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Factors shaping the co-occurrence of two juvenile shark species along the Texas Gulf Coast

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Abstract As top predators, sharks play important ecological roles in coastal marine ecosystems. Yet, environmental changes in many coastal regions are likely altering the composition of ecological communities, the interspecific interactions sharks have within coastal waters, and subsequently the ecological roles sharks play within these ecosystems. As such, understanding interactions among sharks, and how extrinsic factors shape these interactions, is important for predicting the consequences of future human impacts and environmental changes. Elucidating the contexts under which species co-occur and the implications of co-occurrence is an important step in developing such a predictive framework. Blacktip shark (*Carcharhinus limbatus*) and bull shark (*Carcharhinus leucas*) concentrations were quantified using long-term coastal gill net survey data across five bay systems in Texas. Relationships between co-occurrence, and environmental factors and shark sizes were examined within and across species. Co-occurrence of blacktip sharks and bull sharks varied spatially and temporally, with a significant increase in interspecific co-occurrence from the 1970s to 2010s, and a significant decrease in bull shark concentrations through time. Changes in environmental conditions, specifically increasing salinities, may have been responsible for increased blacktip and bull shark co-occurrence, and potential interspecific competition, which in turn may have led to decreased bull shark concentrations to reduce intraspecific competition. However, more refined questions are needed before predictive frameworks can be developed concerning the contexts under which co-occurrence is prevalent. Quantifying resource use among coastal sharks will help elucidate the drivers and implications of co-occurrence, and the potential for competitive interactions within and across species.

Introduction

Predators serve essential roles in their respective ecosystems through top-down effects and the translocation of biomass and nutrients that stimulate bottom-up processes (e.g., Helfield and Naiman 2006; Schmitz et al. 2010). These ecological roles are shaped by community composition, including co-occurrence and competition with other predators and conspecifics (e.g., Owen-Smith and Mills 2008; Bolnick et al. 2011; Browning et al. 2014). When resources are limited, ecological theory predicts that niche partitioning will occur within and across species to promote coexistence (Pianka 1973; 1974; Schluter and McPhail 1992). However, natural and anthropogenic disturbances continue

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to affect many predator populations and are reshaping population and community structure, which may be affecting competitive interactions and niche overlap among sharks (reviewed by Heithaus et al. 2008; Holt 2009; Estes et al. 2011).

Overlap in predator–human habitat use increases vulnerability of species to anthropogenic disturbances (Eero et al. 2011; Maxwell et al. 2013; Dulvy et al. 2016), and coastal sharks have been particularly affected due to exploitation, unintended captures, and deterioration of essential habitats (Ferretti et al. 2010; Dulvy et al. 2014). Natural or anthropogenically stimulated changes in species presence/absence within shark populations can lead to considerable differences in shark behavior and niche widths (Chase and Leibold 2003; Papastamatiou et al. 2006; Brena et al. 2015), and reductions in co-occurrence and niche similarity may destabilize coastal food webs (Pace et al. 1999; Jackson et al. 2001; Estes et al. 2011). As such, elucidating shark community dynamics within coastal ecosystems, and the factors that shape species co-occurrence, is important for understanding how ecological communities may respond to changes in shark abundances, distributions, and behaviors (Cornelius et al. 2001; Ruppert et al. 2013).

Ecosystems where sharks co-occur across a gradient of environmental conditions and human disturbance provide ideal study areas to investigate the response of ecological communities to changing shark populations. The Texas coastline provides habitat for diverse elasmobranch assemblages, which include juvenile and adult blacktip sharks (*Carcharhinus limbatus*) and bull sharks (*Carcharhinus leucas*), and serves as nurseries for at least bull sharks (Hueter and Tyminski 2007; Froeschke et al. 2010a). Published studies in Texas and other Gulf Coast states suggest several extrinsic factors affect catch rates of these species, providing a foundation for developing and testing hypotheses concerning the factors that may shape shark co-occurrence in the Western Gulf of Mexico. Using catch rates and movement data, published studies show that both blacktip sharks and bull sharks exhibit preferences for warm temperatures, moderate salinities, and shallow depths throughout the Gulf of Mexico (Baughman and Springer 1950; Norden 1966; Simpfendorfer et al. 2005; Blackburn et al. 2007; Parsons and Hoffmayer 2007; Wiley and Simpfendorfer 2007; Heupel and Simpfendorfer 2008; Carlson et al. 2010; Drymon et al. 2010, 2014; Froeschke et al. 2010b; Heupel et al. 2010; Bethea et al. 2015; Ward-Paige et al. 2015). However, these patterns are not consistent across regions (e.g., Grace and Henwood 1997; Shipley 2005; Heithaus et al. 2009), and other factors, including dissolved oxygen content (Shipley 2005; Heithaus et al. 2009; Drymon et al. 2014), prey availability (Ortega et al. 2009; Drymon et al. 2013; Sargarese et al. 2016), predation risk (Matich and Heithaus 2015), habitat type (Carlson 2002; Steiner et al. 2007; Curtis et al. 2013; Drymon et al. 2014), and red tides (Sagarese et al. 2017) play a role in shaping the distribution patterns of these sharks, with suggestions that bull sharks may be more robust to environmental variability than blacktip sharks (Steiner et al. 2007). Using catch rate data, Froeschke et al. (2010b) found that salinity, water temperature, and depth were the most important factors affecting the relative abundances of blacktip sharks and bull sharks in coastal Texas, with spatial variability in catch rates potentially attributed to bay-specific differences in nursery quality (Froeschke et al. 2010a). As such, co-occurrence of blacktip sharks and bull sharks is likely driven by these factors.

Here, spatial and temporal differences in blacktip shark and bull shark distributions are investigated in five coastal bay systems within Texas across the last 40 years, to explore the extrinsic and intrinsic factors that lead to co-occurrence within and across species. Specifically, data were used to determine (1) if blacktip sharks and bull sharks co-occur over time and space, and (2) what extrinsic (i.e., environmental) and intrinsic (body size) factors correlate with events when more than one shark is captured.

Methods

Study sites

The Texas coast comprises a series of bay systems geographically separated from the Gulf of Mexico by seven barrier islands that limit physical and biological connectivity (Fig. 1). These systems range from predominantly freshwater (Sabine Lake) to hypersaline habitats (Laguna Madre) that support distinct ecological communities (e.g., Froeschke et al. 2010b; Kim et al. 2014). Many of these bay systems are heavily influenced by precipitation and freshwater inputs from rivers (Kim et al. 2014), and spatial variability in precipitation and freshwater input typically leads to a salinity gradient across the Texas coast, with decreasing salinities within bay systems as latitude increases (Froeschke et al. 2010b; Mohan and Walther 2015). Similarly, water temperatures are typically cooler as latitude increases, with higher dissolved oxygen concentrations in mid-latitudinal bay systems (i.e., San Antonio Bay and Aransas Bay; Froeschke et al. 2010b).

Among the seven bay systems that comprise the Texas coastline, blacktip sharks and bull sharks predominantly co-occur at a broad geographical scale in five of these systems (listed north to south)—Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, and Corpus Christi Bay (Froeschke et al. 2010b). Blacktip sharks exhibit minimal use of Sabine Lake, likely because of low salinity conditions, and bull sharks exhibit minimal use of Laguna

