2012

Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, Carcharhinus leucas

Philip Matich
Marine Sciences Program, Florida International University, pmati001@fiu.edu

Michael R. Heithaus
Department of Biological Sciences and Marine Sciences Program, Florida International University, heithaus@fiu.edu

Recommended Citation

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

This material is based upon work supported by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research program under Cooperative Agreements #DBI-0620409 and #DEB-9910514. Any opinions, findings, conclusions, or recommendations expressed in the material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator (*Carcharhinus leucas*)

Philip Matich* and Michael R. Heithaus
Marine Sciences Program
Florida International University
3000 NE 151st
North Miami, FL 33181, USA

Running head: temperature stress on marine predator

*To whom correspondence should be addressed, pmati001@fiu.edu, (305) 919-5602 voice, (305) 919-4030 fax

Abstract

The frequency of extreme environmental events is predicted to increase in the future. Understanding the short- and long-term impacts of these extreme events on large-bodied predators will provide insight into the spatial and temporal scales at which acute environmental disturbances in top-down processes may persist within and across ecosystems. Here, we use long-term studies of movements and age structure of an estuarine top predator - juvenile bull sharks - to identify the effects of an extreme 'cold snap' from 2-13 Jan 2010 over short (weeks) to intermediate (months) time scales. Juvenile bull sharks are typically year-round residents of the Shark River Estuary until they reach 3-5 years of age. However, acoustic telemetry revealed that almost all sharks either permanently left the system or died during the cold snap. For 116 days after the cold snap, no sharks were detected in the system with telemetry, or were captured during longline sampling. Once sharks returned, both the size structure and abundance of the individuals present in the nursery had changed considerably. During 2010, individual longlines were 70% less likely to capture any sharks, and catch rates on successful longlines were 40% lower than during 2006-2009. Also, all sharks caught after the cold snap were young-of-the-year or neonates, suggesting that the majority of sharks in the estuary were new recruits and several cohorts had been largely lost from the nursery. The longer-term impacts of this change in bull shark abundance to the trophic dynamics of the estuary, and the importance of episodic disturbances to bull shark population dynamics will require continued monitoring, but are of considerable interest due to the ecological roles of bull sharks within coastal estuaries and oceans.

Key words: acoustic telemetry, *Carcharhinus leucas*, cold snap, demographic change, environmental variability, estuary, extreme weather event, shark, temperature stress

Introduction

Many ecosystems experience predictable disturbances in their physical environment, and these shifts in conditions can be important in structuring and/or restructuring communities (e.g. Doan 2004, Tabacchi et al. 2009, Tyler 2010). Less attention has been given to the impacts of unpredictable extreme environmental events on ecosystem dynamics (Turner 2010). However, these acute events may also be important in shaping communities, and their effects can be widespread and long-lasting (e.g. Mulholland et al. 2009, Byrnes et al. 2011, Foster et al. 2011). Gaining an understanding of extreme weather events is important because their frequency is expected to increase in the future (Easterling et al. 2000, Meehl et al. 2000, IPCC 2007).

Acute changes in environmental conditions generally require a rapid behavioral response from animals, and in the case of extreme events, individuals may not have previously encountered such conditions and populations may not have adapted to cope with them physiologically. Thus, rapid and extreme changes can lead to both short- and long-term alterations in the size and structure of populations (e.g. Gabbert et al. 1999, Chan et al. 2005, Daufresne et al. 2007). These shifts in population density and structure can lead to considerable shifts in the habitat use, trophic and social interactions, and resource use of both individuals and populations after extreme events (e.g. Frederick & Loftus 1993, Frederiksen et al. 2008, Lea et al. 2009). In turn, these changes in populations and behaviors can be transmitted through communities and ultimately affect ecosystem stability (e.g. Bennets et al. 2002, Thibault & Brown 2008, Mantzouni & MacKenzie 2010).

Bull sharks (*Carcharhinus leucas*; Müller & Henle 1839) are a widely distributed, coastal predator found in tropical, subtropical, and temperate ecosystems worldwide (Compagno 1984). Because bull sharks are highly efficient osmoregulators, they can travel between fresh and marine waters, and respond to sudden changes in salinity with minimal metabolic costs (Anderson et al. 2006). Subadult and mature individuals typically reside in coastal waters, while juveniles use coastal estuaries as nurseries during early years (Heithaus et al. 2007, Wiley & Simpfendorfer 2007, Castro 2011). Within estuaries, juvenile bull sharks experience environmental variability, including acute and seasonal shifts in local salinities and temperatures (e.g. Simpfendorfer et al. 2005, Steiner et al. 2007, Wiley & Simpfendorfer 2007). This variability in the physical environment can lead to seasonal and intermittent patterns in shark occurrence within nurseries (e.g. Heupel & Simpfendorfer 2008, Yeiser et al. 2008, Heupel et al. 2010). However, seasonal variability in temperature and/or salinity does not cause all populations to leave the confines of their respective nurseries (e.g. Heithaus et al. 2009), and whether acute changes in water temperature may cause large changes in behavior or survivorship are unknown. Understanding the impacts of acute events on bull sharks in nurseries is important, however, because of their possible roles in linking coastal and estuarine food webs (Matich et al. 2011), and their position as an upper trophic level predator in these habitats.

