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Does proximity to freshwater refuge affect the size structure of an estuarine predator (*Carcharhinus leucas*) in the north-western Gulf of Mexico?

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Abstract. The life histories of estuarine species are often adapted to the environmental variability they experience. However, estuaries are increasingly vulnerable to natural and anthropogenic changes, necessitating an understanding of how shifting conditions affect the survival, behaviour and population structure of estuarine-dependent animals. In this study we used data from fisheries-independent surveys collected across six estuaries with variable salinity regimes in Texas, USA, from 1975 to 2016 to investigate the role sources of freshwater inflow play in shaping juvenile bull shark *Carcharhinus leucas* size structure. High frequencies of co-occurrence with similarly sized conspecifics (59% of capture events) suggest bull sharks segregated within Texan estuaries based on body size. Bull shark sizes increased with distance to the nearest source of freshwater inflow, although effect sizes were small and access to freshwater habitats may be more important in shaping size-dependent distribution patterns. River mouths were disproportionately used by smaller juveniles (<90-cm total length, TL) and avoided by larger juveniles (>135 cm TL). However, the use of river mouths decreased in estuaries characterised by limited freshwater inflow and greater variability in salinities at river mouths, highlighting geographic differences in the functions these habitats provide as potential environmental and predator refugia. Young-of-the-year (i.e. age-0) sharks also increased their use of river mouths throughout the 40-year study period, revealing the growing importance of river mouths as potential nursery habitats.

Additional keywords: bull shark, estuary, euryhaline, nursery, ontogenetic shift.

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Introduction

At the intersection of saltwater and freshwater ecosystems, estuaries provide unique niches for a diverse array of species (Constanza *et al.* 1993; Kupschus and Tremain 2001; Vasconcelos *et al.* 2015). Many estuarine fauna thrive partly because their life history strategies are specifically adapted to the spatial and temporal variability in environmental conditions that typify these ecosystems (e.g. Franco *et al.* 2008; Elliott and Whitfield 2011). However, anthropogenic and natural perturbations across coastal ecosystems and river systems

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threaten these gradients at multiple scales, with implications for ecosystem productivity, ecological function and resilience (Beck *et al.* 2001; Day *et al.* 2012; Ribeiro *et al.* 2016; Mahoney and Bishop 2017). Furthermore, sea level rise, shifts in rainfall patterns and changing salinities are predicted to interact with local human impacts to alter hydrological regimes, as well as the ecological communities that estuaries support (Nicholls *et al.* 2008; Harvey *et al.* 2012; Williams *et al.* 2017). As such, there is a growing need to improve our understanding of the factors responsible for regulating the functions that estuaries provide, and predict how species will respond to perturbations of estuarine systems (Simenstad *et al.* 2006; Mahoney and Bishop 2017; Maxwell *et al.* 2017).

Mobile predators, including fishes, reptiles, mammals and birds, help structure estuaries by generating top-down effects, transporting nutrients and biomass across habitats and connecting disparate food webs (Heithaus *et al.* 2008; Rosenblatt *et al.* 2013). Among these predators, many sharks rely on estuaries as nurseries (McCandless *et al.* 2007), including more than a dozen species in the south-eastern US and northern Gulf of Mexico (e.g. Castro 1993; Bethea *et al.* 2015; Bangley and Rulifson 2017). Geographically widespread and abundant, bull sharks *Carcharhinus leucas* inhabit estuaries globally, ranging from freshwater rivers to coastal oceans, linking multiple habitats through their movements and trophic interactions (e.g. Boesman 1964; Heupel and Simpfendorfer 2008; Tillett *et al.* 2012; Drymon *et al.* 2014). Nursery habitats function as refugia and provide important services for young bull sharks, including food for growth and development (Heithaus 2007). In general, as juvenile bull sharks grow to ~1.5 m in total length (TL), their dependence on estuaries as nursery habitats decreases as their habitat preferences shift increasingly to more saline, coastal waters (e.g. Simpfendorfer *et al.* 2005; Froeschke *et al.* 2013; Matich and Heithaus 2015).

Proposed drivers of habitat use among bull sharks include predation risk, competition, physiological tolerances and energetic needs (e.g. Hueter and Tyminski 2007; Heupel and Simpfendorfer 2008; Werry *et al.* 2011; Clua *et al.* 2014). Some of these drivers are relatively widespread; for example, cooling winter water temperatures in many estuaries trigger seasonal emigrations among bull sharks in pursuit of more suitable conditions (Jones and Grace 2002; McCandless *et al.* 2007; Yeiser *et al.* 2008; Curtis *et al.* 2011; Bangley *et al.* 2018). However, residency patterns, ontogenetic niche shifts and spatial partitioning among age classes usually vary geographically among nurseries. For example, juvenile bull sharks avoid freshwater habitats in some estuaries because of the apparent physiological and energetic stress induced by these habitats based on the osmoregulatory costs of using hypotonic environments (e.g. Parsons and Hoffmayer 2007; Steiner and Michel 2007; Heupel and Simpfendorfer 2008; Ortega *et al.* 2009). In contrast, juvenile bull sharks in other estuaries exhibit affinity for waters with salinities <5, presumably because of the refuge function they provide from marine predators (e.g. Norden 1966; Sosa-Nishizaki *et al.* 1998; Hueter and Tyminski 2007; Thorburn and Rowland 2008; Heithaus *et al.* 2009; Curtis *et al.* 2013; Drymon *et al.* 2014). These conflicting conclusions make predicting specific estuarine habitat use patterns of bull sharks challenging, resulting in a need for local- and regional-level research to understand bull shark population dynamics at these scales.

The coastline of Texas is more than 5000 km long, and its estuaries support shark communities dominated by juvenile bull sharks (Froeschke *et al.* 2010*a*, 2013; Plumlee *et al.* 2018). However, bull sharks are relatively understudied in the western Gulf of Mexico beyond assessments of abundance and the effects of abiotic factors at large regional scales (e.g. Froeschke *et al.* 2010*a*, 2010*b*, 2013; Plumlee *et al.* 2018), making comparisons with more extensively studied juvenile populations in the eastern Gulf of Mexico difficult (e.g. Wiley and Simpfendorfer 2007; Steiner and Michel 2007; Heupel and Simpfendorfer 2008; Heithaus *et al.* 2009). As with most estuaries, salinities in Texan estuaries typically increase as the distance from freshwater sources (i.e. rivers and tributaries) increases, approaching marine conditions at tidal inlets (Froeschke *et al.* 2010*a*). Considering size-specific affinities of bull sharks for certain salinities and microhabitats in other regions, size-mediated differences in distribution may also exist in Texan estuaries (e.g. Heithaus *et al.* 2009; Ortega *et al.* 2009; Curtis *et al.* 2011; Werry *et al.* 2011). However, reverse and hypersaline conditions are common at lower-latitude estuaries in Texas (Mohan and Walther 2015), and frequent perturbations (e.g. severe thunderstorms, water management alterations) can lead to highly dynamic environmental conditions, including rapid shifts from marine to hyposaline waters (Orlando *et al.* 1993; Longley 1994). Unless conditions approach or exceed physiological limits, euryhaline species with broad salinity tolerances, like bull sharks (Pillans *et al.* 2005), are unlikely to track short-term changes in salinity and make energetically demanding migrations within and across estuaries (Marshall 2012; Kültz 2015). Indeed, juvenile bull sharks occur across a wide range of salinities (0–40) in Texan estuaries (Froeschke *et al.* 2010*a*) and are found in rivers connected to these systems (Table 1), suggesting habitat suitability is likely driven by more than salinity alone (Carlson 2002). Proximity to sources of freshwater inflow may be a more robust long-term indicator of salinity regimes that affect bull shark habitat use and size structuring (Longley 1994; Carlson 2002) and provide insights beyond our current understanding of bull sharks in the region. In this study, we investigated the effects of proximity to freshwater inflow sites on juvenile bull shark presence, concentration, co-occurrence and size structure across six different estuaries in Texas to better understand the role low salinity habitats (i.e. river mouths) play in shaping nurseries and ontogenetic habitat shifts.

