Long-term monitoring provides insight into estuarine top predator (*Carcharhinus leucas*) resilience following an extreme weather event

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ABSTRACT: Chronic environmental change threatens biodiversity, but acute disturbance events present more rapid and immediate threats. In 2010, a cold snap across south Florida had wide-ranging impacts, including negative effects on recreational fisheries, agriculture, and ecological communities. Here, we use acoustic telemetry and historical longline monitoring to assess the long-term implications of this event on juvenile bull sharks *Carcharhinus leucas* in the Florida Everglades. Despite the loss of virtually all individuals (ca. 90%) within the Shark River Estuary during the cold snap, the catch per unit effort (CPUE) of age 0 sharks on longlines recovered through recruitment within 6–8 mo of the event. Acoustic telemetry revealed that habitat use patterns of age 0–2 sharks reached an equilibrium in 4–6 yr. In contrast, the CPUE and habitat use of age 3 sharks required 5–7 yr to resemble pre-cold snap patterns. Environmental conditions and predation risk returned to previous levels within 1 yr of the cold snap, but abundances of some prey species remained depressed for several years. Reduced prey availability may have altered the profitability of some microhabitats after the cold snap, leading to more rapid ontogenetic shifts to marine waters among sharks for several years. Accelerated ontogenetic shifts coupled with inter-individual behavioral variability of bull sharks likely led to a slower recovery rate than predicted based on overall shark CPUE. While intrinsic variation driven by stochasticity in dynamic ecosystems may increase the resistance of species to chronic and acute disturbance, it may also increase recovery time in filling the diversity of niches occupied prior to disturbance if resistive capacity is exceeded.

KEY WORDS: Extreme climate event · Resilience · Shark · Nursery · Elasmobranch · Coastal Everglades · Acoustic telemetry

1. INTRODUCTION

The projected speed and magnitude of warming temperatures and rising sea levels associated with climate change vary widely based on model selection, input data, and geographic region (Flato et al. 2013, Rummukainen 2016). It is clear, however, that environmental change will persist globally in the immediate future, and some ecosystems and species are better suited to changing landscapes and seascapes than others (Grimm et al. 2013, Butt et al. 2016).

Indeed, changing environments have led to responsive shifts in species abundances, distributions, behaviors, and physiologies, which have been associated with both positive and negative changes in fitness and survival (Lytle & Poff 2004, Jentsch et al. 2007, Grimm et al. 2013). The properties of resistance and resilience mitigate some of these effects and aid in the functional maintenance of ecological communities (Holling 1973). These qualities, however, are often context-dependent, and vary with the severity of environmental change and species-

specific traits (Jentsch et al. 2007, Butt et al. 2016, van de Pol et al. 2017).

Environmental disturbances vary in their effects on ecological systems and processes based on their frequency, duration, and intensity, as well as the properties of ecosystems (Jentsch et al. 2007, Miller et al. 2011). Slow, chronic shifts in abiotic factors have been a primary focus of climate scientists, because of the predicted global scale of their effects on ecological and economic systems (IPCC 2014, 2018, Butt et al. 2016). Yet, acute disturbance events, such as hurricanes, floods, droughts, cold snaps, and heat waves are also of great interest due to their rapid and forceful nature, and the limited ability of humans and other species to predict such events (Bailey & Secor 2016, Moran-Ordonez et al. 2018). Furthermore, climate models predict that these events are likely to change in their frequency of occurrence and severity in the near future (reviewed in IPCC 2012, Ummenhofer & Meehl 2017, Maxwell et al. 2019).

Long-term monitoring used to study chronic environmental change can provide data and insight into the effects of acute events before, during, and after a disturbance (Thibault & Brown 2008, Scheele et al. 2012). As such, advancing our understanding of acute disturbance effects is an important facet of climate science, and fits within the framework of predicting the long-term effects of warming temperatures and rising seas (IPCC 2012, Maxwell et al. 2019). Identifying species traits (e.g. physiology and life history) and the properties of communities (e.g. biodiversity) that promote or limit resilience to such disturbance also broadens the scope of such research, and enables more flexible management strategies to promote timely recovery of species and ecosystems, and minimize the effects of these perturbations.

Ecosystems with disturbance regimes of significant frequency, duration, and/or intensity can serve as model systems in which to test hypotheses of resistance/resilience. South Florida experiences predictable chronic disturbances as well as unpredictable acute perturbations, which shape its ecosystems and ecological communities (Duever et al. 1994, Boucek & Rehage 2014, Nungesser et al. 2015). Seasonal and annual fluctuations in precipitation and temperature coupled with discrete events such as hurricanes and flooding alter species abundances, behaviors, and biodiversity across a predictable spectrum for both migrant and residential south Florida fauna (Roman et al. 1994, Lytle & Poff 2004, Pirhalla et al. 2015).

In January 2010, south Florida experienced an extreme cold event, with temperatures more than 5°C below average winter temperatures, that was of a magnitude unobserved over the previous century (NOAA 2010, Rehage et al. 2010). The cold snap had wide-ranging impacts on agriculture, fisheries, eco-tourism, and ecological communities. In response to the rapid and extended decline in temperatures, Florida's citrus crop crashed (Cave 2010), recreational fisheries were closed for several years (e.g. *Albula vulpes*, *Centropomus undecimalus*; Frezza & Clem 2015, Santos et al. 2016), reef-building corals experienced mass mortality (Kemp et al. 2011, Schopmeyer et al. 2012), and many other tropical and subtropical fauna died in large numbers (e.g. Stith et al. 2012, Rehage et al. 2016, Scharer et al. 2017).

Long-term ecological research in the region, particularly in the coastal Everglades, has provided the opportunity to study the long-term effects of this event, and further develop the science of disturbance ecology and climate change using study species for which we have a comprehensive understanding of their biology and ecology both from the region, and across their geographic ranges (Childers et al. 2019). Here, we investigate the long-term impacts of the 2010 cold snap on juvenile bull sharks *Carcharhinus leucas* in a natal nursery within the Florida coastal Everglades — the Shark River Estuary. Matich & Heithaus (2012) showed that the magnitude and/or duration of the event exceeded the thermal resistive capacity of juvenile bull sharks within the Shark River Estuary, and resulted in behavioral changes among all sharks, along with mass mortality. However, a new cohort of bull sharks repopulated the nursery within 6–8 mo of the event. While definitive differences in recovery to disturbance between *r*- and *k*-selected species provide a framework for hypothesis testing (reviewed by Timpane-Padgham et al. 2017), the resilience of juvenile segments of populations of long-lived and late-maturing species with relatively low fecundity is less evident. Therefore, predicting the magnitude of effects and times for full recovery of abundance, age structure and patterns of space use and species interactions in nurseries is unclear. As such, we aim to test 4 separate hypotheses with the present study:

• H_1: Recruitment of bull sharks was not affected by the 2010 cold snap, because adult bull sharks that inhabit coastal and shelf waters were likely able to find thermal refuges, and able to give birth in the estuary in 2010 and thereafter (Castro 2011).

• H_2: Repopulation of bull sharks after the 2010 cold snap was driven primarily by the arrival of

newborn pups rather than recolonization by animals alive before the cold snap (Matich & Heithaus 2012).

• H₃: Due to rapid return of typical environmental conditions (Matich & Heithaus 2012), pre- and post-cold snap (a) growth rates, (b) size at birth, and (c) habitat use and distribution of bull sharks were similar.

• H₄: After the mass mortality observed from immediate cold shock, survival rates of newly recruited juvenile bull sharks were similar to those observed before the event, because environmental conditions normalized shortly after the cold snap (Matich & Heithaus 2012).

2. MATERIALS AND METHODS

2.1. Study site

The braided river system of the Shark River Estuary serves as the main drainage basin of the Florida Everglades, connecting oligotrophic freshwater marshes with productive marine waters of the Gulf of Mexico (Fig. 1; Childers et al. 2019). Variability in environmental conditions attributed to freshwater and tidal flow provide a matrix of habitats for species within the estuary (Williams & Trexler 2006,

Matich et al. 2017), including juvenile bull sharks, which use the estuary as a nursery for their first 2–5 yr, after which they disperse to coastal marine waters (Wiley & Simpfendorfer 2007, Heithaus et al. 2009, Matich & Heithaus 2015).

