic pressures of this ecosystem.

Table 1. Dominant [1] fish species found in the SABS that were assigned to 11 functional groups based on the estuarine use functional guild methodology developed by Elliott et al. [2], adapted by Franco et al. [23] and recently applied to the nearby Galveston Bay (Gonzalez et al. [12]) [2].

Functional Group (Richness) [3]	Functional Trait: Estuarine Use	Functional Trait: Feeding Guild	Otter Trawl	Gill Net	Dominant Species (Top 90% Abundance of the Dataset)	
ANC (1)	Anadromous	Carnivore				
ERC (22)	Estuarine resident	Carnivore	x		Atlantic croaker	*Micropogonias undulatus*
			x		Bay anchovy	*Anchoa mitchilli*
				x	Black drum	*Pogonias cromis*
				x	Gafftopsail fish	*Bagre marinus*
			x	x	Hardheaded catfish	*Ariopsis felis*
				x	Red drum	*Sciaenops ocellatus*
			x		Silver perch	*Bidyanus bidyanus*
				x	Spotted seatrout	*Cynoscion nebulosus*
ERO (9)	Estuarine resident	Omnivore	x	x	Gulf menhaden	*Brevoortia patronus*
			x	x	Pinfish	*Lagodon rhomboides*
			x	x	Spot	*Leiostomus xanthurus*
				x	Striped mullet	*Mugil cephalus*
FMC (6)	Freshwater migrant	Carnivore		x	Alligator gar	*Atractosteus spatula*
			x	x	Blue catfish	*Ictalurus furcatus*
				x	Longnose gar	*Lepisosteus osseus*
				x	Spotted gar	*Lepisosteus oculatus*
FMO (3)	Freshwater migrant	Omnivore	x	x	American gizzard shad	*Dorosoma cepedianum*
			x		Threadfin shad	*Dorosoma petenense*
FSC (7)	Freshwater straggler	Carnivore				
FSO (3)	Freshwater straggler	Omnivore				

Table 1. *Cont.*

Functional Group (Richness) [3]	Functional Trait: Estuarine Use	Functional Trait: Feeding Guild	Otter Trawl	Gill Net	Dominant Species (Top 90% Abundance of the Dataset)	
MMC (38)	Marine migrant	Carnivore	x		Atlantic bumper	*Chloroscombrus chrysurus*
			x		Atlantic cutlassfish	*Trichiurus lepturus*
			x		Fringed flounder	*Etropus crossotus*
			x		Inshore lizardfish	*Synodus foetens*
			x		Least puffer	*Sphoeroides parvus*
			x		Naked goby	*Croilia mossambica*
			x		Ocellated flounder	*Ancylopsetta ommata*
			x		Pigfish	*Bodianus unimaculatus*
			x		Scaled sardine	*Harengula jaguana*
			x		Silver seatrout	*Cynoscion nothus*
			x		Striped burrfish	*Chilomycterus schoepfi*
MMO (6)	Marine migrant	Omnivore		x	Sheepshead	*Archosargus probatocephalus*
MSC (51)	Marine straggler	Carnivore	x		Atlantic threadfin herring	*Opisthonema oglinum*
				x	Bull shark	*Carcharhinus leucas*
			x		Gulf butterfish	*Peprilus burti*
			x		Gulf toadfish	*Opsanus beta*
MSO (8)	Marine straggler	Omnivore				

[1] Full list of species and details can be found in Table S1. [2] Planktivores (filter feeders) that consume phytoplankton/zooplankton and other smaller animals such as Bay anchovy (*Anchoa mitchilli*) were classified as carnivores. Similarly, Striped mullet (*Mugil cephalus*), which is often classified as a herbivore or detritivore or both, was classified herein as a omnivore. To be consistent with Gonzalez et al. [12] and thereby allow a comparison between Gulf coast estuaries, we acknowledge that (i) estuarine residents (Table 1) may be designated as marine migrants in some studies (depending on the conditions in the estuary and their life cycle stage) and (ii) broader trophic guilds that pool species commonly separated into different guilds in other studies were not used. [3] Richness is the number of species in each functional group.

2. Materials and Methods

2.1. Study Area

The SABS is a semi-arid estuary [30] located along the central Texas Coast, in the northwestern Gulf of Mexico (28°17′ N, 96°44′ W) (Figure 1). Also known as the Guadalupe Estuary, it includes five main sub-bays: San Antonio Bay, Hynes Bay, Guadalupe Bay, Espiritu Santo Bay and Ayres Bay, along with other minor embayments that include Mesquite Bay, Carlos Bay, Mission Lake, and Pringle Lake. This estuary is largely protected from the Gulf of Mexico by Matagorda Island, and it typically does not have a direct connection to the Gulf except through Cedar Bayou when it is occasionally opened by tropical storms [31]. The other closest connection with the Gulf of Mexico is through Pass Cavallo, to the northeast, in the Colorado-Lavaca Estuary [31]. The SABS includes the Aransas National Wildlife Refuge and the Guadalupe Delta Wildlife Management Area (Figure 1). This estuary is a shallow ecosystem that averages 1–2 m in depth, with an area of 551 km^2 [32], with San Antonio Bay being the dominant feature, accounting for 288 km^2. It receives approximately 3.08×10^9 m^3 yr^{-1} (2.5 million acre-feet per year) of freshwater inflows from its major contributing rivers, the Guadalupe River (~70%) on the northeast and San Antonio River (~26%) on the northwest heads of the bay, as well as runoff from surrounding coastal watersheds [33].

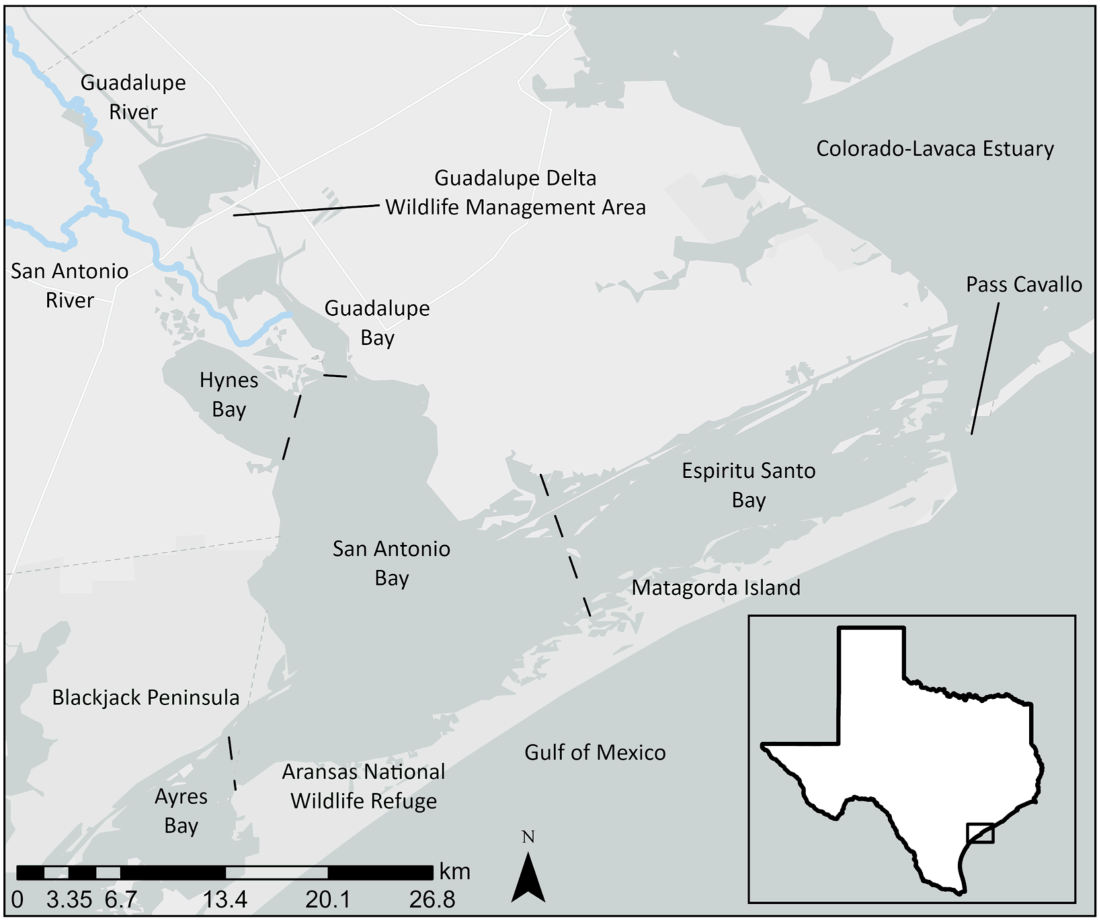

Figure 1. The San Antonio Bay System (also known as the Guadalupe Estuary) is a semi-arid to subtropical estuary located along the central Texas Coast (see arrow in the insert), in the northwestern Gulf of Mexico. Located south of the city of San Antonio (white circle on the Texas map), it has five main sub-bays: San Antonio Bay, Hynes Bay, Guadalupe Bay, Espiritu Santo Bay and Ayres Bay. This estuary is protected from the Gulf of Mexico by Matagorda Island. Pass Cavallo, to the northeast, in the Colorado-Lavaca Estuary provides a connection with the Gulf of Mexico waters. The Aransas National Wildlife Refuge and the Guadalupe Delta Wildlife Management Area along the Blackjack Peninsula are important conservation zones.