Materials and methods

Study sites

Among the eight estuaries that comprise the Texas coastline, bull sharks are abundant in the northernmost six (listed north to south): Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay and Corpus Christi Bay (Fig. 1; Froeschke *et al.* 2010*a*). Seven barrier islands physically separate Texas estuaries from the Gulf of Mexico, and freshwater input from rivers and precipitation leads to a spatial gradient from predominantly cooler, freshwater estuaries in northern latitudes (e.g. Sabine Lake) to warmer, hypersaline estuaries in

Table 1. Published records of bull sharks found in Texan rivers from the Portal to Texas History database (https://texashistory.unt.edu/) searched by authors August 2016–January 2017

TL, total length

Publication date	Publication	Volume and issue or edition	Location	Shark size
17 August 1871	*The Houston Telegraph*	Vol. 37, Issue 17	Neches River; Beaumont	120 cm TL
21 September 1892	*The Galveston Daily News*	Vol. 51, Issue 181	Brazos River; Freeport	11 kg
14 September 1895	*The Galveston Daily News*	Vol. 54, Issue 174	Colorado River; Below Bay City	90 cm TL
20 June 1902	*The Orange Daily Tribune*	Vol. 1, Issue 92	Sabine River	90 cm TL
20 March 1903	*The Bartlett Tribune*[A]	Vol. 17, Issue 48	Red River; near Harris Ferry	270 cm TL
5 September 1907[B]	*The Houston Post*	Vol. 23, Edition 1	Guadalupe River; McFaddin Ranch	160 kg
18 April 1908	*Brownsville Daily Herald*	Vol. 16, Issue 247	Rio Grande River; near Santa Maria	180 cm TL, 68 kg
29 July 1908	*Brownsville Daily Herald*	Vol. 17, Issue 22	Rio Grande River; near Donna	300 cm TL
1 October 1908	*Brenham Daily Banner*[C]	Vol. 43, Issue 46	Sabine River; near Orange	90 cm TL
11 August 1916	*The Dublin Progress*	Vol. 29, Issue 16	Red River; near Sherman	40 cm TL, 1 kg
31 July 1931	*The Schulenburg Sticker*	Vol. 37, Issue 38	Colorado River; south of Alleyton	75 cm TL, 4 kg
11 May 1977	*Věstník*	Vol. 65, Issue 19	San Bernard River	No information
12 July 2001	*Port Aransas South Jetty*[D]	Vol. 31, Issue 28	Colorado River; Bastrop	No information

[A] Also published in the *Denton County News* (Vol. 11, number 46, Ed. 1) and *The Dublin Progress* (Vol. 15, number 44).

[B] Also published on 28 September 1907.

[C] Also published in *The Houston Post* (Vol. 24, Ed. 1).

[D] Story recalled from memory.

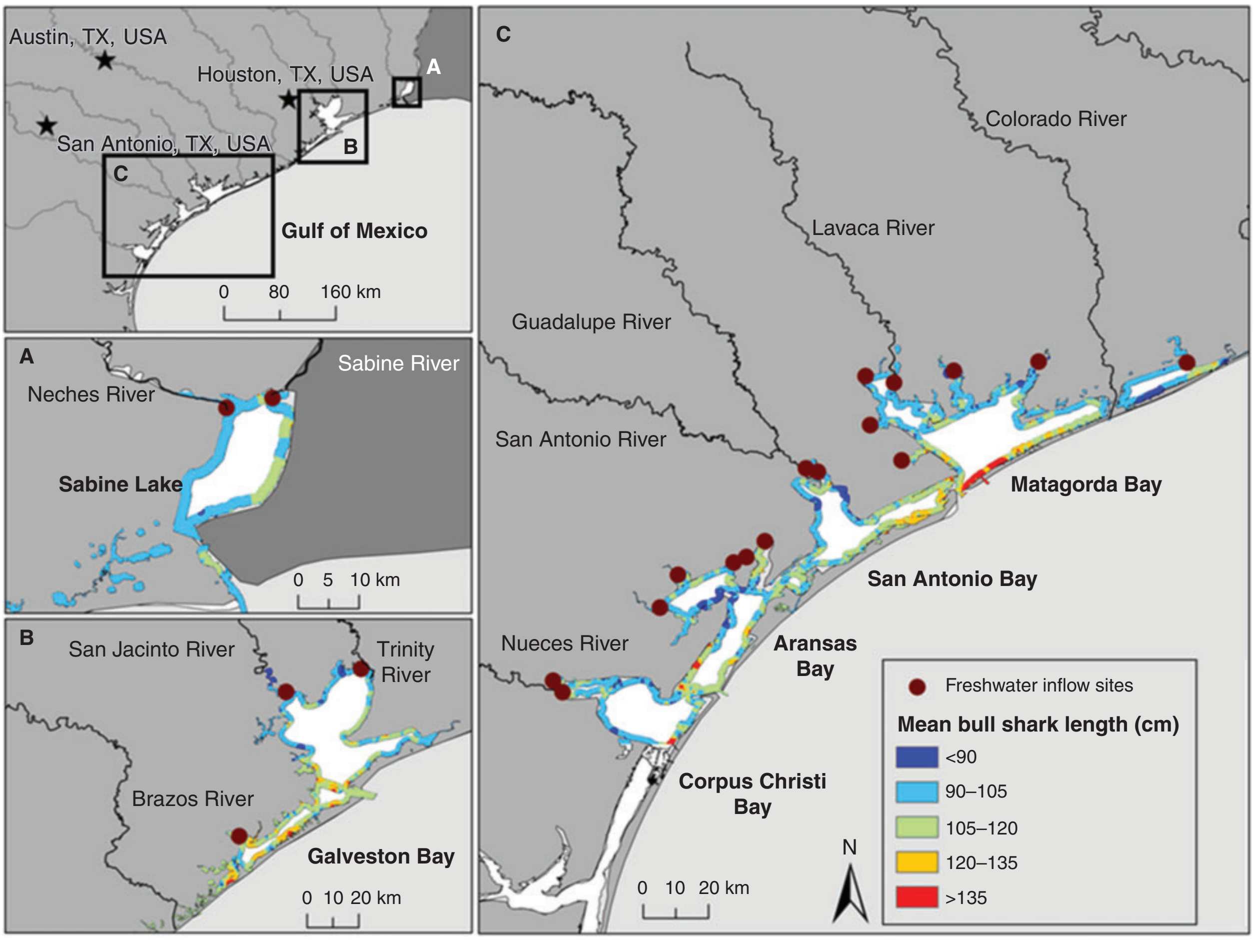

Fig. 1. Bull shark total length (TL) data from 1975 to 2016 from the Texas Parks and Wildlife Department long-term fishery-independent gill net monitoring program were interpolated into a heat map representing the mean TL of bull sharks sampled in each estuary. Circles at river and tributary mouths indicate the locations of freshwater inflow sites used for analyses.

southern latitudes (e.g. Laguna Madre; Longley 1994; US Environmental Protection Agency 1999; Froeschke *et al.* 2010*a*). Spatial variability in precipitation across Texas leads to greater freshwater inflow from north-eastern rivers into estuaries (e.g. Sabine and Neches rivers into Sabine Lake) compared with more south-western rivers (e.g. Nueces River into Corpus Christi Bay; Longley 1994; US Environmental Protection Agency 1999). At least some of these estuaries serve as nurseries for bull sharks (Froeschke *et al.* 2010*b*), providing the opportunity to evaluate the importance of freshwater inflow sites (mouths of rivers and tributaries) in shaping the size structure of juvenile bull sharks across a wide spatial scale.

Gill-net surveys

Data were obtained from ongoing gill-net surveys conducted by the Texas Parks and Wildlife Department (TPWD) long-term fishery-independent monitoring program, which was established in 1975. Sample sizes were variable before 1982 (mean ± s.d., 43.0 ± 17.2 gill-nets deployed per annum), at which point effort was standardised to 45 gill-net sets in each estuary over each 10-week spring (April–June) and autumn (September–November) seasons, thus 90 gill-nets in total deployed per estuary annually. Data were included from sampling conducted in Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay and Corpus Christi Bay from 1975 to 2016 to quantify temporal shifts in juvenile bull shark presence, concentration, co-occurrence and size structure across the entire study period. Sampling sites were randomly chosen by the TPWD without replacement per sampling season for each estuary using a stratified cluster sampling design within a 3.4225-km^2 (1 nautical mile^2) grid based on the presence of shoreline within the selected sites. Sampling was conducted overnight (mean ± s.d., soak time 13.7 ± 1.4 h) with monofilament gill-nets (183 m long, 1.2 m deep, with 45.7-m sections of 7.6-, 10.2-, 12.7- and 15.2-cm stretched mesh tied together in ascending order) set perpendicular from the shoreline. The orientation of the nets was standardised, with the 7.6-cm stretched mesh closest to shore. Sampling was restricted to bays, inlets, river mouths, tidal passes and connected lakes within each estuary. All organisms caught were identified to the lowest possible taxonomic level, counted and measured to stretched TL. Date, capture location and salinity (measured using a handheld water quality meter) were recorded for each net set and haul; salinity was measured at deployment and retrieval of each set and was averaged for analyses.

Data analysis

The presence, concentration, TL and co-occurrence of juvenile bull sharks (conspecifics caught together) were used for analysis. Because gill-net capture efficacy is size limited, and because bull shark life history leads subadults to leave estuaries (e.g. Heithaus *et al.* 2009; Werry *et al.* 2011), only sharks <136 cm TL were retained for analysis, except for the detailed river mouth evaluation, for which all sampled sharks were used (see 'Importance of River Mouths' below; e.g. Branstetter and Stiles 1987; Natanson *et al.* 2014). Sharks >135 cm TL comprised <3% of captured sharks during monitoring; thus, removing them likely had minimal effect on our interpretation of results. All analyses were conducted in IBM SPSS (ver. 22, IBM Corp., Armonk, NY, USA).