Phosphorous limitation and outwelling produce a productivity gradient tied to salinity in the estuary, and allochthonous biomass accumulates in upstream habitats when marsh water levels recede during the dry season, and teleosts are forced into deeper upstream channels (Rehage & Loftus 2007, Childers et al. 2019). Consequently, there is a bimodal distribution of food availability for juvenile bull sharks during marsh dry-down, with peaks in upstream and downstream habitats (Rehage & Loftus 2007, Matich & Heithaus 2014). Food-risk trade-offs shape the behavior of juvenile bull sharks, and predation risk posed by larger sharks is higher in waters adjacent to the Gulf of Mexico (Matich & Heithaus 2015). To quantify general patterns in shark distribution, we divided the estuary into 4 regions based on spatial differences in abiotic (e.g. salinity) and biotic factors (e.g. risk, prey abundance) documented during long-term sampling (i.e. Florida Coastal Everglades Long-Term Ecological Research Project [LTER]; our Fig. 1; see Matich & Heithaus 2012, 2015 for details): Downriver (DR), Shark River (SR), Tarpon Bay (TB), and Rookery Branch (RB).
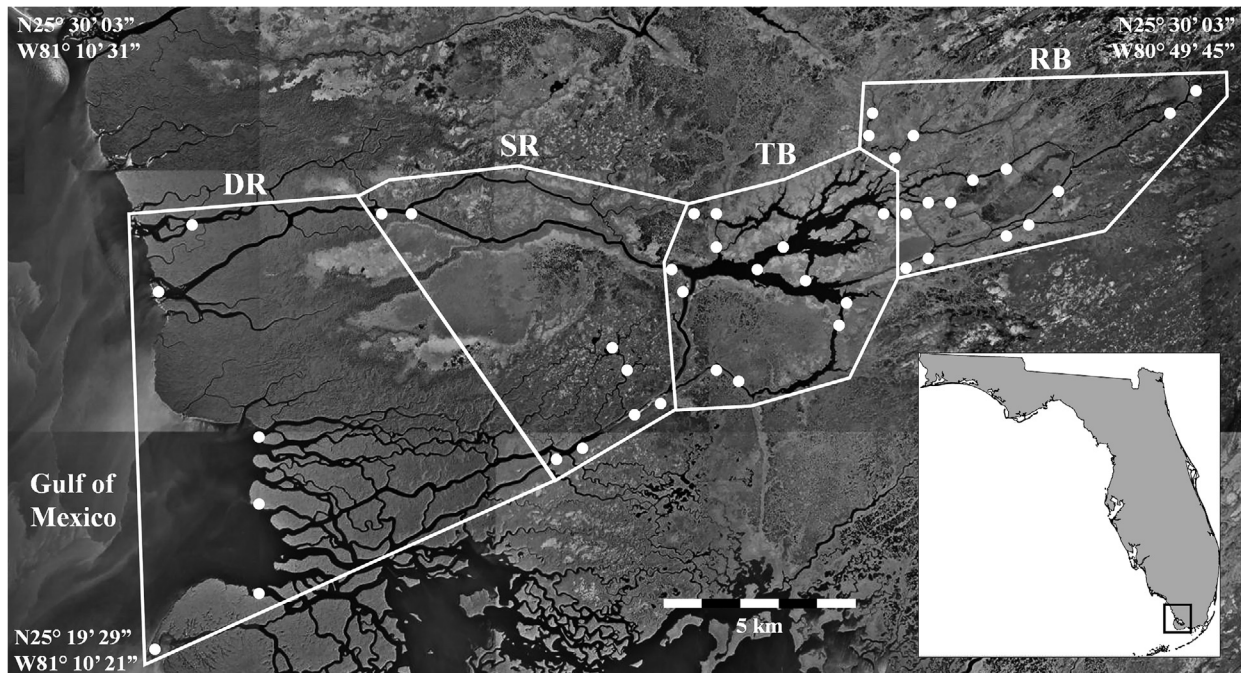

Fig. 1. Acoustic telemetry sampling regions (DR: Downriver; SR: Shark River; TB: Tarpon Bay; RB: Rookery Branch) within the Shark River Estuary (inset: Florida). White dots: locations of acoustic receivers. Catch data are quantified from longline sampling conducted in TB

2.2. Field sampling

Juvenile bull sharks were sampled in TB using ca. 500 m bottom-set longlines fitted with 40–55 Mustad tuna circle hooks (sizes 14/0 and 15/0) baited with mullet (*Mugil* sp.) from March 2006 to August 2017 (see Heithaus et al. 2009 for further details on sampling equipment). Shark total length (TL) was measured to the nearest centimeter, the presence of an umbilical scar was noted to identify neonates, sex was determined by the presence or absence of claspers, and sharks were externally tagged using a numbered roto tag affixed through the first dorsal fin.

A subset of sharks (n = 105) were surgically fitted with a Vemco V16-4H transmitter. Transmitters emitted a unique series of pulses for each shark at a random interval between 30 and 90 s, with a battery life of 2–5 yr. Movements of acoustically tagged sharks were tracked within an array of 43 Vemco VR2 and VR2W acoustic receivers placed throughout the estuary to detect the location and direction of movements of tagged sharks into and out of each region (DR, SR, TB, and RB; Fig. 1). Each receiver had a detection range of ca. 500 m (see Rosenblatt & Heithaus 2011 for further details of the sampling array). Data were downloaded every 3–4 mo and batteries were replaced as needed.

2.3. Quantitative analysis

2.3.1. Catch data

Catch per unit effort (CPUE) was measured as sharks caught per longline set, and was used as an estimate of juvenile bull shark densities. CPUE was quantified for each age class from 0 to 3 yr old, as well as all sharks within this age range (i.e. total juvenile shark CPUE). Because of the limited number of sharks caught with open umbilical scars during the study, shark ages were estimated using size and time of birth, and growth rates. Based on minimum sizes and the presence of umbilical scars, bull sharks in the Shark River Estuary are likely born at 60–70 cm TL between May and August (see also Curtis et al. 2011). Recaptures of tagged individuals in our study and data from other locations (e.g. Neer et al. 2005, Natanson et al. 2014) indicate growth rates of 10–20 cm yr^{-1}. Broadly, sharks ≤85 cm TL were classified as age 0 (including individuals with umbilical scars), sharks 86–100 cm TL were age 1, sharks 101–115 cm TL were age 2, and sharks 116–130 cm TL were age 3; although smaller sharks may have been classified

into older age classes based on maximum monthly sizes for each age class (see Matich & Heithaus 2015 for more details on monthly determinations of shark age). Sharks were reassigned into the next oldest age class on 1 July each year for age-specific analyses based on tracking data (see our Section 2.3.2 below; Matich & Heithaus 2015).

To assess differences in the CPUE of sharks attributed to the 2010 cold snap and recovery thereafter, we used a general linear model (GLM) from March 2006 to August 2017. We used post hoc Tukey tests to detect significant differences across years. No significant differences were found between years prior to the cold snap (2006–2009) in CPUE ($F_{3,148}$ = 0.79, p = 0.50), or CPUE of sharks in any age class (age 0: $F_{3,148}$ = 0.50, p = 0.78; age 1: $F_{3,148}$ = 1.16, p = 0.33; age 2: $F_{3,148}$ = 2.04, p = 0.11, age 3: $F_{3,148}$ = 0.48, p = 0.70). Thus, pre-cold snap data were pooled for 2006–2009 for hypothesis testing (see H$_1$, H$_2$, and H$_3$ in Section 1 above).

We used logistic regression to examine (1) differences across sampling years in sex ratios of juvenile bull sharks from age 0 to 3, and (2) differences in size structure (proportion of individuals in age classes 0–3) across years. We observed no difference in size structure prior to the 2010 cold snap (chi-squared test; χ^2 = 15.50, p = 0.08); thus 2006–2009 data were pooled for hypothesis testing (see H$_1$ and H$_2$).

Linear regression was used to assess differences in predicted growth rates and size at birth among cohorts based on age estimates (see H$_3$). Slopes of best-fit lines were used as estimates of growth rates, and *y*-intercepts were used as estimates of birth size annually on 1 July (see Matich & Heithaus 2015). We used *t*-tests to determine differences in growth rates across cohorts by testing pairwise differences in regression slopes, with Hochberg's step-up procedure to correct for multiple comparisons (Hochberg & Tamhane 1987).

2.3.2. Acoustic telemetry data

Using the methodology of Heupel et al. (2012), survival rates of acoustically tagged bull sharks were estimated based on telemetry data (see H$_4$ in Section 1 above) — individuals that ceased movement within the study site or showed movement patterns inconsistent with previous or typical movements were considered dead. All mortality events were identified during the study by the lack of movement of tagged sharks. A *z*-test was used to quantify differences in survival rates of tracked sharks before (2008–2009)

and after (2012–2014) the cold snap when mortalities were identified with telemetry data.

The monthly proportions of time acoustically tagged sharks spent in each sampling region (DR, SR, TB, and RB) were calculated. We used these proportions to assess annual differences in shark distribution patterns relative to the 2010 cold snap until Hurricane Irma in August 2017 (see H_3). During the late dry season (March–May), bull sharks exhibit significant changes in their movement patterns in response to influxes of potential prey from adjacent freshwater marshes (Matich & Heithaus 2014). To investigate juvenile bull shark movements outside of this 3 mo period, we removed movement data from March to May annually (see Matich & Heithaus 2015). In addition, data were only analyzed for sharks that were tracked within the estuary for at least 4 mo. Using this subset of data, we performed a GLM to individually investigate annual differences in the distribution of sharks in each age class within the estuary (2009, 2012–2017). We used post hoc Tukey tests to detect significant differences in habitat use across years.

Movement data were also used to assess interannual variability in residency patterns of sharks in response to the 2010 cold snap. A Kruskal-Wallis 1-way ANOVA was used to quantify annual differences in estimated age at emigration from the estuary, with post hoc Mann-Whitney tests used to

identify differences among years. Among the sharks tracked in 2017, 3 individuals permanently emigrated from the estuary prior to September when Hurricane Irma passed over south Florida (Strickland et al. 2019); 1 bull shark emigrated in July, and 2 emigrated in August. Nine additional bull sharks left the estuary in 2017 in response to Hurricane Irma, but returned after conditions in the estuary normalized, and were thus not included in the analysis. All statistical analyses were conducted in IBM SPSS 22. We evaluated significance at $\alpha = 0.05$, and report means with ±1 SD.

3. RESULTS

3.1. Catch data

From 2006 to 2017, we sampled 251 bull sharks in TB (2006: 36, 2007: 11, 2008: 12, 2009: 35, 2010: 9, 2011: 16, 2012: 15, 2013: 32, 2014: 12, 2015: 6, 2016: 36, 2017: 31), ranging from 66 to 178 cm TL (mean: 94.1 ± 18.7 cm).