Water exchange also occurs with the Colorado-Lavaca Estuary (Matagorda Bay) to the northeast and the Mission-Aransas Estuary to the southwest (Aransas Bay and Copano Bay). Freshwater inputs from the Guadalupe and San Antonio Rivers flow along the western boundary of the bay toward the Aransas National Wildlife Refuge along the Blackjack Peninsula, whereas waters from the Gulf of Mexico enter primarily through Pass Cavallo and penetrate San Antonio Bay from the east—through Espiritu Santo Bay [34]. The SABS is directly adjacent to three counties: Aransas, Refugio, and Calhoun, with a total human population of 50,677 people [35]. Land use in these counties is primarily agricultural (39% or 1456 km^2), while developed land accounts for only 4% of the land area (148 km^2). Upland habitats of scrub shrub (woody vegetation less than or equal to 5 m in height), forested, and grassland habitats cover 30% of the land area (1224 km^2), while woody and emergent wetlands comprise 25% (1006 km^2) of the land [36].

2.2. Data Sources

The Texas Water Development Board (TWDB) calculates the annual freshwater inflows to the SABS by summing the gaged and ungaged inflows from the Guadalupe and San Antonio River basins and other small coastal basins and portions of the Lavaca-Guadalupe and San Antonio-Nueces basins [37]. Gaged flows are those measured by United States Geological Survey (USGS) stream flow gages located at Coleto Creek near Victoria (USGS 8177500), Coleto Creek near Schroeder (USGS 8177000), Guadalupe River at Victoria (USGS 8176500), and San Antonio River at Goliad (USGS 8188500). Downstream of the USGS gages, between the gage and the point where the stream meets the estuary, the streamflow is ungaged and must be estimated by summing the computed streamflow, using (a) the Texas Rainfall-Runoff (TxRR) model; (b) flows diverted from streams by municipal, industrial, agricultural and other users; and (c) unconsumed flows returned to streams [33,37,38]. Using these data, the annual freshwater inflow values were defined in this study as "Low" and "High" by comparing the total annual inflow to the median annual inflows from 1993–2018: 2.94×10^9 m^3 yr^{-1} ($\pm 2.01 \times 10^9$ m^3 yr^{-1}).

The Texas Parks Wildlife Department (TPWD) regularly monitors the fish community (species, abundance, size range) and environmental data in the SABS using a variety of sampling gears [39]. Every month, the TPWD collects 20 otter trawl samples using a geographically random sampling design. Otter trawls (6.1 m wide with 38 mm stretched nylon multifilament mesh) sample open waters at depths $\geq$ 1 m to target juvenile and sub-adult size fishes. Per the TPWD sampling design, the SABS is partitioned into two zones with 10 otter trawl samples randomly collected from each zone per month. Each zone is divided into sample grids (one-minute latitude by one-minute longitude) and each sample grid is comprised of 144 sample gridlets (5 s latitude by 5 s longitude). Sample grids are randomly selected in each zone, followed by the random selection of a sample gridlet within the selected zone [39]. All the trawls are towed at ~4.8 km per hour for 10 min in a circular manner.

Gill nets are deployed seasonally by the TPWD in the spring (10 consecutive weeks beginning in mid-April) and fall (10 consecutive weeks beginning in mid-September). Gill nets are deployed from one hour before sunset to four hours after the following sunrise and are set perpendicular to the shoreline to sample sub-adult and adult fish. The frequency of the gill net deployment by the TPWD in the SABS totaled 45 collections per month during the sampling season [39]. Gill nets are 182.9 m in length and 1.2 m deep, with four 45.7 m long sections of monofilament mesh ranging from 76 mm to 152 mm in mesh size [39].

The catch within each otter trawl and gill net sample is identified to the lowest possible taxonomic level; only individuals identified to the level of the genus and species were used in this study. The present study used data collected in 6240 otter trawl and 2282 gill net samples from 1993 to 2018. Environmental data describing the dissolved oxygen (DO, mg O_2 L^{-1}), water temperature (°C), turbidity (NTU) and salinity (on the unitless practical salinity scale) are collected with every biological sample using a calibrated YSI or HACH meter. Trawl-associated environmental data are collected at 0.3 m above the bay bottom before trawling begins [39]. Gill-net-associated environmental data are collected via surface samples taken from the top 15 cm of the water column at the end of the gill net farthest from shore before net retrieval begins [39].

2.3. Functional Trait Classification

The TPWD sampling efforts yielded 154 fish species (Table S1) that were assigned to functional groups (Table 1) based on the estuarine use functional guild methodology developed by Elliott et al. [2], adapted by Franco et al. [23], and recently applied to Texas estuaries [12]. The trophic guild designations (e.g., carnivore, detritivore, herbivore, omnivore) were also included (Tables 1 and S1); no species were identified as exclusively detritivore or herbivore. The assignment of functional groups was also based on documentation of estuarine habitat use and diet habits by Livingston [40], Bowling [41] and Gonzalez et al. [12]. Fish were also partitioned based on their migratory behavior. Marine and freshwater migrant species exploit estuaries during different parts of their life cycles, while estuarine resident species depend on these ecosystems year-round. Stragglers are somewhat rare, ranging from species that occur "accidentally" in estuaries to those that are opportunistic [24]. The classification approach yielded 11 functional groups: anadromous carnivores (ANC), estuarine resident carnivores (ERC), estuarine resident omnivores (ERO), freshwater migrant carnivores (FMC), freshwater migrant omnivores (FMO), freshwater straggler carnivores (FSC), freshwater straggler omnivores (FSO), marine migrant carnivores (MMC), marine migrant omnivores (MMO), marine straggler carnivores (MSC) and marine straggler omnivores (MSO) (Table S1).

2.4. Statistical Analysis

Multivariate analyses of the environmental and fish assemblage data were conducted using PRIMER v7 [42]. The salinity, water temperature, and DO parameters exhibited normal distributions and were not transformed. Turbidity data yielded a skewed distribution and were transformed (logx + 1; base e) to approximate a normal distribution. All four environmental parameters were normalized in PRIMER to create a common measurement scale. Species abundance counts were used directly and were not converted to catch per unit effort (CPUE) due to the uniform deployment of effort across the sampling period (20, randomized 10 min trawls deployed each month over a 26-year period). Sample abundance was log transformed (logx + 1) to reduce the contribution of the high abundances of common species in relation to rare species.

Multivariate statistical methods were used to assess changes in the annual functional abundance in each of the five sub-bays. By sub-bay, the transformed abundances were averaged for each functional group by year to determine the annual average functional abundance across all the samples for each functional group. The transformed abundances were also averaged for the 26-year period by sub-bay for each functional group (the long-term, period average). For each of the five sub-bays, the annual average abundance for each functional group was normalized to the long-term average. This was performed by calculating the difference between the annual average abundance and the long-term average for each functional group. The resulting value, referred to as the departure from the period average, was plotted against the bay-wide annual TWDB total freshwater inflows. The departure from the period average method uses the long-term average (1993–2018) as a reference level against which the interannual change in functional group abundance can be calculated and compared as a community response to the change in annual freshwater inflows.

Distance-based linear modeling (DISTLM) using the BEST selection procedure and R^2 selection criterion ($R \geq 0.30$) were applied to the sub-bay-scale abundance (Bray–Curtis) and environmental similarity (Euclidian distance) matrices to determine the statistical correlations between candidate environmental predictor variables and annual functional abundance response variables. The alpha significance for the DISTLM marginal tests was set to $p < 0.05$. ANOSIM analysis was performed on the transformed abundance data to determine the percent contribution of functional groups to the overall abundance across the estuary. SIMPER analysis was also carried out on the transformed abundance data to observe the percent contribution of functional groups to the overall abundance across the estuary. Only fish species that accounted for the top 90% were included.

3. Results

3.1. Environmental Conditions

The annual freshwater inflow values were defined in this study as "Low" and "High" by comparing the total annual inflow to the median annual inflows from 1993 to 2018: 2.94×10^9 m^3 yr^{-1} ($\pm$ 2.01×10^9 m^3 yr^{-1}) (Figures 2 and 3; dashed line). Low inflow years occurred in 1994–1996, 1999, 2000, 2003, 2005–2006, 2008–2009, and 2011–2014. The last time range (2011–2014) coincided with the period of a prolonged statewide drought [43]. High flow years were 1993, 1997–1998, 2001–2002, 2004, 2007, 2010, and 2015–2018 (Figures 2 and 3). Floods are not uncommon in this part of Texas. Historic river crests determined to be in the major flood category for the San Antonio and Guadalupe Rivers occurred in 1998, 2002, 2004, 2007, and 2010 (https://water.weather.gov/ (accessed on 15 July 2022)).