Salinity trends

All gill-net deployment and retrieval data were used (i.e. from nets with and without sharks; $n = 20\,525$) to analyse the relationships of salinity and salinity variance with distance from source of freshwater inflow across each estuary. The distance from sampling locations to the nearest site of freshwater inflow based on hydrologic connectivity, namely the straight line distance from sampling locations to the nearest river or tributary (i.e. ecotone habitats where rivers and tributaries meet estuaries), was quantified using Google Earth Pro (see https://www.google.com/earth/versions/, accessed May 2019). If land masses impeded a direct measurement from the sampling location to freshwater inflow site, multiple measurements were summed based on the shortest in-water distance. Although submarine groundwater discharge can provide a source of freshwater for estuaries, these sources were not considered based on the relationship between bull shark ontogenetic niche shifts and rivers and tributaries (e.g. Heithaus *et al.* 2009; Werry *et al.* 2011). We then used a general linear model (GLM) to test the effects of distance to nearest source of freshwater inflow and estuary (and their interaction) on salinity and long-term variance in salinity for sites in which at least six sampling events occurred in order to reduce bias from outliers among sites that were sampled a limited number of times during the 40-year study period. Pearson's Chi-Square test was used to determine the independence of data. Normal probability plots were used to test for normal distributions of the residuals, and plots of residuals *v.* predicted values were used to test for homogeneity of variance of the model and factors. Tests and plots indicated that the use of a GLM was appropriate. *Post hoc* Tukey's tests were used to determine the significance of differences among estuaries, and *post hoc* linear regression was used to assess trends in the distance to nearest source of freshwater inflow with salinity and variance in salinity for each estuary; *t*-tests were used determine differences in linear trends across estuaries by testing pairwise differences in regression slopes, with Hochberg's step-up procedure used to correct for multiple comparisons (Hochberg and Tamhane 1987).

Juvenile bull shark size structure

Another GLM was used to quantify the effects of distance to the nearest source of freshwater inflow on trends in bull shark size across space (i.e. estuaries) and time (i.e. seasons (spring and autumn) and decades). Estuary, decade and season were categorical variables used for analysis. Sampling periods were assessed broadly (i.e. decadally) because of the spatially randomised nature of gill-net sampling within estuaries and the lack of statistical power using shorter temporal periods (Plumlee *et al.* 2018).

All factors and two-way interactions were included in models. Mean TL was used as the dependent variable to avoid pseudoreplication for capture events with more than one shark. Effect sizes were calculated to evaluate the utility of predictor variables. Independence of data, normal distributions of residuals and homogeneity of variance of the model and factors were tested, and the results indicated that the use of a GLM was appropriate. *Post hoc* Tukey's tests were used to determine the significance of differences in size structure among estuaries and decades, and *post hoc* linear regression was used to assess the trends in mean TL with distance to freshwater inflow for significant interactions.

Conspecific co-occurrence

A generalised linear model with a Gaussian distribution was used to evaluate the effects of distance to the nearest source of freshwater inflow, and interactions with estuary, decade and season, on the difference in size of co-occurring bull sharks (size difference data were cube root transformed to account for skewness). Extrinsic factors (i.e. distance to the nearest source of freshwater inflow, estuary, decade and season) followed model parameters used for the GLM evaluating bull shark size structure (see above) to ensure consistency and comparability when interpreting results across analyses. Co-occurring sharks were classified as individuals caught during the same sampling event (Kohler and Turner 2001; Matich *et al.* 2017*a*), and the difference in total length (Δ_{TL}) of each capture pair was calculated for each event when sharks co-occurred. *Post hoc* Tukey's tests were used to determine the significance of differences in size structure among estuaries and decades.

Juvenile bull sharks in the Gulf of Mexico grow ~15 cm TL year^{-1} for the first 2–3 years of life (Branstetter and Stiles 1987; Natanson *et al.* 2014) and may preferentially associate with conspecifics of the same cohort, as exhibited by other carcharhinids (e.g. Guttridge *et al.* 2013; Keller *et al.* 2017; Finger *et al.* 2018). As such, we also calculated the proportion of bull sharks co-occurring with individuals based on Δ_{TL} using 15-cm Δ_{TL} bins: 0–15, 16–30, 31–45 and >45 cm proximate TL. Chi-Square tests were used to quantify the effects of estuary, decade and season on Δ_{TL} bins.

Importance of river mouths

Because of the important role riverine habitats can play in bull shark nurseries (e.g. Heupel and Simpfendorfer 2008; Werry *et al.* 2011; Tillett *et al.* 2012), we specifically investigated the importance of river mouths (habitat <3 km from rivers) on bull shark capture rates. Chi-Square tests were used to quantify the likelihood of capturing juvenile bull sharks in river mouths compared with other habitats within estuaries sampled (all habitat >3 km from rivers was pooled) across space (estuaries) and time (decades and sampling seasons). The analysis tested the assumption that bull shark catch per unit effort (CPUE) at river mouths would be the same as CPUE in all other parts of the estuaries. If CPUE was higher at river mouths than at all other parts of an estuary, then catch rates were higher than expected (i.e. river mouth CPUE : remainder of estuary CPUE > 1). If CPUE was lower at river mouths than all other parts of an estuary, then catch rates were lower than expected, with statistics from Chi-Square tests indicating significance at $\alpha = 0.05$. Bull sharks were pooled into 15-cm TL size classes based on growth rates (see above), with individuals pooled into wider size classes for the analysis of estuary and decadal differences because of low sample sizes, namely <90 cm TL (young-of-the-year, YOY), 90–135 cm TL (smaller juveniles) and >135 cm TL (larger juveniles and subadults). Extrinsic factors followed model parameters used for the GLM and the generalised linear model (excluding distance to the nearest source of freshwater inflow) to ensure consistency and comparability when interpreting results. *Post hoc* *Z*-tests and linear regression were used to interpret differences among estuaries, decades and sampling seasons.

Results

From 1975 to 2016, 7635 bull sharks with TL <136 cm were captured during 3312 sampling events. In all, 549 sharks were caught in Sabine Lake (mean ± s.d., salinity 9.01 ± 6.63), 995 were caught in Galveston Bay (mean ± s.d. salinity, 17.57 ± 8.52), 2467 were caught in Matagorda Bay (mean ± s.d. salinity, 20.95 ± 8.99), 2118 were caught in San Antonio Bay (mean ± s.d. salinity, 17.08 ± 10.56), 1062 were caught in Aransas Bay (mean ± s.d. salinity 19.56 ± 9.84) and 444 were caught in Corpus Christi Bay (mean ± s.d., salinity 29.49 ± 7.22). The distance to the nearest source of freshwater inflow was a significant predictor of salinity ($F = 4047.23$, $P < 0.01$, $\eta = 0.38$) and variance in salinity ($F = 205.45$, $P < 0.01$, $\eta = 0.37$) during sampling, with significant differences across estuaries (salinity: $F = 218.49$, $P < 0.01$, $\eta = 0.20$; variance in salinity: $F = 32.84$, $P < 0.01$, $\eta = 0.33$). The rate of change in salinity as distance to the source of freshwater inflow increased was greatest in San Antonio Bay and lowest in Galveston and Corpus Christi bays (Fig. 2; see Table S1, available as Supplementary Material to this paper). Variance in salinity increased significantly with the distance to the source of freshwater inflow in Sabine Lake, and decreased significantly in Matagorda, Aransas and Corpus Christi bays (Table S1; Fig. S1).

Juvenile bull shark size structure

Decade ($\eta = 0.130$), estuary ($\eta = 0.095$), season ($\eta = 0.032$), distance to the source of freshwater inflow ($\eta = 0.167$) and the interaction between distance to the source of freshwater inflow and estuary ($\eta = 0.114$) were significant factors correlated with mean bull shark size (Table S2). Mean capture sizes exhibited small but significant differences across estuaries ($F = 6.25$, $P < 0.01$; Fig. 3) and decades ($F = 14.80$, $P < 0.01$; Fig. 4; Table S2). Sharks tended to be larger in Galveston, San Antonio and Aransas bays (Fig. 3). Temporally, more than 40% of sharks caught in the 1970s were YOY individuals (<90 cm TL), with fewer YOY sharks caught in the 1980s (22%), 1990s (15%), 2000s (18%) and 2010s (23%). Mean TL increased directly with distance from the source of freshwater inflow (~0.20 cm TL km^{-1}; $F = 82.76$, $P < 0.01$), but significant relationships between mean TL and distance from the source of freshwater inflow were only found in Matagorda Bay (0.36 cm TL km^{-1}; $r^2 = 0.04$) and San Antonio Bay (0.37 cm TL km^{-1}; $r^2 = 0.05$) based on *post hoc* tests (Fig. 5).