When data were pooled, no significant differences in shark CPUE were detected before and after the event ($F_{1,429} = 0.01$, p = 0.91). However, differences were apparent across years, with higher CPUE in 2016 and 2017 than 2010 ($F_{7,281} = 2.69$, p = 0.01; Fig. 2). Neither age 0 nor age 1 sharks exhibited
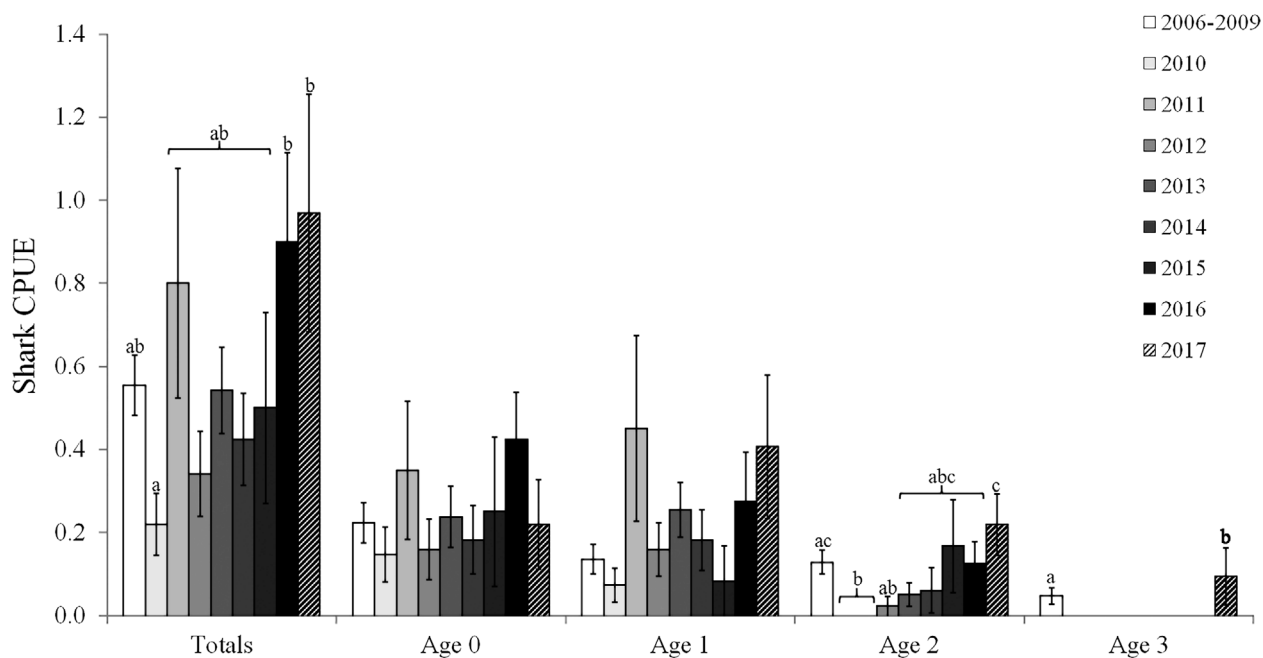

Fig. 2. Longline catch per unit effort (CPUE) of juvenile bull sharks age 0–3 in Tarpon Bay, 2006–2017. Data collected before the 2010 cold snap were not significantly different ($F_{3,148} = 0.79$, p = 0.50), and were pooled. Error bars are ±SE, and bars with different letters are significantly different within ages / across totals (p < 0.05, post hoc Tukey tests)

differences in CPUE across sampling years, supporting H_1 and H_2 ($F_{age\ 0,8,429} = 1.02$, p = 0.42; $F_{age\ 1,8,429} = 1.81$, p = 0.07; Fig. 2). However, there were temporal differences in age 2 and age 3 CPUE ($F_{age\ 2,7,281} = 2.92$, p < 0.01; $F_{age\ 3,7,281} = 3.14$, p < 0.01; Fig. 2). CPUE of age 2 sharks were lower in 2010–2012 than prior to the 2010 cold snap, with increasing CPUE of age 2 sharks from 2010 to 2017 (Fig. 2). Age 3 sharks were only caught prior to the 2010 cold snap and in 2017 (Fig. 2).

There was no differences in the sex ratio (M:F) of juvenile bull sharks before (55:45) or after (48:52) the 2010 cold snap ($\chi^2 = 2.49$, p = 0.29); however, there was a temporal shift in the age structure within the nursery ($\chi^2 = 37.99$, p = 0.04; Fig. 3, Table 1). No sharks older than age 1 were caught in 2010 and 2011, with a significantly higher proportion of age 1 sharks caught in 2011 than prior to the 2010 cold snap. A smaller proportion of age 2 sharks were caught in 2012 than prior to 2010. Age structure did not resemble 2006–2009 until 2017.

Estimated growth rates and estimated sizes at birth for each cohort varied annually, ranging from 9.4 to 23.0 cm TL yr^{-1} (growth rate) and 66.3–80.9 cm TL (birth size; Table 2, Fig. 4). There was a significant negative correlation between growth rate and birth size estimates (r = −0.72, $t_9 = 3.13$, p = 0.01). Growth rates varied across years (Table 3, Fig. 4), with faster growth rates among the 2005, 2006, and 2011 cohorts, and slower growth rates among the 2014, 2015, and 2016 cohorts. However, no direct effects from the cold snap were apparent, supporting H_{3a} and H_{3b}. Data were insufficient to produce a best-fit line for the 2008 cohort.

3.2. Acoustic telemetry data

Among the 105 sharks that were surgically implanted with acoustic transmitters, 86 individuals were tracked within the acoustic array for at least 4 mo (Table A1 in the Appendix), with an average tracking duration of 15.3 ± 8.5 mo (maximum: 27 mo), and a total tracking time of 1315 mo among the 86 sharks.

Mortality rates of acoustically tagged sharks did not differ before (8% of all acoustically tagged sharks from 2008 to 2009) versus after (10% of acoustically tagged sharks from 2012 to 2017) the 2010 cold snap (z = 0.29, p = 0.77), excluding the acute
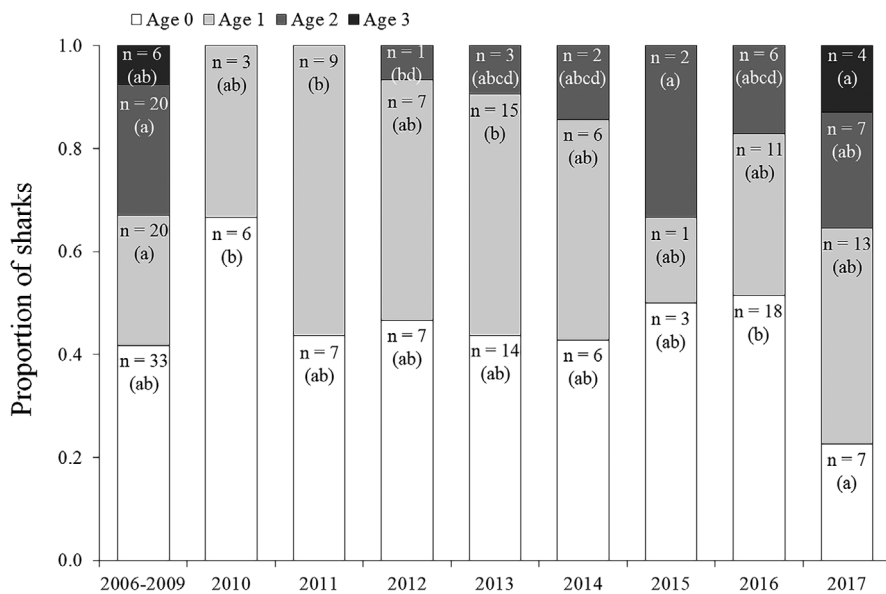

Fig. 3. Annual variability in the proportion of juvenile bull sharks in each age class, with sample sizes. Data collected before the 2010 cold snap were not significantly different ($\chi^2 = 15.50$, p = 0.08), and were pooled. Letters within bars indicate significant interannual differences (p < 0.05, post hoc chi-squared test)

Table 1. Chi-squared and p-values for post hoc test of temporal differences in bull shark age structure. **Bold**: significant (α = 0.05)

	2006–2009	2010	2011	2012	2013	2014	2015	2016
2010	4.29, 0.23							
2011	**9.45, 0.02**	1.21, 0.27						
2012	5.17, 0.16	1.26, 0.53	1.22, 0.54					
2013	**8.60, 0.04**	1.89, 0.39	1.69, 0.43	0.11, 0.95				
2014	2.99, 0.39	2.01, 0.37	2.56, 0.28	2.15, 0.34	0.25, 0.88			
2015	0.85, 0.84	3.54, 0.17	**6.88, 0.03**	**6.19, 0.04**	3.34, 0.19	1.63, 0.44		
2016	4.21, 0.24	1.86, 0.40	**6.28, 0.04**	4.93, 0.09	1.99, 0.37	0.58, 0.75	1.07, 0.59	
2017	5.06, 0.17	**9.27, 0.03**	**11.11, 0.01**	**10.49, 0.02**	**9.70, 0.02**	3.51, 0.32	3.26, 0.35	**8.87, 0.03**

