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RESEARCH ARTICLE

Long-term effects of climate change on juvenile bull shark migratory patterns

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Abstract

1. Seasonal variability in environmental conditions is a strong determinant of animal migrations, but warming temperatures associated with climate change are anticipated to alter this phenomenon with unknown consequences.
2. We used a 40-year fishery-independent survey to assess how a changing climate has altered the migration timing, duration and first-year survival of juvenile bull sharks (*Carcharhinus leucas*).
3. From 1982 to 2021, estuaries in the western Gulf of Mexico (Texas) experienced a mean increase of 1.55°C in autumn water temperatures, and delays in autumn cold fronts by ca. 0.5 days per year. Bull shark migrations in more northern estuaries concomitantly changed, with departures 25–36 days later in 2021 than in 1982. Later, migrations resulted in reduced overwintering durations by up to 81 days, and the relative abundance of post-overwintering age 0–1 sharks increased by >50% during the 40-year study period.
4. Yet, reductions in prey availability were the most influential factor delaying migrations. Juvenile sharks remained in natal estuaries longer when prey were less abundant. Long-term declines in prey reportedly occurred due to reduced spawning success associated with climate change based on published reports. Consequently, warming waters likely enabled and indirectly caused the observed changes in shark migratory behaviour.
5. As water temperatures continue to rise, bull sharks in the north-western Gulf of Mexico could forgo their winter migrations in the next 50–100 years based on

current trends and physiological limits, thereby altering their ecological roles in estuarine ecosystems and recruitment into the adult population. It is unclear if estuarine food webs will be able to support changing residency patterns as climate change affects the spawning success of forage species.

6. We expect these trends are not unique to the western Gulf of Mexico or bull sharks, and migratory patterns of predators in subtropical latitudes are similarly changing at a global scale.

KEYWORDS
climate change, nursery, overwintering, phenology, prey declines, sea surface temperature

1 | INTRODUCTION

Animal migrations are responsible for the largest natural changes in biodiversity on the planet, altering species densities and the structure of ecological communities (Dingle, 1996). As such, changes in migration dynamics attributed to climate change have become one of the most important conservation issues of the 21st century (Kubelka et al., 2022; Lennox et al., 2016). While shifts in migration are well documented in many terrestrial systems (Harris et al., 2009; Joly et al., 2019), they have been more challenging to assess in the marine realm due to observational challenges and data limitations (Hays et al., 2016; Renshaw et al., 2023).

Migrations are driven by shifts in environmental conditions, resource availability, predation risk and/or reproductive biology to maximize fitness and survival (Dingle, 1996; Hays et al., 2016; Secor, 2015; Shaw, 2016). Yet, migrations can place animals at risk. In addition to energetic costs (Braithwaite et al., 2015), many animals face environmental, ecological and anthropogenic threats during these journeys (Queiroz et al., 2019; Stepanuk et al., 2023). For example, pre-wintering female baleen whales migrate to lower latitudes to give birth, where environmental conditions are optimal for newborn development in waters absent of predators (Cockeron & Connor, 1999). These mother–calf pairs remain in low latitudes for weeks-months and upon returning to temperate and polar feeding grounds, they are at substantial risk of attack from killer whales (*Orcinus orca*), which intercept mother–calf pairs along spring migration routes (Cockeron & Connor, 1999). Blacktip sharks (*Carcharhinus limbatus*) seasonally migrate in schools of thousands in the northwestern Atlantic in response to changes in water temperature and prey availability (Kajiura & Tellman, 2016), and larger predators like great hammerheads (*Sphyrna mokarran*) are attracted to these aggregations and hunt blacktip sharks at the southern range of their migration (Doan & Kajiura, 2020).

In many ecosystems, cooling temperatures and a reduction in productivity occurring between autumn and winter forces many animals to migrate because of physiological and/or energetic restrictions (e.g. Clark, 1968; Fancy et al., 1989; Zuniga et al., 2017). Yet as climates warm, the timing (Walther et al., 2002), distance (Bowers & Kajiura, 2023; Hammerschlag et al., 2022), and in some cases, the need to migrate (Fiedler et al., 2004; Pulido & Berthold, 2010) are being altered for many populations. To date, these changes have been viewed by many in a negative light given the potential alteration to ecosystem structure and function (Nagelkerken & Munday, 2016). However, climate change-induced shifts in migration dynamics could also offer benefits. For example, if migrations become shorter in distance and/or duration, resultant reductions in energetic costs and lower risk of encountering predators could lead to increased fitness and survival (Buchan et al., 2020; de Zoeten & Pulido, 2020). Consequently, warming temperatures may favour some species if the benefits of reduced risk associated with shortened migrations outweigh the costs of increased metabolic needs and/or latitudinal range shifts attributed to warming temperatures (Santos et al., 2021; Secor, 2015). The inherent vulnerability of many marine species to climate change has been assessed, and the concept of climate change 'winners' and 'losers' is reflected in these analyses (Hare et al., 2016; Somero, 2010). However, there remains significant concerns that the current and predicted speed of environmental change is outpacing many species' abilities to respond physiologically and/or behaviorally to warming waters (Blois et al., 2013).

Here, we use a historical 40-year data set to assess how climatic changes have altered the migration timing and survival of juvenile bull sharks (*Carcharhinus leucas*) in the western Gulf of Mexico. Globally and regionally, bull sharks are important predators in coastal ecosystems and use estuaries as nursery habitat (e.g. Blackburn et al., 2007; Froeschke et al., 2010; Heupel & Simpfendorfer, 2008; Werry et al., 2011). Their seasonal distributions and migratory patterns are strongly influenced by water temperatures, and a mix of other factors including dissolved oxygen, prey availability and predation risk (e.g. Cottrant et al., 2021; Drymon et al., 2014; Heithaus et al., 2009; Lofthus et al., 2024; Matich & Heithaus, 2012, 2015). Recent shifts in the distribution of juvenile bull sharks in the northwestern Atlantic have been attributed to climate change (Bangley et al., 2018), and warming waters are increasing habitat suitability for juvenile bull sharks in the northern Gulf of Mexico (Mullins et al., 2024). Therefore, our findings offer a long-term perspective into the changing nature of migration dynamics in juvenile sharks, which are applicable to many other seasonally migrating predators, and may improve our ability to characterize ecological shifts in response to climate change.

2 | MATERIALS AND METHODS

2.1 | Study system and species

Bull sharks tolerate wide salinity ranges due to their euryhaline nature (Anderson et al., 2006), and can thus be found from freshwater to marine habitats along the Texas coast (Froeschke et al., 2010). The ca. 5400 km of the Texas coastline is comprised of estuaries that are largely isolated from the Gulf of Mexico by seven barrier islands (Figure 1). With the exception of Laguna Madre, all Texas estuaries provide extensive habitat for juvenile bull sharks (Froeschke et al., 2010), where they exhibit an ontogenetic shift from low to high salinity waters during their first few years (Matich et al., 2020). Two of these estuaries—Matagorda Bay and San Antonio Bay—serve as nurseries for bull sharks, with others projected to serve this role in the future (e.g. Galveston Bay; Froeschke et al., 2010).

2.2 | Data collection

Data were obtained from standardized gillnet sampling conducted by Texas Parks and Wildlife Department (TPWD) from 1982 to 2021. Annual sampling consisted of 45 gillnets set in each estuary (*n* = 6) of the Texas coast in each 10-week spring (April–early June) and autumn (mid-September–November) season (90 total per year per estuary), with the exception of Spring 2020 due to Covid-19. Monofilament gillnets were 183 m long, 1.2 m deep and set overnight perpendicular to shore (mean soak time = 13.68 h). Within each estuary, sampling sites were randomly chosen without replacement per sampling season per annum using a stratified cluster design within a 3.4225 km^2 grid based on the presence of shoreline (e.g. see Figure S1), with all estuaries sampled concurrently during 10-week spring and autumn seasons. All organisms captured were identified, counted and measured. Date,