Conspecific co-occurrence

Bull sharks <136 cm TL co-occurred with at least one conspecific in 1618 sampling events (49% of capture events), with 5988 sharks (78%) captured with at least one conspecific in the same net during the study period. The proportion of sharks co-occurring decreased gradually across sampling decades (Table 2), and was relatively consistent across estuaries with the exception of Corpus Christi Bay, where only 58% of sharks were

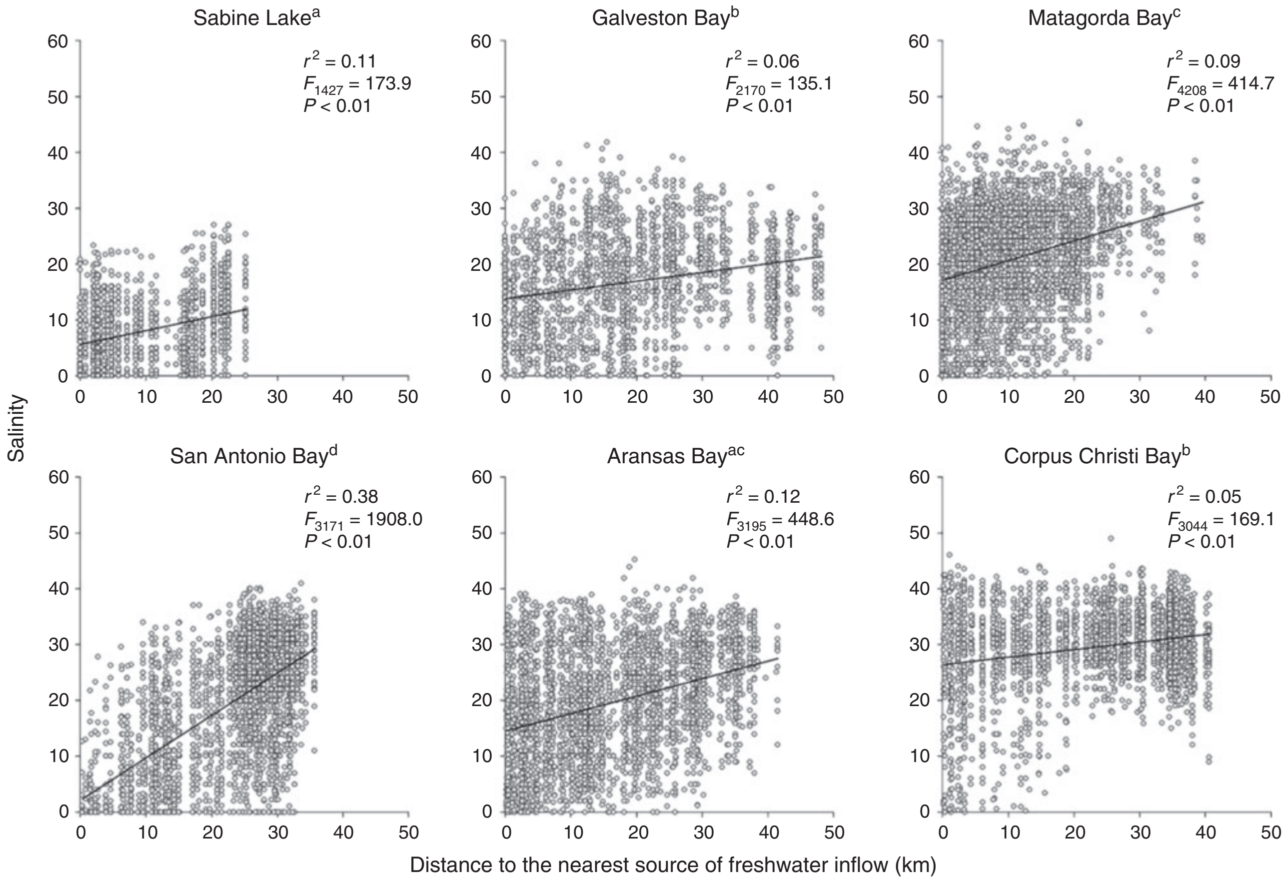

Fig. 2. Lines of best fit for estuary-specific relationships between salinity and the distance to the nearest source of freshwater inflow from all gill net deployment and retrieval data (i.e. from nets with and without sharks; $n = 20\,525$). Different superscript letters next to estuary names indicate significant differences in slope based on *post hoc t*-tests and Hochberg's step-up procedure to adjust for multiple comparisons at $\alpha = 0.05$.

caught with conspecifics (Table 2). The mean ± s.d. size difference of co-occurring sharks was 10.48 ± 10.00 cm TL for the entire study system, with small but significant differences across estuaries, decades and seasons (Tables 2, S3).

Chi-Square tests showed significant differences across estuaries, decades and seasons in the likelihood of bull sharks co-occurring with conspecifics in different size classes (Fig. 6). Sabine Lake and Corpus Christi Bay exhibited higher than expected frequencies of co-occurring conspecifics within 15 cm TL of one another ($Z = 2.3$ ($P = 0.02$) and $Z = 3.8$ ($P < 0.01$) respectively), and Galveston Bay exhibited significantly lower frequencies of co-occurring conspecifics within 15 cm TL of one another ($Z = -3.2$, $P < 0.01$). Gill-net sets in the 1980s and 1990s yielded higher than expected co-occurrence of similarly sized ($\Delta_{\mathrm{TL}} < 15$ cm) conspecifics ($Z = 9.6$ ($P < 0.01$) and $Z = 6.2$ ($P < 0.01$) respectively), whereas a significantly higher co-occurrence of dissimilarly sized conspecifics was found in the 2000s ($Z = -11.3$, $P < 0.01$) and 2010s ($Z = -5.8$, $P < 0.01$).

Importance of river mouths

Based on the total frequency of net deployments (i.e. all gillnets, not just those resulting in the capture of bull sharks) in river mouths during the spring sampling season, bull sharks exhibited a negative trend in capture frequency at river mouths as shark size increased ($r^2 = 0.97$, $F = 145.33$, $P < 0.01$; Fig. 7). YOY sharks were caught in river mouths more frequently than expected in both spring and autumn; sharks 90–120 cm TL were also caught in river mouths more frequently than expected in spring and sharks >135 cm TL were caught in river mouths less frequently than expected in spring (Fig. 7). YOY sharks varied spatially ($\chi^2 = 55.43$, $P < 0.01$) and by decade ($\chi^2 = 67.19$, $P < 0.01$) in their likelihood of being captured at river mouths, whereas sharks 90–135 cm TL varied spatially in their likelihood of being captured at river mouths ($\chi^2 = 70.56$, $P < 0.01$; Fig. 7). The frequencies of shark captures in river mouths compared with expected frequencies decreased as latitude decreased for both YOY sharks ($r^2 = 0.78$, $F_{1,4} = 13.81$, $P = 0.02$) and sharks 90–135 cm TL ($r^2 = 0.83$, $F_{1,4} = 19.53$, $P = 0.01$). Capture frequency in river mouths was significantly lower than expected in Aransas and Corpus Christi bays and higher than expected in Sabine Lake, Galveston Bay and Matagorda Bay (Fig. 7). Both YOY sharks ($r^2 = 0.70$, $F_{1,4} = 6.87$, $P = 0.08$) and sharks >135 cm TL ($r^2 = 0.74$, $F_{1,4} = 8.67$, $P = 0.06$) exhibited marginally significant increases in their likelihood of being captured at river mouths across decades (Fig. 7).