South Florida, USA experiences predictable seasonal changes in air temperature that contribute to annual shifts in the community composition of aquatic and terrestrial ecosystems (e.g. McIvor et al. 1994, Ruetz et al. 2005, Rehage & Loftus 2007). These changes are typically moderate and gradual (Duever et al. 1994), but from 2-13 Jan 2010, South Florida experienced a dramatic and extended drop in air temperature (mean low air temperature = 6.1°C ± 0.7 SD; NOAA 2010) that led to an extreme mortality event of both terrestrial and aquatic species on a scale not recorded in Everglades National Park for more than 50 years (Rehage et al. 2010). Here, we take advantage of an ongoing long-term study conducted before, during, and after this event, to investigate the effects of this extreme cold event on the behavior and age structure of bull sharks that typically exhibit year-round residency within a South Florida coastal estuary.

Methods

Study location

The Shark River Estuary of Everglades National Park, Florida, USA (Fig. 1) is primarily a braided stream system lined by mangroves that extends from the Gulf of Mexico to freshwater vegetated marshes ~30 km upstream (Childers 2006). Juvenile bull sharks use the estuary as a nursery year-round, and reside in the ecosystem for their first 3-5 years of life (Wiley & Simpfendorfer 2007, Heithaus et al. 2009). For the purpose of this study, the area was divided into four different sampling regions based on spatial variability in salinity documented during long-term sampling. The Downriver (DR) region includes the coastal waters of Ponce de Leon Bay and relatively deep (3-5 m) and wide (50-400 m) channels extending up to 5 km upstream, with an annual salinity range of 16-39 parts per thousand (ppt) (mean = 29 ppt ± 4.9 SD). The Shark River (SR) region includes relatively deep (3-7 m) channels 6-14 km upstream, and salinity varies seasonally from 1-34 ppt (mean = 14 ppt ± 8.9 SD). Tarpon Bay (TB) is a relatively shallow bay (1-3 m deep) with several smaller bays 15-19 km upstream, and salinity ranges from 0.3-25 ppt annually (mean = 5 ppt ± 6.0 SD). And finally, the Upriver (UR) region includes relatively narrow channels 2-4 m deep, which are 20-27 km upstream, that temporally vary in salinity from 0.2-21 parts per thousand (ppt) (mean = 3 ppt ± 4.6 SD) (Fig. 1).

Field sampling

Spatial and temporal variability in water temperature were measured using Hobo Pro v2 data loggers (Onset, Cape Cod, MA) deployed at 13 locations throughout the system (Fig. 1) from Jul 2007 - Jan 2011. Water temperature was measured by loggers every 10-15 minutes throughout the study, and data were downloaded every 3-4 months. Throughout the study, water temperatures also were measured during all sampling events using a YSI 85 handheld water quality meter (YSI Incorporated, Yellow Springs, OH). Because of the superior spatial and temporal resolution of data from Hobo data loggers, we used only these data in analyses from Jul 2007 - Jan 2011.

Spatial and temporal variability in bull shark abundance was quantified from 2006-2010 using ~500 m longlines fitted with 40-55 14/0 or 15/0 Mustad tuna circle hooks. Hooks were baited with mullet (*Mugil* sp.) and attached to ~2 m of 400 kg monofilament line (see Heithaus et al. 2009 for details of sampling equipment). Longline sampling took place in all four regions (DR, SR, TB, and UR) quarterly for the duration of the study (Table 1, Appendix 1). In 2008, however, sampling only took place during Jan and Oct-Dec. We therefore excluded data from 2008 in our analyses of bull shark relative abundance. Captured sharks (n = 121 from 2006-2007 and 2009-2010) were tagged, measured, and sexed alongside the sampling vessel, or within a water-filled, aerated cooler on board. Shark stretched total length was measured over the top of the body to the nearest centimeter, the presence or absence of an umbilical scar on the ventral side of the body was recorded, and sharks were externally tagged using a plastic roto tag affixed through the first dorsal fin prior to being released.