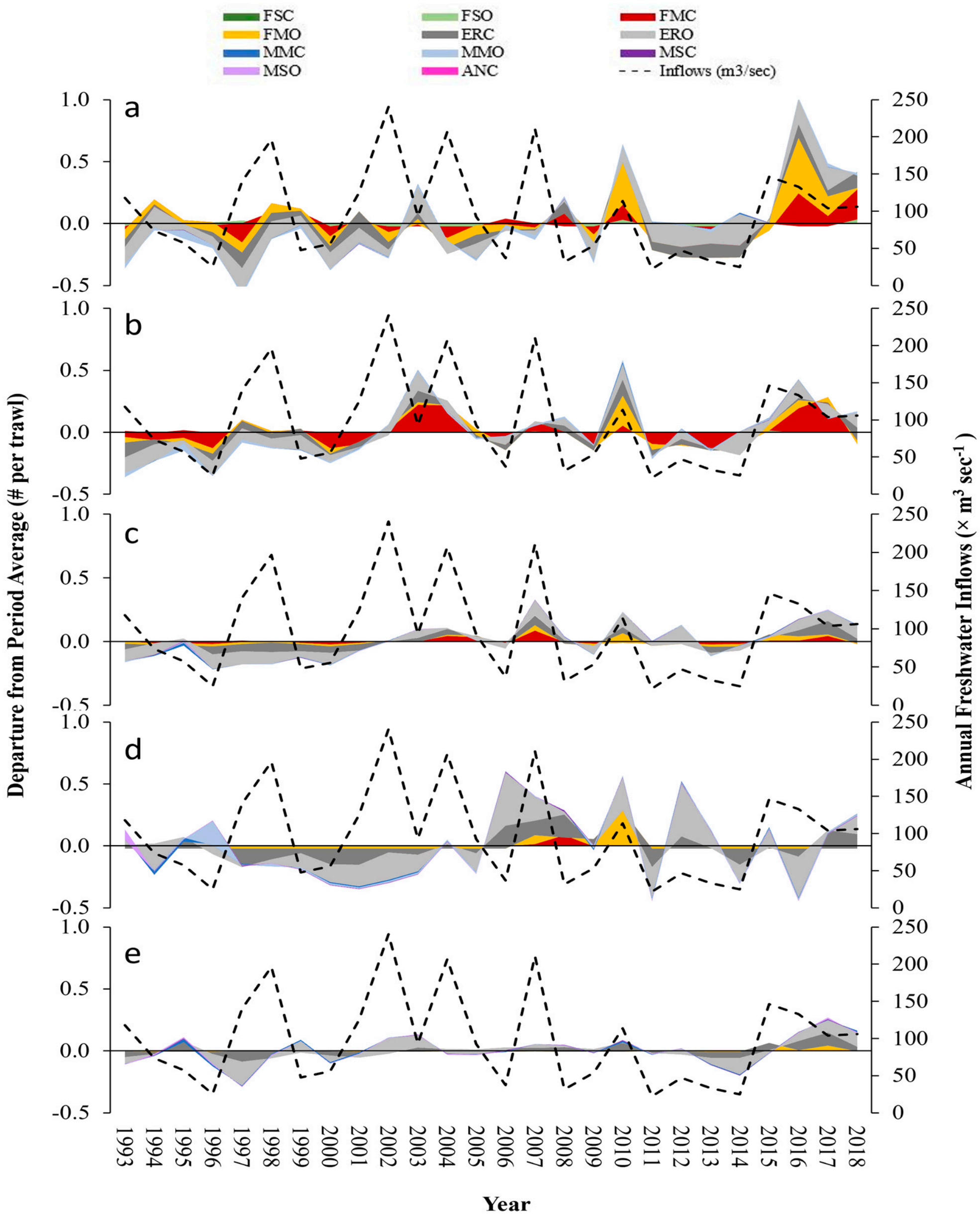

Figure 2. Functional group abundance departure from the average for species captured in otter trawls (1993–2018) in the San Antonio Bay System: (**a**) Guadalupe Bay, (**b**) Hynes Bay, (**c**) San Antonio Bay, (**d**) Ayres Bay, and (**e**) Espiritu Santo Bay. Annual freshwater inflows (dashed line; $\times 10^9$ m^3 yr^{-1}) were defined as "Low" or "High" relative to the median annual inflow from 1993 to 2018.

The environmental conditions in the SABS were summarized by sub-bay (standard deviations of means are presented) and by low and high flow conditions (Table 2). There were between 4461 and 4469 otter trawls and gill net samples collected during the low inflow years and between 3770 and 3378 during the high inflow years. The sample sizes differed between years and sub-bays because of missing values (typically due to equipment failures). The 26-year average temperature and DO were similar between low and inflow years, but the salinity and turbidity were much more variable during low compared to high inflow years. The Guadalupe Bay salinities were the lowest, on average 6.5 (±8.2, 0–29.6) and 2.0 (±4.2, 0–23.2) during low and high inflow years, followed by those in Hynes Bay (11.7 ± 8.8 and 4.1 ± 4.5, respectively), with intermediate values in San Antonio Bay (20.6 ± 9.8 and 12.2 ± 9.7, respectively). The salinities in Ayres Bay were generally lower than those measured in Espiritu Santo Bay, and high flow periods freshened these areas by more than seven compared to low flow periods. The differences in salinities across the sub-bays reflect the primary freshwater and marine end members, respectively (Figure 1). The temperature and DO did not vary significantly between sub-bays, low and high inflows when performing a side-by-side comparison (Table 2). As with salinity, the turbidity was highly variable. The turbidities were lowest in Espiritu Santo Bay, on average 8.4 NTU ± 10.1 and 10.9 NTU ± 23 during low and high inflows, while those in Ayres Bay were higher (average 24.3 NTU ± 26.2 and 40.5 NTU ± 46.4, respectively). On average, the turbidities in Guadalupe Bay and Hynes Bay (averages > 29.7 NTU) where twice those in San Antonio Bay and four-times those in Espiritu Santo Bay (Table 2).

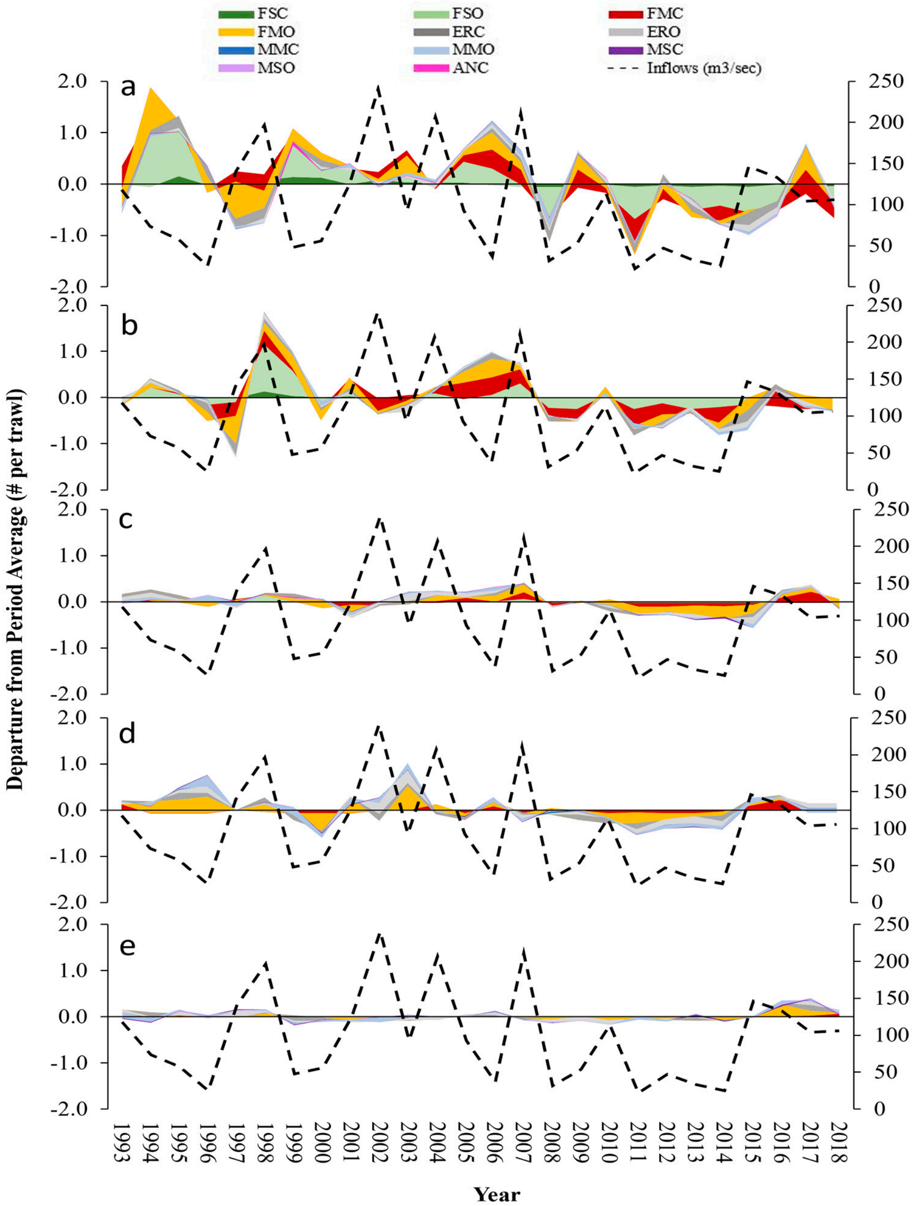

Figure 3. Functional group abundance departure from the average for species captured in gill nets (1993–2018) in the San Antonio Bay System: (**a**) Guadalupe Bay, (**b**) Hynes Bay, (**c**) San Antonio Bay, (**d**) Ayres Bay, and (**e**) Espiritu Santo Bay. Annual freshwater inflows (dashed line; $\times 10^9$ m^3 yr^{-1}) were defined as "Low" or "High" relative to the median annual inflow from 1993 to 2018.