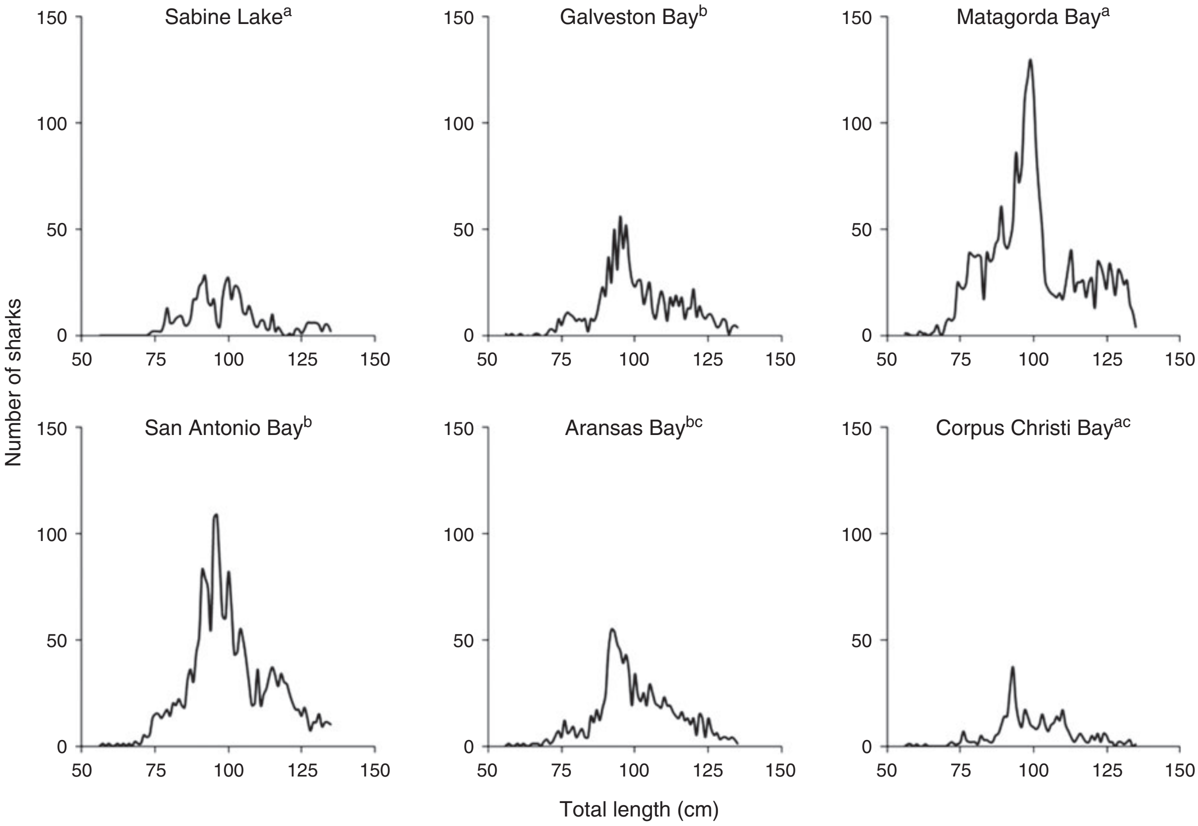

Fig. 3. Density plots of the size distribution of juvenile bull sharks captured during the study period in each estuary. Different superscript letters next to estuary names indicate significant differences in size structure based on *post hoc* Tukey's test at $\alpha = 0.05$.

Discussion

Changes in hydrology and environmental conditions driven by sea level rise, climate change and human development will likely exert heterogeneous effects on animal populations, which may be amplified for species that exhibit size specific distribution patterns attributed to ontogenetic niche shifts (e.g. Barton 2010; Sinclair *et al.* 2016). Species that undergo more pronounced niche shifts, including habitat shifts across ecosystem boundaries, may be comprise individuals that experience vastly different conditions and disturbance regimes (e.g. Klockmann *et al.* 2017; Matich *et al.* 2019). As such, elucidating the distribution patterns and factors that shape size structuring within populations is of value for predicting intraspecific variability in response to future perturbation.

Based on more than 40 years of TPWD fisheries-independent monitoring data conducted across six estuaries in Texas, ~59% of bull sharks co-occurred with conspecifics within 15 cm TL of one another, which is consistent with spatial partitioning based on bull shark size found in other estuarine nurseries (e.g. Heithaus *et al.* 2009; Ortega *et al.* 2009; Curtis *et al.* 2011; Werry *et al.* 2011). Only 19% of bull sharks captured during 20 525 TPWD surveys were with conspecifics that differed by >15 cm TL (likely one or more age class apart), and only 22% of bull sharks were captured individually. Co-occurrence with similarly sized conspecifics was more frequent in less saline ecosystems, suggesting environmental conditions may shape intraspecific interactions or similarly sized individuals could move in response to similar environmental cues (e.g. tide and freshwater inflow). Distance to the nearest source of freshwater inflow (i.e. mouths of rivers and tributaries) served as a significant predictor of bull shark size in Matagorda Bay and San Antonio Bay, supporting our understanding of bull shark ontogenetic shifts from freshwater to marine habitats in the Gulf of Mexico (e.g. Carlson 2002; Ortega *et al.* 2009; Curtis *et al.* 2011). Previous studies suggested that the use of low-salinity habitats may reduce predation risk and lower interspecific competition due to physiological limitations of other shark species, leading to high survival rates among juvenile bull sharks in these environments (Werner and Hall 1988; Compagno 2002; Heithaus 2007; Heupel and Simpfendorfer 2011). High hepatosomatic indices (i.e. liver : body ratio) among smaller bull sharks may also help facilitate the use of these habitats by optimising buoyancy (Gleiss *et al.* 2015; Iosilevskii and Papastamatiou 2016), and foraging opportunities may provide energetic benefits to using low-salinity waters (e.g. Matich and Heithaus 2014).

Despite statistical significance, the predictive power ($r^2 = 0.01$) and effect size ($\eta = 0.28$) of the bull shark size structure GLM were low, with considerable variability in trends between the distance to the source of freshwater inflow and shark TL across estuaries. Bull sharks of all sizes were captured throughout all estuaries sampled, as reported previously by

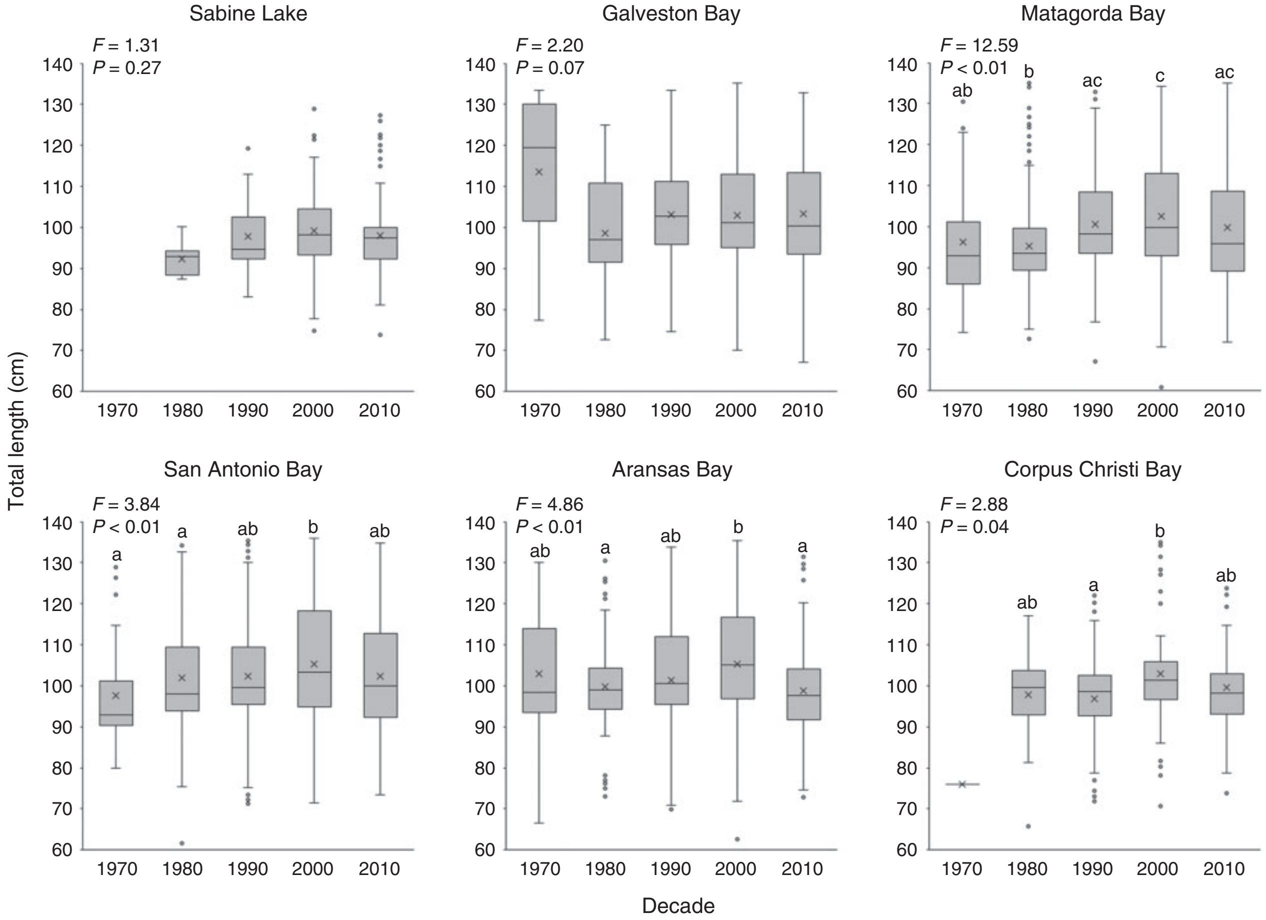

Fig. 4. Box plots showing bull shark total length across decades in different estuaries. The boxes show the interquartile range, with the median value indicated by the horizontal line and the mean indicated by the '×'. Whiskers show the range and individual symbols indicate outliers. Different letters above boxes indicate significant differences across decades in each estuary ($P < 0.05$, *post hoc* Tukey's test).