Passive acoustic tracking was used to quantify the movement patterns of individual bull sharks. From Dec 2007 - Dec 2009 sharks caught in excellent condition (swimming strongly upon capture) ranging from 67-149 cm total length (n = 40 individuals with active transmitters at the time of full acoustic array establishment; see below; Appendix 2) were surgically fitted with a Vemco V16-4H transmitter (Vemco, Halifax, NS). Transmitters were set to emit a unique series of pulses for each shark at a random interval between 30-90 sec (mean emission interval = 60 sec; mean battery life = 2 yr). Movements of acoustically tagged sharks were tracked within an array of 43 Vemco VR2 and VR2W acoustic receivers (Fig. 1), that was fully established by October 2008. In most areas, acoustic receivers were deployed in pairs, such that the location and direction of movement for each acoustically tagged shark could be monitored continuously throughout most of the study system. Due to the complexity of the channels at the mouth of the estuary this could not be achieved in the DR region. However, based on the detection ranges of the acoustic receivers (in situ measurements revealed mean detection ranges were ~500 m; see Rosenblatt & Heithaus 2011 for detection ranges of individual receivers), and their locations at the estuary mouth, sharks entering the Gulf of Mexico would have been detected by at least one of the receivers as they exited the Shark River Estuary. Between the DR and SR regions, there are several exit points from the estuary that lead into Whitewater Bay, but there are no connecting bodies of water that allow for sharks to travel between the Gulf of Mexico and Whitewater Bay (i.e. the only exit points from the system are at the mouths of the Shark and Harney Rivers, where acoustic receivers were in place; Fig. 1). Each receiver was attached to a PVC pipe set in a 10 kg cement anchor. Data from receivers were downloaded every 3-4 months for the duration of the study, and batteries were replaced as needed.

Data analysis

Passive acoustic telemetry was used to assess the effects of the cold snap on bull shark behavior and survival. Data downloaded from acoustic receivers were converted to times of entry into and exit from the sampling regions (DR, SR, TB, and UR; Fig. 1) using a custom computer program (GATOR; Andrew Fritz, FritzTech, Houston, TX). Logistic regression was used to test the effects of sampling month, year, region and their interactions on 1) the probability of detecting all sharks with active transmitters within the system, and 2) the probability of detecting at least one shark with an active transmitter within the system. After analyses of full models with all factors and interactions, interactions with P >0.10 were sequentially removed from models. All main factors (month, year, and region) were included in final models regardless of p-values. Logistic regression was used to test the probability that each shark had left the system (i.e. emigrated) or was 'lost' in the system (i.e. last detected by an acoustic receiver within the array that was not adjacent to an exit point of the estuary) each month from Nov 2008 - Jan 2010.

Longline catch data were analyzed to assess changes in bull shark abundance, distribution and size/age structure relative to the cold snap. Due to the large number of zeros in the data, we used a conditional approach (e.g. Fletcher et al. 2005, Serafy et al. 2007) to quantify the change in shark abundance and distribution in relation to the cold snap. First, we used logistic regression to test the effects of sampling month, year, region, and their interactions on the probability of catching at least one juvenile bull shark on a particular longline set ("occurrence"). Next, we used a general linear model to determine how these factors and possible interactions influenced the number of sharks caught on longlines when they were present ("concentration"). We pooled months into four sampling periods: Jan-Mar, Apr-Jun, Jul-Sep, and Oct-Dec for each year. Concentration data were transformed using Box-Cox transformations. All interactions with P >0.10 were sequentially removed from models, but main factors were included in final models regardless of significance level. Post hoc Tukey's test was used to test for significant differences across treatments.

To determine the effects of the cold snap on the size structure of the bull shark nursery, we used a Kruskal-Wallis one-way analysis of variance to investigate whether the sizes of sharks caught from May-Dec varied across sampling years. Sharks caught from Jan-Apr for all years were not included in body size analyses because no sharks were caught from Jan-Apr in 2010 (sharks were captured during these months in other years; Table 1, Appendix 1), and including sharks from these months in other years could have confounded our ability to investigate changes in size structure between previous years and that present in 2010 after the cold snap. In addition, logistic regression was used to examine the effects of capture year on the probability of capturing sharks with umbilical scars (i.e. neonates <2 months old; Compagno 1984) and of the probability of capturing sharks <90 cm total length (i.e. young of the year; Branstetter & Stiles 1987, Neer et al. 2005). All statistical analyses were conducted in JMP 6.0.0.