Table 2. Descriptive statistics of environmental data in low inflow versus high inflow years collected in 8522 otter trawl and gill net samples deployed in the five sub-bays of the San Antonio Bay System from 1993 to 2018.

	Low Inflow		High Inflow	
	n	**Mean ± SD (Range)**	**n**	**Mean ± SD (Range)**
Salinity	*4461*	*21.4 ± 10.3 (0.0–43.0)*	*3776*	*14.1 ± 10.0 (0.0–37.0)*
Guadalupe	203	6.5 ± 8.2 (0.0–29.6)	164	2.0 ± 4.2 (0.0–23.2)
Hynes	319	11.7 ± 8.8 (0.0–35.0)	272	4.1 ± 4.5 (0.0–20.0)
San Antonio	2709	20.6 ± 9.8 (0.0–43.0)	2326	12.2 ± 8.7 (0.0–37.0)
Ayres	74	22.5 ± 9.1 (0.0–39.6)	70	15.1 ± 7.9 (0.0–35.0)
Espiritu Santo	1156	28.6 ± 5.3 (5.0–41.0)	944	23.6 ± 7.2 (0.0–36.8)
***Temperature* (°C)**	*4465*	*23.7 ± 6.0 (6.6–34.0)*	*3778*	*23.7 ± 6.1 (5.9–34.8)*
Guadalupe	203	24.4 ± 5.9 (9.8–33.1)	164	24.3 ± 6.0 (5.9–32.5)
Hynes	318	24.3 ± 6.1 (8.0–32.3)	272	23.7 ± 6.1 (8.1–32.0)
San Antonio	2713	23.5 ± 6.3 (6.6–34.0)	2327	23.6 ± 6.3 (6.5–34.8)
Ayres	75	24.9 ± 6.1 (7.4–31.5)	71	26.7 ± 4.1 (13.6–33.2)
Espiritu Santo	1156	23.8 ± 5.3 (9.3–32.9)	944	23.5 ± 5.5 (9.0–33.3)
***Dissolved Oxygen* (mg O_2 L^{-1})**	*4469*	*7.7 ± 1.8 (1.1–18.5)*	*3776*	*7.9 ± 1.9 (0.4–19.7)*
Guadalupe	203	7.9 ± 1.9 (2.0–16.9)	164	8.0 ± 2.4 (1.7–19.6)
Hynes	319	8.1 ± 2.1 (1.1–16.3)	272	8.3 ± 2.1 (2.3–17.3)
San Antonio	2715	7.7 ± 1.8 (1.4–18.5)	2326	8.0 ± 1.8 (0.4–19.7)
Ayres	76	7.8 ± 1.9 (4.7–14.0)	71	7.6 ± 1.6 (2.6–14.0)
Espiritu Santo	1156	7.5 ± 1.6 (2.2–16.0)	943	7.7 ± 1.6 (1.4–14.6)
***Turbidity* (NTU)**	*4465*	*17 ± 29.0 (0.0–771.0)*	*3770*	*25.9 ± 39.3 (0.0–565.0)*
Guadalupe	202	37.3 ± 48.4 (1.0–426.0)	164	43.5 ± 50.9 (4.0–494.0)
Hynes	319	29.7 ± 39.3 (1.0–390.0)	271	54.3 ± 58.0 (2.0–454.0)
San Antonio	2712	17.4 ± 29.7 (0.0–771.0)	2324	27.1 ± 38.0 (0.0–565.0)
Ayres	76	24.3 ± 26.2 (1.0–109.0)	71	40.5 ± 46.4 (1.0–234.0)
Espiritu Santo	1156	8.4 ± 10.1 (0.0–125.0)	940	10.9 ± 23.0 (0.0–452.0)

3.2. Functional Assemblage of Fish Community

The TPWD otter trawls and gill nets captured 154 species of fish in the SABS (n = 201,648 individuals), representing 11 functional groups (Tables 1 and S1). The functional groups with the greatest species richness were the MSC (51 species), MMC (38 species), and ERC (22 species), while the rare functional groups included the FMO (3 species), FSO (3 species) and ANC (1 species) (Table S1). The most abundant species collected in the otter trawl and gill net samples were Atlantic croaker (*Micropogonias undulatus*, Linnaeus, 1766), spot (*Leiostomus xanthurus*, Germain de Lacépède, 1802), hardhead catfish (*Ariopsis felis*, Linnaeus, 1766), pinfish (*Lagodon rhomboides*, Linnaeus, 1766) and black drum (*Pogonias cromis*, Linnaeus, 1766) (Table 1). These five species accounted for 15.8%, 12.3%, 10.4%, 7.7%, and 7.3% of the total catch in the SABS over the study area period.

3.3. Spatial-Temporal Distribution of Functional Abundance

The spatial distributions of the fish caught in the otter trawls differed among the sub-bays (Figure 2). Guadalupe Bay and Hynes Bay had five and four functional groups, representing most fish in each sub-bay, respectively. Ayres Bay exhibited the highest functional diversity, with seven functional groups represented in the otter trawl catch, while San Antonio and Espiritu Santo Bay had intermediate numbers (Figure 2). In the early 1990s, marine species were captured in all the lower sub-bays, particularly Ayres Bay, but less so toward the end of the study period (Figure 2). The ERC functional group was present in all five sub-bays in relatively similar proportions each year (Figure 2). We found that the ERO group was more commonly present in the lower reaches of the SABS, with Guadalupe Bay and Hynes Bay together having about one-third of the functional group catch (Figure 2). Espiritu Santo Bay had a largest fraction of EROs (28%), much more than San Antonio Bay (19%) and Ayres Bay (24%) (Figure 2c–e). Freshwater stragglers were present, albeit only accounting for a small fraction (<5%) of the total abundance, in Guadalupe Bay and largely absent from Hynes Bay. FMC species were very abundant in Guadalupe Bay and Hynes Bay (58% and 34% of the total FMC abundance, respectively), while FMOs were most abundant in Guadalupe Bay, accounting for 47% of the total FMO abundance (Figure 2a,b).

The gill net patterns (Figure 3) were very different from those observed for the otter trawls (Figure 2). The freshwater stragglers accounted for the greatest abundance (almost 70% of freshwater fishes at different times) in Guadalupe Bay and Hynes Bay (Figure 3a,b) but were present in almost negligible quantities in the rest of the SABS (Figure 3c–e). FSOs were most prevalent in the upper sub-bays, accounting for most of the freshwater fish community relative to the FSC, FMO and FMC (Figure 3a,b), with a few exceptions (1997–1998 and 2017 in Guadalupe Bay and 2015–2018 in Hynes Bay). FMC and FMO were present in all the sub-bays and so were important contributors to the functional diversity of the SABS (Figure 3). In terms of the relative abundance, FMC and FMO were present in relatively higher densities in the upper bays, intermediate levels in San Antonio Bay and Ayres Bay, and the fewest were observed in Espiritu Santos Bay. In the gill nets, ANC were frequently caught in Guadalupe Bay but not in Hynes Bay. San Antonio Bay, Ayres Bay and Espiritu Santo Bay had greater numbers of functional groups present (Figure 3), with both estuarine and marine species were frequently caught. There was a greater abundance of fish in San Antonio Bay and Ayres Bay relative to Espiritu Santo Bay, with FMC, FMO, ERC, ERO and MMO being common functional groups, with their relative abundance being variable between years and locations.

The annual abundance across functional groups was associated with changes in the freshwater inflows—low inflow years corresponded to declines in the overall functional group abundance and high inflow years corresponded to increases in the overall functional group abundance (Figures 2 and 3). The patterns in Guadalupe Bay and Hynes Bay were driven by the FMC, FMO, ERC and ERO functional groups in the otter trawls (Figure 2). FSC and FSO, along with FMC and FMO, were more important in defining the functional group distributions in the gill nets than ERCs and EROs in Guadalupe Bay and Hynes Bay (Figure 3). The relationships between the functional diversity, abundance, and freshwater inflows were less apparent in the lower reaches of this ecosystem when examining the otter trawl data (Figure 2). When examining the gill nets, the patterns related to freshwater inflows were primarily driven by FMO and FMC, and to a lesser extent by the ERO and ERC functional groups, in San Antonio Bay and Ayres Bay but not Espiritu Santo Bay (Figure 3). The relationship between the freshwater inflow volume and the patterns in functional group abundance weakened with increasing distance from major freshwater inflows sources.