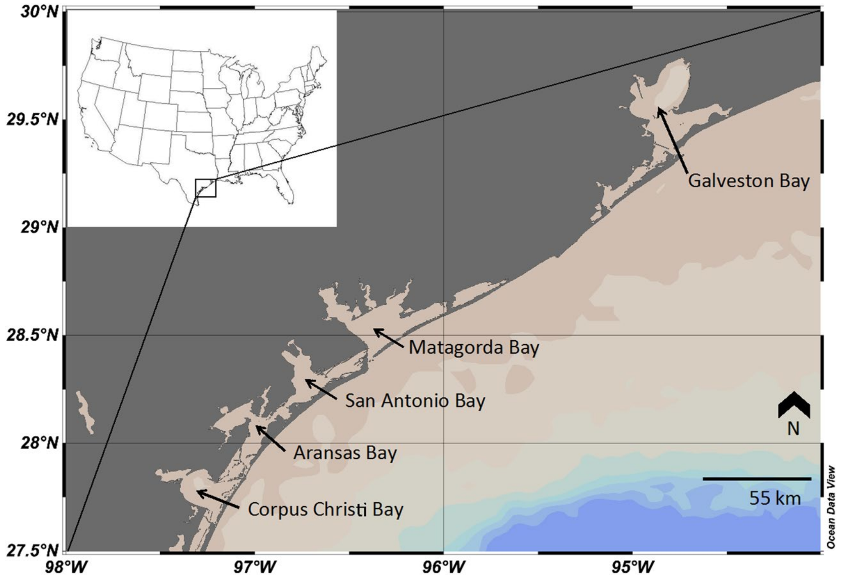

Fig. 1 Location of the five major bay systems along the coast of Texas where sharks were sampled

Madre, likely because of hypersaline conditions (Froeschke et al. 2010b). Each of the five bay systems where blacktip sharks and bull sharks co-occur regionally exhibit different physical characteristics as described above (e.g., Thronson and Quigg 2008; Froeschke et al. 2010b). Each bay system also has different historical patterns in human development and disturbance, including recreational and commercial fishing communities that are typically most active in Galveston Bay (e.g., McEachron and Green 1984; Ditton et al. 1992), because of the large human population the Houston metropolitan area supports (ca. 2.2 million people; U.S. Census Bureau 2010). As such, the spatial variability in conditions and disturbance among bay systems provides both a physical and anthropogenic gradient in which to investigate shark co-occurrence patterns.

Field sampling

Data were obtained from gill net surveys conducted by the Texas Parks and Wildlife Department long-term fishery-independent monitoring program that was established in 1975 and is ongoing. Beginning in 1982, 45 gill nets were set in each bay system in each 10-week spring (April–June) and fall (September–November) season. Sample sizes were variable before 1982. Sampling consists of 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 stretched mesh tied together in ascending order) set overnight (mean soak time ± SD = 13.7 ± 1.4 h), perpendicular to the shoreline with the 7.6 cm stretched mesh on the shoreward end, from randomly selected locations. All organisms caught were identified to the lowest taxonomic level (typically species), counted, and measured [total length (from the tip of the snout to the tip of the tail fully extended; TL) in mm]. Date, location, water depth (m), salinity (psu), water temperature (°C), and dissolved oxygen (mg L^{-1}) were recorded for each sample and used to estimate environmental conditions while nets soaked. Environmental conditions may have changed overnight, but were only recorded at deployment and retrieval; thus, the sampling regime did not enable us to test how changes in environmental conditions during sampling affected shark captures and co-occurrence. The average environmental conditions of each sampling event at deployment and retrieval were used for analyses.

Species caught in gill nets were not exclusively sharks (see e.g., McEachron et al. 1998; Matich et al. 2016), and some teleosts may provide food for sharks and/or attract sharks to gill nets during deployments (Cortés 1997). To assess the effects of teleost abundance on shark co-occurrence and concentrations, the catch per unit effort (CPUE) values of teleost species most abundant in gill net surveys, and known to be consumed by blacktip sharks and bull sharks, were pooled and quantified to estimate food availability (i.e., the CPUE values of the seven “bait” species were combined). Species included in analyses were Atlantic croaker (*Micropogonias undulatus*), finescale menhaden (*Brevoortia gunteri*), gizzard shad (*Dorosoma cepedianum*), Gulf menhaden (*Brevoortia patronus*), ladyfish (*Elops saurus*), spot (*Leiostomus xanthurus*), and striped mullet (*Mugil cephalus*) (Snelson and Williams 1981; Snelson et al. 1984; Cliff and Dudley 1991; Castro 1996; Bethea et al. 2004; Barry et al. 2008; Tavares 2008; Bornatowski et al. 2014; Tillett et al. 2014; Plumlee and Wells 2016).

Data analysis

Using gill net data, the presence and absence of blacktip sharks and bull sharks, the co-occurrence of blacktip sharks and bull sharks, the co-occurrence of conspecifics, and species-specific concentrations (i.e., individually for each species) were quantified. Co-occurrence is an event in which at least two sharks were captured from different species (i.e., at least one bull shark and at least one blacktip shark—interspecific co-occurrence) or the same species (i.e., at least two bull sharks or at least two blacktip sharks—intraspecific co-occurrence). Concentration is defined as the number of sharks captured during a single event when sharks were caught (Maunder and Punt 2004) and used to quantify intraspecific co-occurrence as a continuous variable. Gill nets that did not result in the capture of at least one blacktip shark or at least one bull shark were not included in the analyses (Maunder and Punt 2004; Fletcher et al. 2005; Serafy et al. 2007). Absence data (i.e., when sharks were not captured) was not included to avoid overlapping with the findings of Froeschke et al. (2010b), who investigated the impacts of environmental conditions on catch rates of these species in Texas. However, findings are presented within the context of Froeschke et al.'s results to broaden the scope of our study.

Forward, stepwise logistic regression (i.e., factors were added sequentially and kept if significant at $\alpha = 0.05$) was used to quantify the effects of extrinsic and intrinsic factors on the likelihood of capturing at least one blacktip shark and at least one bull shark (i.e., interspecific co-occurrence). Predictor variables included (as extrinsic factors) bay system, decade (1970s, 1980s, 1990s, 2000s, 2010s), season (spring and fall), mean water temperature, mean salinity, mean dissolved oxygen, mean deepest water depth sampled by gill nets, and prey CPUE. Intrinsic factors in analyses included mean shark TL and shark TL range. Only significant interactions and main effects at $\alpha = 0.05$ were included in the models. A post hoc Mann–Whitney test was used to quantify differences among parameters for significant factors and interactions. Results were used to elucidate the factors leading to interspecific co-occurrence, which is defined as a sampling event during which at least one blacktip shark and at least one bull shark were captured. An identical analytical framework with post hoc Mann–Whitney tests was used to identify the factors leading to intraspecific co-occurrence (i.e., when more than one individual of the same species was captured during a sampling event—presence/absence).

Sharks of the same or different species may have entered gill nets at different times, and thus data may indicate the capture of sharks that would otherwise not exhibit intra- or interspecific co-occurrence. The sampling scheme did not enable us to test the assumption that sharks captured in the same gill net were captured at the same time. However, the small spatial coverage of the gill nets (183 m long) relative to the spatial coverage of bay systems (ca. 500–1500 km^2) should limit interpretation bias of sharks co-occurring that may have entered habitats sampled by nets, hours apart.

Forward stepwise general linear models (GLMs) were used to investigate the effects of extrinsic and intrinsic factors (those used for logistic regression) affecting shark concentrations when more than one individual was captured, independently for each species. A post hoc Tukey's test was used to quantify differences among parameters for significant factors and interactions. 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 versus predicted values were used to test for variance homogeneity of the models and factors. GLMs were also used with post hoc Tukey's tests to investigate the spatial and temporal differences in blacktip and bull shark size structure (i.e., total lengths and length ranges). Data were appropriately transformed to meet assumptions of GLMs, including log transformation of blacktip and bull shark concentrations, and square root transformation of blacktip and bull shark size ranges. All analyses were conducted in IBM SPSS 22.

Results

From 1975 to 2014, 20,540 gill nets were deployed in Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, and Corpus Christi Bay, during which 2912 blacktips were captured during 993 sampling events and 7841 bull sharks were captured during 3331 sampling events (Table 1). Blacktip sharks ranged from 39 to 210 cm TL, and bull sharks ranged from 56 to 211 cm TL, with 98% of sharks of both species <150 cm TL.

