Community structure of elasmobranchs in estuaries along the northwest Gulf of Mexico

Jeffrey D. Plumlee [a, b, *], Kaylan M. Dance [a], Philip Matich [c], John A. Mohan [a], Travis M. Richards [a], Thomas C. TinHan [a], Mark R. Fisher [d], R.J.David Wells [a, b]

[a] Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Rd., Galveston, TX, 77553, USA
[b] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, 77843, USA
[c] Texas Research Institute for Environmental Studies, Sam Houston State University, 2424 Sam Houston Avenue Ste. B-8, Huntsville, TX, 77341, USA
[d] Coastal Fisheries Division, Texas Parks and Wildlife, 702 Navigation Circle, Rockport, TX, 78382, USA

A B S T R A C T

Estuaries promote high levels of productivity and biodiversity by providing habitat for many biological communities due to their wide range of environmental conditions. Estuarine systems serve as nurseries, areas for parturition, and feeding grounds for elasmobranchs. However, estuaries face an array of anthropogenic pressures, including overfishing, altered flow regimes, pollution, and habitat destruction. Given the vulnerability of estuarine ecosystems, observing long-term changes in community structure is essential to understanding the effects of anthropogenic stressors. Elasmobranch community structure was analyzed among eight estuaries in the northwest Gulf of Mexico to evaluate spatial and temporal variability in species abundance and diversity using bi-annual fisheries independent gillnet survey data over three decades (1985—2014). Ten species comprised 99.4% of elasmobranchs caught which included 35.3% bull sharks (*Carcharhinus leucas*), 18.1% bonnetheads (*Sphyrna tiburo*), 17.0% cownose rays (*Rhinoptera bonasus*), 13.4% blacktip sharks (*Carcharhinus limbatus*), 5.9% Atlantic stingrays (*Dasyatis sabina*), 3.1% Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), 2.7% spinner sharks (*Carcharhinus brevipinna*), 2.1% scalloped hammerheads (*Sphyrna lewini*), 1.7% finetooth sharks (*Carcharhinus isodon*), and 0.7% lemon sharks (*Negaprion brevirostris*). During the study period, elasmobranch community structure changed among estuaries and among decades. Bull sharks, bonnetheads, cownose rays, blacktip sharks, and spinner sharks all increased in abundance during the study period, whereas finetooth sharks and lemon sharks decreased over time. Higher latitude estuaries were dominated by bull sharks while lower latitude estuaries were dominated by cownose rays. Salinity was the most important environmental variable in predicting individual elasmobranch species abundance (deviance explained: 14.4 ± 6.5 SD), while temperature and depth also played a role in shaping community structure. Diversity was greatest in mid-latitudinal estuaries with spatially and temporally dynamic salinity regimes. As environmental change and human impacts persist across much of the world, understanding environmental drivers of community structure using long-term datasets will provide insight to how these changes influence coastal ecosystems, and enable more comprehensive and scale-independent models to be developed for the management and conservation of coastal ecotones.

1. Introduction

Estuarine systems are vitally important and provide essential habitat to both freshwater and marine fishes (Beck et al., 2001).

Estuaries are shaped by considerable spatial and temporal variability in habitat composition and environmental conditions, a characteristic of ecotone regions, which can drive species presence/absence and community structure responsible for food web stability (Akin et al., 2003). For marine predators, including coastal elasmobranchs, estuaries can serve as areas for parturition (Castro, 1993), nurseries (Heupel et al., 2007), and foraging grounds (Bethea et al., 2004). Degradation of estuarine systems, coinciding with

species declines, illustrate the importance of estuaries to elasmobranch fishes across different life history stages (Knip et al., 2010). Because of the important role elasmobranchs play in their respective food webs (Heithaus et al., 2008) monitoring spatial and temporal shifts in elasmobranch community structure can improve our understanding of the effects environmental variability and habitat degradation have on estuaries and coastal ecosystems.

Many elasmobranch species use coastal estuaries throughout their various life history stages, and for some species, estuaries serve as neonate and juvenile refuges because of the food resources and protection they provide (Heupel et al., 2007; Heupel and Simpfendorfer, 2011; Parsons and Hoffmayer, 2007). Specifically, estuaries in the northwestern Gulf of Mexico (NW GoM) have been identified as primary and secondary nurseries for elasmobranchs species such as bull sharks (*Carcharhinus leucas*) (Froeschke et al., 2010b). In addition to the role estuaries serve as nurseries, several species of elasmobranchs exhibit residency in estuaries throughout mature life stages, including Atlantic stingrays (*Dasyatis sabina*) (Snelson et al., 1988), bonnetheads (*Sphyrna tiburo*), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) (Bethea et al., 2015), and cownose rays (*Rhinoptera bonasus*) (Collins et al., 2007), highlighting the importance of these ecosystems throughout ontogeny for coastal elasmobranchs.

The distribution of coastal elasmobranchs in the GoM has been correlated with physical, (salinity, temperature, depth) (Drymon et al., 2010; Froeschke et al., 2010a) and biological parameters (chlorophyll a, fish and crustacean biomass) (Drymon et al., 2013), which are hypothesized to work in conjunction to create suitable habitat for individual species (Heithaus et al., 2007). However, many environmental parameters are transient and change over timescales ranging from days to years, potentially altering individual distributions, species niche widths, ecological roles, and community structure. In the northeastern GoM (NE GoM), Bethea et al. (2015) found that shark species diversity was greatest in coastal habitats where salinity was highly variable, including river mouths and barrier islands, suggesting that temporally and spatially dynamic estuaries may support highly diverse elasmobranch communities in other parts of the GoM.

Within the NW GoM, the coast of Texas consists of barrier islands that span 591 km (Texas Natural Resources Information System, 2015), and eight major estuarine systems that include Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay, Upper Laguna Madre, and Lower Laguna Madre, covering an area of 5911 square kilometers (Texas Natural Resources Information System, 2014a) (Fig. 1). Texas estuaries are sourced from 10 major rivers; Neches, Trinity, San Jacinto, Brazos, Colorado, Lavaca, Guadalupe, San Antonio, Nueces, Rio Grande that drain 510,263 square kilometers of watershed, with regional variability in freshwater inflow rates (Texas Natural Resources Information System, 2014b). A longitudinal precipitation gradient increasing from $<40\,cm^3\,yr^{-1}$ in the west to $>140\,cm^3\,yr^{-1}$ in the east (Lyons, 1990), and a latitudinal salinity gradient increasing from 0 salinity in the north to >40 salinity in the south creates environmental variability along the Texas coast (Mohan and Walther, 2015; Tolan, 2007). Climatic gradients within Texas estuaries likely influence the distribution and relative abundance of at least some elasmobranch species (Bethea et al., 2015; Drymon et al., 2014; Froeschke et al., 2010a; Wiley and Simpfendorfer, 2007).