Results

Environmental Conditions

Prior to the cold snap, water temperatures in the estuary ranged from 14.2 °C (6 Feb 2009) to 33.1 °C (15 Jul 2009), with the coldest temperatures occurring from Jan-Mar (mean = 22.0 °C ± 3.0 SD), and the warmest temperatures occurring from Jul-Sep (mean = 30.6 °C ± 1.2 SD) (Fig. 2). Water temperatures in the Shark River Estuary during the cold snap were considerably lower (mean = 12.9 °C ± 2.8 SD, 4-15 Jan 2010) than any other time period during the study (Figs. 2 & 3), and mean daily water temperatures dropped as low as 9.1 °C at the peak of the event (12 Jan 2010 at DR). Mean daily air temperature lows in the Florida Everglades were below 10°C from 1-14 Jan 2010 (Flamingo Ranger Station NOAA).

Effects on Bull Sharks

From 2006-2009, we captured 112 juvenile bull sharks (66-200 cm TL; 57 females and 55 males; Table 1). After 20 Dec 2009, no sharks were caught until 22 May 2010, and only nine sharks were caught from 22 May 2010 to 16 Dec 2010 despite sampling effort similar to previous years (68-86 cm TL; 2 females, 8 males, one individual escaped before its sex was determined; Table 1, Appendix 1). During sampling in Jan 2010, two bull sharks (~100 cm TL) were found dead within the confines of the estuary, presumably from temperature-induced mortality - these were the only sharks found dead during the study (2006-2011).

From Oct 2008 - Dec 2009, 40 bull sharks (67-149 cm TL; 21 females and 19 males, Appendix 2) with surgically implanted acoustic transmitters were active in the tracking array. Of these, 14 individuals were present during the cold snap (2-25 Jan 2010) and had transmitters that were implanted at least 18 days before the event. Six of the 14 individuals present during the cold snap (43%) were 'lost' within the confines of the system during the cold snap (see Fig. 1 for the last detection locations of these individuals), suggesting they probably died in the system. The other eight individuals left the system (i.e. were last detected in the DR region) during the cold snap. The proportion of acoustically tagged sharks that were lost (43%) and that left the system (57%) were considerably greater than any other month during the study ($F_{46,211} = 3.56$, $p < 0.01$; $F_{46,211} = 2.72$, $p < 0.01$, respectively; Fig. 4). The 26 acoustically tagged individuals not present during the cold snap either 1) left prior to the cold snap - permanently emigrating to other estuaries or coastal waters (n = 17), 2) had acoustic transmitter malfunctions (e.g. battery failure) immediately after release (n = 5), 3) likely died due to stress incurred during surgery (n = 2), or 4) disappeared inside the array because of natural or anthropogenic mortality (e.g. fishing, boat traffic, other research projects; n = 2; Appendix 2). The acoustically tagged sharks lost during the cold snap (n = 6) were last detected by the receivers within the southeast part of the Shark River region (Fig. 1) where it is highly unlikely that they could have left the system or entered Whitewater Bay without being detected by at least one of the two receivers farther downstream in the SR region. The region where acoustically tagged sharks were last detected during the cold snap (i.e. DR or SR) was not influenced by shark total length (t = 1.13, p = 0.28, df = 12). No acoustically tagged sharks were detected on acoustic receivers after the cold snap until 24 Jun 2010.

The probability of detecting at least one shark and all sharks on acoustic receivers within the Shark River Estuary varied with all main factors (region, month, and year) and the interaction between sampling region and year (Table 2; Fig. 2). From Nov 2008 - Dec 2009, more sharks were detected in Tarpon Bay (6.18 sharks/day ± 0.18 SE) than any other region, and the fewest number of sharks were detected in the Downriver region (0.13 sharks/day ± 0.03 SE). The Shark River (2.06 sharks/day ± 0.10 SE) and Upriver (1.39 sharks/day ± 0.10 SE) regions had intermediate numbers of sharks detected (Fig. 2). In Jan 2010, the cold snap caused a considerable shift in detections at all sites. Detections decreased sharply in TB (1.92 sharks/day ± 0.68 SE) and UR (0.24 sharks/day ± 0.14 SE), but increased in DR (1.88 sharks/day ± 0.36 SE) before all sharks exited the system or were no longer detected within the system by 26 Jan 2010 (Figs. 2 & 3). Most acoustically tagged sharks present during the cold snap were no longer detected after 11 Jan 2010, however three individuals (54801, 54802, 58258), which moved into DR during the cold snap, remained in the vicinity throughout the cold snap and were detected intermittently on DR monitors before disappearing permanently by 26 Jan 2010 (Fig. 3). All acoustically tagged individuals that were detected immediately before and during the cold snap had transmitters that should have been active at the time of the last acoustic monitor download on 22 Jan 2011. Only one shark (59903) reappeared in the system after the cold snap on 24 Jun 2010, and remained in the system until it was last detected heading into the DR region (based on detection sequence in SR) on 29 Aug 2010 (Fig. 2).