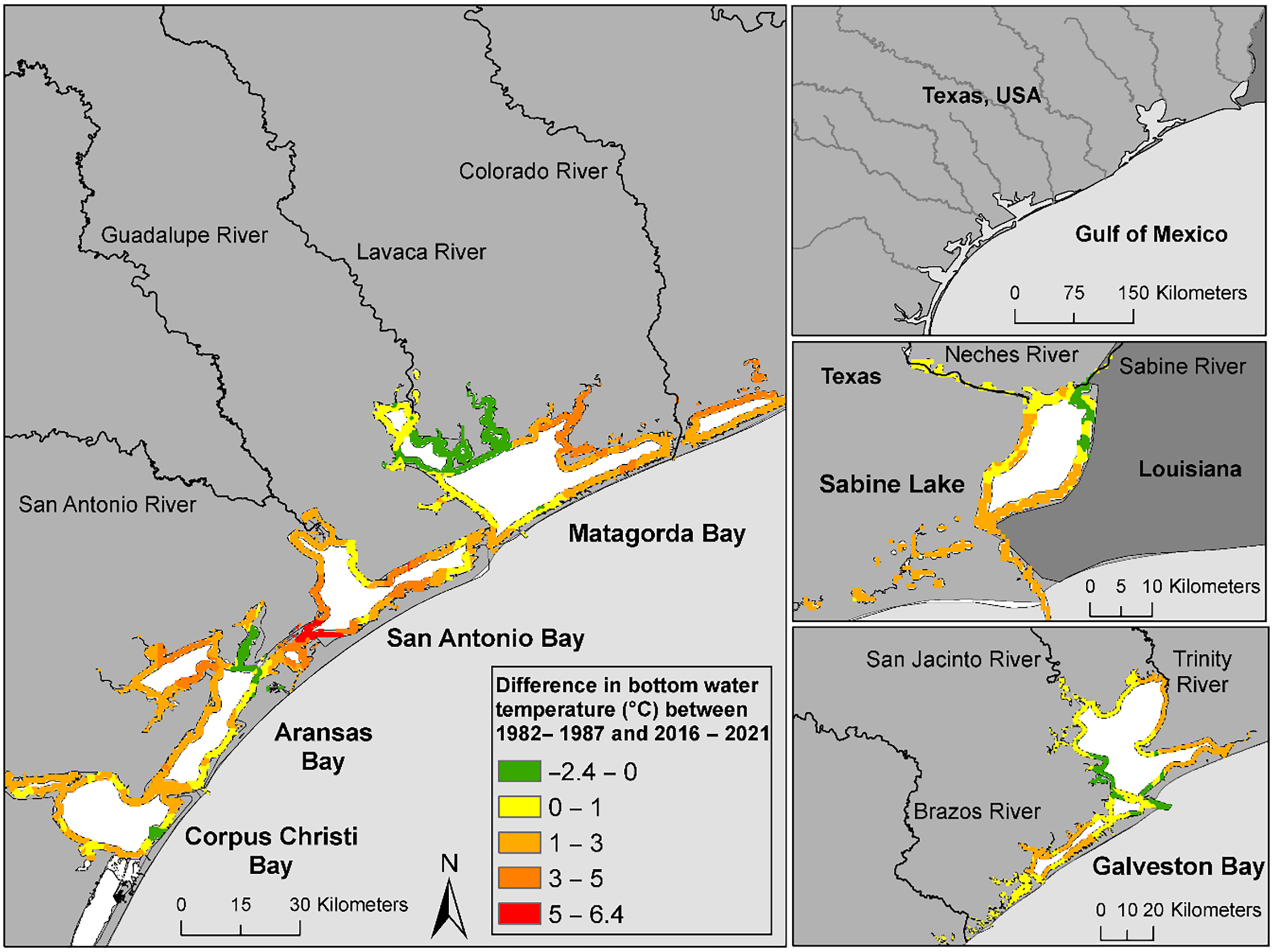

FIGURE 1 Map of the difference in water temperature (°C) measured at maximum depth (on bottom) for years 1982–1986 compared to 2016–2021 interpolated across all six evaluated Texas estuaries. The difference in bottom water temperature (measured by Texas Parks and Wildlife Department in situ) was calculated from measurements made during gillnet sampling in 1980s and 2010s–2020s within the same month and at the same geographic location.

capture location, salinity and water temperature were recorded for each sampling event, with data collection standardized across all estuaries and years. Sampling was conducted by TPWD starting in 1975; however, gillnet surveys were not standardized until 1982, and thus data from 1975 to 1981 were not included in the analyses.

Bull sharks were classified into age-classes following the framework of Matich, Plumlee, and Fisher (2021). Young-of-the-year (YOY) sharks were <86 cm total length (TL) in spring based on histogram valley and <101.1 cm in autumn based on rapid histogram decline (Figure S2). Age 0–1 sharks caught in spring were ≥86 cm TL and ≤111.5 cm TL based on histogram valleys (Figure S2). These identified size ranges are comparable to bull sharks in other parts of the Gulf of Mexico (e.g. Heithaus et al., 2009; Heupel & Simpfendorfer, 2008), and fit within anticipated growth rates (Branstetter & Stiles, 1987; Natanson et al., 2014).

Many wildlife populations exhibit behavioural responses to changing autumn weather patterns, including the onset of winter weather indicated by strong cold fronts (e.g. Bauer et al., 2011; Cameron et al., 2021; Springer, 1950). To assess the potential impacts of changes in autumn weather on YOY shark migration timing, hourly air temperature, barometric pressure, wind speed and wind direction data from Copernicus Climate Change Service (C3S; https://cds.climate.copernicus.eu/) were acquired for September–November from 1982 to 2021 for each estuary at 0.1° spatial resolution. Data were plotted to identify the day of year (DOY) of the first major cold front annually for each estuary (Allen et al., 1996). Cold fronts were classified based on (1) barometric pressure reaching a low point and then rapidly rising, (2) wind shifting considerably in direction and speed and (3) temperature dropping substantially (Allen et al., 1996; Millsap & Zook, 1983; e.g. see Figure S3).

Acknowledging the importance of prey availability in juvenile bull shark habitat selection (Cottrant et al., 2021; Lubitz et al., 2023; TinHan & Wells, 2021), we integrated data on secondary productivity across the study site. To assess secondary productivity and its impacts on migration timing, data from bag seine sampling conducted by TPWD from 1982 to 2021 was used to quantify the relative abundance of striped mullet (*Mugil cephalus*), one of the most abundant forage fish across Gulf of Mexico estuaries (Leard et al., 1995), and the most important prey species of small juvenile bull sharks in Texas (Marsaly et al., 2023; TinHan & Wells, 2021). Within each estuary, 20 standardized bag seines (18.3 m long, 1.8 m deep and 1.3 cm stretched mesh) were pulled parallel to shore across an area of 0.03 ha monthly within the same grid system as gillnets for the duration of the study period. Within each estuary, sampling sites were randomly chosen without replacement each month using a stratified cluster design, with all estuaries sampled concurrently.

No ethical approval or permits were required for the use of long-term monitoring data collected by TPWD.

2.3 | Data analysis

Linear regression was used to assess how bull shark migrations and potential drivers of migrations changed in each estuary across the study period (1982–2021) after analytical assumptions were met (linearity and homoscedasticity tested with plots of residuals vs predicted values; normality tested with Shapiro–Wilk tests; autocorrelation tested with Durbin–Watson tests). Each of the dependent variables below were assessed against sampling year (independent variable) for each estuary:

1. YOY Autumn DOY: The 95th percentile of the DOY of the last YOY shark caught in gillnets in autumn. Annual DOY of the last YOY shark caught in gillnets was prior to the last week of autumn for 67% of sampling (Figure 2; see Section 3) indicating an appropriate estimate. Unpublished telemetry data (TinHan, 2020) also show that YOY bull sharks annually depart from estuaries in autumn, supporting this as a proxy for migration timing.
2. DOY of cold front: DOY of the first major cold front in September–November based on C3S weather data.
3. Autumn temperature: Mean water temperatures measured during gillnet sampling in October–November.
4. Summer–Autumn Mullet catch per unit effort (CPUE): Sum of monthly CPUE (mullet caught per bag seine) from June to November. Both summer and autumn were included because of the importance of foraging and building of energy reserves for YOY sharks prior to overwintering (e.g. Lyons et al., 2020; McMillan et al., 2021)
5. Autumn salinity: Variance of salinity measured during gillnet sampling October–November (Matich et al., 2022).

Linear regression was also used to assess how bull shark overwintering duration and survival changed in each estuary across the study period:

6. Overwintering duration (sensu TinHan, 2020): Duration of time between (a) the 95th percentile of the DOY of the last YOY shark caught in autumn gillnets (variable 1 above), and (b) the

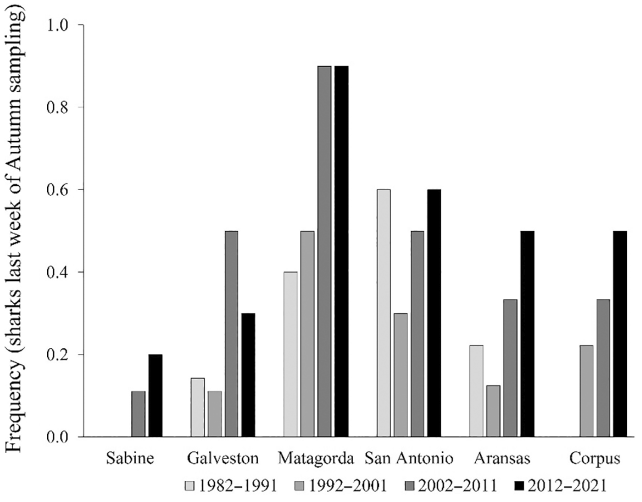

FIGURE 2 Frequency of years sharks were caught in gillnets the last week of autumn sampling per decade.