Previous research has investigated long-term trends in the distributions of several elasmobranch species in the NW GoM (Froeschke et al., 2010a; Matich et al., 2017). However, patterns and drivers of spatial and temporal variability in elasmobranch community structure are unclear, despite their importance to statewide biodiversity management and conservation, as well as gaining a broader geographic understanding of elasmobranch communities in the GoM (Bethea et al., 2015; Drymon et al., 2013; Grace and Henwood, 1997; McCandless et al., 2007). Describing regional differences in elasmobranch community structure is needed in order to gain a more comprehensive understanding of recent and projected shifts in species abundances (Bubley and Carlson, 2012; Froeschke et al., 2012), and to weigh the importance of abiotic and biotic parameters in maintaining ecosystem stability.

The objectives of this study were to 1) examine spatial and temporal patterns of elasmobranch community structure in estuaries along the NW GoM coast, and 2) identify the physical drivers of elasmobranch community structure within estuaries in the NW GoM.

2. Materials and methods

All analyses were performed on catch data obtained from the Texas Parks and Wildlife Department (TPWD) long-term gillnet monitoring program. Data collection consisted of 45 gillnets set each spring (April—June) and 45 each fall (August—November) in each major estuary system, following a stratified clustered sampling design (see Martinez-Andrade et al. (2009)). One caveat to this sampling program is the size selectivity of the gillnets used. Sharks with a total length (TL) > 2 m typically were excluded from capture (Froeschke et al., 2010a). For some species (e.g. bull sharks, lemon sharks, and scalloped hammerheads) these gillnets exclusively capture juveniles and neonates (based on shark sizes; Compagno (2001)). Gillnets were set overnight from approximately 1 h before sunset to 3—4 h after sunrise (mean 13.7 ± 1.4 h standard deviation, SD). Records were obtained for all gillnet sets from 1985 through 2014 for all major estuaries (Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay, Upper Laguna Madre, and Lower Laguna Madre). Upon retrieval of each gillnet, salinity, temperature (C°), and dissolved oxygen (mg l^{-1}) were measured in the upper 15 cm of surface water. Turbidity (NTU) was measured from collected water using a calibrated turbidimeter at the nearest field station within 24 h, and depth (m) was measured from the deepest end of the gillnet set. The dataset was assembled using the 10 most abundant elasmobranch species captured during the gillnet sampling: bull sharks, bonnetheads, cownose rays, blacktip sharks (*Carcharhinus limbatus*), Atlantic stingrays, Atlantic sharpnose sharks, spinner sharks (*Carcharhinus brevipinna*), scalloped hammerheads (*Sphyrna lewini*), finetooth sharks (*Carcharhinus isodon*), and lemon sharks (*Negaprion brevirostris*) which together comprised 99.4% of all individual elasmobranchs.

2.1. Spatial and temporal catch composition

Gillnet catch abundance was converted into catch per unit effort (CPUE) for spatial and temporal analyses, dividing the total catch by the individual net soak time in hours. All major estuaries in the TPWD dataset were included in analyses, with the exception of Cedar Lakes and East Matagorda Bay, which were excluded due to irregular sampling and low sample sizes over the sampling period. Species accumulation curves were generated in PRIMER v.7 (Clarke and Gorley, 2015), for 1, 5 and 10 year bins. Due to the infrequency with which some species occurred, temporal analyses were run on 10 year bins (1985—1994, 1995—2004, 2005—2014), hereby referred to as decades.

Spatial and temporal patterns in species abundance (CPUE) and diversity were examined among estuaries and decades, respectively. Analyses were run using a Bray-Curtis similarity matrix with a 4th root transformation to CPUE in order to identify trends among
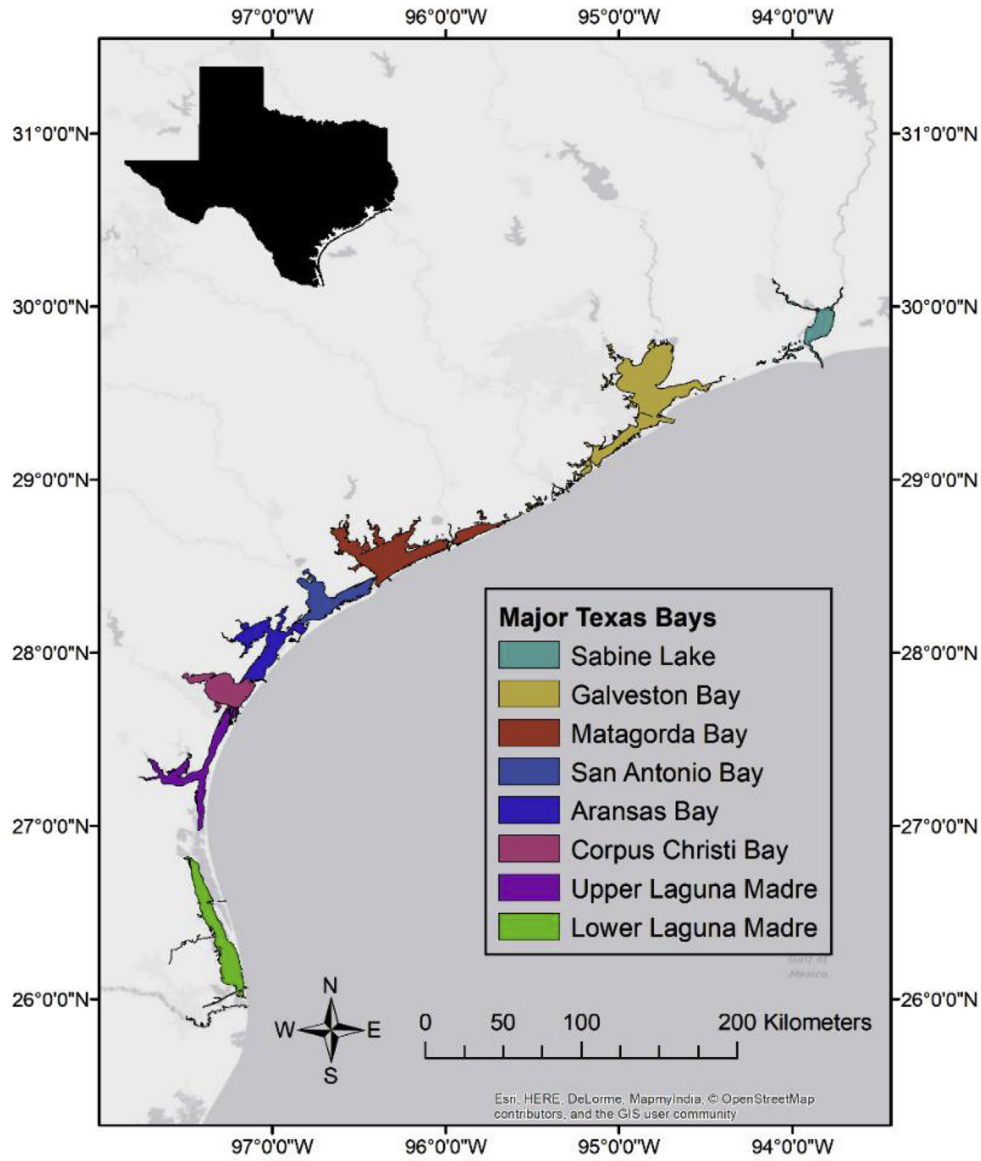
Fig. 1. Map of major estuaries located along the Texas coast in the northwest Gulf of Mexico.

less abundant species. A two-way crossed analysis of similarity (ANOSIM) was then conducted using estuary and decade as factors. Elasmobranch species with the greatest contribution to the dissimilarity between factor comparisons were identified using SIMPER analysis. Additionally, Brillouin's diversity index (H_B) was generated individually for each gillnet set and the Kruskal-Wallis test was used to determine differences in diversity among estuaries and decades. Brillouin's (H_B) diversity is most useful when the randomness of a sample is not guaranteed, for example, when the sampling regime is passive (or baited) which may attract a specific number of species over another (Peet, 1974). The Brillouin index is calculated as:

$$H_B = \frac{lnN! - \sum_{i-1}^{s} lnn_i!}{N}$$

where N is the total number of individuals in the sample, n_i is the number of individuals belonging to the ith species, and s is the species number (Brillouin, 1962).