Co-occurrence of blacktip sharks and bull sharks (i.e., interspecific co-occurrence) varied spatially and temporally (Fig. 2). Interspecific co-occurrence was highest in Matagorda, San Antonio, and Corpus Christi bays (mean ± SE = 8.2% ± 0.7, 8.1% ± 0.8, and 9.1% ± 1.5 of capture events, respectively; $\chi^2_{1,4042} = 10.08$, $p < 0.01$; Fig. 2a). Interspecific co-occurrence of blacktip sharks and bull sharks significantly increased across decades, with the highest frequency of interspecific co-occurrence in the 2010s (12.2% ± 1.1 of capture events; $\chi^2_{1,4042} = 6.13$, $p = 0.01$; Fig. 2b). Interspecific co-occurrence was also higher in the fall (September–November; 8.9% ± 0.7) than the spring (April–June; 5.3% ± 0.5; $\chi^2_{1,4042} = 3.97$, $p = 0.046$).

Extrinsic and intrinsic factors significantly affected the likelihood of interspecific co-occurrence (Table 2; ESM Table 1). Blacktip sharks and bull sharks were

Table 1 Gill net deployments, number of sharks caught, size range of sharks caught (in cm TL), average salinity (±SD in psu), average water temperature (±SD in °C), and average dissolved oxygen content (±SD in mg L^{-1}) across decades within each bay system

Bay	Decade	Gill nets	Blacktip sharks		Bull sharks		Salinity	Temperature	Dissolved oxygen
			N	Size range	*N*	Size range			
Galveston	1970s	221	26	53–130	33	66–166	16.1 (7.3)	18.8 (7.2)	10.4 (2.5)
	1980s	849	137	45–129	83	73–151	17.7 (7.9)	25.1 (4.1)	8.6 (2.8)
	1990s	900	116	51–100	266	75–149	16.3 (8.9)	25.4 (4.0)	7.5 (1.5)
	2000s	900	77	49–126	390	58–163	16.7 (8.5)	26.1 (3.6)	7.5 (1.4)
	2010s	450	87	46–115	444	56–179	22.3 (7.8)	25.8 (3.8)	7.9 (1.6)
Matagorda	1970s	288	21	81–128	145	74–169	15.9 (6.4)	19.9 (7.2)	10.0 (1.9)
	1980s	1242	441	40–145	885	66–150	20.7 (8.2)	24.9 (4.7)	8.5 (1.6)
	1990s	1300	148	44–159	604	56–158	18.6 (9.1)	25.8 (4.2)	7.5 (1.7)
	2000s	1300	357	48–182	977	57–178	21.1 (8.8)	26.6 (3.8)	7.1 (1.4)
	2010s	650	434	39–210	424	61–201	28.0 (7.4)	26.2 (3.9)	7.5 (1.3)
San Antonio	1970s	175	4	81–147	116	74–152	15.2 (10.6)	20.6 (6.8)	8.9 (2.2)
	1980s	849	8	58–164	558	62–185	21.1 (10.2)	25.5 (4.0)	7.7 (2.5)
	1990s	900	179	52–168	648	65–175	18.1 (10.7)	25.9 (3.9)	8.3 (1.7)
	2000s	900	163	49–179	604	57–169	18.7 (11.7)	26.7 (3.5)	7.9 (1.6)
	2010s	450	218	45–181	301	59–211	24.6 (9.4)	26.3 (3.7)	7.7 (1.6)
Aransas	1970s	181	1	56	48	67–136	13.2 (7.2)	20.2 (6.9)	10.1 (2.2)
	1980s	849	27	56–86	275	71–146	20.4 (9.1)	25.4 (4.1)	9.0 (2.2)
	1990s	900	7	56–91	171	60–147	18.0 (9.2)	26.2 (3.9)	8.2 (2.1)
	2000s	900	7	74–167	357	57–169	18.2 (10.1)	26.9 (3.5)	7.6 (1.7)
	2010s	450	25	72–165	168	66–154	26.6 (8.9)	26.6 (3.6)	7.9 (1.4)
Corpus Christi	1970s	169	10	57–81	4	76–147	25.0 (7.1)	21.0 (6.6)	9.4 (2.0)
	1980s	849	126	40–177	32	65–126	30.6 (6.9)	25.3 (3.9)	8.1 (1.8)
	1990s	900	75	49–146	105	57–136	28.5 (6.7)	26.2 (3.8)	7.8 (1.8)
	2000s	900	163	46–107	98	60–174	28.3 (7.7)	26.9 (3.3)	7.1 (1.5)
	2010s	450	55	43–150	105	74–135	33.4 (5.7)	26.6 (3.2)	7.2 (1.2)

caught together at increased salinities (28.3 ± 0.3 psu, $\chi^2_{1,4042} = 67.46$, $p < 0.01$) and deeper depths (1.30 ± 0.03 m, $\chi^2_{1,4042} = 11.47$, $p < 0.01$), compared to homospecific events (i.e., when only one species was caught; 21.6 ± 0.2 psu and 1.17 ± 0.01 m, respectively; Fig. 3a, b). Bull shark size also varied between homospecific and heterospecific capture events. Interspecific co-occurrence was more frequent when bull sharks were larger (110.7 ± 1.7 vs. 102.6 ± 0.3 cm TL, $\chi^2_{1,4042} = 6.86$, $p < 0.01$), and the size range of bull sharks was greater (23.5 ± 1.2 vs. 18.3 ± 0.2 cm TL; $\chi^2_{1,4042} = 5.60$, $p = 0.02$; Fig. 3c, d). There was a moderately significant interaction among bay system and bull shark size range on the likelihood of capturing both blacktip and bull sharks during an event ($\chi^2_{1,4042} = 4.19$, $p = 0.04$). Bull sharks exhibited significantly wider ranges of total length in Matagorda Bay and San Antonio Bay when both shark species were caught (27.2 ± 3.2, and 25.1 ± 3.2 cm TL, respectively) and significantly wider total length ranges in Aransas Bay when only bull sharks were caught (17.2 ± 0.9 cm TL; ESM Fig. 1).

Capture events with more than one individual of a species (intraspecific co-occurrence), also varied spatially and temporally (Fig. 4). The proportion of capture events with more than one blacktip shark was lowest in Aransas Bay (22.7% ± 6.4; $\chi^2_{1,993} = 6.06$, $p = 0.01$), and the proportion of capture events with more than one bull shark was highest in Matagorda Bay (57.5% ± 1.5) and lowest in Corpus Christi Bay (32.6% ± 3.2; $\chi^2_{1,3331} = 11.61$, $p < 0.01$; Fig. 4a). The proportion of capture events with more than one individual was significantly higher during the fall than the spring for blacktip sharks ($\chi^2_{1,993} = 8.68$, $p < 0.01$) and bull sharks ($\chi^2_{1,3331} = 7.81$, $p < 0.01$; Fig. 4b). Intraspecific co-occurrence did not vary across decades for blacktip sharks ($\chi^2_{1,993} = 0.37$, $p = 0.54$) or bull sharks ($\chi^2_{1,3331} = 0.52$, $p = 0.47$).

Solitary blacktip sharks and bull sharks were caught in significantly different environmental conditions

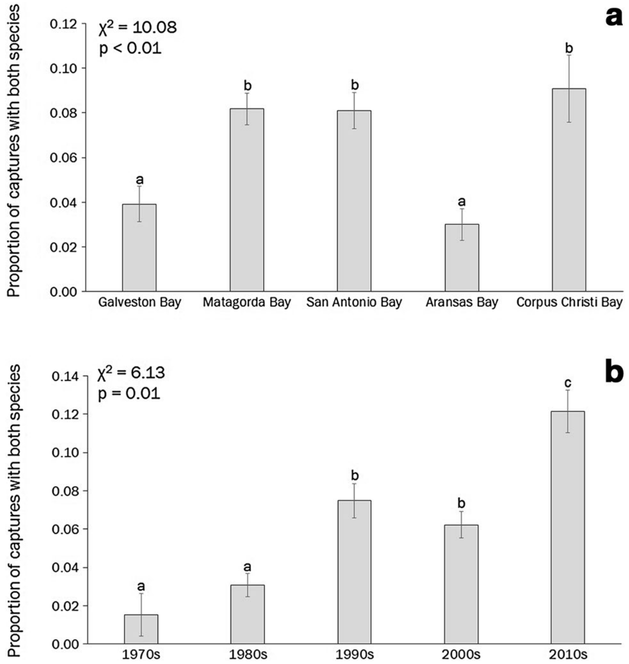

Fig. 2 The frequency of interspecific co-occurrence varied both spatially (**a**) and temporally (**b**). *Bars* indicate SE, and *bars with different letters* indicate significant differences between bay systems or decades based on Mann–Whitney post hoc test