3.4. *Effect of Environmental Parameters on Functional Assemblage*

Distance-based linear modeling (DISTLM) was used to determine the correlation between environmental variables and functional group annual abundance in the otter trawls and gill nets. The DISTLM results for water temperature, DO, and turbidity were not statistically significant in any of the sub-bays of this estuary (Tables 3 and 4). The DISTLM marginal results showed salinity having a significant correlation with functional abundance in fish caught in otter trawls in Guadalupe Bay ($p = 0.001$) and Hynes Bay ($p = 0.001$), but not in the other sub-bays (Table 3). The DISTLM results showed turbidity had a significant correlation in San Antonio Bay ($p = 0.031$), while temperature was significantly correlated in Espiritu Santo Bay ($p = 0.002$). In Ayres Bay, both temperature ($p = 0.001$) and DO ($p = 0.001$) had significant correlations with functional abundance in fish caught in otter trawls (Table 3). Based on the BEST overall model for otter trawls, the variance in functional abundance was explained by all four environmental parameters in Ayres Bay and Espiritu Santo Bay ($R^2 = 0.40$ and 0.27, respectively). The four environmental variables explained only ~22% of the variation in annual functional abundance in the otter trawls in Guadalupe Bay, Hynes Bay and San Antonio Bay (Table 3).

Table 3. Marginal test results of DISTLM and resulting BEST R^2 between environmental variables in five sub-bays of the San Antonio Bay System and abundance of 11 functional groups collected using otter trawls.

	Salinity	Temperature (°C)	Dissolved Oxygen (ppm)	Turbidity (NTU)
Guadalupe Bay R^2 = 0.22	p = 0.001	p = 0.484	p = 0.441	p = 0.902
Hynes Bay R^2 = 0.23	p = 0.001	p = 0.349	p = 0.243	p = 0.256
San Antonio Bay R^2 = 0.22	p = 0.13	p = 0.48	p =0.505	p = 0.031
Ayres Bay R^2 = 0.40	p = 0.166	p = 0.001	p = 0.001	p = 0.286
Espiritu Santo Bay R^2 = 0.27	p = 0.353	p = 0.002	p = 0.634	p = 0.559

Table 4. Marginal test results of DISTLM and resulting BEST R^2 between environmental variables in five sub-bays of the San Antonio Bay System and abundance of 11 functional groups collected using gill nets.

	Salinity	Temperature (°C)	Dissolved Oxygen (ppm)	Turbidity (NTU)
Guadalupe Bay R^2 = 0.31	p = 0.001	p = 0.059	p = 0.658	p = 0.582
Hynes Bay R^2 = 0.48	p = 0.001	p = 0.007	p = 0.024	p = 0.091
San Antonio Bay R^2 = 0.17	p = 0.016	p = 0.394	p = 0.016	p = 0.716
Ayres Bay R^2 = na	p = 0.293	p = 0.60	p = 0.20	p = 0.149
Espiritu Santo Bay R^2 = na	p = 0.093	p = 0.209	p = 0.715	p = 0.111

The correlations between environmental variables and functional group annual abundance in the gill nets determined using DISTLM (Table 4) were not identical to those for otter trawls (Table 3). The DISTLM marginal results showed salinity (p = 0.001) and temperature (p = 0.007) had a significant correlation with functional abundance in fish caught in gill nets in Hynes Bay, but only salinity (p = 0.001) was significant in Guadalupe Bay (Table 4). In San Antonio Bay, the DISTLM results found salinity (p = 0.016) and DO (p = 0.016) had a significant correlation. There were no significant correlations in Espiritu Santo Bay or Ayres Bay between environmental variables and functional abundance in gill nets (Table 4). Based on the BEST overall model for gill nets, the variance in functional abundance was explained by all four environmental parameters in Guadalupe Bay and Hynes Bay (R^2 = 0.48 and 0.31, respectively). The four environmental variables explained only 17% of the variation in annual functional abundance in gill nets in San Antonio Bay (Table 4) and could not explain the variability in Ayres or Espiritu Santo Bays.

3.5. Functional Group and Species Response to High and Low Inflows

The effects of inflows on the functional group and species abundance in high and low inflow years were analyzed using SIMPER (Figures 4 and 5). As part of this analysis, only the fishes in the top 90% abundance of the dataset were included. In the otter trawls, SIMPER analysis showed that the greatest contributions to similarity resulted from the abundances of the FMC, FMO, ERC, and ERO functional groups in Guadalupe Bay and Hynes Bay; the FMO, ERC, and ERO functional groups in San Antonio Bay; and the ERC, ERO, MMC, and MSC functional groups in Ayres Bay and Espiritu Santo Bay (Figure 4). The effects of inflows on the functional group abundance in gill nets in high and low inflow years analyzed in the SIMPER analysis showed that the greatest contributions to similarity resulted from the abundances of the FMC, FMO, ERC, and FSO functional groups in Guadalupe Bay and Hynes Bay; the ERC, ERO, and FMO functional groups in San Antonio Bay and Ayres Bay; and the ERC, ERO, and MMO functional groups in Espiritu Santo Bay (Figure 5). FSOs were present in higher abundances than EROs in these sub-bays; larger freshwater species (e.g., smallmouth buffalo, *Ictiobus bubalus*, Rafinesque, 1818) able to move downstream with favorable/lower salinities. The abundant groups in the upper sub-bays were the freshwater functional groups, while those in the lower sub-bays had a stronger relationship to the marine environment present in the lower estuary. Further, MMC and MSC are transitory marine species entering sub-bays nearer the Gulf, similar to the pattern observed in the nearby Galveston Bay [12].

In the otter trawls, the analysis showed that the two functional groups (ERC and ERO) provided the greatest contributions to the overall similarity of the catch across the five sub-bays during high and low inflow periods (Figure 4). The ERC functional group was dominated by Atlantic croaker (62–77%), bay anchovy (8.9–10.2%) and silver perch (*Bidyanus bidyanus*, Mitchell, 1838, 5.8–7.4%), while the ERO functional group was dominated by Gulf menhaden (*Brevoortia patronus*, Goode, 1878 52–67%) and spot (26–38%) during high flow years in Guadalupe Bay (Figure 4a). In low inflow years, the ERC also included hardheaded catfish (11%) in this sub-bay (Figure 4b). During high inflows in Hynes Bay, Atlantic croaker contributed to 57% of the ERC, while bay anchovy and silver perch both contributed ~14% and hardheaded catfish only 5% (Figure 4c), and the ERO functional group was dominated by Gulf menhaden (84%) and spot (9%) (Figure 4b). During low flow years in Hynes Bay, the ERC were dominated by the same for fishes with similar contribution, but the ERO functional group now included pinfish (5%) (Figure 4d). The fish species contributed significantly and in similar proportions to the ERC and ERO functional groups in Antonio Bay, with them collectively accounting for 90% of the fish populations during both high and low flows (Figure 4e,f). In the Ayres Bay otter trawls, the ERC functional group dominated and was composed of Atlantic croaker, silver perch, hardheaded catfish and bay anchovy; these fishes accounted for a greater abundance of the fish population during high inflows than the ERO functional group, which was dominated by pinfish and spot (Figure 4g), with these species contributing to 56%, 14.1%, 12.9% and 8.8% and 52% and 40%, respectively. By contrast, during low inflow periods in Ayres Bay, the ERC community shifted to Atlantic croaker (66%), bay anchovy (14%) and silver perch (10%), while the ERO shifted to pinfish (43%), spot (43%) and Gulf menhaden (8.6%) (Figure 4h). Only in Espiritu Santo Bay did the ERO (spot and pinfish) functional group contribute to a larger fraction of the fish community than the ERC (Atlantic croaker, bay anchovy, silver perch, hardheaded catfish) functional group during both high and low inflow years (Figure 4i,j).

The FMC functional group in the otter trawls was dominated by blue catfish (*Ictalurus furcatus*, Valenciennes, 1840) during both high and low inflow years (Figure 4). This species contributes to a decreasing fraction of the community from Guadalupe Bay (99.8%) to Hynes Bay (98.45%) to San Antonio Bay (73.1%), and it was absent in Ayres Bay and Espiritu Santo Bay. American gizzard shad (*Dorosoma cepedianum*, Lesueur, 1818; FMO) was present during high inflows in all five sub-bays (>66.7%) but contributed to a decreasing proportion of the community with increasing distance from the river mouths (Figure 4). During low inflows, American gizzard shad was present in the upper portions of the estuary (Guadalupe Bay, Hynes Bay, and San Antonio Bay) as the dominant species of the FMO functional group (>97.8%) of the community in Guadalupe Bay, Hynes Bay, and San Antonio Bay. Threadfin shad (*Dorosoma petenense*, Günther, 1867), which is also part of FMO was important during high inflows in San Antonio Bay and Espiritu Santo Bay only and absent in low inflow years (Figure 4). A notable functional group shift in the otter trawl samples was observed in Ayres Bay between high inflow and low inflow years: FMO shifted to MMC and MSC functional groups respectively (Figure 4g,h). During high inflow years, FMO were 100% American gizzard shad. However, in low inflow years, four MMC species were caught: least puffer (*Sphoeroides parvus*, Shipp and Yerger, 1969 45%), fringed flounder (*Etropus crossotus*, Jordan and Gilbert, 1882, 23%), inshore lizardfish (*Synodus foetens*, Linnaeus, 1766, 13%), and naked goby (*Croilia mossambica*, Lacepède, 1800, 11%); and three MSC species: Gulf toadfish (*Opsanus beta*, Goode and Bean, 1880, 37%), Gulf butterfish (*Peprilus burti*, Fowler, 1944, 32%), and Atlantic threadfin herring (*Opisthonema oglinum*, Lesueur, 1818, 32%).