2.2. Environmental trends

The influence of environmental variables on the abundance of individual species of elasmobranchs was investigated using generalized additive models (GAMs). Species-habitat relationships are commonly characterized using GAMs, which are semi-parametric analogs of generalized linear models (GLM) that allow for non-linear relationships between predictor and response variables (Dance and Rooker, 2016; Rooker et al., 2012). GAMs were constructed using a negative binomial distribution and logarithm link in the mgcv package in the statistical program R v.3.41 (R Core Team, 2014; Wood, 2017). Models were initially run using the default degrees of freedom (k), and then constrained for the final model based on the gam.check function in mgcv. The general GAM construction is given by the equation:

$$E[y] = g^{-1} \left[\beta_0 + \sum_k S_k(X_k) \right]$$

where E[y] is equal to the expected value of the response variable (catch), g is the link function, β_0 is the intercept, X represents one of k predictor variables, and S_k is the smoothing function of the predictor variable, X_k (Wood, 2006).

Seven predictor variables, two categorical (month and year) and five numeric (salinity, temperature, dissolved oxygen, turbidity, and depth) predictor variables were included in each initial model. For the categorical variable month, we used a cyclic cubic regression spline which allows for the variable to be cyclically continuous. Elapsed gillnet soak time was included as an offset to account for variability in soak times among gillnet samples. Manual stepwise backwards variable selection minimizing Akaike information criterion (AIC) was used to optimize variable contribution to the model where only significant, p-value ($\alpha < 0.05$), variables were retained within the model. Collinearity between variables was identified using the VIF function in R (Wood, 2017). If collinearity was identified (VIF score > 4), collinear variables were tested individually using separate models, and the variable that was attributed to a better model fit (lowest AIC and highest DE) was used in the final model.

3. Results

The dataset consisted of 21,597 individual gillnet sets, with 6,032 (27.9%) gillnets containing elasmobranchs, and 20,091 individuals caught over 30 years (1985–2014). The percent distribution of the 10 species caught in NW GoM estuaries were 35.3% bull sharks ($n = 7,089$), 18.1% bonnetheads ($n = 3,640$), 17.0% cownose rays ($n = 3,421$), 13.4% blacktip sharks ($n = 2,699$), 5.9% Atlantic stingrays ($n = 1,185$), 3.1% Atlantic sharpnose sharks ($n = 620$), 2.7% spinner sharks ($n = 532$), 2.1% scalloped hammerheads ($n = 429$), 1.7% finetooth sharks ($n = 332$), and 0.7% lemon sharks ($n = 144$) (Table 1). Matagorda Bay ($n = 5,728$), San Antonio Bay ($n = 4,877$), and Corpus Christi Bay ($n = 3,410$) contained 70% of the elasmobranchs caught (Table 1).

3.1. Spatial and temporal trends

Elasmobranch community structure differed among estuaries (ANOSIM, Global R = 0.123, p = 0.001) and by decade (Global R = 0.019, p = 0.001). Successive pairwise analyses among estuaries and decades indicated decadal shifts in elasmobranch community structure, as well as significant variability among individual estuaries (Supplemental Table 1). Each species had varied CPUE across all estuaries. Five species had their max average CPUE in Matagorda Bay, bull sharks (0.070 ± 0.16 SD), blacktip sharks (0.028 ± 0.16),

Atlantic sharpnose sharks (0.006 ± 0.05), spinner sharks (0.009 ± 0.13), and lemon sharks (0.003 ± 0.04). Additionally, three species had their max average CPUE in Corpus Christi Bay, bonnetheads (0.031 ± 0.22), cownose rays (0.024 ± 0.11), and scalloped hammerheads (0.004 ± 0.04). The remaining two species had their max average CPUE in San Antonio Bay, Atlantic stingrays (0.009 ± 0.03) and finetooth sharks (0.003 ± 0.04) (Fig. 2a and b). Analysis of estuary pairwise comparisons indicated a shift in dominant elasmobranch species between northern and southern estuaries. Bull sharks were the dominant species for all estuaries north of Corpus Christi (Fig. 1), with a decrease in percent of community composition from Sabine Lake (94.5%) to Aransas Bay (52.0%) (Fig. 2a). Cownose rays were the dominant species south of Corpus Christi Bay, with a peak relative abundance in Upper Laguna Madre (Fig. 2b). Atlantic stingrays, blacktip sharks, and bonnetheads were more evenly dispersed among the estuaries, with variable abundance for each species (Fig. 2a and b). Bull sharks, cownose rays, Atlantic stingrays, blacktip sharks, and bonnetheads had consistently high abundances across decades in the estuaries. However, individually, there were shifts in each species average abundances. Average relative abundance of cownose rays increased by 50% from Decade 1 (1985–1994) to Decade 2 (1995–2004), but declined for blacktip sharks and bonnetheads by 20% and 23%, respectively, during this time period. From Decade 2 (1995–2004) to Decade 3 (2005–2014) blacktip sharks increased by 27% and bonnetheads increased by 100%, while Atlantic stingrays declined by 20%. Additionally, there were differences in diversity using both estuary and decade as factors. Diversity (H_B) was lowest ($p < 0.05$) in the most northern estuary (Sabine Lake; mean 0.005 ± 0.060 SD) and highest ($p < 0.05$) in the central Texas coast (Matagorda Bay; mean 0.310 ± 0.436, San Antonio Bay; mean 0.311 ± 0.422, Corpus Christi Bay; mean 0.277 ± 0.423). Diversity (H_B) also stayed constant from 1985 to 2004 (1985–1994; mean 0.187 ± 0.354, 1995–2004; mean 0.191 ± 0.355) but increased in 2005–2014 (mean 0.269 ± 0.419) ($p < 0.05$).

### 3.2. Generalized additive models

Overall deviance explained (DE) by generalized additive models (GAMs) ranged from 11.5% (Atlantic stingray) to 58.8% (lemon shark) with an average 36.4% DE (Table 2). Salinity (DE; 14.4 ± 6.5% SD) was the most important environmental factor for every species except bull sharks and Atlantic stingrays, where salinity was the second most important variable following temperature for bull sharks, and month was the most important variable for Atlantic stingrays (Table 2). Response plots demonstrate that the majority

Table 1
Total abundance and mean size for elasmobranchs caught in each major estuary from 1985 through 2014. Size for shark species is total length (TL) and maximum disc width (DW) for ray species.