than capture events that resulted in more than one individual (Table 2; ESM Tables 2, 3). Individual blacktip sharks were caught at cooler temperatures (27.2 ± 0.1 °C, $\chi^2_{1,993} = 11.54$, $p < 0.01$) and shallower depths (1.3 ± 0.02 m, $\chi^2_{1,993} = 9.20$, $p < 0.01$) than blacktip sharks caught with at least one conspecific (27.5 ± 0.1 °C, 1.4 ± 0.03 m; Fig. 5a, b). Individual bull sharks were caught in cooler water temperatures (27.6 ± 0.1 °C, $\chi^2_{1,3331} = 39.98$, $p < 0.01$), higher salinities (21.6 ± 0.2 psu, $\chi^2_{1,3331} = 17.44$, $p < 0.01$), and water with less dissolved oxygen (7.5 ± 0.04 mg L^{-1}, $\chi^2_{1,3331} = 4.96$, $p = 0.03$) than bull sharks caught with at least one conspecific (28.1 ± 0.1 °C, 20.1 ± 0.2 psu, 7.6 ± 0.04 mg L^{-1}; Fig. 5c–e). The interaction between water temperature and season had a significant effect on the likelihood of capturing more than one blacktip shark ($\chi^2_{1,993} = 7.49$, $p < 0.01$)—individual blacktip sharks were caught in cooler waters than multiple blacktip sharks during the spring (27.4 and 28.3 °C, respectively), but there was no difference in capture temperatures of individual blacktip sharks and blacktip shark groups during the fall (26.8 and 26.8 °C, respectively).

Blacktip shark and bull shark concentrations (i.e., the number of conspecifics caught together) also varied in space and time (Table 2; Fig. 6; ESM Tables 4, 5). When more than one blacktip shark was caught, concentrations of individuals were highest in Matagorda Bay (6.1 ± 0.5 individuals per event) and lowest in Aransas Bay (3.1 ± 0.3 individuals per event; $F_{4,452} = 3.06$, $p = 0.02$), while bull shark concentrations were lowest in Corpus Christi Bay (2.9 ± 0.2 individuals per event; $F_{4,1633} = 2.39$, $p < 0.05$; Fig. 6a, c). Blacktip sharks exhibited no decadal changes in concentration ($F_{4,453} = 1.24$, $p = 0.29$); however, bull sharks exhibited a 26% decrease in concentration across decades through the 2000s, with no difference between the 2000s and 2010s ($F_{4,1633} = 2.59$, $p = 0.04$; Fig. 6b, d). Decadal differences in bull shark concentrations also varied across bay systems ($F_{16,1633} = 2.39$, $p < 0.01$). There was no significant temporal shift in bull shark concentrations in Aransas and Corpus Christi bays. Bull shark concentrations fluctuated temporally in Galveston Bay, with significantly lower concentrations in the 1980s (3.3 ± 0.4 individuals per event) and the 2000s (3.3 ± 0.3 individuals per event). There was a decrease in bull shark concentrations in San Antonio Bay after the 1970s, and there was a decadal decrease in bull shark concentrations in Matagorda Bay during the study period (ESM Fig. 2).

Shark concentrations were also influenced by shark size. Both blacktip and bull shark concentrations decreased as mean shark size increased ($F_{1,430} = 17.34$, $p < 0.01$, and $F_{1,1588} = 16.00$, $p < 0.01$, respectively; Fig. 7a, c). Blacktip and bull shark concentrations increased as the range in total lengths increased

Table 2 Final logistic regression and general linear models for (1) blacktip shark and bull shark co-occurrence, (2) blacktip shark conspecific co-occurrence, (3) bull shark conspecific co-occurrence, (4) blacktip shark concentrations, and (5) bull shark concentrations, where *a* bay system, *b* decade, *c* season, *d* salinity, *e* water temperature, *f* dissolved oxygen, *g* depth, *h* blacktip shark total length, *i* blacktip shark total length range, *j* bull shark total length and *k* bull shark total length range

Model	Interaction	Final model	Model *df*	χ²	*F*	*p*
(1) Species co-occurrence	Interspecific	$Y_{\mathrm{lmnoruv}} = \mu + a_{\mathrm{l}} + b_{\mathrm{m}} + c_{\mathrm{n}} + d_{\mathrm{o}} + g_{\mathrm{r}} + j_{\mathrm{u}} + k_{\mathrm{v}} + (ak)_{\mathrm{lv}} + \varepsilon_{\mathrm{lmnoruv}}$	17	176.0	–	<0.01
(2) Blacktip shark co-occurrence	Intraspecific	$Y_{\mathrm{lnpr}} = \mu + a_{\mathrm{l}} + c_{\mathrm{n}} + e_{\mathrm{p}} + g_{\mathrm{r}} + (ce)_{\mathrm{np}} + \varepsilon_{\mathrm{lnpr}}$	8	30.70	–	<0.01
(3) Bull shark co-occurrence	Intraspecific	$Y_{\mathrm{lnopq}} = \mu + a_{\mathrm{l}} + c_{\mathrm{n}} + d_{\mathrm{o}} + e_{\mathrm{p}} + f_{\mathrm{q}} + (ac)_{\mathrm{ln}} + \varepsilon_{\mathrm{lnopq}}$	14	134.9	–	<0.01
(4) Blacktip shark concentration	Intraspecific	$Y_{\mathrm{l}} = \mu + a_{\mathrm{l}} + \varepsilon_{\mathrm{l}}$	4	–	3.06	0.02
(5) Bull shark concentration	Intraspecific	$Y_{\mathrm{lm}} = \mu + a_{\mathrm{l}} + b_{\mathrm{m}} + \varepsilon_{\mathrm{lm}}$	24	–	3.49	<0.01

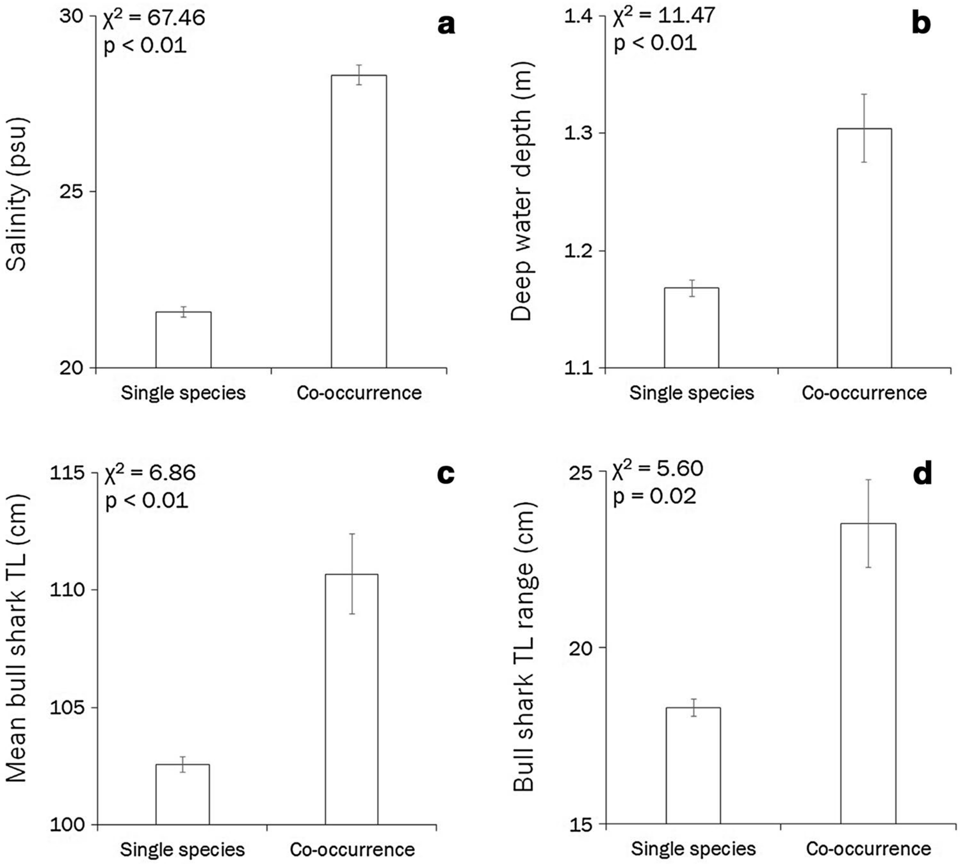

Fig. 3 Salinity (**a**), water depth (**b**), bull shark total length (**c**), and bull shark total length range among individuals captured during an event (**d**) were significantly different between capture events with one species and capture events with both species. *Bars* are SE