95th percentile of the DOY of the first age 0–1 shark caught in spring gillnets the following year (i.e. time between last autumn capture and first spring capture).

7. Age 0–1 Spring CPUE: CPUE [age 0–1 sharks caught per gillnet standardized for soak time (Matich et al., 2022)] from April to early June in the following year. Age 0-1 is used to delineate these sharks due to uncertainty in parturition timing.

Additional variables were included in subsequent analysis (see boosted regression tree [BRT] below) of trends in age 0–1 Spring CPUE (variable 7) as potential drivers of post-overwintering survival of YOY sharks:

8. Spring water temperature: Mean water temperature measured during gillnet sampling in April.
9. Spring Mullet CPUE: CPUE (mullet caught per bag seine) in April.

We developed BRT models of catch data from gillnet monitoring to investigate (1) what extrinsic variables best predicted the timing of autumn migrations (i.e. YOY Autumn DOY), (2) how extrinsic variables correlated with the overwintering duration of YOY bull sharks and (3) how extrinsic variables correlated with the relative abundance of first year bull sharks when they return from overwintering (i.e. age 0–1 Spring CPUE). We first assembled BRT models using data combined for all Texas estuaries, then ran analyses for the three most northern estuaries (Sabine Lake, Galveston Bay and Matagorda Bay) and the three most southern estuaries (San Antonio Bay, Aransas Bay and Corpus Christi Bay) independently to assess geographic differences (TinHan et al., 2020).

We investigated the first question using annual YOY autumn DOY as the dependent variable (variable for linear regression 1 above); DOY of cold front, autumn temperature, summer–autumn mullet CPUE and autumn salinity were independent variables. The second question was investigated using annual overwintering duration (of YOY bull sharks) as the dependent variable (variable for linear regression 6 above); YOY autumn DOY, DOY of cold front, autumn temperature, summer–autumn mullet CPUE and autumn salinity were independent variables. The third question included annual age 0–1 Spring CPUE as the dependent variable (proxy for YOY overwintering survival; variable for linear regression 7 above); overwintering duration, YOY Autumn DOY, autumn temperature, summer–autumn mullet CPUE, autumn salinity, spring water temperature and spring mullet CPUE were included as independent variables. Estuary was included as an independent variable for the global model (i.e. model in which data from all estuaries were included), but not in north and south coast analysis.

Boosted regression tree models were developed using trees built from binary splits from the relationships of the predictor variables using the gbm function in the R package 'dismo' (Hijmans et al., 2017). Model parameters were dependent on the question and region; however, we set fixed parameters of 75% of the out-of-the-bag occurrence observations. Tree complexity (the number of tree nodes) varied from 5 for the models including all estuaries and 3 for the regional (north/south) models. Learning rate (influence of each tree to the overall model) was also model-specific and ranged from 0.01 to 0.0001. Model variables were selected for optimal tree prediction using best practices outlined in Elith et al. (2008). The number of trees used to identify the consensus model were determined using *k*-fold cross-validation optimization with the gbm.step function in 'dismo'. A consensus tree was achieved when the holdout residual deviance was minimized, and the predictive power of the consensus model was measured using cross-validation correlation. Models were run using a Gaussian distribution. Within each model, variables were ranked using 'model importance' which was determined using the average number of times a variable was selected to split the data within the trees and squaring the predictive improvement resulting from these tree splits (Froeschke et al., 2010). Two independent, normally distributed variables generated using a random number generator (rand1 between 0 and 1; rand2 between 0 and 100) were included in each model and created using a random number generator with the 'rnorm' function in base R (R Core Team, 2014). Variables that had a lower model importance than the random numbers were not reported as their predictive power was effectively negligible. Analyses were conducted in R (version 4.3.1; R Core Team, 2014).

3 | RESULTS

From 1982 to 2021, 3978 age 0 and 7059 age 0–1 bull sharks were sampled in gillnets across the Texas coast, during which mean annual water temperatures increased by 0.83°C ± 0.60 SD coast-wide. However, the change in mean autumn water temperatures that may govern the timing of bull shark migrations was greater, significantly increasing by 1.55°C ± 0.89 SD. Warming temperatures exhibited a negative correlation with latitude, with the more northern Sabine Lake and Galveston Bay warming at rates approximately half that of the more southern Aransas and Corpus Christi Bays based on the slopes of best fit lines (Figure 3; Table 1).

The timing (DOY) of the first major autumn cold front was delayed by ca. 0.5 days per year across the 40-year study period, with similarities in magnitude and significance across each estuary (Figure 3; Table 1). Temporal trends in summer–autumn mullet CPUE also occurred in Sabine Lake, Galveston Bay, Matagorda Bay and Aransas Bay. Each of these four estuaries exhibited a significant decrease in mullet during the study period ranging from 0.18 to 0.46 fewer fish caught per sampling event per year, equating to 78%–94% declines in mullet relative abundance from 1982 to 2021 (Figure 3; Table 1).

Coast-wide, shifts in the timing of YOY autumn migrations (ca. 0.3 days later per year), mean YOY overwintering duration (ca. 1.2 days shorter per year) and age 0–1 spring (shark) CPUE (ca. 0.22 more sharks/gillnet from 1982 to 2021) were observed during the study period (Figure 4; Table 1). The largest and most consistent changes in the timing of YOY autumn migrations, YOY overwintering duration and age 0–1 spring CPUE occurred in northern estuaries