Froeschke *et al.* (2010*a*), which may be due to considerable variability in environmental conditions throughout large portions of the study systems. The capture of bull sharks with smaller or larger conspecifics was relatively infrequent (<20% of capture events), suggesting bull sharks of similar size use similar habitats or respond similarly to movement stimuli (e.g. tidal stage; Simpfendorfer *et al.* 2005; Grubbs 2010; Keller *et al.* 2017). However, a suite of factors likely shapes habitat use decisions among bull sharks in different size classes when considered at broad spatial scales, such as entire estuaries (for a review, see Guisan and Thuiller 2005). Spatial heterogeneity in benthic habitat, depth and proximity to human-altered shorelines (Armstrong 1987; Britton and Morton 1989), coupled with seasonal and acute shifts in temperatures, precipitation and salinity (Orlando *et al.* 1993; US Environmental Protection Agency 1999), may mask clearer ontogenetic habitat shifts apparent in other bull shark nurseries. More nuanced approaches may be needed to understand ontogenetic habitat relationships for bull sharks in Texas, and models that incorporate factors specific to individual estuaries could account for variability in salinity regimes that may affect bull shark distributions within nurseries based on size (e.g. Gillmore and Herrema 1981; Carlson 2002; Simpfendorfer *et al.* 2005). Trends in the CPUE of juvenile bull sharks in river mouths and geographic variability in freshwater inflow provide insights into this hypothesis.

As expected, salinity sampled at gill-net set locations was significantly related to the distance from sources of freshwater inflow (Orlando *et al.* 1993; Longley 1994). As such, capture location may serve as an indicator of long-term salinity conditions within each estuary. However, the relationship between variability in salinity and sampling location exhibited significant spatial differences. Southern estuaries (i.e. Aransas and Corpus Christi bays) exhibited decreased variability in salinity as the distance from sources of freshwater inflow increased, whereas Sabine Lake exhibited an opposite trend, with greater stability in salinity as the proximity to freshwater inflow sources increased. The results were not unexpected based on geographic differences in freshwater inflow: spatial variability in precipitation across Texas leads to a direct relationship between freshwater inflow into estuaries and latitude, providing more consistent, low-salinity habitats at river mouths in Sabine Lake than in Aransas and Corpus Christi bays (Orlando *et al.* 1993; Longley 1994; US Environmental Protection Agency 1999). Consequently, increased evaporation and salt water

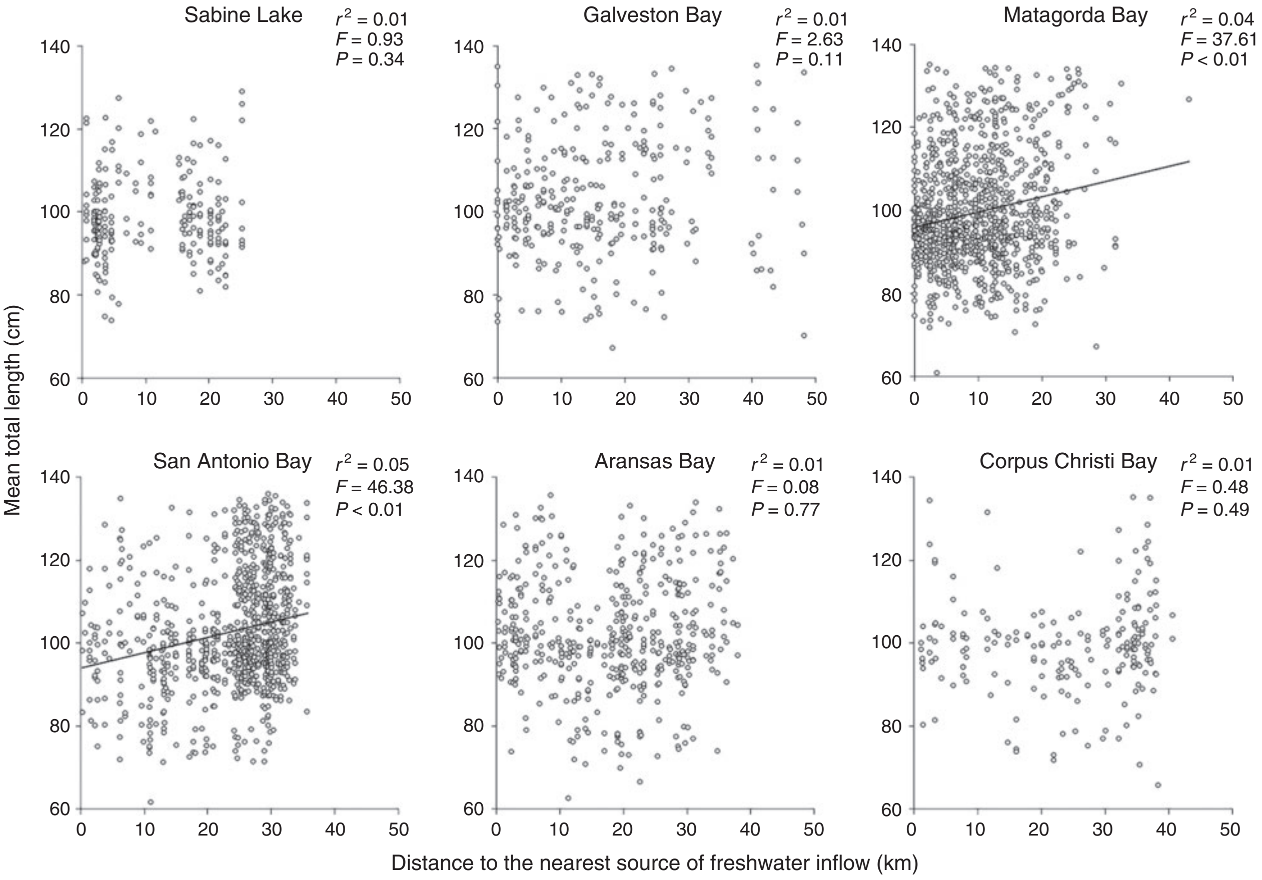

Fig. 5. Effect of distance to the nearest source of freshwater inflow on mean shark total length in different estuaries. Trend lines are only shown for significant relationships.

Table 2. Proportion of bull sharks co-occurring with conspecifics and mean (±s.d.) size difference of co-occurring sharks

Different letters indicate significant differences ($P < 0.05$) in mean size differences of co-occurring sharks across estuaries, decades, or seasons based on *post hoc* Tukey tests. TL, total length

	Proportion of co-occurring sharks	Mean size difference (cm TL)
Sabine Lake	0.76	9.71 ± 8.60^{a}
Galveston Bay	0.80	11.18 ± 9.95^{bcd}
Matagorda Bay	0.84	10.65 ± 10.33^{ef}
San Antonio Bay	0.76	10.57 ± 9.95^{be}
Aransas Bay	0.72	9.06 ± 9.26^{cf}
Corpus Christi Bay	0.58	10.20 ± 10.48^{ad}
1970s	0.85	10.57 ± 11.40^{a}
1980s	0.80	8.91 ± 8.06^{b}
1990s	0.80	9.49 ± 8.94^{b}
2000s	0.77	12.06 ± 11.24^{c}
2010s	0.75	11.42 ± 10.59^{c}
Spring	0.77	10.98 ± 10.53^{a}
Autumn	0.78	9.80 ± 9.07^{b}

intrusion from the Gulf of Mexico may serve as greater regulating agents of salinity in southern estuaries than freshwater inflow, creating more stable environmental conditions adjacent to tidal passes and distinct ecosystems that lead to geographic variability in the distributions of bull sharks across the Texas coast (Armstrong 1987; US Environmental Protection Agency 1999; Plumlee *et al.* 2018).