Table 2. Equations, test statistics, and p-values of linear regression estimates of growth rates and size at birth for each cohort based on age estimates of captured bull sharks (Matich & Heithaus 2015). Growth rates are based on the slopes of best-fit lines, and birth sizes are based on *y*-intercepts at 1 July per annum. Values in parentheses: 95% CI. TL: total length

| Cohort	Best-fit line	R^2	F	p	Growth rate (cm TL yr^{-1})	Birth size (cm TL)
2005	$y = 0.055x + 69.33$	0.96	393.5	<0.01	20.2 (18.0–22.4)	69.3 (64.3–74.3)
2006	$y = 0.063x + 63.28$	0.94	246.6	<0.01	23.0 (19.8–26.2)	63.3 (56.8–69.8)
2007	$y = 0.050x + 75.61$	0.70	28.0	<0.01	18.1 (10.6–25.6)	75.6 (64.3–86.9)
2009	$y = 0.043x + 66.76$	0.92	252.4	<0.01	15.6 (13.6–17.7)	66.3 (63.7–69.9)
2010	$y = 0.036x + 70.02$	0.94	185.1	<0.01	13.2 (11.1–15.3)	70.0 (67.0–73.1)
2011	$y = 0.047x + 70.31$	0.92	223.3	<0.01	17.3 (14.9–19.7)	70.3 (66.1–74.5)
2012	$y = 0.037x + 78.98$	0.90	96.0	<0.01	13.4 (10.4–16.4)	79.0 (76.2–81.8)
2013	$y = 0.031x + 80.88$	0.91	290.4	<0.01	11.4 (10.0–12.7)	80.9 (78.3–83.5)
2014	$y = 0.026x + 76.28$	0.91	87.5	<0.01	9.6 (7.6–11.6)	76.3 (72.6–80.0)
2015	$y = 0.026x + 79.04$	0.70	32.4	<0.01	9.4 (5.7–13.1)	79.0 (73.9–84.3)
2016	$y = 0.028x + 73.93$	0.44	22.9	<0.01	10.0 (5.8–14.2)	73.9 (70.9–76.9)
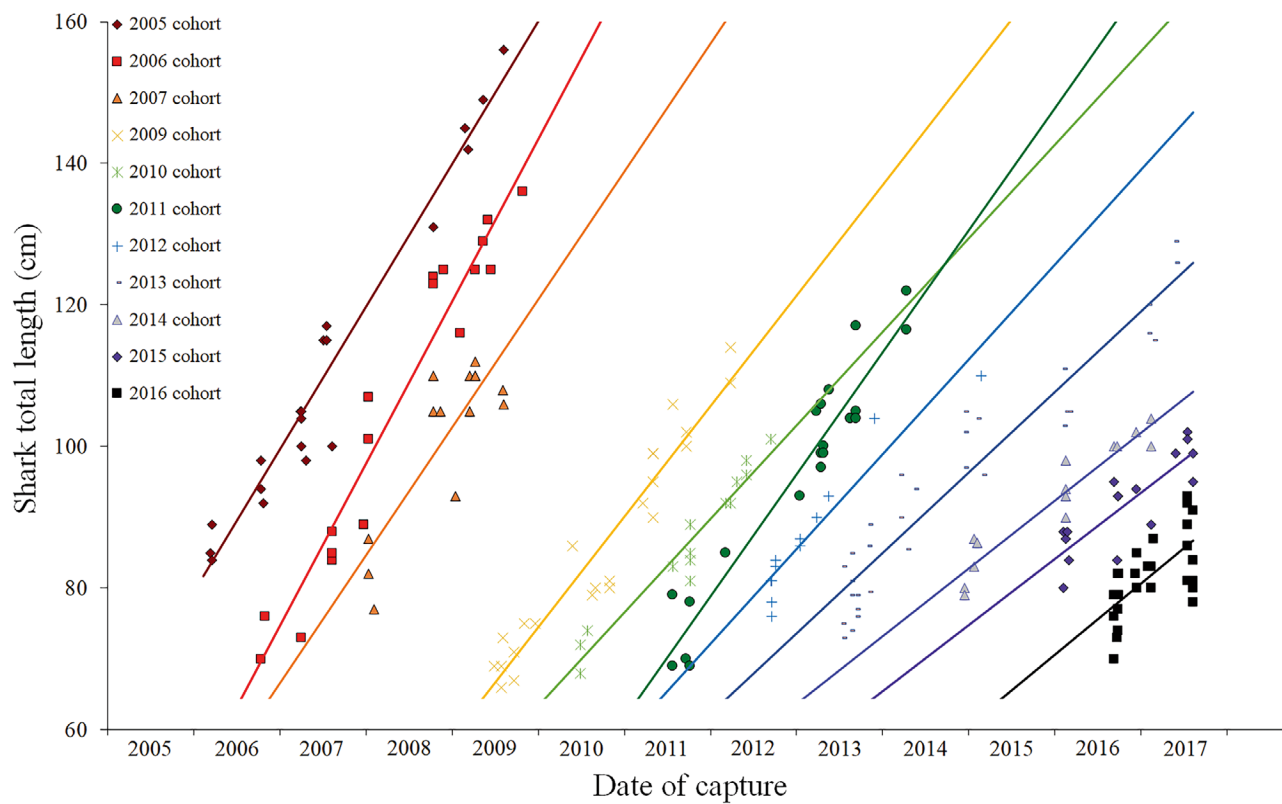
Fig. 4. Body size upon capture date used to quantify growth rate and size at birth estimates of juvenile bull shark cohorts based on age estimates of captured sharks (Matich & Heithaus 2015). Lines are best fit lines from linear regressions

effects of the event itself (in January 2010), supporting H_4. The spatial distributions of juvenile bull sharks did, however, vary across the study period, counter to H_{3c}. Age 0 sharks exhibited limited differences in spatial distributions, with greater use of upstream waters (RB) in 2014, and greater use of more saline waters (SR) in 2016 and 2017 (Fig. 5).

Age 1 sharks exhibited greater temporal differences in distributions, with significantly greater use of downstream (DR) habitats and lower use of upstream habitats (TB and RB) in 2012, with subsequently less time spent in higher-salinity waters (DR and SR) and increased time spent in lower-salinity waters (TB and RB) until 2016. Age 2 and age 3 sharks exhibited sim-

Table 3. *t*-values and p-values for pairwise cohort slope comparisons of estimated juvenile bull shark growth rates. **Bold**: significant based on adjusted α-value (0.003) using Hochberg′s step-up procedure

|	2006	2007	2009	2010	2011	2012	2013	2014	2015	2016
2005	−1.64, 0.118	0.51, 0.617	3.09, 0.006	**4.93, <0.001**	1.90, 0.072	**3.85, 0.002**	**7.20, <0.001**	**7.77, <0.001**	**5.24, <0.001**	**4.22, <0.001**
2006		1.27, 0.223	**4.15, <0.001**	**5.62, <0.001**	3.14, 0.006	**4.74, <0.001**	**7.27, <0.001**	**7.86, <0.001**	**5.93, <0.001**	**4.99, <0.001**
2007			0.72, 0.485	1.44, 0.173	0.30, 0.766	1.29, 0.221	1.99, 0.067	2.47, 0.029	2.28, 0.039	2.00, 0.066
2009				1.85, 0.086	−0.96, 0.353	1.30, 0.216	**3.68, 0.002**	**4.64, <0.001**	3.09, 0.008	2.36, 0.033
2010					−2.66, 0.019	−0.22, 0.832	1.55, 0.144	2.75, 0.018	7.83, 0.089	1.26, 0.228
2011						2.04, 0.062	**4.37, <0.001**	**5.22, <0.001**	**3.66, 0.002**	2.89, 0.009
2012							1.44, 0.176	2.45, 0.031	1.81, 0.095	1.31, 0.215
2013								1.62, 0.131	0.98, 0.344	0.5, 0.623
2014									0.00, 0.999	−0.32, 0.755
2015										−0.27, 0.793
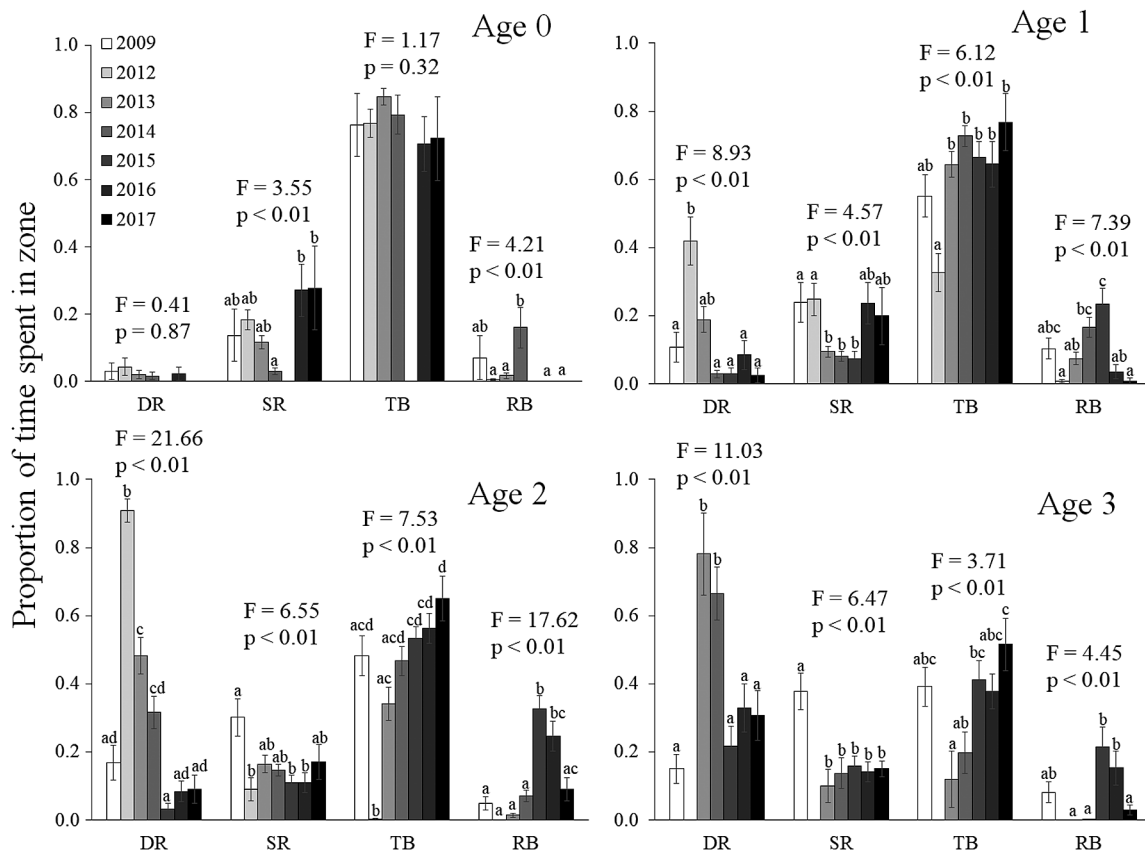
Fig. 5. Proportion of time spent in each sampling region (see Fig. 1 for abbreviations) for juvenile bull sharks age classes 0–3 from 2009 to 2017 (n_{age0} = 7, 11, 19, 9, 0, 7, 4; n_{age1} = 13, 8, 22, 19, 10, 8, 7; n_{age2} = 14, 2, 15, 21, 19, 13, 7; n_{age3} = 7, 0, 3, 12, 10, 6, 8 sharks tracked for each sampling year, respectively). Data are unavailable for 2010 and 2011, because no sharks were tracked during this period. Error bars are ±SE, and bars with different letters are significantly different (p < 0.05, post hoc Tukey tests)