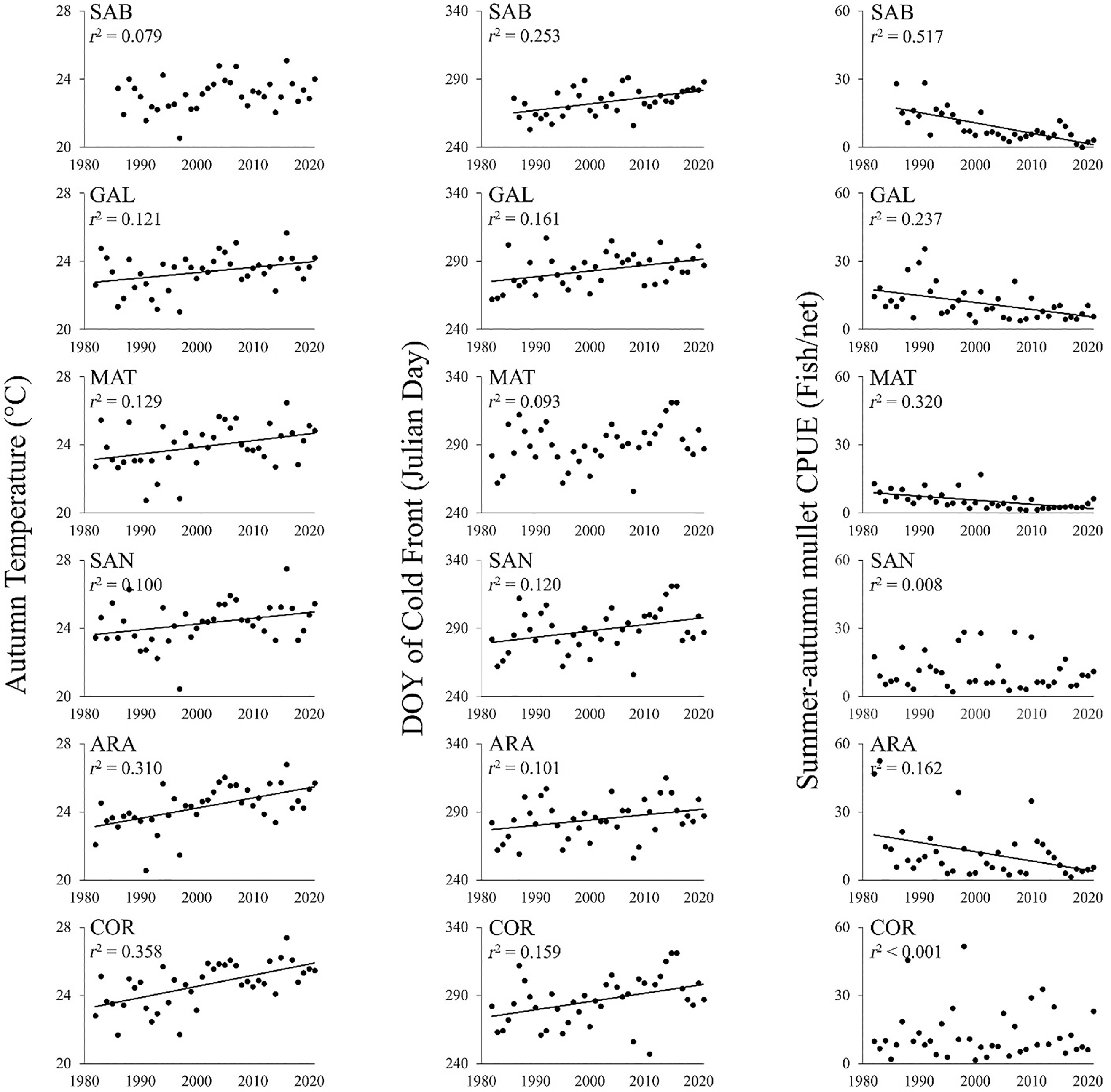

FIGURE 3 Left column: Annual average late autumn (October–November) water temperatures. Middle column: Day of year (DOY) of the first major autumn cold front (January 1 ~ DOY = 1). Right column: Summer–autumn striped mullet relative abundance (catch per unit effort [CPUE]; fish/bag seine). Panels include annual mean values for Sabine Lake (SAB; first row), Galveston Bay (GAL; second row), Matagorda Bay (MAT; third row), San Antonio Bay (SAN; fourth row), Aransas Bay (ARA; fifth row) and Corpus Christi Bay (COR; sixth row). Best fit lines are only included for significant linear regression models (see Table 1 for equations and statistics); the coefficient of determination (r^2) is included for all models.

(Sabine Lake, Galveston Bay and Matagorda Bay; Figure 4; Table 1). The timing of YOY autumn migrations were 37.2 and 27.8 days later in 2021 than 1982 in Sabine Lake and Galveston Bay, respectively (Figure 4). Estimated YOY overwintering duration was 70.5 and 80.8 days shorter in 2021 than 1982 in Sabine Lake and Galveston Bay, respectively (Figure 4). Age 0–1 spring CPUE increased more than sixfold in both Sabine Lake and Galveston Bay from 1982 to 2021 (Figure 4). Later migrations, shorter YOY overwintering durations and/or higher age 0–1 spring CPUE occurred in other estuaries; however, changes were smaller in magnitude or absent, and trends among all three parameters were only detected in Sabine Lake and Galveston Bay (Figure 4; Table 1).

Boosted regression trees (Table S1) indicated that autumn water temperatures warmer than 23.7°C, and autumn cold front DOYs after 288 Julian day (JD) led to later YOY migrations coast-wide, with decreasing summer–autumn mullet CPUE correlated with later

TABLE 1 Effect of year on dependent variables for Figures 3 and 4 with regression models.

	Sabine	Galveston	Matagorda	San Antonio	Aransas	Corpus
Autumn temperature	y = 0.025x − 26.99 2.912 (1,34), 0.097	y = 0.031x − 39.21 **5.427** (1,38), **0.028**	y = 0.039x − 54.84 **5.626** (1,38), **0.023**	y = 0.034x − 43.13 **4.229** (1,38), **0.047**	y = 0.060x − 95.50 **17.050** (1,38), **<0.001**	y = 0.066x − 107.08 **21.230** (1,38), **<0.001**
DOY of cold front	y = 0.473x − 675.16 **11.540** (1,34), **0.002**	y = 0.420x − 556.15 **7.301** (1,38), **0.010**	y = 0.404x − 518.06 3.887 (1,38), 0.056	y = 0.466x − 644.36 **5.187** (1,38), **0.028**	y = 0.388x − 492.02 **4.255** (1,38), **0.046**	y = 0.601x − 916.54 **7.716** (1,38), **0.011**
Autumn salinity	y = 0.055x − 92.381 0.178 (1,34), 0.676	y = −0.356x + 755.82 2.789 (1,38), 0.103	y = 0.182x − 323.49 0.506 (1,38), 0.481	y = −0.252x + 579.60 0.361 (1,38), 0.551	y = −0.526x + 1083.06 3.923 (1,38), 0.055	y = −0.294x + 617.12 0.657 (1,38), 0.423
Summer–Autumn Mullet CPUE	y = −0.459x + 928.09 **36.400** (1,34), **<0.001**	y = −0.307x + 625.28 **11.820** (1,38), **0.001**	y = −0.180x + 365.74 **17.920** (1,38), **<0.001**	y = −0.059x + 128.38 0.301 (1,38), 0.587	y = −0.410x + 831.83 **7.351** (1,38), **0.010**	y = 0.001x + 12.03 <0.001 (1,38), 0.998
YOY Autumn DOY	y = 0.954x − 1623.50 **8.339** (1,28), **0.007**	y = 0.712x − 1128.64 **6.359** (1,34), **0.017**	y = 0.723x − 1131.93 **13.960** (1,38), **<0.001**	y = 0.076x + 155.19 0.151 (1,38), 0.700	y = 0.478x − 654.98 3.151 (1,34), 0.085	y = 0.168x − 41.85 0.143 (1,28), 0.708
Overwintering duration	y = −1.808x + 3812.63 **4.869** (1,21), **0.041**	y = −2.073x + 4333.40 **49.710** (1,30), **<0.001**	y = −0.834x + 1821.70 **10.940** (1,37), **0.002**	y = 0.154x − 149.15 0.333 (1,37), 0.567	y = −1.030x + 2230.42 **12.240** (1,33), **0.001**	y = −1.372x + 2923.78 **5.338** (1,25), **0.029**
Age 0–1 Spring CPUE	y = 0.012x − 22.91 **5.104** (1,24), **0.033**	y = 0.018x − 35.16 **27.630** (1,36), **<0.001**	y = −0.004x + 8.68 0.727 (1,36), 0.400	y = −0.004x + 8.92 1.021 (1,36), 0.319	y = 0.009x − 17.07 **15.940** (1,36), **<0.001**	y = 0.004x − 7.58 **18.120** (1,36), **<0.001**

Note: Bold *F*- and *p*-values indicate significant linear trends with year at $\alpha = 0.05$. Values in parentheses are degrees of freedom.

Abbreviations: CPUE, catch per unit effort; DOY, day of year.

migrations (Figure 5). Coast-wide BRT models assessing YOY autumn DOY explained 12.8% of the total model deviance (Table S1). Later migrations (after 296 JD) were correlated with shorter overwintering duration of YOY sharks and accounted for 71.5% of modelled variability, with the full model explaining 61.3% of total deviance (Figure 5; Table S1). Longer overwintering duration (>172 days) and higher summer–autumn mullet CPUE (>12.6 fish/seine) from the previous year were largely responsible for lower age 0–1 spring CPUE (i.e. sharks in their second spring; deviance explained = 21.7%; Figure 5; Table S1).

Warmer autumn temperatures (>23.7°C in northern estuaries, and >23.9°C in southern estuaries), and later autumn cold fronts (after 293 JD in northern estuaries, and after 285 JD in southern estuaries) were correlated with later YOY migrations (Figures 6a and 7a). Lower summer–autumn mullet CPUE was only correlated with later migrations in northern estuaries (<9.5 fish/seine; Figure 6a). The BRT model explained 16.2% of the modelled deviance in northern estuaries, whereas the BRT model explained less than zero (−3%) of the modelled deviance in southern estuaries (Table S1). The relative effect of extrinsic variables on YOY autumn DOY was also 1–2 orders of magnitude greater for northern estuaries than southern estuaries (Figures 6a and 7a), indicating limited predictive power of the variables included in the model for the timing of autumn migrations in southern estuaries.

Overwintering duration of YOY sharks was largely explained by later migrations in northern (after 292 JD; 71% of modelled variability; Figure 6b) and southern estuaries (after 294 JD; 78% of modelled variability; Figure 7b; Table S1). The BRT model for overwintering duration explained 68.7% of modelled deviance in northern estuaries and 36.6% of deviance explained in southern estuaries. Age 0–1 spring CPUE was reliably predicted by shorter YOY overwintering duration for both northern and southern estuaries (<174 days in northern estuaries, and <180 in southern estuaries; Figures 6c and 7c). Additionally, lower age 0–1 spring CPUE in southern estuaries was predicted by higher summer–autumn mullet CPUE (>9 fish/seine) from the previous year (Figure 7c). All other variables included in the BRT models but not mentioned above had model importance lower than the included random variables, and as such were not considered useful as predictors.