	Bull shark	Bonnethead	Cownose ray	Blacktip shark	Atlantic stingray	Atlantic sharpnose shark	Spinner shark	Scalloped hammerhead	Finetooth shark	Lemon shark
Sabine Lake	567	25	2	2	4	1	0	0	0	0
Galveston Bay	1155	136	88	338	118	59	105	20	13	7
Matagorda Bay	2396	473	654	1138	202	228	340	106	100	91
San Antonio Bay	1819	1255	561	571	307	146	45	41	98	34
Aransas Bay	752	205	212	45	182	15	3	30	0	5
Corpus Christi Bay	331	1200	916	371	143	130	35	169	112	3
Upper Laguna Madre	3	19	523	7	71	14	1	7	1	0
Lower Laguna Madre	66	327	465	227	158	27	3	56	8	4
Grand Total	**7089**	**3640**	**3421**	**2699**	**1185**	**620**	**532**	**429**	**332**	**144**
Mean Size (mm) ± SD	**1030 ± 178**	**709 ± 134**	**592 ± 150**	**873 ± 402**	**252 ± 100**	**699 ± 179**	**776 ± 233**	**676 ± 160**	**853 ± 247**	**764 ± 121**
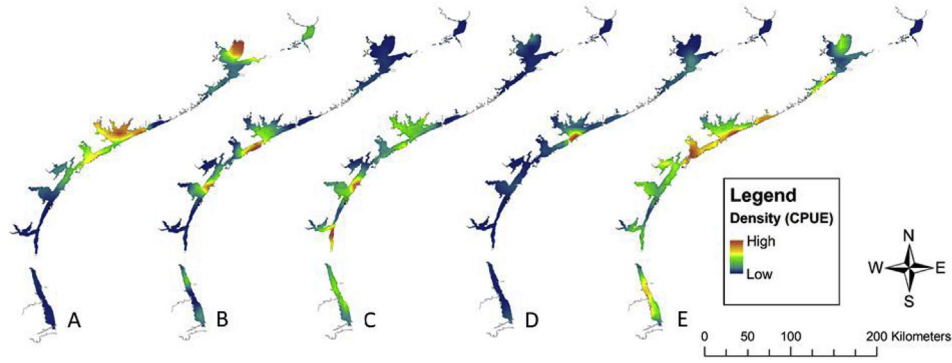
Fig. 2a. Heat maps of the mean density (CPUE) over 30 years along the northwest Gulf of Mexico coast for A) bull sharks (*Carcharhinus leucas*), B) bonnetheads (*Sphyrna tiburo*), C) cownose rays (*Rhinoptera bonasus*) D) blacktip sharks (*Carcharhinus limbatus*), and E) Atlantic stingrays (*Dasyatis sabina*). Abundance (CPUE) estimates are scaled relative to that species for each map.
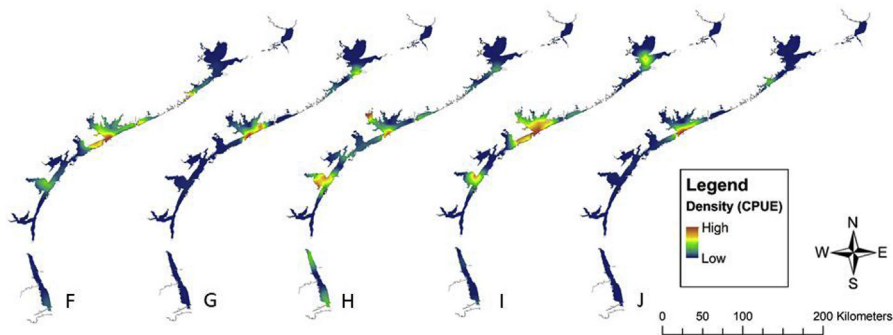
Fig. 2b. Heat maps of the mean density (CPUE) over 30 years along the northwest Gulf of Mexico coast for F) Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), G) spinner sharks (*Carcharhinus brevipinna)*, H) scalloped hammerheads (*Sphyrna lewini)*, I) finetooth sharks (*Carcharhinus isodon*) and J) lemon sharks (*Negaprion brevirostris*). Abundance (CPUE) estimates are scaled relative to that species for each map.

Table 2

Environmental and categorical (c) variables retained in the final generalized additive models (GAMs) after stepwise backwards Akaike information criterion (AIC) selection process for elasmobranch species found in estuaries along the northwest Gulf of Mexico. Model suitability was interpreted from AIC scores and percent deviance explained (DE %). The relative importance of each variable was estimated given the difference in AIC (ΔAIC) and DE (ΔDE) when this variable was removed from the final model.

	Bull shark		Bonnethead		Cownose ray		Blacktip shark		Atlantic stingray	
	AIC	DE	AIC	DE	AIC	DE	AIC	DE	AIC	DE
	27926.8	36.8%	11976.4	47.4%	15524.5	25.8%	11892.4	33.9%	12240.4	11.5%
	ΔAIC	ΔDE	ΔAIC	ΔDE	ΔAIC	ΔDE	ΔAIC	ΔDE	ΔAIC	ΔDE
Salinity	1250.6	9.4	750.7	17.3	533.9	13.4	582.6	15.9	115.6	4.1
Temp	1529.6	9.9	36.2	1.5	148.0	3.8	30.1	0.9	75.6	2.7
DO	19.9	0.2	–	–	13.2	0.4	5.7	0.5	9.6	0.3
Turbidity	33.6	0.3	–	–	–	–	19.0	0.4	–	–
Depth	126.5	1.3	438.7	9.7	90.7	1.3	160.3	3.6	61.1	2.9
Year (c)	148.8	1.0	245.4	5.3	121.7	1.5	90.7	0.7	45.8	2.1
Month (c)	–	–	324.8	4.8	268.6	4.4	218.9	3.2	337.2	6.4

	Atlantic sharpnose shark		Spinner shark		Scalloped hammerhead		Finetooth shark		Lemon shark	
	AIC	DE	AIC	DE	AIC	DE	AIC	DE	AIC	DE
	4304.3	33.8%	2255.9	47.1%	3282.8	46.7%	2689.9	35.2%	1374.3	58.8%
	ΔAIC	ΔDE	ΔAIC	ΔDE	ΔAIC	ΔDE	ΔAIC	ΔDE	ΔAIC	ΔDE
Salinity	171.1	5.3	98.2	14.1	282.8	22.6	151.3	25.7	80.2	16.5
Temp	7.3	1.4	–	–	9.5	1.1	–	–	–	–
DO	16.8	1.4	20.9	1.5	22.4	1.4	–	–	–	–
Turbidity	–	–	8.6	0.9	–	–	–	–	30.9	1.8
Depth	40.0	2.4	22.1	4.4	116.1	6.4	46.1	8.1	21.2	2.4
Year (c)	45.7	3.4	13.0	1.1	–	–	2.9	1.6	82.9	6.6
Month (c)	31.4	2.7	104.4	13.8	39.8	0.2	39.9	0.5	113.9	6.3

(80%) of elasmobranchs (blacktip sharks, Atlantic sharpnose sharks, Atlantic stingrays, bonnetheads, finetooth sharks, lemon sharks, spinner sharks, scalloped hammerheads) found in NW GoM estuaries were found in salinities between 15 and 40. Only cownose rays and bull sharks were found to have positive response to salinities ≤15, with bull sharks having a positive response down to 0 salinity (Fig. 3a).