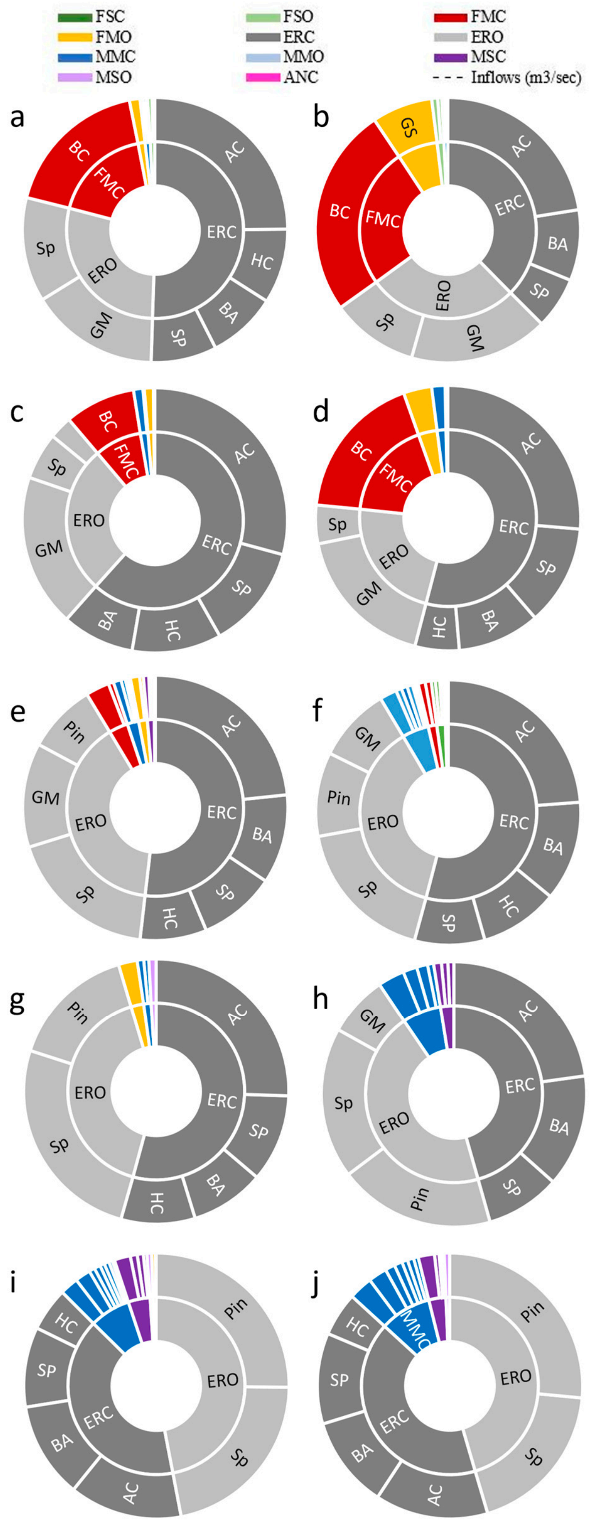

Figure 4. Otter trawl average species abundance by functional group in each sub-bay during low (left) versus high (right) inflow in the San Antonio Bay System, respectively. (**a**,**b**) Guadalupe Bay, (**c**,**d**) Hynes Bay, (**e**,**f**) San Antonio Bay, (**g**,**h**) Ayres Bay, and (**i**,**j**) Espiritu Santo Bay. Functional groups (color coded) are shown in the inner circle and the corresponding fish species are given in the outer circle. Full fish names are given in Table S1, along with the abbreviations used in this figure. The most common fish named in alphabetical order are Atlantic croaker (AC), bay anchovy (BA), blue catfish (BC), gafftopsail catfish (GC), Gulf menhaden (GM), hardheaded catfish (HC), pinfish (Pin), silver perch (SP), and spot (Sp).

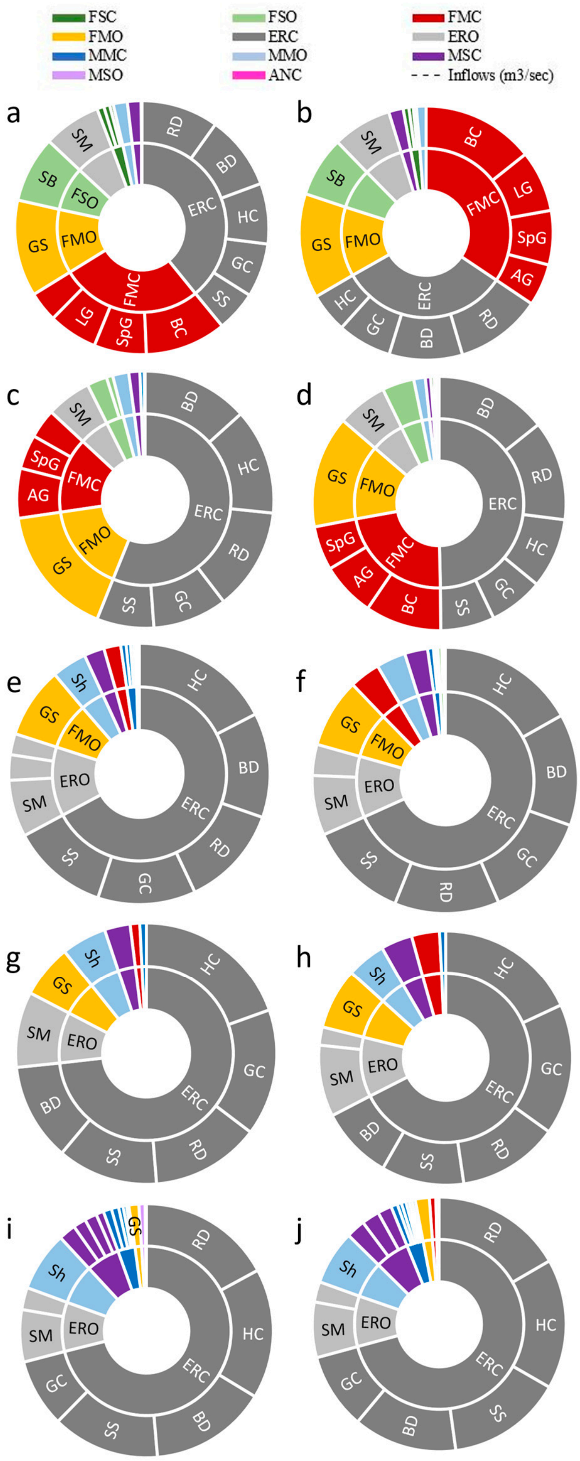

Figure 5. Gill net average species abundance by functional group in each sub-bay during low (left) versus high (right) inflow in the San Antonio Bay System, respectively. (**a**,**b**) Guadalupe Bay, (**c**,**d**) Hynes Bay, (**e**,**f**) San Antonio Bay, (**g**,**h**) Ayres Bay, and (**i**,**j**) Espiritu Santo Bay. Functional groups (color coded) are shown in the inner circle and the corresponding fish species are given in the outer circle. Full fish names are given in Table S1, along with the abbreviations used in this figure. The most common fish named in alphabetical order are alligator gar (AG), black drum (BD), blue catfish (BC), gafftopsail catfish (GC), gizzard shad (GS), hardheaded catfish (HC), longnose gar (LG), red drum (RD), sheepshead (Sh), smallmouth buffalo (SB), spotted gar (SpG), spotted seatrout (SS), and striped mullet (SM).

In the lower reaches of the estuary, the MMC and MSC functional groups contributed to a larger fraction of the otter trawls' community than what was present in the upper reaches of the estuary (Figure 4). Unlike ERC, ERO, FMC and FMO, these two functional groups consisted of a greater diversity of species. In Espiritu Santo Bay during high inflows (Figure 4i), the following MMC were present (and their relative abundances): pigfish (*Bodianus unimaculatus*, Günther, 1862, 38%), Atlantic bumper (*Chloroscombrus chrysurus*, Linnaeus, 1766, 22%), Atlantic cutlassfish (*Trichiurus lepturus*, Linnaeus, 1758, 10.5%), fringed flounder (7.3%), least puffer (4.5%), silver seatrout (*Cynoscion nothus*, Holbrook, 1848, 3%), ocellated flounder (*Ancylopsetta ommata*, Jordan and Gilbert, 1883, 3.3%) and striped burrfish (*Chilomycterus schoepfi*, Walbaum, 1792, 1.9%). In contrast, during low inflows, inshore lizardfish appeared but ocellated flounder and striped burrfish disappeared (Figure 4j). The MMC fish community assemblage was very different in Ayres Bay during high and low inflows, with scaled sardine (*Harengula jaguana*, Poey, 1865, 39%) and fringed flounder (60%) comprising the majority of the MMC community during high inflows, while least puffer (45%), fringed flounder (23%), inshore lizardfish (13%) and naked goby (11%) made up the community during low inflows (Figure 4).