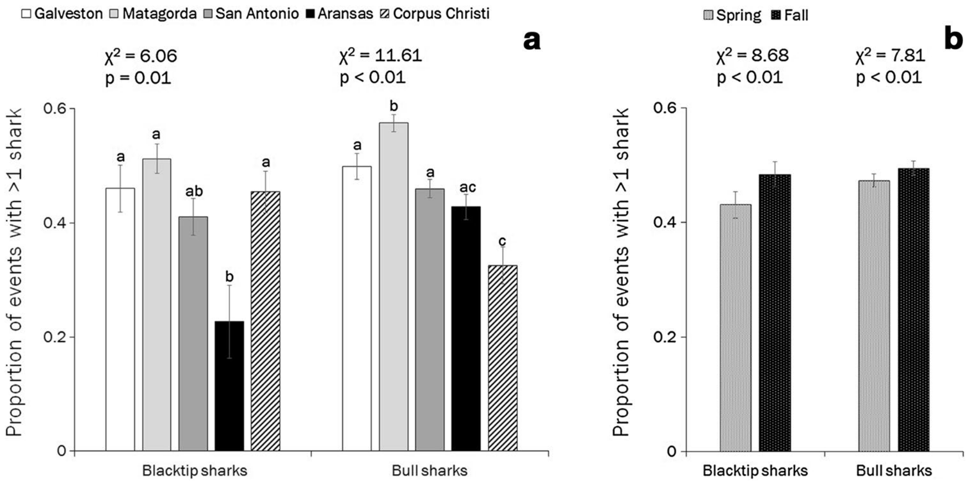

Fig. 4 The proportion of events when more than one blacktip shark or more than one bull shark were capture varied spatially (**a**) and seasonally (**b**). *Bars* indicate SE, and *bars with different letters* in **a** indicate significant differences between bay systems

among individuals captured during the same event ($F_{1,430} = 15.61$, $p < 0.01$, and $F_{1,1588} = 421.1$, $p < 0.01$, respectively; Fig. 7b, d). Teleost CPUE did not affect shark co-occurrence, the likelihood of capturing more than one individual of either species, or shark concentrations (ESM Tables 1, 3–5).

Size structure among blacktip and bull sharks varied spatially and temporally (Fig. 8). Among captured sharks, mean TL was highest in San Antonio Bay (mean ± SE = 104.3 ± 2.2 cm TL) and smallest in Galveston Bay (76.1 ± 1.4 cm TL) for blacktip sharks ($F_{4,445} = 7.33$, $p < 0.01$), with significant but small spatial differences among bull sharks ($F_{4,1633} = 6.16$, $p < 0.01$; Fig. 8a). The size range of sharks captured also varied spatially for blacktip sharks and bull sharks ($F_{4,445} = 12.61$, $p < 0.01$, $F_{4,1633} = 5.99$, $p < 0.01$, respectively). The largest size ranges among blacktip sharks was in Matagorda Bay (28.8 ± 2.2 cm TL) and San Antonio Bay (27.1 ± 2.7 cm

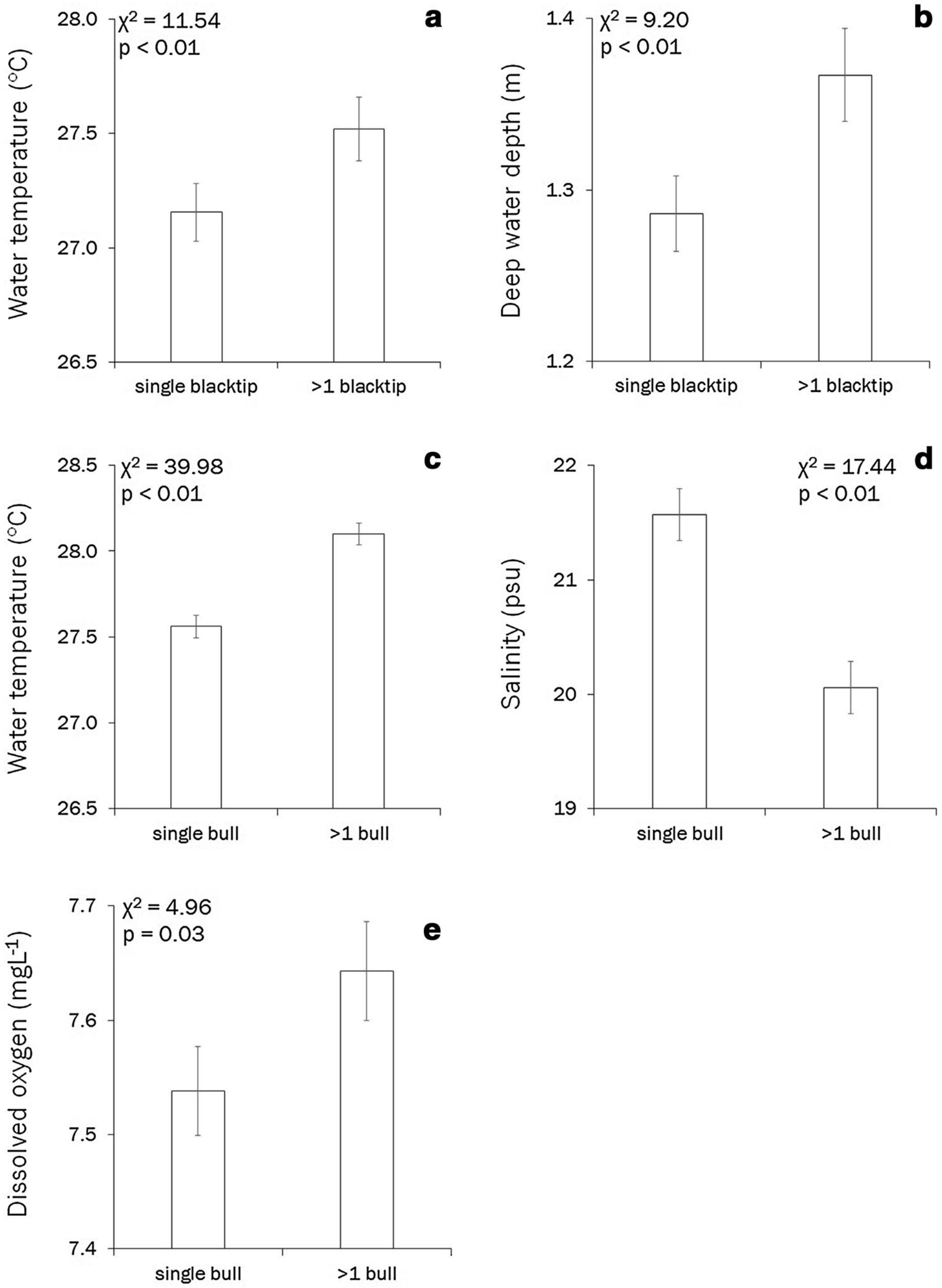

Fig. 5 Variability in water temperature (**a**) and depth (**b**) lead to significant differences in the likelihood of capturing an individual blacktip shark or more than one blacktip shark; and variability in water temperature (**c**), salinity (**d**), and dissolved oxygen (**e**) lead to significant differences in the likelihood of capturing an individual bull shark or more than one bull shark. *Bars* indicate SE

TL), and the smallest size ranges among bull sharks was in Corpus Christi Bay (13.9 ± 2.0 cm TL) (Fig. 8b). Blacktip shark sizes also varied across decades, with significantly smaller individuals captured in the 1980s and 1990s (77.3 ± 1.4, and 74.9 ± 1.4 cm TL, respectively; $F_{4,445} = 14.68$, $p < 0.01$). There was no decadal change in bull shark mean total lengths (Fig. 8c). The mean range of blacktip shark total lengths among individuals captured during the same event significantly increased in the 2000s and 2010s (22.1 ± 2.2, and 34 ± 2.7 cm TL, respectively, $F_{4,445} = 14.83$, $p < 0.01$), with a small but significant increase in mean range of bull shark total length among individuals captured during the same event through time ($F_{4,1633} = 2.91$, $p = 0.02$; Fig. 8d).