Month had high relative DE (4.7 ± 3.8%) for all species, excluding bull sharks. For all species for which month was significant, the response plots indicated a positive relationship between abundance and the onset of the summer months, with declining and negative responses in the fall (September/October) (Fig. 4a and b). Depth was also found to have high DE (4.3 ± 2.8%), with most elasmobranch species (bull sharks, bonnetheads, cownose rays, blacktip sharks, Atlantic sharpnose sharks, spinner sharks, scalloped hammerheads, and finetooth sharks) having positive responses to depths > 1 m. Atlantic stingrays and lemon sharks both had positive responses to <1 m depth, with lemon sharks having a negative response to depths >1 m (Fig. 3a and b). Turbidity (DE; 0.9 ± 0.7) and dissolved oxygen (DE; 0.8 ± 0.6) were not included in the final model for most species, or were included in the final model but accounted for low overall DE (Table 2).

4. Discussion

Coast-wide diversity in elasmobranchs was comparable to other estuaries in the GoM (Bethea et al., 2008; Wiley and Simpfendorfer, 2007) and the Western Atlantic (Bangley and Rulifson, 2017). Of the 10 elasmobranch species that were found in estuaries of the NW GoM, there were six species of requiem sharks (Carcharhinidae), two species of hammerhead sharks (Sphyrnidae), one whiptail ray (Dasyatidae), and one eagle ray (Myliobatidae). Using fishery independent gillnet surveys, Bethea et al. (2015) found that 11 species of sharks frequently occur in estuarine and coastal waters of

Florida, Alabama, and Mississippi, with Atlantic sharpnose sharks, bonnetheads, and blacktip sharks comprising 84% of the overall catch in the NE GoM. Similarly, Drymon et al. (2013) found that Atlantic sharpnose sharks, blacktip sharks, and blacknose sharks were the most abundant sharks across the northern GoM. Our study found similar abundances of bonnethead and blacktip sharks; however, Atlantic sharpnose sharks were found to be less abundant in NW GoM estuaries (3.1% of species in NW GoM vs. 51% in NE GoM). Atlantic sharpnose shark abundance was positively correlated with depth in this study, and in others (Ward-Paige et al., 2015), and the shallow nature of most estuaries in the NW GoM may have resulted in fewer Atlantic sharpnose sharks than other northern Gulf of Mexico estuaries. Bull sharks were found to be more abundant in this study relative to the NE GoM (38.1% of the species in NW GoM vs. 1% NE GoM). The bull sharks captured in the Bethea et al. (2015) study were almost exclusively caught in Mobile Bay, AL, which is a shallow, low salinity, mixed estuary (Drymon et al., 2014), similar to many of the estuaries found in the NW GoM (Froeschke et al., 2010a). Additionally, the high levels of freshwater inflow and lower salinities in NW GoM estuaries may have led to increased abundances of bull sharks, which show a strong affinity for moderate to low salinities (Froeschke et al., 2010a).