In the gill nets, the analysis showed that the ERC functional group provided the greatest contribution to the overall similarity of the catch across the five sub-bays during high and low inflow periods (Figure 5), but particularly in the lower reaches. In Guadalupe Bay, during high and inflows (Figure 5a), the ERC and FMC functional groups dominated the catch (Figure 5a,b). The ERC during high flows included primarily red drum (*Sciaenops ocellatus*, Linnaeus, 1766, 42%), black drum (24%), gafftopsail fish (*Bagre marinus*, Mitchill, 1815, 19%) and hardheaded catfish (9%). During low inflows, in Guadalupe Bay (Figure 5b), the ERC functional group comprised similar fishes as during high inflows, but in this case also included spotted seatrout (*Cynoscion nebulosus*, Cuvier, 1830, 10%). FMC were important during both high and low inflows and in similar proportions, with blue catfish (43–51%), longnose gar (*Lepisosteus osseus*, Linnaeus, 1758, ~19%), spotted gar (*Lepisosteus oculatus*, Winchell, 1864, 16–24%) and alligator gar (*Atractosteus spatula*, Lacépède, 1803, ~13%) comprising the greatest similarity. The FMO functional group was entirely compromised of American gizzard shad in both inflow conditions (Figure 5a,b); likewise, smallmouth buffalo and striped mullet were the dominant members of the FSO and ERO groups.

Unlike Guadalupe Bay, Hynes Bay was dominated by estuarine fishes, including ERCs and EROs, and to a lesser extent, freshwater fishes in the FMC and FMO (Figure 5). The similarity of the catch during high and low inflows in Hynes Bay is reflected in the similarity in contributions by black drum, red drum, hardhead catfish, gafftopsail catfish and spotted seatrout (ERCs) and stiped mullet (ERO), accounting for 56% and 62% of the catch in high and low flow years, respectively (Figure 5c,d). FMC (blue catfish, alligator gar and spotted gar) accounted for a larger proportion of the community in high than low flow years, while FMOs (American gizzard shad) and FSOs (smallmouth buffalo) were similar. The fishes in these functional groups contributed similarly to the community composition (Figure 5c,d).

The contributions of FMC, FMO and FSO to the overall abundance and similarity decreased with distance from the mouths of the freshwater rivers (Figure 5). In the middle of the SABS, ERCs and EROs dominated (~80%) populations in San Antonio Bay. The estuarine fishes present had similar abundances irrespective of high or low flows (Figure 5e,f), with hardhead catfish, black drum, gafftopsail catfish, red drum, spotted seatrout, striped mullet, Gulf menhaden and spot accounting for 80% of the community. MMO and MSC appeared in increasing abundance in San Antonio Bay relative to the upper bay segments (Guadalupe and Hynes Bays), with sheepshead (*Archosargus probatocephalus*, Walbaum, 1792) and bull shark (*Carcharhinus leucas*, Valenciennes, 1839), respectively, frequently making up 6% of the catch.

The Ayres Bay fish catch was also dominated by the ERC and ERO functional groups, together accounting for 78% and 83% of the species during high and low inflow years, respectively (Figure 5g,h). Hardhead catfish (~26), gafftopsail catfish (~22%), red drum

(~18%), spotted seatrout (~14%) and black drum (~11%) were the commonly found ERC. During high flow years, striped mullet and Gulf menhaden were important, while in low years, the striped mullet contributed. Gizzard shad (FMO) accounted for between 6 and 8% of the community in Ayres Bay, while sheepshead (MMO) and bull shark (MSC) accounted for ~5% and 3%, respectively. There were three times more alligator gar present during high flows than low flows.

While the Espiritu Santo Bay gill net samples had similar proportions and populations during high and lows flows in terms of ERC, ERO and MMO and those present in Ayres Bay, distinct patterns were observed for MSC and MMC which accounted for both a greater proportion of the fish population as well as its diversity compared to that observed in Ayres Bay (Figure 5i,j). In Espiritu Santo Bay, bonnethead (*Sphyrna tiburo*, Linnaeus, 1758), bull shark and blacktip shark (*Carcharhinus limbatus*, Valenciennes, 1839) were often caught, accounting for 6% of the population present during high flow years. In low flow years, Spanish mackerel (*Scomberomorus maculatus*, Mitchill, 1815) was also part of the MSC catch in this bay. MMCs, when present, were most often found in the Espiritu Santo Bay gill nets (Figure 5i,j). Florida pompano (*Trachinotus carolinus*, Linnaeus, 1766), crevalle jack (*Caranx hippos*, Linnaeus, 1766), cownose ray (*Rhinoptera bonasus*, Mitchill, 1815), pigfish, Gulf flounder (*Paralichthys albiguttata*, Jordan and Gilbert, 1882), southern kingfish (*Menticirrhus americanus*, Linnaeus, 1758) and grey snapper (*Lutjanus griseus*, Linnaeus, 1758) contributed to this functional group in similar abundances regardless of being caught in high or low flow years.

4. Discussion

Given the inherent environment of estuaries, the ecological effects of anthropogenic stressors can be difficult to differentiate from natural variation [1,18,19,21,29]. In functional classification approaches, the characteristics of fishes are used to identify the ecological community structure and connectivity [2,23,26,27,29,44–46], thereby increasing the specificity of information that can be used to understand the relationships between species responses and environmental impacts [24,29,45–47]. This approach has been used worldwide, and recently, in the nearby Galveston Bay, which is also located on the upper Texas coast in the northwestern Gulf of Mexico [12]. This tool provides information at a time when increasing pressures are being placed on freshwater resources upstream and extreme weather events such as drought and floods are altering the hydrological characteristics of estuaries downstream of riverine sources [7,22,48–50]. In addition, given that estuarine ecosystem health is fundamentally dependent on freshwater inflows, there is an ongoing need to find a balance between the supply and demand of this resource [11,12] and sustain ecosystem services despite increasing external pressures [13]. Further, some ecosystems are seeing species shifts associated with the tropicalization of fish [8,18,19]. As such, some fish species may be used as bioindicators to assess the ecological quality and function of estuarine ecosystems [10,11,13,22,47,51], but others may not be a viable option. Herein, we show that the distribution of functional groups of fish present in the SABS varies throughout this estuarine system, with freshwater inflows having a greater influence on some system components over the others (Figures 2 and 3). In addition, the prevalence of fish species in each system component varies with high and low freshwater inflow conditions (Figures 4 and 5); some of these fish may be useful as bioindicator species to understand the health and function of this ecosystem.

4.1. Functional Redundancy in the Functional Groups

Ichthyofaunal communities are often studied to understand ecosystem resilience and/or responses to climate change [18,28,47,50,52]. In terms of the functional redundancy in the functional groups, if the ecosystem starts losing species in a functional group, does that mean the group will be less resilient to climate change? This is a difficult question to answer because it is not always clear what the underlying cause of species loss is and when that loss is permanent versus transient. For example, Atlantic croaker estimates are now once again within acceptable ranges in the SABS [28], reflecting a recovery due to the shrimp fisheries closures in the early 1990s [53,54]. This species was once a substantial component of the shrimping industry by catch (unintended catch), making the recovery a significant finding. On the other hand, southern flounder, which has also been declining since the early 1990s (based on available records) in the SABS, has not recovered. Both warming bay waters and overfishing were implicated as contributors to their population decline. Fisheries' closures have also led to an increase in abundances of black drum, one of the more dominant large fish in the SABS, as well as redfish and the sought-after spotted seatrout [28]. These fishes were each targeted both commercially and recreationally but in recent decades have been the subject of harvest restrictions in the SABS to protect the population and affect recovery [53]. And indeed, their populations have been increasing since gill nets were banned in 1988 [54]. The fishes mentioned here (Atlantic croaker, southern flounder, black drum, spotted seatrout) are representatives of the ERC functional group; their distribution and prevalence in the SABS were also found to be influenced by high and low freshwater inflows on the system components, supporting our hypotheses. However, these fish are not good bioindicators for freshwater inflows given their estuarine nature (see more below).

In terms of the functional diversity and functional abundance in the SABS, red drum, gafftopsail catfish and spotted seatrout made up a large fraction of the ERCs in the gill nets under high and low inflows, respectively, while black drum are more important under high inflows and hardhead catfish during low inflows. In the otter trawls, the ERC functional group was dominated by Atlantic croaker, while the ERO functional group was dominated by Gulf menhaden and spot. All these species are euryhaline with broad salinity tolerances [55,56]. Other important ERC members are the bay anchovy, silver perch and hardheaded catfish, while in the ERO functional group, pinfish were important mid-bay and closer to the Gulf of Mexico. Only in Espiritu Santo Bay did the ERO functional group (with mostly spot and pinfish) contribute to a larger fraction of the fish community than the ERCs (Atlantic croaker, bay anchovy, silver perch, hardheaded catfish) during both high and low inflow years. In the gill nets, red drum, black drum, gafftopsail fish, spotted seatrout and hardheaded catfish were common ERC species throughout the estuary irrespective of flow conditions. Many of these fishes are important commercially and/or recreationally.