Within estuaries, both mean and variability in environmental conditions can shape fish populations and communities (Flint 1985; Constanza *et al.* 1993; Kupschus and Tremain 2001; Elliott and Whitfield 2011). For example, fish assemblages in coastal lagoons of Maryland were less diverse during periods of high variability in salinity, which was attributed to transient species moving out of lagoons to account for increased physiological stress (Love *et al.* 2009). Similarly, fish species richness and diversity was lower in areas of Biscayne Bay, Florida, with variable salinity than in areas with stable salinity based on species osmoregulatory abilities (Serafy *et al.* 1997). Estuary-specific differences in the use of river mouths by juvenile bull sharks suggest that stability or variability in salinity may be an important driver of habitat use, as well as size structuring within some Texas estuaries. YOY captures in river mouths approached and fell below expected frequencies in lower-latitude estuaries that receive limited freshwater inflow from

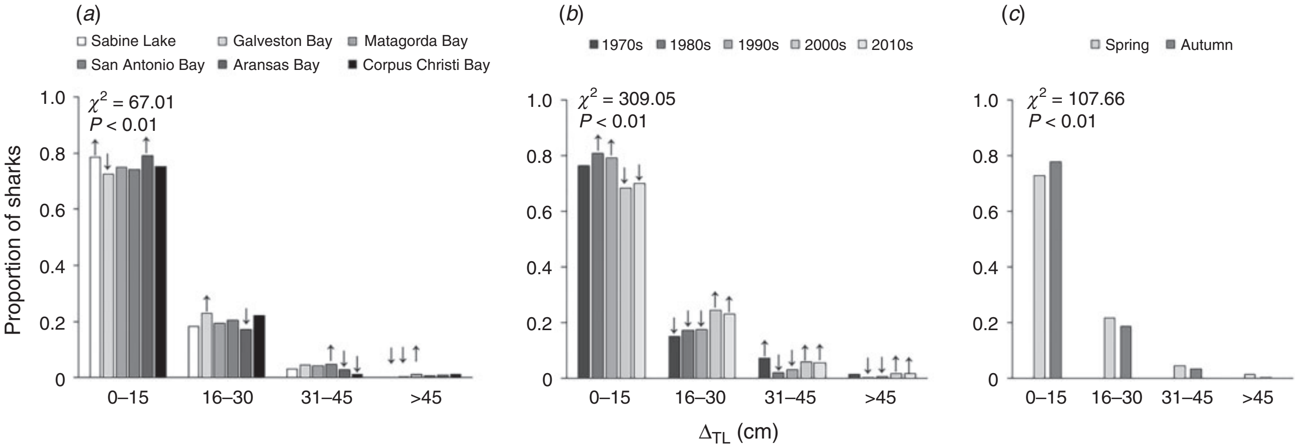

Fig. 6. Proportion of co-occurring sharks with differences in total length (Δ_{TL}) of 0–15, 16–30, 31–45 and >45 cm varied across (*a*) estuaries, (*b*) decades and (*c*) season. Arrows above bars indicate significant differences from expectations based on *post hoc* *Z*-scores, with upward and downward pointing arrows indicating significantly higher and lower than expected frequencies of co-occurring conspecifics within Δ_{TL} bins respectively.

rivers and exhibit greater stability in salinity within habitats distant from river mouths. If biotic factors, such as predictability in prey resources, play important roles in shaping bull shark populations (Wirsing *et al.* 2007; Gaitán-Espitia *et al.* 2017; Weideli *et al.* 2019), then bull sharks may seek out more environmentally stable habitats within Texan estuaries that support more predictable, consistent prey populations (Gelwick *et al.* 2001; Cortés and Waessle 2017; Byrne *et al.* 2019). Similar latitudinal trends in the use of river mouths were observed among juvenile bull sharks 90–135 cm TL, suggesting that the ecological functions these habitats provide may vary based on freshwater inflow and salinity variability (Gillmore and Herrema 1981; Carlson 2002; Simpfendorfer *et al.* 2005; Froeschke *et al.* 2010*a*). Alternatively, bull sharks using more dynamic estuaries may exhibit greater movement patterns in order to remain within preferred conditions (e.g. Heupel and Simpfendorfer 2008; Drymon *et al.* 2014).

In contrast to YOY and smaller juveniles, larger juvenile bull sharks and subadults (sharks >135 cm TL) did not preferentially use river mouths, indicating a size-based shift in distribution patterns in some ecosystems, which was more prominent during spring sampling. All sharks >90 cm TL were captured in river mouths at a frequency expected based on sampling effort during the autumn season. Yet, there was an interaction between shark size and the use of river mouths during the spring, with a significant decrease in the expected use of river mouths with shark size. Smaller sharks (<121 cm TL) exhibited a preference for river mouths compared with other estuarine habitats, whereas larger sharks (>135 cm TL) avoided river mouths in spring. Owing to a lack of sampling in summer months, it is unclear why such partitioning among size classes occurred in river mouths in spring but not autumn. Increased freshwater inflow in early spring may have increased the spatial scale over which salinity gradients formed in estuaries, consequently increasing the scale over which size partitioning occurred and improving our ability to detect such patterns (Werry *et al.* 2011; US Geological Survey National Water Information System, see https://waterdata.usgs.gov/nwis/rt, accessed May 2019). Fewer, less energetically rewarding prey may be available in spring due to reduced winter productivity, leading to more pronounced niche partitioning among smaller and larger conspecifics (Akin *et al.* 2003; Svanbäck and Bolnick 2007; Taylor and Bennett 2008; Zimmerman *et al.* 2009; Simpson *et al.* 2019). Temporal variability in freshwater inflow, salinities and temperatures may have also led to seasonal differences in partitioning based on differences in physiological tolerances and preferences across bull shark size classes (Parsons and Hoffmayer 2007; Ortega *et al.* 2009; Curtis *et al.* 2011). A transition from preferring low-salinity waters to avoiding such habitats fits the current model for ontogenetic niche shifts among bull sharks (e.g. Simpfendorfer *et al.* 2005; Werry *et al.* 2011; Matich and Heithaus 2015), but sharks did not follow this pattern in all estuaries, suggesting differences in intraspecific interactions may be driven by estuary-specific differences in freshwater inflow.

Predation risk is proposed as an important factor shaping size structuring within bull shark nurseries, in which the smallest, most-vulnerable individuals seek out the safest habitats to improve survival rates (Castro 1993; Heithaus 2007; Grubbs 2010). YOY bull sharks preferentially used consistent, low-salinity habitats at river mouths in northern estuaries, yet the connection between rivers and bays in providing nursery habitat within Texan estuaries is still unclear because gill-net monitoring did not occur in river habitats. Historical records suggest that bull sharks have been observed in Texan rivers (Table 1), but there have been no studies of bull shark use of riverine systems in Texas. As estuaries become more saline due to climate change and sea level rise (Ribeiro *et al.* 2016; Mahoney and Bishop 2017), rivers may become increasingly important as low-salinity refugia from predation and competition within estuarine ecosystems. Decadal increases in the use of river mouths by YOY bull sharks support the hypothesis that more stable, low-salinity habitats are becoming increasingly preferred. However, the drivers of these patterns may be due to interspecific interactions with other shark species rather than direct changes in environmental conditions. Indeed, the abundance of blacktip sharks *Carcharhinus limbatus* has recently increased in the Gulf of Mexico (Bubley and Carlson 2012), potentially in response to regional changes in fisheries management (Peterson *et al.* 2017).

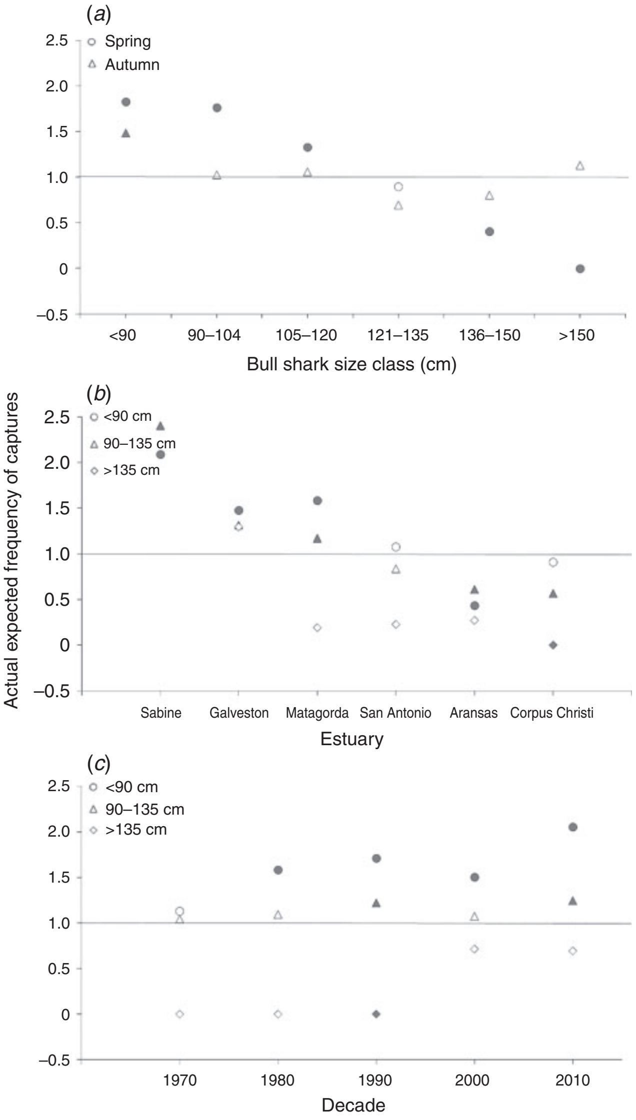

Fig. 7. Deviation of bull sharks captured at river mouths from expected capture rates based on gill net deployments in river mouths (*a*) decreased with age class, (*b*) decreased as latitude decreased and (*c*) increased through time. The horizontal lines represent expected frequencies of captures at river mouths if the frequency of shark captures did not differ from the frequency of gill net deployments; values >1 indicate more shark captures than expected and values <1 indicate fewer shark captures than expected. Open symbols were not significantly different than expected, whereas filled symbols were significantly different than expected based on Chi-Square tests. Age classes are grouped for spatial and temporal assessment due to low individual sample sizes.