Despite spatial variability in species abundances and community compositions, the 10 elasmobranch species most commonly caught in NW GoM estuaries were consistently correlated with shifting environmental variables. Our results indicate that salinity and depth, and to a lesser extent temperature, play an important role in shaping the distribution of elasmobranchs in NW GoM estuaries. Estuaries exhibit dynamic, physicochemical properties, where habitats can experience rapid shifts in abiotic conditions and community structure (Akin et al., 2003; Blaber and Blaber, 1980; Gelwick et al., 2001). Physical factors (salinity, temperature, depth) found to drive estuarine teleost and invertebrate abundance are
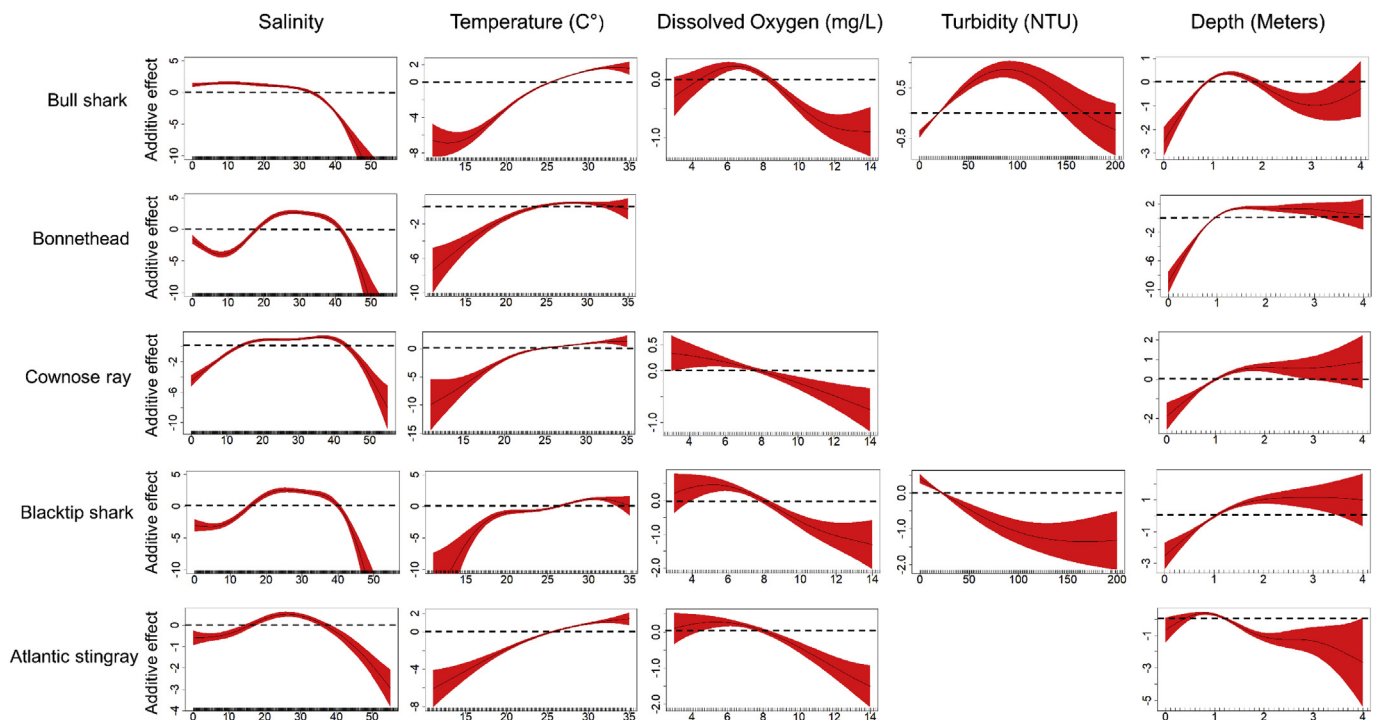
Fig. 3a. Response plots showing the influence of retained environmental variables on the distribution of elasmobranchs: bull sharks (*Carcharhinus leucas*), bonnetheads (*Sphyrna tiburo*), cownose rays (*Rhinoptera bonasus*), blacktip sharks (*Carcharhinus limbatus*), and Atlantic stingrays (*Dasyatis sabina*). Variables include salinity, temperature, dissolved oxygen, turbidity, and depth.
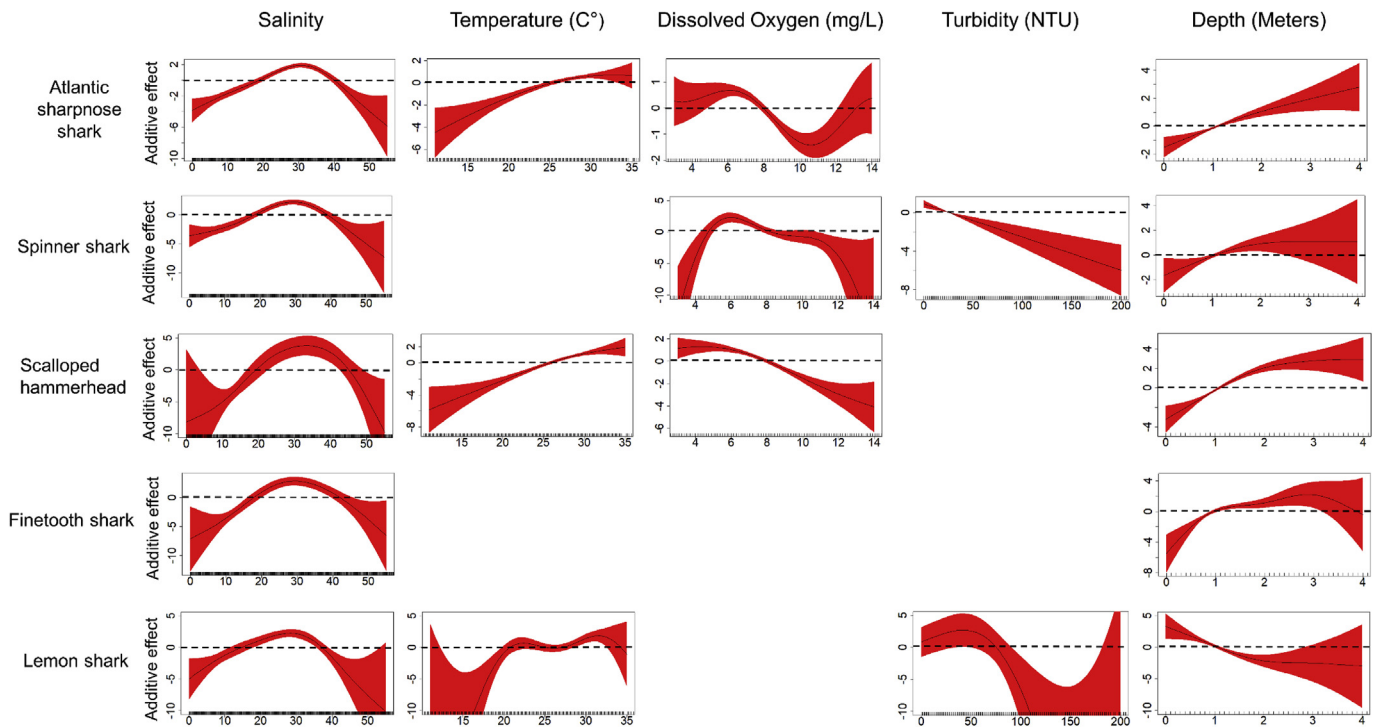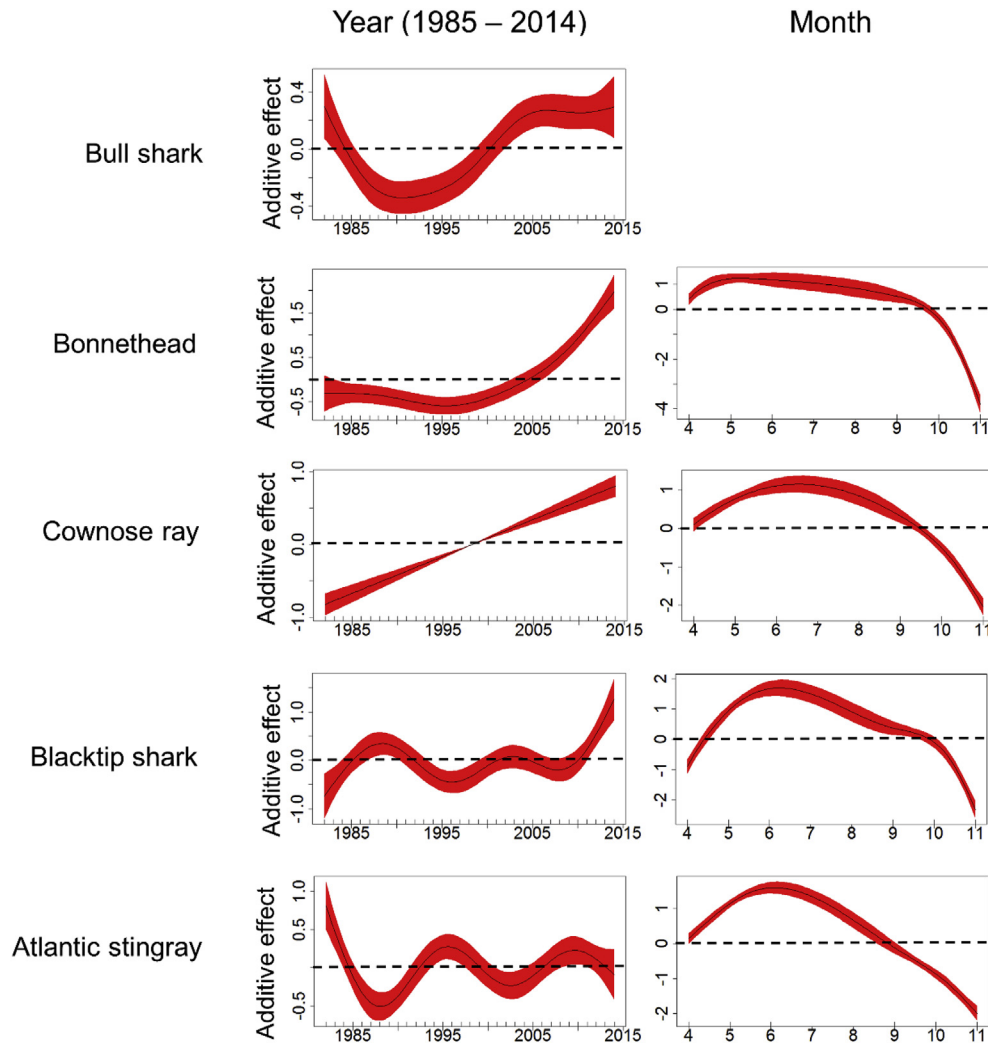
Fig. 3b. Response plots showing the influence of retained environmental variables on the distribution of elasmobranchs: Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), spinner sharks (*Carcharhinus brevipinna*), scalloped hammerheads (*Sphyrna lewini*), finetooth sharks (*Carcharhinus isodon*), lemon sharks (*Negaprion brevirostris*). Variables include salinity, temperature, dissolved oxygen, turbidity, and depth.