Discussion

Environmental change and anthropogenic effects continue to impact many marine ecosystems (Jackson et al. 2001; Yang and Rudolf 2010; Doney et al. 2012), and the detrimental effects attributed to the extensive overlap between

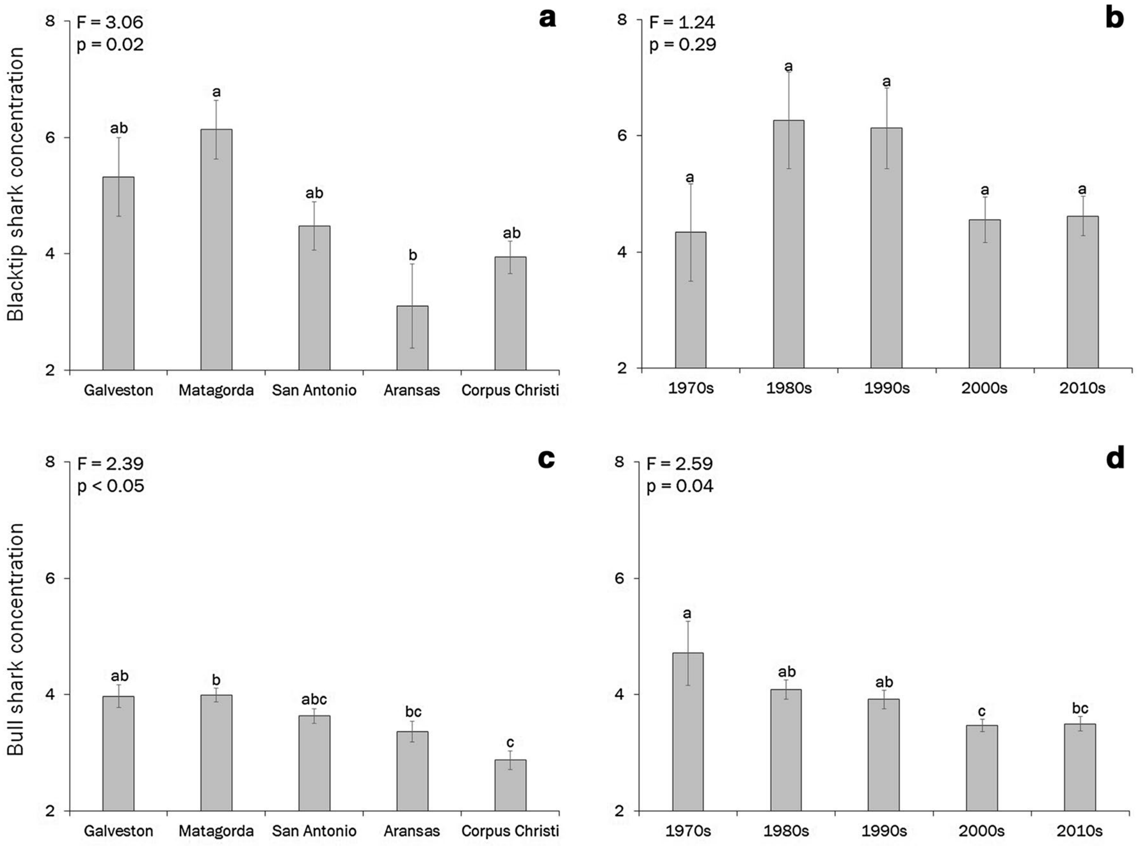

Fig. 6 Blacktip shark (**a**, **b**) and bull shark (**c**, **d**) concentrations varied spatially (**a**, **c**) and temporally (**b**, **d**). *Bars* indicate SE, and *bars with different letters* indicate significant differences between bay systems or decades based on Tukey's post hoc test

humans and sharks are predicted to have wide ranging implications, leading to the loss of ecological role(s) in some contexts (Heithaus et al. 2008; Estes et al. 2011; Ripple et al. 2014), and niche filling in others (Kitchell et al. 2002; Owen-Smith and Mills 2008). However, gaining an understanding of species interactions is needed, before questions concerning shifts in niche widths and the loss of ecological roles can be investigated. Our findings suggest that interspecific co-occurrence of blacktip sharks and bull sharks has significantly increased over the last 40 years, and changes in environmental conditions may be responsible.

Spatiotemporal variability in interspecific co-occurrence

Interspecific co-occurrence of blacktip sharks and bull sharks varied spatially across the study area. Sampling in Matagorda Bay, San Antonio Bay, and Corpus Christi Bay led to the highest frequency of events during which both species were captured, and habitat quality within at least some of these bay systems may promote spatial overlap between blacktip sharks and bull sharks. Froeschke et al. (2010a) suggested that Matagorda Bay and San Antonio Bay each provides important nursery habitat for juvenile bull sharks, potentially because of food availability, predator refuge, and/or salinity regimes. Other studies in the Gulf of Mexico also suggest that these factors play an important role in shaping bull shark distributions (Simpfendorfer et al. 2005; Wiley and Simpfendorfer 2007; Heupel and Simpfendorfer 2008; Ortega et al. 2009; Froeschke et al. 2010b; Heupel et al. 2010; Drymon et al. 2014; Matich and Heithaus 2015). During the study period, most (ca. 98%) sharks caught among both species were juveniles based on total length (Branstetter and Stiles 1987; Baremore and Passerotti 2013; Natanson et al. 2014), supporting this hypothesis proposed by Froeschke et al. (2010a). Middle and lower bay systems along the coast of Texas also tend to have moderate–high salinities conducive for blacktip shark habitation (Steiner et al. 2007; Froeschke et al. 2010b; Bethea et al. 2015). Thus, significantly higher interspecific co-occurrence and spatial overlap between blacktip sharks and bull sharks in these bay systems was not unexpected when compared to Galveston Bay and Aransas Bay.

However, habitat use among bull sharks and blacktip sharks in coastal ecosystems is not uniform within and across estuaries (e.g., Heupel et al. 2004; Steiner and