In terms of habitat use, Franco et al. [23] found that European estuarine fish assemblages were significantly dominated by marine species, either migrants or stragglers, followed by estuarine, freshwater, anadromous and catadromous species. In the SABS and Galveston Bay, estuarine fish dominate estuaries, with inflows determining the presence and abundance of freshwater species in the upper reaches near rivers, while marine species particularly juvenile and sub-adult size fishes are located near the mouth of the bay [12]. This is also the case when considering a global perspective, with freshwater and marine stragglers accounting for the lowest abundance [27]. The presence of freshwater species is highly variable, depending on the large variability of freshwater inflows in the sub-bays. In European estuaries, the freshwater functional groups were most variable, while in Texas it was the estuarine groups that showed the greatest variability. The present study shows that most fish species use Texas estuaries for spawning and as a permanent residence, with some using them for diadromous migrations; this is opposite to what was observed in European estuaries, which are used as temporary habitats by fish, as feeding or nursery grounds [23]. Estuarine habitats offer high densities of prey and other food not encountered in marine areas, and their turbid shallow waters provide protection from predators [57]. For estuarine species, our results support theories of the estuarine ichthyofauna stress–subsidy continuum [1,23].

In some cases, there is a mismatch between the capacity of ecosystems to supply sufficient oxygen and fisheries' demand for oxygen [58]. In other cases, there may be an increase in the occupancy probability of predator species in estuaries experiencing a decreasing trend in the occupancy of freshwater-associated prey species [18]. For the latter, these species are often associated with freshwater outflow and marsh tidal creeks, so the decrease in their occupancy probability is related to the availability of habitats. In the SABS, it is well documented that wetland loss since the early 2000s due to sea level rises [28] and concurrently decreasing freshwater inflows due to diversions upstream for agriculture and human populations [59] have collectively influenced some fish species more than others. Further studies are needed to understand how this is impacting fish diversity in the SABS. Fujiwara et al. [18] found a significant increasing trend in the Shannon diversity index of fish species in San Antonio Bay from 1982 to 2016, which they attributed to the expansion of tropical species into the region. Thus, climate change factors are complicating analyses of historical data when endeavoring to understand how hydrologic changes are important.

4.2. Bioindicators

The functional classification methodology herein can be used to identify bioindicators of environmental change for the SABS. Bioindicators can be a species, a population or community that reflects the state of an ecosystem and can represent when changes are occurring at the habitat or community level [51,52]. Studies looking at the common communities observed across multiple bay systems may exclude the species that are sensitive to changing environmental conditions in preference for those that have a narrower range of tolerable conditions [10,11]. Gulf menhaden and pinfish, for example, have a wide salinity tolerance and can be found in estuaries across the Atlantic and Gulf of Mexico, so it is not surprising that some studies have found these fish to be a beneficial indicator of changing river inflow conditions [10,11]

During high freshwater inflows in the SABS, American gizzard shad (FMO) contributed to a decreasing proportion of the overall community with increasing distance from the river mouths (Figures 1 and 4). On the other hand, during low inflows, American gizzard shad was only a minor component of the community in the upper portions of the estuary (Guadalupe Bay, Hynes Bay, and San Antonio Bay). In the gill nets, American gizzard shad was the only fish species caught during high and low inflows in the upper bay. In previous decades (1982–2011), American gizzard shad comprised > 6% of the gill net catch and were present in over 53% of the samples [54]. These results support the use of this species as a bioindicator for freshwater inflows in the SABS. They also compliment the findings of Gonzalez et al. [12], who proposed that American gizzard shad (and threadfin shad) could be used as candidate bioindicators of freshwater inflows for Galveston Bay.

In addition, the blue catfish was also identified as a possible bioindicator of freshwater inflows for Galveston Bay [60], but not for the SABS [61], as part of a statewide study on bioindicators. The rationale for choosing blue catfish was that their distribution and abundance had a significant inverse correlation with salinity [11], and during drought periods, they were only present closest to the river mouths. This was consistent with their preference for turbid low salinity (0–8) waters [62]. Blue catfish dominated the FMC functional group in the Galveston Bay study by Gonzalez et al. [12]; these authors recommended the spatial qualification that the FMC functional group be applied as an indicator of freshwater inflows in Trinity Bay, not the entire Galveston Bay estuary. Further, Boyd and Bubley [54] recommended blue catfish only be used to monitor populations in the upper parts of the SABS, which include upper San Antonio Bay and the adjacent Hynes and Guadalupe Bays. Given the abundance (total numbers and functionally) of blue catfish in the SABS, and the importance of this species in food webs, this species could be a suitable bioindicator in parts of this estuary.

In the lower reaches of the estuary, the MMC and MSC functional groups contributed to a larger fraction (abundance) of the otter trawls (Figure 4). Unlike ERC, ERO, FMC and FMO, the marine functional groups had a greater diversity of species, including pigfish, Atlantic bumper, Atlantic cutlassfish, fringed flounder, least puffer, silver seatrout, ocellated flounder and striped burrfish. During low inflows, ocellated flounder and striped burrfish disappeared and inshore lizardfish appeared. The MMC fish community assemblage was very different in Ayres Bay during high and low inflows, with additional fish species observed, such as the scaled sardine and naked goby, compared to Espiritu Santos Bay.

These differences were associated with the unique hydrology of the lower reaches of the SABS [32,61]. As described above, freshwater inflows flow along Ayres Bay, whereas Espiritu Santos Bay is primarily influenced by flows from the Gulf of Mexico. In the nearby Galveston Bay, the MMC and MSC functional groups were dominated by Atlantic bumper and Gulf butterfish [12]. These species move from marine to estuarine environs during portions of their life cycle (in the case of marine migrants) and opportunistically (marine stragglers).

By contrast, Gulf menhaden (ERO), present in high abundance throughout the SABS [53]; present study and Galveston Bay [11,12], cannot be used as a bioindicator species. Given their euryhaline nature, this species shows limited responses to freshwater inflows. Similarly, pinfish was ruled out because it is also present throughout the bay and numerical abundant. Boyd and Bubley [54] examined the patterns in three gear types (seines, otter trawls and gill nets) collected from 1982 to 2011 and found that pinfish often accounted for over 40% of the samples in seines and otter trawls. Because of their small size, they made up less than 1% of the gill net catch, a gear that targets larger fish, but still occurred in over 10% of the samples. Though their population appeared to be increasing slightly, there was substantial year-to-year variability. Steichen and Quigg [11] found that pinfish had a significant positive correlation with salinity, consistent with their preference for higher salinities (>25), but Gonzalez et al. [12] concluded that given its low abundance relative to other species, it would not be a suitable bioindicator species in Galveston Bay.

4.3. Other Approaches

Measures of species richness, abundance, biomass and body size have been used as indicators of ecological community structure, function, and productivity [8,18,19]. These metrics advance our understanding of community organization [2,23,26] but do not provide details of the groups of fish that have a similar response to environmental conditions or similar effects on ecosystem processes; this is the added value of using functional group classifications [26,45]. Single-species studies' outcomes may be subject to species-specific pressures (e.g., overfishing, commercial versus recreational uses), but this can be overcome when using long (>decade) datasets [11,28]. Multi-variate statistical approaches are also very helpful in deconvoluting large datasets and multiple bays and estuaries in one comprehensive effort [10,18,19], particularly when considering the impacts of climate change and other large-scale processes. Collectively, regardless of the approach used, all these approaches ultimately provide us with information about ecosystem functioning, resilience, and/or stability, which is needed to help with conservation and the management of fisheries.

5. Conclusions

Freshwater inflows are a dominant driver of functional shifts in the Gulf of Mexico's coastal ecosystems, determining the functional organization of the fish communities. In the SABS, the annual average functional group abundance reflected the annual freshwater inflow patterns in the upper bay segments. Significant floods in 1998, 2002, 2004, 2007, and 2010, however, decoupled these patterns. Similarly, during the drought of 2011–2014, FMCs and estuarine residents (ERC and ERO) were essentially lost from Hynes Bay in the otter trawls while ERO encroached into Gaudalupe Bay, while freshwater stragglers were found in gill nets in the upper reaches of the bay. After the drought, the functional abundance recovered quickly from 2015 to 2018, aided perhaps by the high freshwater inflows that were recorded in those years. The ability of community-specific functional trait diversity to return after an extreme climatic event is dependent on both the nature of the event itself and its frequency and severity. Freshwater inflows to estuaries change over time due to water uses upstream and episodic extreme events such as droughts and floods, but it takes decades before shifts in the occupancy probability may be detected.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/fishes9110461/s1, Table S1: Fish species found in the SABS that were assigned to 11 functional groups based on the estuarine use functional guild methodology developed by Elliott et al. [2], adapted by Franco et al. [23] and recently applied to the nearby Galveston Bay (Gonzalez et al. [12]).

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