ilar, but more pronounced changes in distribution patterns. Age 2 and age 3 sharks significantly increased their use of DR after 2010 (i.e. 2012), with markedly decreased use thereafter aligned with increasing use of TB.

In addition to the 8 bull sharks that emigrated from the Shark River Estuary during the 2010 cold snap, acoustic tracking showed that 44 individuals permanently emigrated from the estuary before (n = 13) and after (n = 31) the event (batteries on acoustic transmitters died before emigration for the remaining individuals being tracked). Estimated age at emigration varied considerably among individuals (0–5 yr); however, inter-annual differences were apparent
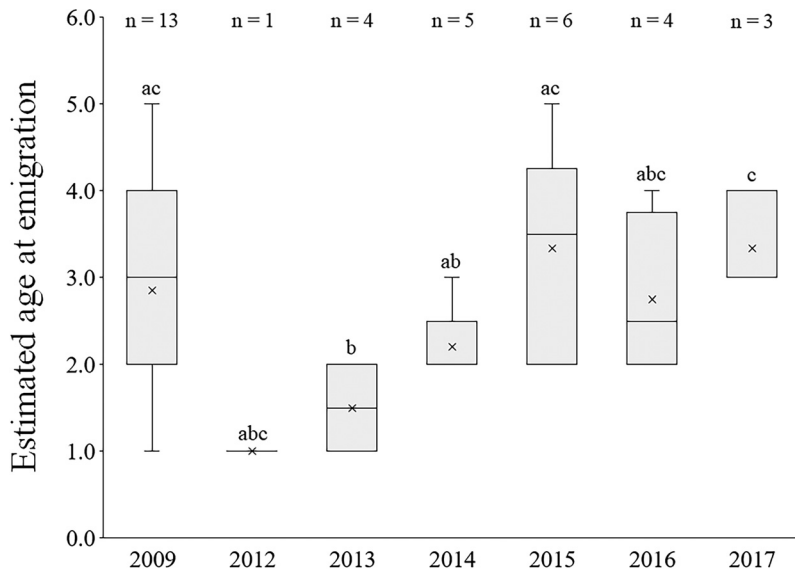
Fig. 6. Estimated age of juvenile bull sharks upon permanent emigration from the Shark River Estuary based on acoustic tracking data. Sharks acoustically tagged after the 2010 cold snap did not begin emigrating from the estuary until 2012. Boxes: 25th–75th percentiles; lines within boxes: medians; ×: means; whiskers: max./min. Different letters indicate significantly different (p < 0.05, post hoc Mann-Whitney tests). All sharks that permanently emigrated from the estuary in July and August 2017 are included

(Kolmogorov-Smirnov test statistic H_3 = 12.6, p = 0.05; Fig. 6). Estimated age at emigration was significantly younger in 2013 (1.5 ± 0.58 yr) than 2009 (2.9 ± 1.14 yr), 2015 (3.3 ± 1.21 yr), and 2017 (3.3 ± 0.58 yr), and the single individual that emigrated from the estuary in 2012 was only 1 yr of age. Movement data do not suggest predation events occurred, based on criteria of Heupel et al. (2012).

4. DISCUSSION

Extreme disturbance events provide challenges for both ecological communities and resource managers due to their unpredictable nature, high intensity, and often rapid onset (Jentsch et al. 2007, Maxwell et al. 2019). These challenges combined with our limited understanding of resilience across contexts make predicting recovery periods for populations and ecosystems difficult (Allen et al. 2010, Butt et al. 2016). In south Florida, unprecedented weather during the 2010 cold snap caused extensive mortality of juvenile bull sharks (Matich & Heithaus 2012); however, several months after the event, the Shark River Estuary nursery began to recover, with survival and birth rates consistent with other bull shark nurseries in the region (Curtis et al. 2011, Natanson et al. 2014, Matich & Heithaus 2015). Yet using traditional

indices (i.e. CPUE and age structure), we found that recovery of multiple characteristics of the bull shark population required a longer duration of time (≥7 yr) than expected based on our hypotheses (ca. 4 yr). Furthermore, the system was perturbed again with another extreme event in September 2017 (Hurricane Irma; Strickland et al. 2019), challenging our descriptions of stable states in highly disturbed systems (Holling 1973, Pimm 1984).

Across south Florida, natural and anthropogenic perturbations shape ecosystems, with many residential species well suited to acute disturbance events nested within chronic environmental variability (Duever et al. 1994, Pirhalla et al. 2015, Childers et al. 2019). The ecosystems of the Florida Everglades experience extreme environmental events every ca. 5–10 yr (Duever et al. 1994, Pirhalla et al. 2015), and sharks are adapted to handle such disturbances, with an array of sensory systems and high levels of mobility that enable them to detect and avoid most unsuitable conditions (Carrier et al. 2012, Klimley 2013). For instance, sharks respond to hurricanes by migrating to safer, deeper waters, and returning to shallower coastal ecosystems soon after such events (i.e. within days to weeks; Heupel et al. 2003, Simpfendorfer & Wiley 2006, Strickland et al. 2019). However, the rapid onset of the 2010 cold snap may not have offered environmental cues early enough for juvenile bull sharks to respond effectively. The 2010 event in south Florida was similar to many other cold weather events defined by rapid declines in temperatures that can have severe short-term (e.g. Lea et al. 2009, Moreno et al. 2015) and long-term effects (e.g. Chan et al. 2005, Tyler 2010, Scharer et al. 2017). Even iteroparous species that are morphologically and physiologically suited to tolerate cold temperatures can be impacted by extreme events through decreased survival and reproduction (e.g. Davidson & Evans 1982, Joly et al. 2011, Deville et al. 2014), with lasting effects for several years after the events (e.g. Post et al. 1997, Chan et al. 2005, Maxwell et al. 2019).

Bull sharks are found in low water temperatures within some estuaries (e.g. 14°C in Caloosahatchee River, FL, Heupel & Simpfendorfer 2008; 15°C in Matagorda Bay, TX, Froeschke et al. 2010; 18°C in Sydney Harbour, Smoothey et al. 2016), but occurrence in colder waters is uncommon (e.g. Curtis et al. 2011, Drymon et al. 2014, Bangley et al. 2018). In most North American nurseries, juvenile bull sharks

make annual winter migrations into more southern waters of the Gulf of Mexico, Caribbean Sea, or Atlantic Ocean to avoid cooling winter waters (McCandless et al. 2007, Curtis et al. 2011, Bangley et al. 2018). Relatively warm average winter temperatures of the subtropical Shark River Estuary enable juvenile bull sharks to remain within the nursery year-round, alleviating the energetic expense of migration, as well as the risk juvenile bull sharks face from large predatory sharks in coastal waters (Wiley & Simpfendorfer 2007, Matich & Heithaus 2012, 2015). However, year-round residency in this shallow estuarine bay makes them more susceptible to cold shock from extreme winter weather events, like that experienced in 2010 (Matich & Heithaus 2012).