also highly correlated with estuarine elasmobranch distributions (Anderson et al., 2017; Furey and Rooker, 2013). For example, Froeschke et al. (2010a) found that salinity, temperature, and depth were three of the four most useful abiotic variables for predicting the individual distributions of bull sharks, blacktip sharks, and bonnetheads in NW GoM estuaries. Ward-Paige et al. (2015) found that for six species of juvenile coastal sharks (blacktip sharks, bonnetheads, finetooth sharks, scalloped hammerheads, Atlantic sharpnose sharks, and spinner sharks) salinity, temperature, and depth were again the most useful predictors in the NE GoM. Globally, salinity, depth, and water temperature are among the most important predictors of coastal elasmobranch distributions (reviewed by Knip et al. (2010)), which is supported by our results.

Among the environmental factors considered, salinity played an especially important role in determining community structure in NW GoM estuaries. Estuaries along the NW GoM coast are characterized by a distinct latitudinal gradient in salinity that is the product of similar gradients in precipitation, evaporation, and freshwater inflow (Mohan and Walther, 2015). Salinities are lowest in the most northern estuary, Sabine Lake (9.09 ± 6.74; mean averaged 1985–2014) and peak in the southern estuary, Upper Laguna Madre (38.73 ± 10.65). Elasmobranch diversity was highest in estuaries that showed moderate, but spatially and temporally dynamic salinity regimes, specifically Matagorda Bay (20.85 ± 9.22 SD), San Antonio Bay (20.20 ± 10.89), Aransas Bay (20.19 ± 9.86), and Corpus Christi Bay (29.94 ± 7.09), which is similar to other studies in the Gulf of Mexico (Bethea et al. 2015; Drymon et al. 2013). Salinity conditions within these estuaries can range from fresh to hypersaline, providing a variety of conditions for species with different environmental preferences and physiological tolerances. Mean salinity estimates for these estuaries correspond to the greatest positive response using GAMs for all 10 individual elasmobranch species in this study. Tolan (2007) described these central Texas estuaries as neutral estuaries that can alternate between

positive (less saline than the surrounding seawater) and negative (more saline than the surrounding seawater) salinity regimes throughout the year, due to seasonal precipitation events. This range of salinity regimes may allow for these central estuaries to accommodate euryhaline elasmobranchs, for example, bull sharks (Drymon et al., 2014; Heupel and Simpfendorfer, 2008) and stenohaline elasmobranchs alike, such as blacktip sharks, bonnetheads, and spinner sharks (Hueter and Tyminski, 2002), which is reflected in the high diversity of elasmobranchs found in central coast estuaries of Texas.

Despite coast-wide trends in species and community responses to abiotic conditions, several species showed temporal changes in abundance that could be driven by both natural and anthropogenic factors (Dulvy et al., 2014; Estes et al., 2011; Heithaus et al., 2008). GAM response plots indicated temporal increases in abundance for bonnetheads, cownose rays, bull sharks, blacktip sharks, and spinner sharks, while the abundance of lemon sharks and finetooth sharks declined over the study period. In the NW GoM, there have been several studies indicating increased abundance for blacktip sharks (Bubley and Carlson, 2012) and bull sharks (Froeschke et al., 2012). Peterson et al. (2017) described the preliminary recovery of many species of coastal shark as a response to shark fishery management plans (FMPs). Following the enactment of the current shark FMP in 1993, spinner sharks have increased in abundance by 14%, as well as bonnetheads, which were also shown to have increased in abundance over the same period in both the Atlantic Ocean and the Gulf of Mexico. Cownose rays, which are not managed by the current shark FMP, also show increasing trends in abundance. Changes in coastal salinities attributed to sea level rise, fluctuations in precipitation, and freshwater diversion for human use might have led to the increase in habitat suitability for cownose rays, which have been observed to use higher salinity waters (Compagno, 1984). Reasons behind declines in lemon sharks and finetooth sharks are less clear and may be influenced by the low
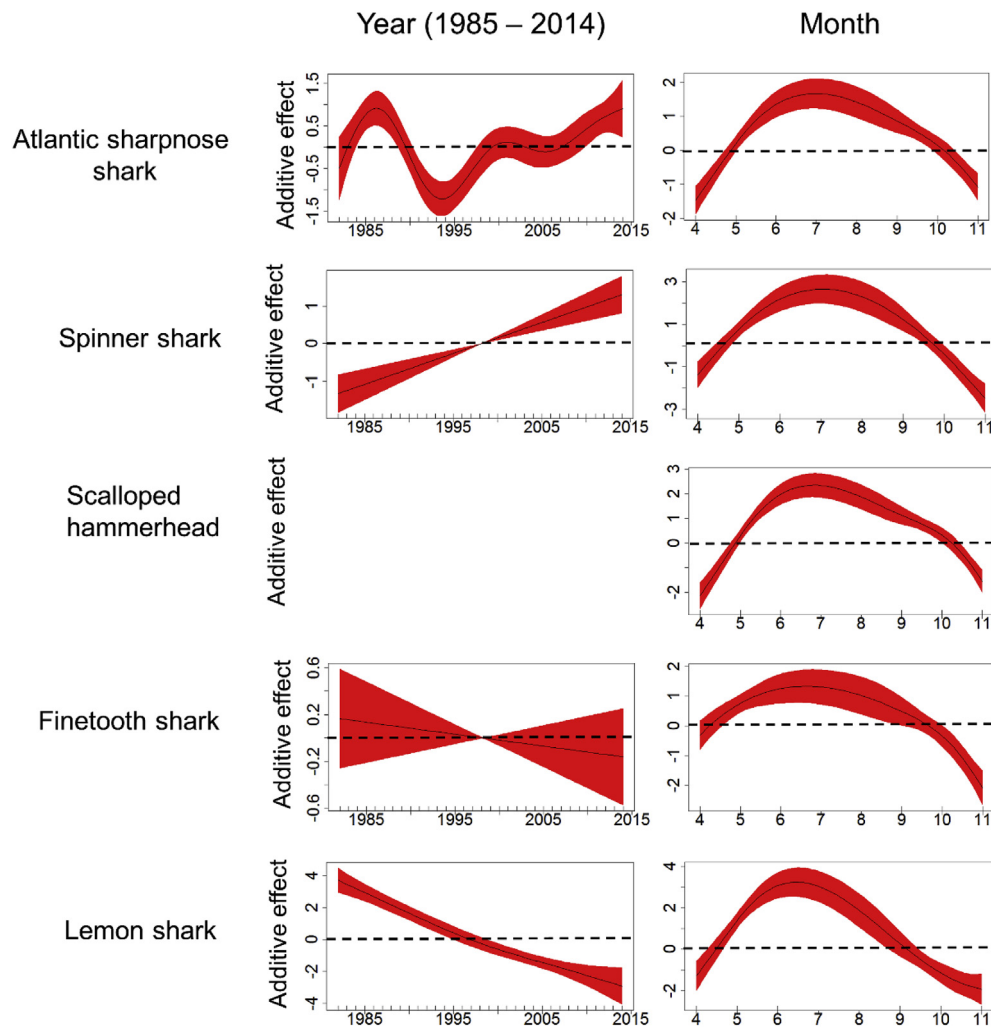
Fig. 4a. Response plots showing the influence of retained categorical variables (year, month) on the distribution of elasmobranchs: bull sharks (*Carcharhinus leucas*), bonnetheads (*Sphyrna tiburo*), cownose rays (*Rhinoptera bonasus*), blacktip sharks (*Carcharhinus limbatus*), and Atlantic stingrays (*Dasyatis sabina*). Variables include year (1985—2014) and month (April—June; August—November), July was interpolated due to missing data from lack of sampling.