4 | DISCUSSION

Climate change poses a threat to ecosystem stability by altering the structure of ecological communities (e.g. Fujiwara et al., 2019). However, wide-ranging generalizations can overlook the potential benefits changing conditions may offer mobile species that are geographically limited by winter temperatures (e.g. Chen et al., 2023; Langan et al., 2021). Based on long-term monitoring in the western Gulf of Mexico, YOY bull sharks in estuaries north of 28°25′ N (delineation of northern and southern estuaries) experienced migratory delays at a rate of ca. 0.75 days per year from 1982 to 2021, with sharks that once emigrated from natal estuaries in September

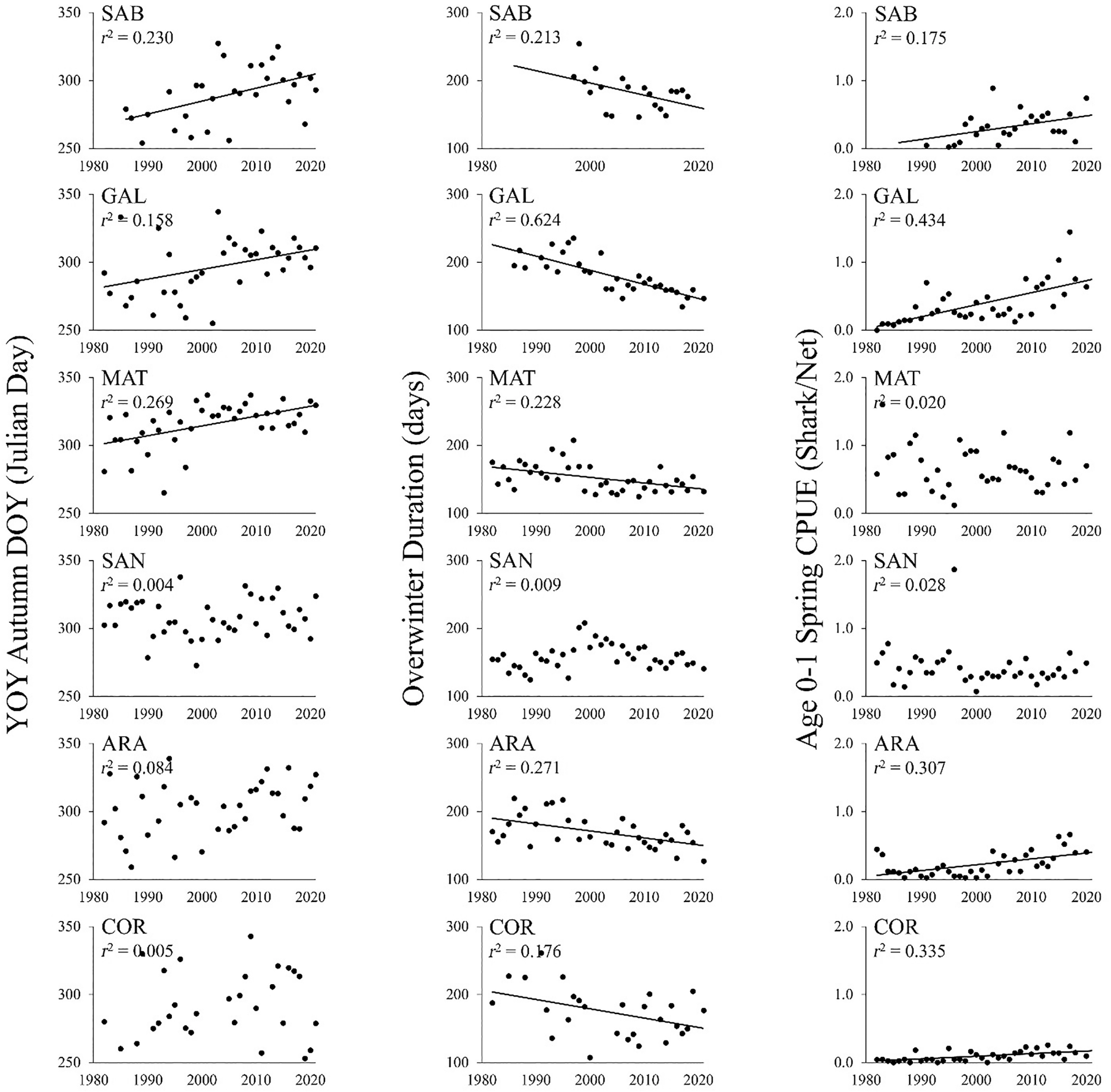

FIGURE 4 Left column: Annual timing of autumn migrations (95th percentile of the day of year [DOY] of the last YOY bull shark caught in gillnets [January 1 ~ DOY = 1]). Middle column: YOY overwintering duration. Right column: Relative abundance of age 0–1 spring sharks (sharks/standardized gillnet). Panels include annual mean values for Sabine Lake (SAB; first row), Galveston Bay (GAL; second row), Matagorda Bay (MAT; third row), San Antonio Bay (SAN; fourth row), Aransas Bay (ARA; fifth row) and Corpus Christi Bay (COR; sixth row). Best fit lines are only included for significant linear regression models (see Table 1 for equations and statistics); the coefficient of determination (r^2) is included for all models.

now leaving in October and November, which aligns with other migratory fishes (e.g. Langan et al., 2021; van Walraven et al., 2017). Considering the linear scaling of migration timing and temperature, overwintering migrations could be eliminated for sharks in some estuaries by the mid-late 21st century if phenotypic plasticity persists. Delayed autumn migrations led to shorter overwintering periods for YOY sharks across the coast, which likely reduced encounters with larger sharks in the Gulf of Mexico that pose predation risks (Matich & Heithaus, 2015), and potentially the metabolic costs of migration if duration is correlated with distance travelled (Lennox et al., 2016). Concomitantly, bull sharks experienced increased overwintering survival of >50% coast-wide across the study period based on changes in the relative abundances of age 0–1 sharks in their second spring season. Consequently, through prolonged access to nursery habitat, juvenile bull sharks in the western Gulf of Mexico could have benefited from climate change from 1982 to 2021. As