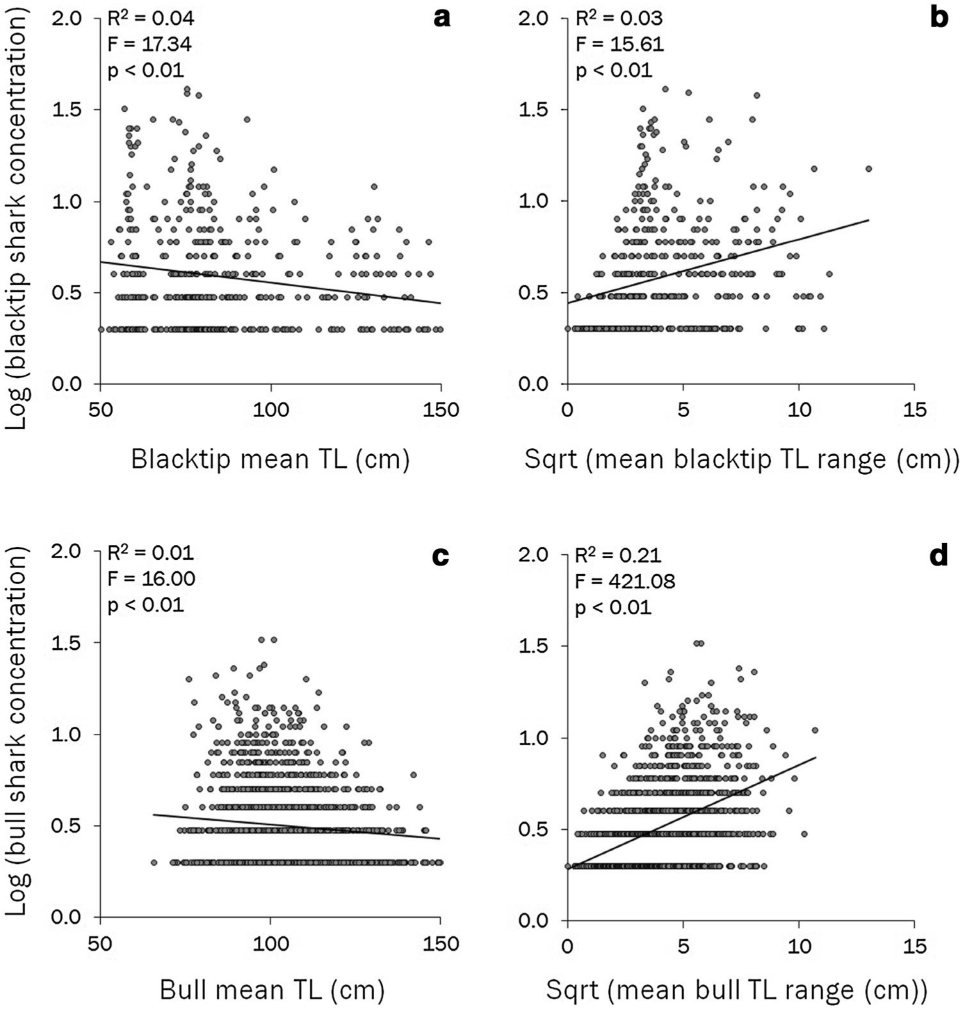

Fig. 7 Blacktip shark (**a**, **b**) and bull shark (**c**, **d**) concentrations varied in response to shark total lengths (**a**, **c**) and the range of total lengths among sharks captured during an event (**b**, **d**)

Michel 2007; Heupel and Simpfendorfer 2008; Froeschke et al. 2010b), which provides insight into the contexts under which these species are more likely to overlap spatially. Juvenile bull sharks use brackish habitats in estuaries and rivers, because they provide refuge from large predatory sharks, as well as release from competitors in marine food webs (e.g., Curtis et al. 2011; Heupel and Simpfendorfer 2011; Werry et al. 2011). In contrast, physiological restrictions are predicted to limit the use of brackish waters by blacktip sharks (Compagno 1984), despite apparent preferences for moderate salinities in some contexts (Froeschke et al. 2010b; Bethea et al. 2015). Such differences in the physiological ecologies of these species suggest that co-occurrence is most likely to occur in more saline waters, and our results support this hypothesis. Sampling events that led to the capture of both bull sharks and blacktip sharks occurred in significantly higher salinities (28.3 ± 0.28 psu SE) than sampling events in which only one species was captured (21.6 ± 0.15 psu SE). However, ca. 20% of these single species capture events occurred among blacktip sharks across a range of salinities (0.0–40.3 psu), suggesting that blacktip sharks are not completely restricted from entering low salinity waters and using habitats in traditional bull shark nurseries. Interactions among blacktip shark and bull sharks in brackish waters may lead to an increase in competition between these two species, and increasing salinities in brackish waters could promote such niche width expansion by blacktip sharks (Compagno 1984; Heithaus 2007; Steiner and Michel 2007), while constricting low–moderate salinity habitats used by bull sharks as nurseries (e.g., Norden 1966; Heuter and Tyminski 2007; Werry et al. 2011; Curtis et al. 2013; Werry and Clua 2013; Drymon et al. 2014).

Temporal changes in the co-occurrence of blacktip sharks and bull sharks provide support for the hypothesis that the higher co-occurrence of blacktip sharks and bull sharks is due to changes in environmental conditions. Texas bays and estuaries have changed over recent history due to adjustments in water management. Along the coast of Texas, estuaries and bays are fed with freshwater from numerous rivers, which humans also rely upon for agricultural, industrial, and urban use (e.g., Musick et al. 1990;

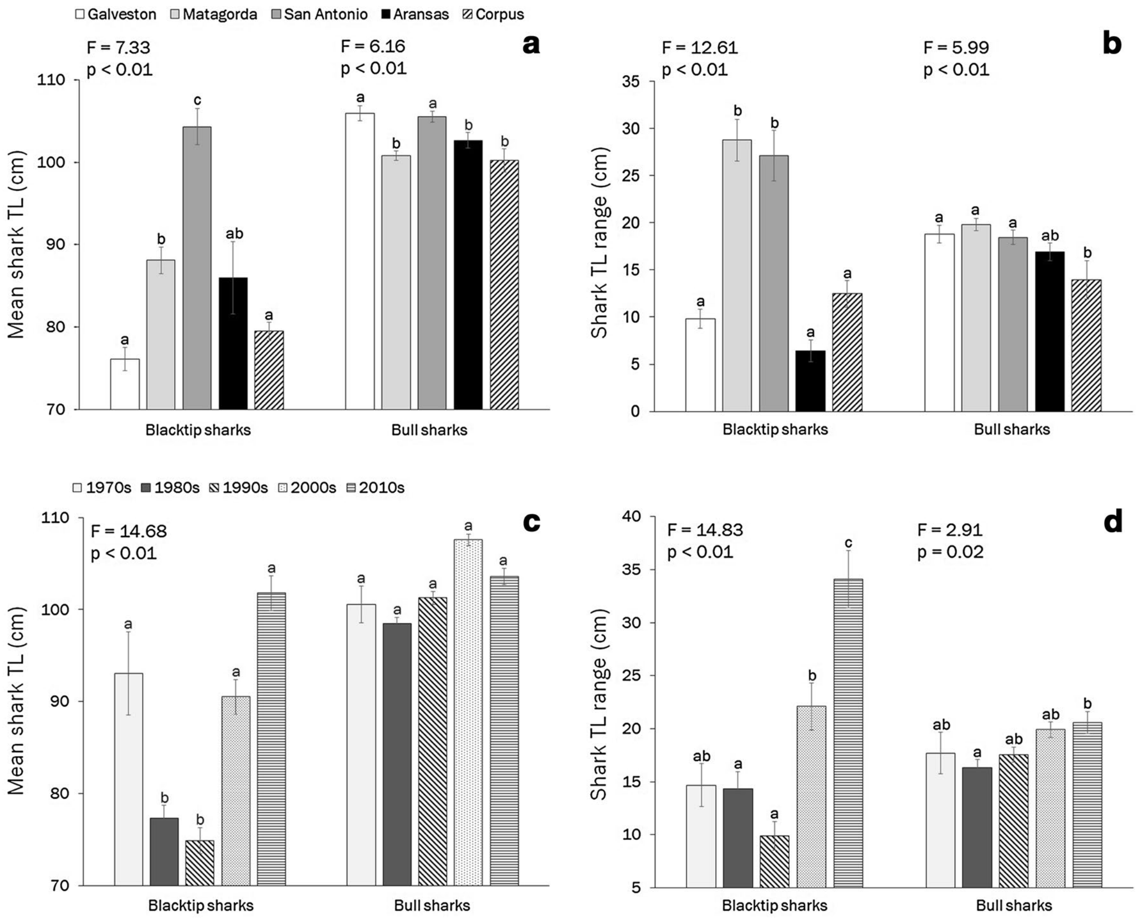

Fig. 8 Mean shark total length (**a**, **c**) and mean range of shark total lengths among individuals captured during an event (**b**, **d**) varied spatially (**a**, **b**) and temporally (**c**, **d**). *Bars* indicate SE, and *bars with different letters* indicate significant differences between bay systems or decades based on Tukey's post hoc test

Kim et al. 2014). Demand for freshwater resources has steadily increased with human population growth across Texas, which in turn may be reducing freshwater inflow into some coastal regions (Wurbs 2014; Venkataraman et al. 2016). Reduced freshwater flow leads to increased salinities, at least among bays where salinity regimes are highly dependent on freshwater inflow (Tolan 2007; Palmer et al. 2011), and increasing salinities would predictably lead to increased spatial overlap and co-occurrence of bull sharks and blacktip sharks based on correlations between salinity and interspecific co-occurrence (NOAA 1998; Froeschke et al. 2010b). Thus, temporal changes in interspecific co-occurrence could be driven by shifts in hydrology. Interspecific co-occurrence was also more frequent when bull sharks were larger, potentially due to ontogenetic shifts of larger individuals into more saline waters more suitable for blacktip sharks (Compagno 1984; Froeschke et al. 2010b; Bethea et al. 2015). However, our analytical framework was not designed to address such questions, and more specific investigations of annual patterns in precipitation, freshwater inflow, salinity regimes, and habitat use patterns of blacktip sharks and bull sharks will provide greater insight into why interspecific co-occurrence has increased by an order of magnitude over the last 40 years.