sample size in this dataset. Changes in turbidity, water temperature, coastal vegetation, and food abundance may play a role in both species' decreased abundances (Carlson et al., 2003; Jennings et al., 2008; Murchie et al., 2010; Newman et al., 2010). Further investigations are necessary on the decline of lemon sharks which have had historically higher abundances within the estuaries of the NW GoM and are also managed by the shark FMP.

Beyond understanding the physical drivers of species abundances and distributions, and community structure, biotic factors also likely play an important role in shaping elasmobranch distributions in NW GoM estuaries. Several species of elasmobranchs in the northern GoM exhibit significant dietary overlap, such as Atlantic sharpnose sharks, blacktip sharks, finetooth sharks, and spinner sharks in the NE GoM (Bethea et al., 2004), or Atlantic sharpnose sharks, and blacktip sharks in the NW GoM (Plumlee and Wells, 2016). Other elasmobranch species, such as bonnetheads, in the northern GoM appear to be trophically distinct from sympatric elasmobranchs (Bethea et al., 2011). Additionally, some species of elasmobranchs exhibit regional differences in diets, for example bonnetheads and Atlantic sharpnose sharks (Bethea et al., 2007; Drymon et al., 2013; Harrington et al., 2016). These complex relationships suggest that biotic factors, such as prey availability, may

drive the abundance and distribution of estuarine elasmobranchs, and subsequent community structure. Species exhibiting trophic plasticity like bull sharks (Matich and Heithaus, 2014) or Atlantic sharpnose sharks (Drymon et al., 2012) have spatial distributions in the estuary that may not be limited by food resources, but by other factors such as predator avoidance (Matich and Heithaus, 2015). However, species with narrow trophic niches may have limited spatial ranges reflective of the distribution of their preferred prey. Plumlee and Wells (2016) found that adult bonnetheads almost exclusively consumed blue crab (*Callinectes sapidus*), in contrast to juveniles who exhibited a wider dietary breadth. This prey specialization may drive adult bonnetheads to pursue blue crab outside of the estuary, which was confirmed using stable isotope analysis showing that adults feed in coastal food webs, and juveniles feed in estuarine food webs. While this study did not investigate trophic relationships bull sharks, cownose rays, Atlantic stingrays, blacktip sharks, and bonnetheads have been observed to prey upon a variety of estuarine-dependent species (Ajemian and Powers, 2012; Castro, 1996; Cortes et al., 1996; Funicelli, 1975; Snelson et al., 1984). These estuarine-dependent predators were in greater abundance in the estuaries of the NW GoM than species that target fewer estuarine species as prey, such as finetooth sharks

Fig. 4b. Response plots showing the influence of retained categorical variables (year, month) on the distribution of elasmobranchs Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), spinner sharks (*Carcharhinus brevipinna*), scalloped hammerheads (*Sphyrna lewini*), finetooth sharks (*Carcharhinus isodon*), and lemon sharks (*Negaprion brevirostris*). Variables include year (1985–2014) and month (April–June; August–November), July was interpolated due to missing data from lack of sampling.

and spinner sharks (Bethea et al., 2004; Higgs, 2016).

Different species of elasmobranchs use estuarine environments at various stages throughout their ontogeny. Some species of elasmobranchs use estuaries in the northern Gulf of Mexico exclusively as neonates and juveniles, (i.e. spinner sharks, finetooth sharks, scalloped hammerheads), while others use estuaries throughout all life stages (i.e. bonnetheads, Atlantic sharpnose sharks, cownose rays, Atlantic stingrays) (Bethea et al., 2015; Collins et al., 2007; Hueter and Tyminski, 2002; Snelson et al., 1988; Ward-Paige et al., 2015). The NW GoM coast has been shown to contain nursery habitat for bull sharks (Froeschke et al., 2010b), and it is hypothesized to provide nursery habitat for other elasmobranch species, including blacktip sharks and bonnetheads (Hueter and Tyminski, 2002). Gillnet sampling targets a narrow size range for many coastal elasmobranchs due to the selectivity of the mesh size used (Froeschke et al., 2010a). This type of sampling selectively targets juveniles and neonates of larger shark species, which may incorrectly identify an area as being exclusively inhabited by young animals. Due to the size selectivity of gillnets used by the Texas Parks and Wildlife Department that typically exclude sharks >2 m TL, we can assume adult sharks that mature at ~2 m (e.g. bull sharks, Branstetter and Stiles (1987); lemon sharks, Brown and Gruber (1988); scalloped hammerheads, Branstetter (1987)), or

adult sharks of species that have been shown to exclusively use estuaries as juveniles in the northern Gulf of Mexico (i.e. finetooth sharks, spinner sharks), will not be present in the sampling and will be excluded from our abundance and distribution estimations.

5. Conclusion

The results of this study show that NW GoM estuaries have diverse elasmobranch communities that vary geographically, and have significantly changed over time. The northern estuaries had communities dominated by bull sharks, while the southern estuaries were shown to have significantly different community structures dominated by cownose rays. Salinity and depth were the most important variables driving estuarine community structure in the NW GoM. Elasmobranch diversity peaked in the central estuaries where salinity regimes were seasonally variable, which accommodated the greatest number of elasmobranch species. Though limited due to gear selectivity and temporal coverage in sampling, this study finds similarities to those investigating coastal elasmobranchs in other parts of the GoM and the northwest Atlantic Ocean. The differences observed in this study highlight the importance of considering management strategies across multiple spatial scales to appropriately consider differences in species

abundances, life histories, and resiliencies. Additional work should focus on the fine-scale species-specific trends in distribution to help illustrate the ecological importance and roles of elasmobranchs in the NW GoM.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2018.02.023.

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