Fecundity, recruitment, and juvenile survival rates often determine the speed at which populations recover after extreme disturbance that can be driven by environmental conditions and food availability after events (e.g. Davidson & Evans 1982, Tyler 2010, Moreno et al. 2015). Based on the CPUE of young-of-the-year individuals (i.e. age 0), it appears that recruitment (H_1 and H_2), litter sizes (H_1), and size at birth (H_{3b}) of bull sharks were similar before and after the 2010 cold snap. Mortality rates of juvenile bull sharks also were not affected in the long-term by the 2010 cold snap (8 and 10% of acoustically tagged sharks before and after the event, respectively; H_4) despite the initial ca. 90% estimated mortality attributed the event. Similarities in recruitment and mortality rates were likely resultant from normalized environmental conditions, which would encourage relatively rapid recovery of the nursery (Matich & Heithaus 2012). However, preferred prey availability within the estuary may have changed, including declines in many tropical euryhaline fishes (e.g. Cichlidae, Gerreidae), and replacement by temperate, freshwater species that may be less accessible in brackish and marine habitats (e.g. Centrarchidae, Mugilidae; Boucek & Rehage 2014). In addition to surpassing physiological tolerances, food limitations attributed to adverse conditions often slow recovery rates after extreme events (e.g. Woodward et al. 2016, Sidorovich et al. 2017). Indeed, many species may survive prolonged periods of adverse weather; however, malnutrition and starvation resulting from lack of food resources can lead to high mortality rates following such events (e.g. Deville et al. 2014, Moreno et al. 2015). For example, harsh winter conditions in Belarus led to declines in the primary prey species (e.g. *Capreolus capreolus*, *Sus scrofa*) of wolves *Canis lupus*, leading to increased predation

on large ungulates, small mammals, and domesticated animals (Sidorovich et al. 2017). Similarly, great egrets *Casmerodius albus* in the Florida Everglades may abandon nests during cold periods due to reduced foraging efficiency in shallow waters when prey fishes increase hiding behavior in vegetation or bury themselves in sediment to reduce thermal stress (Frederick & Loftus 1993). Within the Shark River Estuary, *Eugerres plumieri* and *Mugil cephalus*, important prey items for bull sharks in other coastal ecosystems (e.g. Snelson et al. 1984, Cliff & Dudley 1991, Estupiñán-Montaño et al. 2017), were not affected by the cold temperatures, and exhibited similar abundances before and after the event (Boucek & Rehage 2014). However, other prey taxa (*Mayaheros urophthalmus*, *Eucinostomus harengulus*, *Oreochromis aureus*) decreased significantly, leading to prey communities dominated by temperate freshwater fishes, which could have influenced bull shark recovery based on their preference for brackish habitats within the estuary (Heithaus et al. 2009, Rosenblatt et al. 2013).

Estimated growth rates did vary inter-annually across the study period, but there was no apparent relationship with the cold snap (H_{3a}; Fig. 4). The slowest estimated growth rates (9.6 and 9.4 cm yr^{-1}) were observed among cohorts born several years after the event (2014 and 2015), which exhibited some of the largest estimated sizes at birth (76.3 and 79.9 cm TL). The observed negative correlation between estimated size at birth and growth rate may have been driven by maternal meddling (Olin et al. 2011); however, testing this hypothesis is beyond the scope of our study based on available data. Survival rates were similarly unaffected by the cold snap (H_4), obscuring the mechanisms behind the delayed recovery of the nursery.

Given what appear to be minimal effects of the cold snap on juvenile bull shark recruitment (H_1 and H_2), survival rates (H_4), and growth rates (H_{3b}), coupled with a relatively rapid return of environmental conditions, we hypothesized that habitat-use patterns of juvenile bull sharks would be similar after the cold snap (H_{3c}). Habitat use of age 0 and age 1 bull sharks were consistent with this hypothesis, but age 2 and 3 sharks significantly increased their use of downstream habitats after the 2010 event. By 2015–2017, however, individuals in these age classes used habitats similar to age 2 and 3 sharks present before the cold snap. Reduced use of low-salinity waters by older juvenile bull sharks likely reduced competitive pressure on younger conspecifics (de Roos et al. 2002, Papastamatiou et al. 2006), and may have

reduced cannibalistic encounters (Vorenberg 1962), which could have led to a rapid recovery of young sharks in the nursery after the event. As predicted, age 0 and 1 sharks exhibited immediate recovery from the cold snap based on CPUE in TB, and age 2 sharks recovered within 3 yr of the event, supporting our predictions. Yet, the apparent recovery of the entire nursery was considerably slower than expected based on CPUE (ca. 7 yr instead of 4 yr) — following the cold snap, age 3 sharks were not caught again until 2017. Recovery rates of slow-growing species are often non-linear, thus our results are not anomalous, and support previous studies investigating the long-term impacts of environmental change, and the recovery of highly mobile, large-bodied species (e.g. Chan et al. 2005, Tyler 2010, Elliser & Herzing 2014). Inaccurate age estimation is possible, but it is unlikely based on *in situ* similarities in growth rate estimates among age classes and the extensive work on age and growth of bull sharks within the Gulf of Mexico (Neer et al. 2005, Curtis et al. 2011, Natanson et al. 2014). Alternatively, changes in the behavior of age 3 bull sharks attributed to the ecological conditions of the estuary may be responsible for the observed trends in CPUE.

The oligotrophic nature of the Shark River Estuary leads to more productive food webs in its marine habitats than its low-salinity, upstream waters for much of the year (Rehage & Loftus 2007, Matich & Heithaus 2015, Childers et al. 2019). Thus, despite the protective qualities of brackish and freshwater habitats in reducing encounter rates with marine predators, prey availability is generally higher in riskier, marine waters (Matich & Heithaus 2015). Increased food availability is hypothesized as a driver of ontogenetic niche shifts from estuarine to marine environments for juvenile bull sharks across their geographic range (e.g. Heithaus 2007, Curtis et al. 2011, Werry et al. 2011). After extreme events, some species exhibit changes in ontogenetic shifts in order to improve foraging abilities and energetic gains (e.g. Thorpe 1994, Jeglinski et al. 2012, Bransky & Dorn 2013). Data from our study suggest that bull sharks emigrated from the nursery into coastal waters at a younger age for several years after the event (until 2014) compared to 2009. Despite the recovery of some prey species after the cold snap (*Eugerres plumieri* and *Mugil cephalus*; Boucek & Rehage 2014), other prey taxa were adversely affected (*Mayaheros urophthalmus*, *Eucinostomus harengulus*, *Oreochromis aureus*; Boucek & Rehage 2014), which may have reduced total food availability within the oligotrophic estuary, particularly in brackish waters, leading to changes in foraging behavior of bull sharks, and hastening this niche shift (de Roos et al. 2002). Trade-offs between safer, but less productive upstream habitats and more productive, but risky downstream habitats (Matich & Heithaus 2015) may have intensified due to fewer euryhaline prey species in brackish waters (Anholt & Werner 1995, Heithaus & Dill 2002), and a drought in 2011 that led to declines in allochthonous food inputs into the Shark River Estuary also likely amplified the effects of reduced prey populations (Boucek et al. 2016). Habitat use of age 3 bull sharks supports the hypothesis that the value of microhabitats changed within the nursery — despite no captures of age 3 sharks in TB until 2017, age 3 sharks were detected by acoustic receivers in TB beginning in 2013, and resembled pre-disturbance use patterns by 2015. It is unclear why age 3 sharks were detected in TB for 4 yr prior to the first capture of a shark in this age class after the cold snap, but discrepancies could be attributed to changes in foraging behaviors of age 3 sharks in TB. Reduced prey availability in TB due to changes in fish community structure, coupled with accelerated ontogenetic shifts to downstream foraging locations (Matich & Heithaus 2014), could be responsible for the difference in recovery estimates based on CPUE (ca. 7 yr) and telemetry data (ca. 5 yr). Future research investigating fine-scale habitat use patterns and trophic interactions will provide insight into this hypothesis.

5. CONCLUSIONS

Identifying the resilience of ecosystems and their components (e.g. communities, populations, etc.) is of great importance for predicting outcomes of climate change and associated extreme events (Oliver et al. 2015). However, inherent inter- and intra-annual variation in environmental conditions and community structure in subtropical estuaries like the Shark River Estuary (Duever et al. 1994, Pirhalla et al. 2015, Childers et al. 2019) may mask our ability to accurately identify recovery times (Connell & Sousa 1983, Battisti et al. 2016). In light of an increasing frequency of extreme events that compound intra- and inter-annual environmental variability (reviewed by IPCC 2012; Maxwell et al. 2019), classic definitions of recovery may be inappropriate for the Everglades and similar systems (Holling 1973, Pimm 1984), particularly among species that exhibit high levels of intraspecific variation in behaviors, such as bull sharks (Matich et al.

2011, 2019). Selection pressures in ecosystems prone to acute and chronic disturbance likely lead to greater variability among individuals than those in more stable ecosystems, and in turn these populations may be better suited to handle disturbance events (Moran 1992, Niemelä et al. 2013, Matich et al. 2019). However, greater variability among individuals may lead to slower recovery in filling the diversity of niches occupied before disturbance events, if severity exceeds resistive capacity (Liebsch et al. 2008, Dornelas 2010). Our results suggest that changes in the size structure of juvenile bull sharks within the Shark River Estuary have persisted beyond predictions based on life history as a result of the cold snap, with the nursery comprising more sharks in younger age classes. Increased use of marine habitats and accelerated ontogenetic niche shifts appear responsible for the observed changes in demography. With such long recovery times and increasing frequencies of extreme events, bull shark populations in nursery areas may never reach an equilibrium state and remain in various states of recovery. An important consideration with respect to recovery then, is whether the ecological role and importance of this predator has been retained (Heithaus et al. 2008) — if so, our definition of recovery and resilience should be adjusted to account for inherent ecological and environmental variation, and placed within a community-level context, rather than using standards based on the abundance and structure of populations in the future.