Increased abundances of sharks within Texas bay systems may have also led to increased interspecific co-occurrence among blacktip sharks and bull sharks through time. Within ecological communities, interspecific interactions increase as the relative abundance of individuals within populations increases (Chase and Leibold 2003; Svanbäck and Bolnick 2007). Within Texas, the relative abundance of bull sharks has increased over the last 40 years (Froeschke et al. 2013), and blacktip abundance has also increased in recent years (Bubley and Carlson 2012). Thus, growing blacktip and bull shark subpopulations in coastal bays would potentially lead to increased interspecific co-occurrence through time. However, a large proportion of changes in bull shark abundances is attributed to significant increases in bull sharks within Sabine Lake (Froeschke et al. 2013), which was not considered for this study because of the lack of blacktip sharks that use this ecosystem, and Galveston Bay (Froeschke et al. 2013), which exhibited significantly lower interspecific co-occurrences than Matagorda Bay, San Antonio Bay, and Corpus Christi Bay. Data suggest that Matagorda Bay, San Antonio Bay, and Corpus Christi Bay have all supported relatively stable bull shark subpopulations for the last 30–40 years (Froeschke et al. 2013), suggesting that an increased abundance of at least bull sharks is unlikely to be the primary reason for changes in interspecific co-occurrence among blacktip sharks and bull sharks.

Potential implications of increasing interspecific co-occurrence

Changes in bull shark concentrations, which can provide insight into grouping behavior (Maunder and Punt 2004), however, may improve our understanding concerning the implications of increased interspecific co-occurrence among bull sharks and blacktip sharks through time. In contrast to increased interspecific co-occurrence of blacktip sharks and bull shark through time, bull shark concentrations (i.e., the number of conspecifics caught together during a single event) significantly decreased through time by ca. 25%—fewer bull sharks were caught during individual sampling events from the 1970s to the 2000s and 2010s. Many shark species are considered solitary throughout most of their life histories (e.g., Motta and Wilga 2001; Papastamatiou and Lowe 2012), and thus capture events with few or individual sharks are not unexpected. While relative abundances describe the total number of sharks captured/found across space and time based on sampling effort (Maunder and Punt 2004), concentrations provide information on the number of sharks captured together, which may elucidate the contexts that lead to solitary and grouping behavior (Maunder and Punt 2004). Thus, relative abundances and concentrations provide complementary, but different information on distribution patterns, and temporal shifts in concentrations may indicate changes in intraspecific interactions.

Some shark species form groups to improve feeding success and potentially decrease risk of predation (e.g., Heupel and Simpfendorfer 2005; Dudley and Cliff 2010; Pickard et al. 2016), and elasmobranch groups are not always homospecific (e.g., Williams et al. 2010; Speed et al. 2011; Brunnschweiler et al. 2014; de Leon et al. 2016). Indeed, some species regularly co-occur within particular habitats or under particular contexts (e.g., Vaudo and Heithaus 2011; Kajiura and Tellman 2016), and across the Texas coast, interspecific co-occurrence among blacktip sharks and bull sharks has significantly increased over the last 40 years. Other studies have also found spatial or temporal variability in blacktip and bull shark interspecific co-occurrence, which has been related to habitat quality and environmental conditions (e.g., Castro 1993; de Silva et al. 2001; Steiner and Michel 2007; Fischer et al. 2009; Driggers et al. 2012; Bethea et al. 2015). Changes in interspecific co-occurrence within Texas is likely in response to changes in environmental conditions as previously discussed, and changes in interspecific interactions may have resulted in changes in bull shark behavior. If juvenile bull sharks rely on low–moderate salinity habitats as nurseries (Heuter and Tyminski 2007; Curtis et al. 2011; Werry et al. 2011), and bay systems have increased in salinities (Wurbs 2014; Venkataraman et al. 2016), bull sharks would predictably increase their use of riverine habitats in search of low salinity waters (Heupel and Simpfendorfer 2008; Curtis et al. 2013; Werry et al. 2011; Drymon et al. 2014).

The sampling regime used for this study, however, does not monitor riverine habitats. Thus, if bull sharks increased their use of rivers during the study period, a decrease in bull shark abundance, and potentially concentrations, in bay systems would be expected across time due to a shift in bull shark habitat use. Yet, decreases in bull shark abundances have not been observed (Froeschke et al. 2013). Thus, the hypothesis predicting upstream movements of bull sharks is not supported, and data are not available to test this hypothesis directly. Alternatively, bull sharks may have adjusted their habitat use within bay systems in response to increased interspecific co-occurrence and competition with blacktip sharks by decreasing spatial overlap and competition with conspecifics, which would lead to the observed decrease in bull shark concentrations, but not relative abundances. Ecological theory predicts that as resource availability decreases, which can be due to increased intra- and/or interspecific competition, niche partitioning increases, which can be facilitated through decreased spatial overlap with other species or conspecifics (Pianka 1972, 1973). Bull sharks exhibit niche partitioning within populations based on shark size (e.g., Simpfendorfer et al. 2005; Werry et al. 2011), foraging preferences (e.g., Matich and Heithaus 2015), body condition (e.g., Matich and Heithaus 2015), and individual specializations (e.g., Matich et al. 2011), highlighting the plasticity of their resource use patterns. Thus, shifts in bull shark concentrations may reflect changes in behavior—reduced spatial overlap and intraspecific interactions may enable bull sharks to more suitably partition resources with conspecifics to account for increased competition and niche overlap with blacktip sharks (Pianka 1972, 1973). While speculative, shifts in the behavior of predators in response to intra- and interspecific competition are relatively widespread (reviewed by Brown and Wilson 1956; Bolnick et al. 2003; Pfennig et al. 2010), and plasticity among sharks in coastal ecosystems is promising for their resilience in light of changing environmental conditions and resource availability attributed to human impacts and climate change (Jackson et al. 2001; Yang and Rudolf 2010; Doney et al. 2012; Romero-Lankao et al. 2014; Matich et al. 2017). Future studies quantifying the relative abundance of bull sharks in Texas rivers, and habitat connectivity between rivers and bays through shark movement patterns will help further resolve the drivers and implications of the observed temporal trends.

Conclusion

Our findings suggest that interspecific co-occurrence among blacktip sharks and bull sharks is temporally variable and correlated with salinity; however, our limited understanding of elasmobranch community dynamics along the coast of Texas currently poses challenges for understanding the implications of changes in spatial overlap among these species and interspecific interactions. We speculate that increasing co-occurrence with salinity suggests that environmental changes within Texas bay systems are causing shifts in species distribution patterns, and such changes may be leading to increased interactions among blacktip sharks and bull sharks. However, reduced intraspecific co-occurrence among bull shark conspecifics may alleviate such changes. Gaining a more comprehensive understanding of resource use among sharks within Texas coastal ecosystems will help elucidate the importance of environmental and biological drivers shaping habitat use patterns and co-occurrence among shark species along the western Gulf Coast (e.g., Speed et al. 2010; Vaudo and Heithaus 2011; Plumlee and Wells 2016; Matich et al. 2017). As we strive to improve our understanding of the implications of shifts in salinity regimes and community compositions, future studies should investigate how foraging behavior, life history, and behavioral plasticity in habitat use affect co-occurrence within and across species.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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