As a result, co-occurrence of blacktip sharks and bull sharks in Texan estuaries has increased fourfold over the past 25 years (Matich *et al.* 2017*a*), potentially leading to increased interspecific competition and risk for YOY bull sharks (Brown and Wilson 1956; Pianka 1973; Papastamatiou *et al.* 2006; Castro 2011; Matich *et al.* 2017*b*). As such, access to low-salinity habitats may enable YOY bull sharks to thrive in Texas estuaries.

An important consideration for our work is the limited number of YOY bull sharks caught during the sampling period. The population structure of juvenile bull sharks in Texan estuaries did not fit traditional ecological models, which generally predict the youngest animals to be the most abundant individuals within juvenile populations in the absence of immigration (for a review, see Easterling *et al.* 2000). Bull shark size structure across all estuaries and decades, except for the 1970s, was represented by a bell-shaped curve (Fig. 3, 4), with moderately sized juvenile bull sharks representing the highest proportion of sharks during the study period (i.e. 50% of sharks <136 cm TL were 90–105 cm TL). This deviation was driven by infrequent captures of YOY sharks within the study areas (~20% of sharks <136 cm TL), which was considerably lower than most estuaries that support juvenile bull sharks (30–96% outside of Texas; Table 3). It is unlikely that the patterns observed were due to larger size at birth than in other parts of the Gulf of Mexico, large-scale immigration or emigration or high rates of mortality of YOY, although each is a possible explanation (Thorson 1971; Branstetter and Stiles 1987; Natanson *et al.* 2014; Meynecke *et al.* 2015). The two most likely causes for the observed size distribution curve are gill-net selectivity and inadequate sampling of habitats where YOY sharks aggregate. Indeed, multipanel gill-nets have well-described size selection biases, which can generate bell-shaped size distributions in catch similar to those observed here (Carlson and Cortés 2003; McAuley *et al.* 2007; Baremore *et al.* 2012). Alternatively, the undersampling of YOY sharks may reflect a lack of spatial overlap between YOY sharks and gill-nets. Gill-net monitoring did not sample estuarine rivers, which typically serve as bull shark nurseries around the world and are particularly important for YOY individuals because of the refuge they provide (e.g. Boesman 1964; Hueter and Tyminski 2007; Tillett *et al.* 2012). The lack of river sampling may limit the efficacy of monitoring juvenile bull sharks, which would explain the relatively low YOY encounter rates that should have been 50–360% higher based on other bull shark nurseries (Table 3). The importance of river mouths for YOY sharks in Sabine Lake and Galveston and Matagorda Bays supports our hypothesis that undersampling of rivers contributed to low YOY catch rates, and future monitoring should aim to incorporate estuarine rivers to provide more comprehensive sampling of the full range of bull shark size classes.

Conclusions

Nursery habitats are often unique in their capacity to promote growth and survival among juvenile individuals (Beck *et al.* 2001; Heithaus 2007). In the north-western Gulf of Mexico, our current understanding of bull shark nurseries stems from coast-wide assessments of abundance and distribution patterns, providing a foundation for future research in the region (Hueter and Tyminski 2007; Froeschke *et al.* 2010*b*; Plumlee *et al.* 2018). Yet, the inherent heterogeneity of estuaries (Beck *et al.* 2001; Day *et al.* 2012) and differences in nursery functions across estuaries (McCandless *et al.* 2007) challenges coast-wide management plans. Estuary-specific or regional planners are often met with insufficient local data, funding and other resources, and effective population management of migratory or wide-ranging estuarine species will require compromise and a

Table 3. Estimates of the proportion of bull sharks <136-cm total length (TL) composed of young-of-the-year (YOY) individuals (<90 cm TL) in coastal estuaries

References include studies where length data was available for all individuals. Studies only providing means and a measure of variability were not included

Proportion of YOY (%)	Estuary	Sampling method	Reference
~12	Sabine Pass Inlet (TX, USA)	Entanglement net (12.7- to 24.5-cm stretch mesh)	Shipley (2005)
~20	Texan estuaries (USA)	Gill-net (7.6- to 15.2-cm stretch mesh)	Froeschke *et al.* (2010*b*, 2013); present study
~30	Nerang River (Qld, Australia)	Longline (8/0 tuna hook)	Werry *et al.* (2012)
~34	Indian River Lagoon (FL, USA)	Gill-net (7.9- to 8.9-cm stretch mesh)	Snelson *et al.* (1984)
~36	Shark River Estuary (FL, USA)	Longline (12/0–15/0 tuna circle hook)	Heithaus *et al.* (2009)
~43	Indian River Lagoon (FL, USA)	Longline (12/0 tuna circle hook), rod and reel	Curtis *et al.* (2013)
~45	Rockingham, Bowling Green, Edgecumbe, Repulse Bay (Qld, Australia)	Longline (14/0 tuna circle hook), gill-net (11-cm stretch mesh)	Yates *et al.* (2015)
~51	Barataria Bay and Little Lake (LA, USA)	Gill-net (5.1- to 10.2-cm stretch mesh)	Reviewed by Blackburn *et al.* (2007)
~51	Ten Thousand Islands (FL, USA)	Gill-net (7.6- to 15.2-cm stretch mesh), longline (5/0–18/0 circle and J-hooks), rod and reel, seine (61 m)	Hueter and Tyminski (2007)
~54	Charlotte Harbor (FL, USA)	Gill-net (7.6- to 15.2-cm stretch mesh), longline (5/0–18/0 circle and J-hooks), rod and reel, seine (61 m)	Hueter and Tyminski (2007)
~56	Tampa Bay (FL, USA)	Gill-net (7.6- to 15.2-cm stretch mesh), longline (5/0–18/0 circle and J-hooks), rod and reel, seine (61 m)	Hueter and Tyminski (2007)
~56	Western Australia, Northern Territory (Australia)	Gill-net (5- to 20-cm stretch mesh), longline (5/0 tuna circle hook)	Thorburn and Rowland (2008)
~68	Ten Thousand Islands (FL, USA)	Gill-net (6.5-cm stretch mesh), longline (#1 shark hooks)	Steiner and Michel (2007)
~81	Lake Pontchartrain (LA, USA)	Bag seine (3–30 m), gill-net (20.3-cm stretch mesh)	Reviewed by Blackburn *et al.* (2007)
~87	Mobile Bay (AL, USA)	Gill-net (7.6- to 14.0-cm stretch mesh)	Bethea *et al.* (2015)
~88	Caloosahatchee River (FL, USA)	Longline (12/0–16/0 tuna circle hooks)	Simpfendorfer *et al.* (2005)
~89	Vermillion Bay (LA, USA)	Trammel net (5-cm bar mesh)	Caillouet *et al.* (1969)
~89	Vermillion Bay (LA, USA)	Gill-net (7.6-cm stretch mesh)	Reviewed by Blackburn *et al.* (2007)
~92	Pearl River System (LA, USA)	Trammel net	Reviewed by Blackburn *et al.* (2007)
~96	Rewa, Sigatoka, Navua rivers (Fiji)	Gill-net (10.2-cm stretch mesh)	Glaus *et al.* (2019)

science-based understanding of coast-wide, regional and local patterns in ecology. For example, the results of this study suggest that particular microhabitats (i.e. river mouths) may play a disproportionately important role in bull shark nurseries, with spatial and temporal variability in the use of these habitats driven by differences in freshwater inflow and ontogenetic niche shifts (e.g. Gillmore and Herrema 1981; Carlson 2002; Drymon *et al.* 2014; Matich and Heithaus 2014). Predictable differences in the functionality of river mouths as YOY bull shark habitat across the Texas coast support our understanding of estuarine heterogeneity across multiple spatial scales (Beck *et al.* 2001; Day *et al.* 2012) and suggest that changes to these habitats by natural and anthropogenic perturbations will not uniformly affect the ecological services they provide. Advancing our understanding of how ecological characteristics may change in response to disturbances will improve our ability to appropriately manage estuaries and euryhaline species, like bull sharks, which may respond heterogeneously to extrinsic factors because of size-specific differences in risk and competition (Werner and Hall 1988; Dahlgren and Eggleston 2000; Beck *et al.* 2001; Heithaus 2007; Grubbs 2010).

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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