LITERATURE CITED

Allen CR, Fontaine JJ, Pope KL, Garmestani AS (2010) Adaptive management for a turbulent future. J Environ Manage 92:1339–1345

Anholt BR, Werner EE (1995) Interaction between food availability and predation mortality mediated by adaptive behavior. Ecology 76:2230–2234

Bailey H, Secor DH (2016) Coastal evacuations by fish during extreme weather events. Sci Rep 6:30280

Bangley CW, Paramore L, Shiffman DS, Rulifson RA (2018) Increased abundance and nursery habitat use of the bull shark (*Carcharhinus leucas*) in response to a changing environment in a warm-temperate estuary. Sci Rep 8:6018

Battisti C, Poeta G, Fanelli G (2016) An introduction to disturbance ecology. A road map for wildlife management and conservation. Springer, Cham

Boucek RE, Rehage JS (2014) Climate extremes drive changes in functional community structure. Glob Change Biol 20:1821–1831

Boucek RE, Soula M, Tamayo F, Rehage JS (2016) A once in 10 year drought alters the magnitude and quality of a floodplain prey subsidy to coastal river fishes. Can J Fish Aquat Sci 73:1672–1678

Bransky JW, Dorn NJ (2013) Prey use of wetland benthivorous sunfishes: ontogenetic, interspecific, and seasonal variation. Environ Biol Fishes 96:1329–1340

Butt N, Possingham HP, de Los Rios C, Maggini R, Fuller RA, Maxwell SL, Watson JEM (2016) Challenges in assessing the vulnerability of species to climate change to inform conservation actions. Biol Conserv 199:10–15

Carrier JC, Musick JA, Heithaus MR (2012) Biology of sharks and their relatives, 2nd edn. CRC Press, Boca Raton, FL

Castro JI (2011) The sharks of North America. Oxford University Press, Oxford

Cave D (2010) Cold still hurting Florida's farmers. New York Times, 13 January. www.nytimes.com/2010/01/14/us/14florida.html (accessed 1 Feb 2010)

Chan KS, Mysterud A, Oritsland NA, Severinsen T, Stenseth NC (2005) Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. Oecologia 145:556–563

Childers DL, Gaiser EE, Ogden LA (2019) The Coastal Everglades: the dynamics of social-ecological transformation in the south Florida landscape. Oxford University Press, Oxford

Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. S Afr J Mar Sci 10:253–270

Connell J, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. Am Nat 121:789–824

Curtis TH, Adams DH, Burgess GH (2011) Seasonal distribution and habitat associations of bull sharks in the Indian River Lagoon, Florida: a 30-year synthesis. Trans Am Fish Soc 140:1213–1226

Davidson NC, Evans PR (1982) Mortality of redshanks and oystercatchers from starvation during severe weather. Bird Study 29:183–188

de Roos AM, Leonardsson K, Persson L, Mittlebach GG (2002) Ontogenetic niche shifts and flexible behavior in size-structured populations. Ecol Monogr 72:271–292

Deville AS, Labaude S, Robin JP, Béchet A and others (2014) Impacts of extreme climatic events on the energetics of long-lived vertebrates: the case of the greater flamingo facing cold spells in the Camargue. J Exp Biol 217:3700–3707

Dornelas M (2010) Disturbance and change in biodiversity. Philos Trans R Soc B 365:3719–3727

Drymon JM, Ajemian MJ, Powers SP (2014) Distribution and dynamic habitat use of young bull sharks *Carcharhinus leucas* in a highly stratified northern Gulf of Mexico estuary. PLOS ONE 9:e97124

Duever M, Meeder JF, Meeder LC, McCollom JM (1994) The climate of south Florida and its role in shaping the Everglades ecosystem. In: Davis S, Ogden JC (eds) Everglades: the ecosystem and its restoration. St. Lucie Press, Boca Raton, FL, p 225–248

Elliser CR, Herzing DL (2014) Social structure of Atlantic spotted dolphins, *Stenella frontalis*, following environmental disturbance and demographic changes. Mar Mamm Sci 30:329–347

Estupiñán-Montaño C, Estupiñán-Ortiz JF, Cedeño-Figueroa LG, Galván-Magaña F, Polo-Silva CJ (2017) Diet of the bull shark, *Carcharhinus lecuas*, and the tiger shark, *Galeocerdo cuvier*, in the eastern Pacific Ocean. Turk J Zool 41:1111–1117

Flato G, Marotzke J, Abiodun B, Braconnot P and others (2013) Evaluation of climate models. In: Stocker TF, Qin D, Plattner G-K, Tignor M and others (eds) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, p 741–866

Frederick PC, Loftus WF (1993) Responses of marsh fishes and breeding wading birds to low temperatures: a possible behavioral link between predator and prey. Estuaries 16:216–222

Frezza PE, Clem SE (2015) Using local fishers' knowledge to characterize historical trends in the Florida Bay bonefish population and fishery. Environ Biol Fishes 98:2187–2202

Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279–292

Grimm NB, Chapin FS, Bierwagen B, Gonzalez P and others (2013) The impacts of climate change on ecosystem structure and function. Front Ecol Environ 11:474–482

Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. Am Fish Soc Symp 50: 3–16

Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting the ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210

Heithaus MR, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. Limnol Oceanogr 54:472–482

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277–289

Heupel MR, Simpfendorfer CA, Hueter RE (2003) Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. J Fish Biol 63:1357–1363

Heupel MR, Simpfendorfer CA, Olson EM, Moland E (2012) Consistent movement traits indicative of innate behavior in neonate sharks. J Exp Mar Biol Ecol 432-433:131–137

Hochberg Y, Tamhane AC (1987) Multiple comparison procedures. Wiley, Hoboken, NJ

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

IPCC (Intergovernmental Panel on Climate Change) (2012) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change (Field CB, Barros V, Stocker TF, Qin D and others [eds]). Cambridge University Press, Cambridge

IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Core Writing Team, Pachauri RK, Meyer LA [eds]). IPCC, Geneva

Jeglinski JWE, Werner C, Robinson PW, Costa DP, Trillmich F (2012) Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. Mar Ecol Prog Ser 453:279–296

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374

Joly K, Klein DR, Verbyla DL, Rupp TS, Chapin FS III (2011) Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography 34: 345–352

Kemp DW, Oakley CA, Thornhill DJ, Newcomb LA, Schmidt GW, Fitt WK (2011) Catastrophic mortality on inshore coral reefs of the Florida Keys due to sever low-temperature stress. Glob Change Biol 17:3468–3477

Klimley AP (2013) The biology of sharks and rays. University of Chicago Press, Chicago, IL

Lea MA, Johnson D, Ream R, Sterling J, Melin S, Gelatt T (2009) Extreme weather events influence dispersal of naïve northern fur seals. Biol Lett 5:252–257

Liebsch D, Marques MCM, Goldenbeg R (2008) How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. Biol Conserv 141:1717–1725

Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. Trends Ecol Evol 19:94–100

Matich P, Heithaus MR (2012) Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. Mar Ecol Prog Ser 447:165–178

Matich P, Heithaus MR (2014) Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. J Anim Ecol 83:199–213

Matich P, Heithaus MR (2015) Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). Oecologia 178:347–359

Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J Anim Ecol 80:294–305

Matich P, Ault J, Boucek R, Bryan D and others (2017) Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. Limnol Oceanogr 62: 934–953

Matich P, Kiszka JJ, Heithaus MR, Le Bourg B, Mourier J (2019) Inter-individual differences in ontogenetic trophic shifts among three marine predators. Oecologia 189: 621–636

Maxwell SL, Butt N, Maron M, McAlpine CA and others (2019) Conservation implications of ecological responses to extreme weather and climate events. Divers Distrib 25: 613–625

McCandless CT, Kohler NE, Pratt HL Jr (eds) (2007) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. Am Fish Soc Symp 50. American Fisheries Society, Bethesda, MD

Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversity-disturbance relationships. Proc Natl Acad Sci USA 108:5643–5648

Moran NA (1992) The evolutionary maintenance of alterative phenotypes. Am Nat 139:971–989

Moran-Ordonez A, Briscoe NJ, Wintle BA (2018) Modelling species responses to extreme weather provides new insights into constraints on range and likely climate change impacts for Australian mammals. Ecography 41:308–320

Moreno J, González-Braojos S, Ruiz-de-Castañeda R (2015) A spring cold snap is followed by an extreme reproductive failure event in a mountain population of pied flycatchers *Ficedula hypoleuca.* Bird Study 62: 466–473

Natanson LJ, Adams DH, Winton MV, Maurer JR (2014) Age and growth of the bull shark in the western North Atlantic Ocean. Trans Am Fish Soc 143:732–743

Neer JA, Thompson BA, Carlson JK (2005) Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. J Fish Biol 67: 370–383

Niemelä PT, Vainikka A, Forsman JT, Loukola OJ, Kortet R (2013) Hoes does variation in the environment and individual cognition explain the existence of consistent behavioral differences? Ecol Evol 3:457–464

NOAA (2010) Summary of historic cold episode of January 2010. Coldest 12-day period since at least 1940. NOAA, Miami, FL

Nungesser M, Sauders C, Coronado-Molina C, Obeysekera J, Johnson J, McVoy C, Benscoter B (2015) Potential effects of climate change on Florida's Everglades. Environ Manage 55:824–835

Olin JA, Hussey NE, Fritts M, Heupel MR, Simpfendorfer CA, Poulakis GR, Fisk AT (2011) Maternal meddling in neonatal sharks: implications for interpreting stable isotopes in young animals. Rapid Commun Mass Spectrom 25:1008–1016