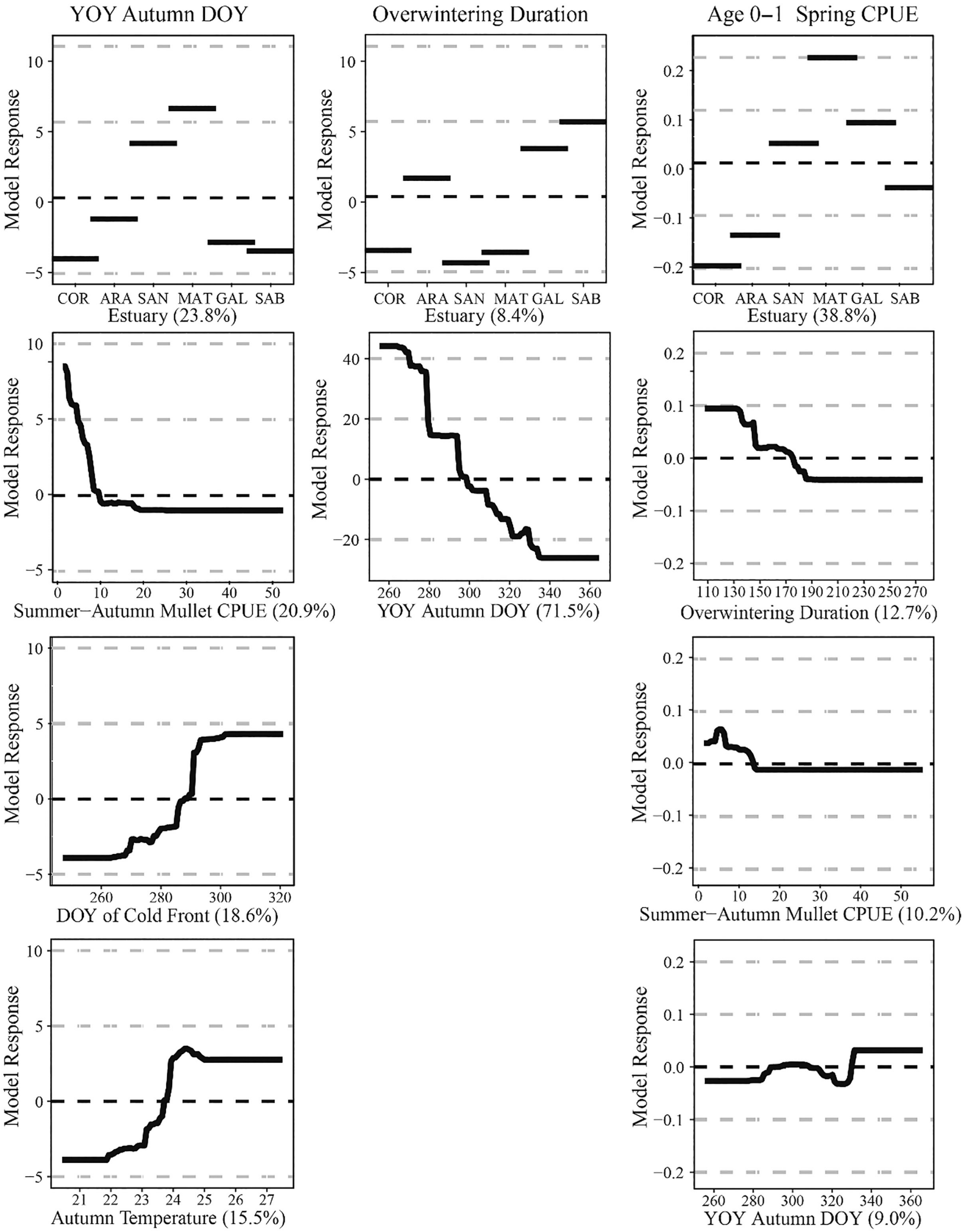

FIGURE 5 Results from coast-wide boosted regression trees. Individual figures are labelled with percent model importance. Left column: Annual timing of YOY autumn migrations. Middle column: YOY overwintering duration. Right column: Relative abundance of age 0–1 spring sharks. Independent variables in the figure are those that exhibited greater explanatory power than a random variable indicative of influencing the dependent variables. CPUE, catch per unit effort; DOY, day of year.

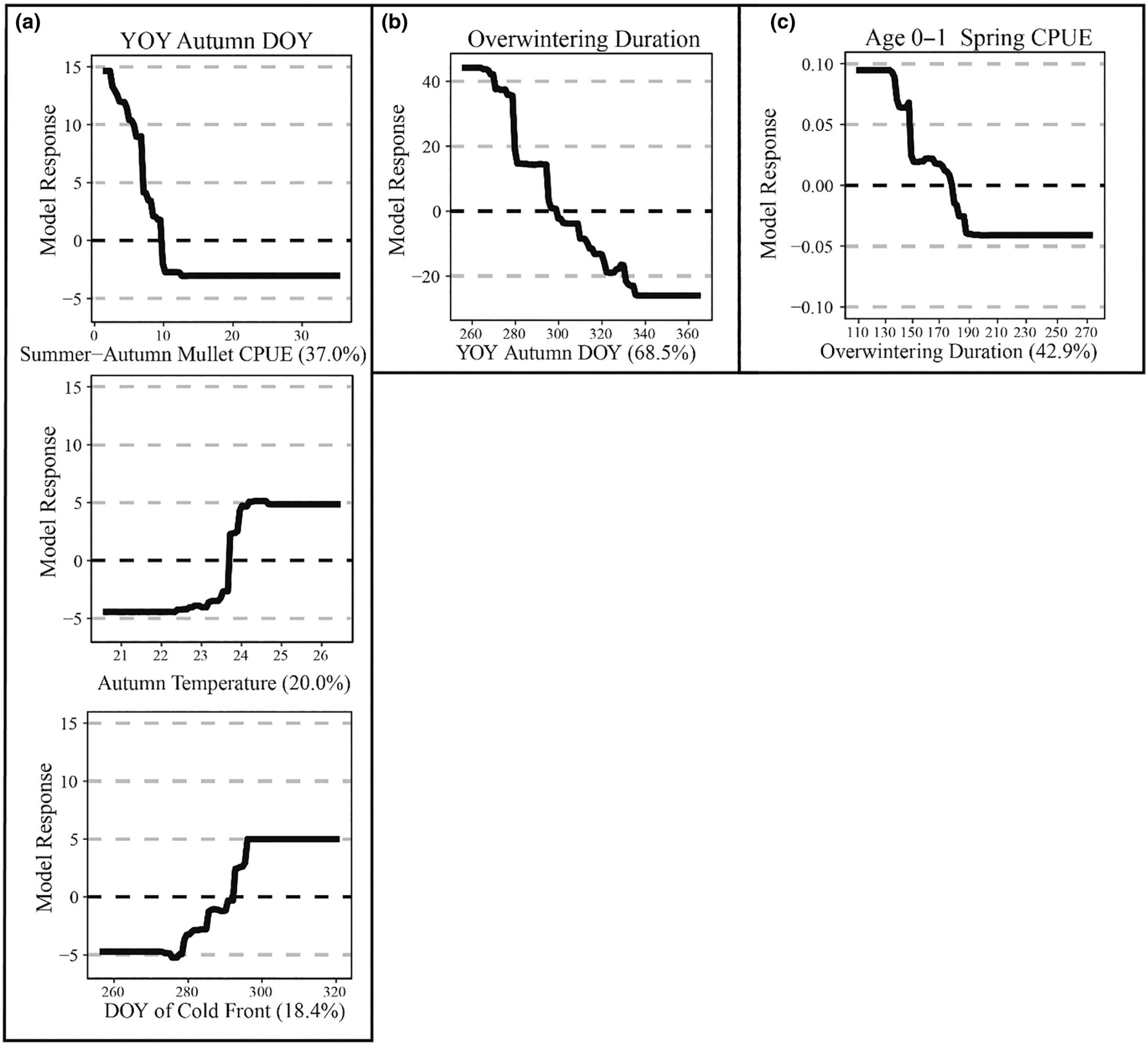

FIGURE 6 Results from boosted regression trees of northern estuaries (Sabine Lake, Galveston Bay and Matagorda Bay) assessing the annual timing of autumn migrations among YOY sharks (a), YOY overwintering duration (b) and age 0–1 spring shark catch per unit effort (CPUE) (c). Individual figures are labelled with percent model importance. Independent variables in the figure are those that exhibited greater explanatory power than a random variable indicative of influencing the dependent variables. DOY, day of year.

water temperatures continue to rise globally (Cheng et al., 2022), we expect that the changes observed in the western Gulf are not unique (e.g. Bangley et al., 2018; Goldner et al., 2022). Sharks and other ectotherms that currently undergo obligatory winter migrations in subtropical latitudes may forego these long-distance movements in the future due to warming temperatures, which will affect their ecological roles (Hammerschlag et al., 2019; Tanaka et al., 2021), economic values (Braun et al., 2023; Rogers et al., 2019) and conservation statuses (Birkmanis et al., 2020). However, our results indicate other extrinsic factors will play a role and lead to more complex outcomes.

The effects of climate change on elasmobranchs have been challenging to characterize, although there is a growing body of scientific information (e.g. Braun et al., 2023; Crear et al., 2023; Hare et al., 2016; Mullins et al., 2024; Tanaka et al., 2021). For example, tiger shark (*Galeocerdo cuvier*) migrations in the Atlantic have extended poleward in recent years, with arrival times in northern latitudes occurring earlier in part due to warming waters (Hammerschlag et al., 2022). Similarly, blue shark (*Prionace glauca*) distributions are predicted to shift poleward in the Pacific (Birkmanis et al., 2020; Cheung et al., 2015) and Atlantic Oceans (Braun et al., 2023). Range shifts for juvenile sharks have also been attributed to warming waters (e.g. Niella et al., 2020, 2022). Bangley et al. (2018) identified the establishment of a bull shark nursery in coastal North Carolina, USA due to temperature increases from 2003 to 2016, reportedly extending the northern nursery range of this species in the western Atlantic. Similarly, Crear et al. (2020) characterized a net gain of

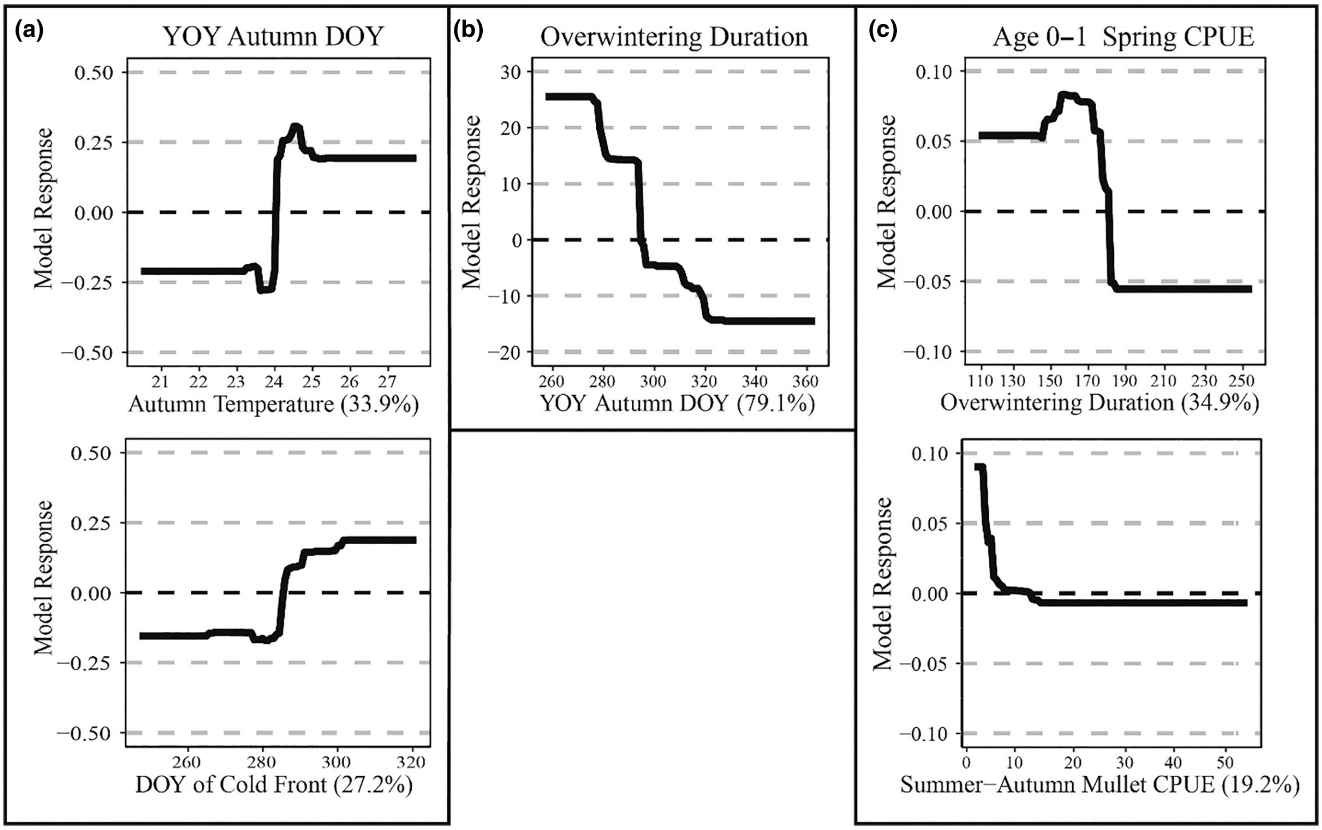

FIGURE 7 Results from boosted regression trees of southern estuaries (San Antonio Bay, Aransas Bay and Corpus Christi Bay) assessing the annual timing of autumn migrations among YOY sharks (a), YOY overwintering duration (b) and age 0–1 spring shark catch per unit effort (CPUE) (c). Individual figures are labelled with percent model importance. Independent variables in the figure are those that exhibited greater explanatory power than a random variable indicative of influencing the dependent variables. DOY, day of year.

suitable nursery habitat for sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, USA in response to changing environmental conditions associated with climate change when considering the entire water column.

The value of many nurseries includes the protective function they provide juvenile sharks during vulnerable life history stages (Heithaus, 2007). However, in temperate and subtropical latitudes, sharks undergo seasonal migrations into riskier habitats to avoid cold stress (Grubbs, 2010). Given its physiological importance, water temperature is a well-documented driver of shark behaviour and distribution (Schlaff et al., 2014). In other estuaries, juvenile bull sharks avoid water temperatures <18°C (e.g. Blackburn et al., 2007; Curtis et al., 2011; Drymon et al., 2014; Wiley & Simpfendorfer, 2007). Our data fits within this framework, with YOY sharks leaving at ca. 23–24°C on average across the study period. Bull sharks can tolerate colder conditions (e.g. Heithaus et al., 2009), but hypothermic stress and mortality are consequences of extended exposure to cold temperatures (reviewed in Curtis et al., 2011; Matich & Heithaus, 2012), and bull sharks, like other ectotherms, are adapted to maintain a buffer between their temperature preferences and critical tolerances (Schlaff et al., 2014). Thus, YOY bull sharks leave estuaries prior to approaching their critical thermal minimum, which is triggered by autumn cold fronts in the western Gulf. The change in timing of autumn cold fronts aligned with changes in water temperatures, with delays in cold fronts of ca. 0.5 days per year across the study period. Changing weather patterns and cooling temperatures associated with cold fronts therefore serve as a good indicator of migration timing. Compared to sharks in higher latitudes, many sharks in more equatorial waters exhibit year-round residencies in their respective nurseries (e.g. Murchie et al., 2010), which can offer survival advantages (Heupel et al., 2007). The tropicalization of higher latitude estuaries could thus provide sharks with similar benefits if their protective functions and prey availability are not negatively impacted by climate change.

In Texas, sharks are born in spring when prey densities are highest, with later parturition dates leading to reduced survival (e.g. Matich, Plumlee, & Fisher, 2021). Based on the relationship between overwintering departure dates and prey populations, temperature and cold front timing were not the only factors responsible for changes in migrations of YOY bull sharks. In Tasmania, the timing of overwintering among school sharks (*Galeorhinus galeus*) is based on juvenile body size rather than temperature in order to reduce energetic costs and risk during migration (McMillan et al., 2021). Beyond somatic growth, YOY sharks also prioritize the replenishment of energetic reserves. Newborn sharks catabolically rely upon energy-rich liver lipids after parturition to meet metabolic needs while they develop foraging skills (Olin et al., 2011), and sharks in some nurseries replenish these reserves prior to their first winter (e.g. Lyons et al., 2020), with individuals in poorer condition taking greater risks to compensate (e.g. Matich & Heithaus, 2015; Matich, Plumlee, & Fisher, 2021).

During the 40-year study period, the primary prey species of YOY bull sharks in Texas, striped mullet (TinHan & Wells, 2021), exhibited declines of 78%–94% in four of the estuaries evaluated, which appear to be the primary driver of YOY migratory delays based on the global BRT model. Across the Gulf of Mexico, winter spawners, including striped mullet, southern flounder (*Paralichthys lethostigma*) and blue crabs (*Callinectes sapidus*), have recently exhibited significant declines, resulting in changes in management policies (Anderson et al., 2017; Erickson et al., 2021; Smith et al., 2021). While fishing pressure has likely played a role, warming winter temperatures and shorter periods of cold temperatures that reduce spawning efficacy are suspected to be the primary reason for widespread declines (Anderson et al., 2017; Erickson et al., 2021). With declines in preferred prey from 1982 to 2021, YOY bull sharks may have remained in estuaries longer to reach minimum sizes (e.g. McMillan et al., 2021) and/or accumulate energy reserves (e.g. Lyons et al., 2020) prior to overwintering. Indeed, the TL of YOY bull sharks in autumn did not change across the study period as would be expected with longer times spent within the nursery habitat if prey availability was consistent (1982 = 93.4 cm TL ± 1.9 SD; 2021 = 90.4 cm TL ± 2.9 SD). If migrations were delayed in response to prey availability, then warmer waters may have enabled YOY sharks to remain in natal nurseries longer in later years of the study period, particularly in northern estuaries (Sabine Lake, Galveston Bay) where late autumn temperatures previously limited first-year residency. Thus, warmer waters may have facilitated extended autumn residency and indirectly caused the observed shifts in migratory timing, but more in-depth evaluations are warranted to identify climate change winners and losers in the region, and to adjust management accordingly as conditions continue to change.

Temporal patterns in migration, overwintering and relative abundances were not ubiquitous across the six estuaries though. Delayed migrations, shorter overwintering duration, and elevated spring CPUE of age 0–1 sharks were more pronounced in northern estuaries. Globally, climate change has and is expected to have the most immediate impacts in higher latitudes because of the rapidity of warming temperatures, shifting weather conditions and resultant changes in productivity (Free et al., 2019). The latitudinal range of the western Gulf of Mexico offers a natural gradient in which to test these predictions, and our results fit expectations. YOY sharks that once exhibited substantial geographic differences in the timing of overwintering departure in the 1980s became less heterogeneous throughout the 40-year study period, because YOY sharks in Sabine Lake and Galveston Bay left much later (37.2 and 27.8 days, respectively) in more recent years as opposed to southern estuaries where departure dates were more static. Differences in the timing of migrations were up to 30 days earlier in northern estuaries at the beginning of the study period, which have been nearly eliminated in recent years (<7 days difference). Despite warming water temperatures in southern estuaries, YOY sharks exhibited no observable change in migratory departure dates. As such, migration cues may vary geographically in the region, and temperature thresholds are likely more consequential in the timing of migration among northern sharks that currently experience colder water temperatures earlier in autumn (Bauer et al., 2011; Buchan et al., 2020; Dingle, 1996).