Oliver TH, Heard MS, Isaac NJB, Roy DB and others (2015) Biodiversity and resilience of ecosystem functions. Trends Ecol Evol 30:673–684

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar Ecol Prog Ser 320:239–251

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307:321–326

Pirhalla DE, Sheridan SC, Ransibrahmanakul V, Lee CC (2015) Assessing cold-snap and mortality events in south Florida coastal ecosystems: development of a biological cold stress index using satellite SST and weather pattern forcing. Estuar Coasts 38:2310–2322

Post E, Stenseth NC, Langvatn R, Fromentin JM (1997) Global climate change and phenotypic variation among red deer cohorts. Proc R Soc B 264:1317–1324

Rehage JS, Loftus WF (2007) Seasonal fish community variation in headwater mangrove creeks in the southwestern Everglades: an examination of their role as drydown refuges. Bull Mar Sci 80:625–645

Rehage J, Gaiser E, Heithaus M, Ross M, Ruiz P (2010) Effects of a rare cold snap on Everglades biota: What are the long-term consequences for the ecosystem? LTER Network News, Spring 2010. http://news.lternet.edu/article348.html (accessed 1 Jul 2010)

Rehage JS, Blanchard JR, Boucek RE, Lorenz JJ, Robinson M (2016) Knocking back invasions: variable resistance and resilience to multiple cold spells in native vs. nonnative fishes. Ecosphere 7:e01268

Roman CT, Aumen NG, Trexler JT, Fennema RJ, Loftus WF, Soukup MA (1994) Hurricane Andrew's impact on freshwater resources. BioScience 44:247–255

Rosenblatt AE, Heithaus MR (2011) Does variation in movement tactics and trophic interactions among American alligators create habitat linkage? J Anim Ecol 80:786–798

Rosenblatt AE, Heithaus MR, Mather ME, Matich P, Nifong JC, Ripple WJ, Silliman BR (2013) The roles of large top predators in coastal ecosystems: new insights from Long-Term Ecological Research. Oceanography 26:156–167

Rummukainen M (2016) Added value in regional climate modeling. Wiley Interdiscip Rev Clim Change 7:145–159

Santos RO, Rehage JS, Boucek R, Osborne J (2016) Shift in recreational fishing catches as a function of an extreme cold event. Ecosphere 7:e01335

Scharer RM, Stevens PW, Shea CP, Poulakis GR (2017) All nurseries are not created equal: large-scale habitat use patterns in two smalltooth sawfish nurseries. Endang Species Res 34:473–492

Scheele BC, Driscoll DA, Fischer J, Hunter DA (2012) Decline of an endangered amphibian during an extreme climatic event. Ecosphere 3:art101

Schopmeyer SA, Lirman D, Bartels E, Byrne J and others (2012) In situ coral nurseries serve as genetic repositories for coral reef restoration after an extreme cold-water event. Restor Ecol 20:696–703

Sidorovich V, Schnitzler A, Schnitzler C, Rotenko I, Holikava Y (2017) Responses of wolf feeding habits after adverse climatic events in central-western Belarus. Mamm Biol 83:44–50

Simpfendorfer CA, Wiley TR (2006) Impact of Hurricane Charley on the movements and habitat use of juvenile smalltooth sawfish. Tech Rep 1133. Center for Shark Research, Mote Marine Laboratory, Sarasota, FL

Smoothey AF, Gray CA, Kennelly SJ, Masens OJ, Peddemors VM, Robinson WA (2016) Patterns of occurrence of sharks in Sydney Harbour, a large urbanised estuary. PLOS ONE 11:e0146911

Snelson FF Jr, Mulligan TJ, Williams SE (1984) Food habits, occurrence, and population structure of the bull shark, *Carcharhinus leucas*, in Florida coastal lagoons. Bull Mar Sci 34:71–80

Stith BM, Slone DH, de Wit M, Edwards HH and others (2012) Passive thermal refugia provided warm water for Florida manatees during the severe winter of 2009-2010. Mar Ecol Prog Ser 462:287–301

Strickland BA, Massie JA, Viadero N, Santos R and others (2019) Movements of juvenile bull sharks in response to a major hurricane within a tropical estuar-

ine nursery area. Estuar Coasts, doi:10.1007/s12237-019-00600-7

Thibault KM, Brown JH (2008) Impact of an extreme climatic event on community assembly. Proc Natl Acad Sci USA 105:3410–3415

Thorpe JE (1994) Salmonid flexibility: responses to environmental extremes. Trans Am Fish Soc 123:606–612

Timpane-Padgham BL, Beechie T, Klinger T (2017) A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. PLOS ONE 12:e0173812

Tyler NJC (2010) Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rengifer tarandus* L.). Ecol Monogr 80:197–219

Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. Philos Trans R Soc B 372:20160135

van de Pol M, Jenouvrier S, Cornelissen JHC, Visser ME (2017) Behavioral, ecological, and evolutionary responses to extreme climatic events: challenges and directions.

Philos Trans R Soc B 372:20160134

Vorenberg MM (1962) Cannibalistic tendencies of lemon and bull sharks. Copeia 1962:455–456

Werry JM, Lee SY, Otway NM, Hu Y, Sumpton W (2011) A multi-faceted approach for quantifying the estuarine nearshore transition in the life cycle of the bull shark, *Carcharhinus leucas.* Mar Freshw Res 62:1421–1431

Wiley TR, Simpfendorfer CA (2007) The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. Bull Mar Sci 80:171–189

Williams AJ, Trexler JC (2006) A preliminary analysis of the correlation of food-web characteristics with hydrology and nutrient gradients in the southern Everglades. Hydrobiologia 569:493–504

Woodward G, Bonada N, Brown LE, Death RG and others (2016) The effects of climatic fluctuations and extreme events on running water ecosystems. Philos Trans R Soc B 371:20150274

Appendix

Table A1. Capture and tracking information for acoustically tagged bull sharks from 2008 to 2017 used for analyses

Shark	Capture date	Size at capture (cm)	Tracking duration (mo)	Shark	Capture date	Size at capture (cm)	Tracking duration (mo)
4558	18 Dec 2007	90	14	52210	13 Jan 2013	86	27
4563	31 Jan 2008	77	14	34181	22 Mar 2013	90	13
49663	10 Oct 2008	105	7	34182	22 Mar 2013	127	7
49664	10 Oct 2008	124	8	52204	22 Mar 2013	105	10
49667	10 Oct 2008	110	11	34183	12 Apr 2013	97	5
49668	10 Oct 2008	123	10	34185	12 Apr 2013	106	24
49669	10 Oct 2008	131	14	34186	12 Apr 2013	99	17
4562	7 Nov 2008	105	13	34816	12 Apr 2013	99	5
49670	7 Nov 2008	83	5	34187	21 Apr 2013	100	6
49672	11 Jan 2009	93	8	34817	21 Apr 2013	100	7
49673	11 Jan 2009	82	3	34188	11 May 2013	93	24
49671	31 Jan 2009	116	6	34189	17 May 2013	108	13
54801	15 Feb 2009	75	7	33565	7 Jul 2013	75	26
54799	14 Mar 2009	75	5	33566	10 Jul 2013	73	26
54803	14 Mar 2009	75	7	33567	10 Jul 2013	83	26
54804	14 Mar 2009	105	9	33568	13 Aug 2013	79	26
54800	4 Apr 2009	110	6	33569	13 Aug 2013	81	26
54802	4 Apr 2009	112	7	33570	7 Sep 2013	117	19
54806	5 Apr 2009	125	8	33571	7 Sep 2013	76	26
54805	8 May 2009	129	7	33573	7 Sep 2013	77	26
58250	8 May 2009	86	4	33574	27 Oct 2013	86	25
58252	8 May 2009	81	7	33575	30 Oct 2013	80	26
58253	12 Jun 2009	125	6	33576	30 Oct 2013	89	26
58254	12 Jun 2009	75	6	33577	23 Nov 2013	104	18
59901	25 Jul 2009	79	4	33578	9 Mar 2014	96	21
58258	4 Aug 2009	115	4	56130	3 Feb 2016	111	17
52202	3 Mar 2012	92	29	56131	3 Feb 2016	88	19
52195	23 Mar 2012	109	19	56147	3 Feb 2016	103	17
52198	23 Mar 2012	114	29	56148	3 Feb 2016	80	4
52200	23 Mar 2012	92	30	56129	12 Feb 2016	94	11
52205	18 Apr 2012	95	29	56132	12 Feb 2016	98	19
52196	30 May 2012	96	18	56133	12 Feb 2016	93	4
52203	30 May 2012	98	24	56134	12 Feb 2016	105	17
52199	9 Sep 2012	101	26	56137	12 Feb 2016	87	19
52207	9 Sep 2012	81	26	56136	19 Feb 2016	88	19
52206	14 Sep 2012	76	26	56145	26 Feb 2016	105	13
52208	14 Sep 2012	81	25	56146	26 Feb 2016	84	19
52194	30 Sep 2012	84	26	56139	2 Sep 2016	95	12
52209	30 Sep 2012	84	6	56140	2 Sep 2016	70	12
52211	30 Sep 2012	83	29	56143	2 Sep 2016	100	12
34184	13 Jan 2013	87	16	56144	2 Sep 2016	79	12
34814	13 Jan 2013	87	5	56138	15 Sep 2016	79	12
52197	13 Jan 2013	93	27	56141	15 Sep 2016	73	12