Extended migratory delays in northern estuaries appear beneficial for YOY bull sharks based on reductions in overwintering duration and increases in relative abundances in subsequent spring seasons across the study period. However, the long-term consequences of this phenological shift are unclear. Estuaries from Terminos Lagoon, Mexico (Pérez-Jiménez et al., 2020) to Louisiana, USA (Blackburn et al., 2007) offer habitat for juvenile bull sharks in the western Gulf of Mexico. Sharks in each estuary are likely suited for their local conditions, but may vary in their propensity to respond to change (Lubitz et al., 2023). Juvenile bull sharks exhibit genetic heterogeneity in the region (Laurrabaquio-A et al., 2019; TinHan et al., 2020); thus, it is perceivable that phenotypic variability and migratory triggers are linked to haplotypic differences across estuaries. Indeed, if warming waters, later cold fronts and/or reductions in prey availability prompt YOY bull sharks to extend autumn residency, then we would have expected migratory delays across all estuaries, which was not observed. It is plausible that the lower relative abundances and thus higher variance of catches of YOY bull sharks in Aransas and Corpus Christi Bays masked observable changes in phenology. Yet, San Antonio Bay had the second highest density of YOY sharks, and changes in migration, overwintering and survival did not occur. There are several possible explanations for this, as the hydrographic profiles in these Texas estuaries vary in freshwater input, ocean access and fresh and saltwater transport throughout the system, and any number of these factors could mask an effect of climate change along the coast (Armstrong, 1987). It is also possible that monitoring data did not capture when sharks departed southern estuaries. Yet, the frequency of sharks caught in the final week of monitoring was comparable across estuaries, suggesting the lack of shift in migratory timing in southern estuaries was not a sampling artefact. Future telemetry studies assessing geographic differences in the timing of migrations and where sharks overwinter will help address this question, and offer insight into how changing conditions may affect sharks more broadly.

Unlike other regions where range expansion is possible (e.g. Bangley et al., 2018), the Gulf of Mexico is limited latitudinally. Based on migration delays of 0.08–0.95 days per year and warming winter temperatures (0.04°C per year), winter migrations could be eliminated for sharks in some Texas estuaries before the end of the 21st century. However, it is not clear that prey populations will be able to support year-round residency in more crowded ecosystems, and carrying capacities could change for bull sharks and other increasingly abundant predators (e.g. *Carcharhinus limbatus*; Matich et al., 2017). Indeed, bull sharks are not the only predator that has increased in relative abundance in recent decades (Matich, Plumlee, Weideli, & Fisher, 2021; Plumlee et al., 2018), while the densities of some prey species have concurrently decreased (Matich, Plumlee, Weideli, & Fisher, 2021).

Bull sharks in southern estuaries could also be at risk as summer water temperatures continue to rise towards the species' upper thermal preferences of 31–37°C (Drymon et al., 2014; Heupel & Simpfendorfer, 2008; Steiner et al., 2007; Wiley & Simpfendorfer, 2007). Peak summer water temperatures in southern estuaries of Texas already exceeded 38°C in the latter part of the study period. While juvenile bull sharks reside in more equatorial estuaries in the region that presumably have warmer summer temperatures (e.g. Bonfil, 1997; Pérez-Jiménez et al., 2020), if there are genetic/local differences in thermal tolerances (Fangue & Bennett, 2003; Osgood et al., 2021), warming waters in Corpus Christi and Aransas Bays are of concern. If summer temperatures exceed thermal tolerances, YOY bull sharks may exhibit obligatory migrations into the Gulf, considering their limited use of low salinity habitats in these estuaries (Matich et al., 2020). Consequently, summer migrations would pose greater risk than winter migrations, because of their immediacy (weeks/months after birth) and due to higher densities and metabolic rates of coastal predators compared to winter (Bernal et al., 2012). Warmer temperatures that lead to more pervasive evapotranspiration and higher salinities could also increase the abundances of more stenohaline sharks that use Texas estuaries as nurseries (e.g. *Carcharhinus brevipinna*, *C. limbatus*; Matich et al., 2022; Swift & Portnoy, 2021), increasing competition with or predation on bull sharks (Matich & Heithaus, 2015), as well as overlap between bull sharks at different life stages (Lofthus et al., 2024). The co-occurrence of juvenile blacktips with juvenile bull sharks has increased fourfold since the 1980s (Matich et al., 2017), indicating such a transition is already occurring.

Sustained or accelerated warming could therefore impact the suitability of estuaries for bull sharks (Mullins et al., 2024), with sharks in northern estuaries benefiting and sharks in southern estuaries becoming disadvantaged. The most recent nursery evaluation in the western Gulf of Mexico included data through 2006 (Froeschke et al., 2010); thus, a new evaluation is needed to assess if the changes observed in our study have led to a change in nursery dynamics. More broadly, assessing shifts in the status of essential fish habitat for migratory species in response to climate change, including parturition and nursery grounds, is imperative moving forward (Braun et al., 2023).

Climate change is not considered as great of a threat to shark populations as fishing mortality and habitat loss (Dulvy et al., 2021). However, many coastal shark populations are vulnerable to the compounding effects of these human-induced stressors and the impacts of ocean warming on habitat quality, physiology and exposure to risk (Cheung et al., 2018; Osgood et al., 2021). Shorter overwintering periods in the Gulf of Mexico attributed to delayed migrations led to increased first-year survival for bull sharks in some estuaries, which should increase recruitment. However, if warming temperatures are coupled with declines in prey populations, then apparent positive consequences of climate change for bull sharks may be limited unless other prey populations replace those currently in decline.

Bull sharks are presently managed as a single population in the north-western Atlantic and Gulf of Mexico based on population genetics (Devloo-Delva et al., 2023) and movements between these neighbouring regions (Kohler & Turner, 2019; Rider et al., 2021). While the stock has not yet been formally assessed, regulation on shark fisheries in recent decades has resulted in the rebuilding of the stock that experienced historic declines due to overfishing (Carlson et al., 2012). Other species have exhibited similar positive responses to management (e.g. Pacoureau et al., 2023; Peterson et al., 2017), but recent changes in the relative abundances of sharks may be more complex due to range and behavioural shifts associated with climate change. Froeschke et al. (2012) attributed increases in the abundance of bull sharks in the western Gulf of Mexico to federal restrictions on the use of gillnets, reduction in shrimp trawl effort and changes in environmental conditions (including temperature). Our results provide further evidence that the increase in bull shark relative abundance could in part be explained by changes in residency within natal estuaries. As such, understanding distribution and phenological shifts due to climate signals will improve the interpretation of CPUE trends and its utility for population monitoring across marine species (Crear et al., 2023). Recently, NOAA Fisheries began to incorporate the potential impacts of changing climate through Climate Vulnerability Assessments (CVAs; Hare et al., 2016; Giddens et al., 2022; McClure et al., 2023; Morrison et al., 2015). Through CVAs, climate effects can be included in population assessments, which is particularly important for large-bodied, long-lived species (Cheung et al., 2018) and fit within ecosystem-based management initiatives that are becoming more pervasive (Karnauskas et al., 2021). As climate change persists, adapting current analytical and management frameworks to account for environmental, biological and ecological variability will be increasingly important to ensure sustainability and healthy ecosystems.

AUTHOR CONTRIBUTIONS

P. Matich led the study conception, data analysis and writing; J.D. Plumlee co-led the study conception, data analysis and writing; W. Bubley, T.H. Curtus, J.M. Drymon, L.L. Mullins, O.N. Shipley and T.C. TinHan contributed to the writing; and M.R. Fisher led the data collection and management.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this study are owned by and publicly available from Texas Parks and Wildlife Department Coastal Fisheries upon request: mark.fisher@tpwd.texas.gov; +1-361-729-2328. The data can also be accessed via Dryad: https://doi.org/10.5061/dryad.69p8cz99w—*Bull* *shark and prey catch data with environmental variables in the western Gulf of Mexico.*

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Boosted regression tree model parameters for models built for the three hypotheses.

Figure S1. Galveston Bay 3.4225 km^2 grid system used by Texas Parks and Wildlife Department to identify sampling locations for gillnets and bag seines.

Figure S2. Frequency distribution of bull sharks caught in gillnets in spring and autumn from 1982 to 2021 across the Texas coast.

Figure S3. Example delineation of first major autumn cold front timing.

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