Nine juvenile bull sharks were caught on longlines from 22 May 2010 to 16 Dec 2010 (Table 1). Occurrence and concentration of bull sharks varied across sampling years, and occurrence varied across regions (Table 2; Fig. 5). The probability of catching at least one shark on a longline set (i.e. occurrence) was highest in 2006 and lowest in 2010, and was highest in Tarpon Bay and lowest Upriver (Fig. 5a). The number of sharks caught on longlines when present (i.e. concentration) was highest in 2007 and lowest in 2010, and exhibited minimal variability across regions (Fig. 5c). Thus, sharks were encountered less often after the cold snap, and when they were encountered in 2010, they were in smaller numbers than when encountered in previous years. Both occurrence and concentration were least variable across years and regions from Apr-Sep, and exhibited considerable variability between years and regions from Oct-Mar (Fig. 5d).

Mortality and abandonment of the system during the cold snap resulted in changes in the size structure of bull sharks directly following the event. Bull sharks caught after the cold snap from May-Dec 2010 were significantly smaller (mean total length = 77 cm ± 1.7 SE) than all previous sampling years (mean TL = 106 cm ± 4.7 SE) during these months ($\chi^2 = 17.33$; $p < 0.01$; Fig. 6a). The probability of catching a shark less than 90 cm total length, and the probability of catching a shark with an umbilical scar (neonate) varied significantly across years ($F_{3,38} = 8.28$, p

<0.01; $F_{3,38} = 6.37$, $p < 0.01$, respectively). All of the bull sharks caught in 2010 were young-of-the-year and 67% were neonates, which was higher than other years (of the sharks caught from 2006-2009, 41% were young-of-the-year, and only 11% were neonates, respectively; Fig. 6).

Discussion

Population-level Effects

Populations often experience daily and seasonal shifts in environmental conditions, and individuals adjust to these predictable changes by making local or long-distance migrations, changing their behavior, and/or making metabolic adjustments (e.g. Heupel & Hueter 2001, Klimley et al. 2002, Swenson et al. 2007, Holdo et al. 2009, Speed et al. 2010). However, unpredictable and rapid fluctuations in environmental conditions may occur too quickly for individuals to appropriately adjust their behavior or respond physiologically in order to meet metabolic needs and survive (e.g. Aebischer 1986, Schoener et al. 2001). An inability to adapt to such events may have important consequences for the structure and function of populations and ecosystems (e.g. Easterling et al. 2000, Daufresne et al. 2007, Thibault & Brown 2008), and is a concern for conservation because the frequency of extreme environmental events is predicted to increase in the future (IPCC 2007).

Extreme cold events have led to fish kills in Florida about every ten years in the last 100 years (Gilmore et al. 1978, Snelson & Bradley 1978 and references within), suggesting the cold snap in 2010 was not unique. However, in comparison to previous cold events, the magnitude of individuals killed as a result of cold temperatures in Jan 2010 was considerably greater. During the cold snap of 1976-77 in the Indian River Lagoon, central Florida, USA - the last published account of an extensive fish kill in Florida attributed to an extended drop in temperature - mean water temperatures were 10.8 °C, which is comparable to water temperatures in the Shark River Estuary in Jan 2010, and resulted in dead individuals from 56 species, including bull sharks (n = 2; Gilmore et al. 1978, Snelson & Bradley 1978). Yet, the number of fish reported dead in 1977 was several orders of magnitude lower (tens to hundreds), compared to the effects of the cold snap in Jan 2010 (thousands to tens of thousands of fishes killed; Rehage et al. 2010, personal observation), suggesting the impacts on survivorship were much greater in general in the Shark River Estuary during the 2010 event, and the recovery period may be longer.

Before the cold snap, bull shark use of the Shark River Estuary was characterized by individuals <3 years old being year-round residents (Heithaus et al. 2009, P Matich & MR Heithaus *unpublished data*), which may be facilitated by the relatively warm winter water temperatures (e.g. Garla et al. 2006, Chapman et al. 2009, Cortes et al. 2011). The absolute temperatures in Jan 2010, and the duration of the extreme cold event, appear to have exceeded the thermal tolerance of bull sharks using the Shark River Estuary, and resulted in profound impacts on abundance and subsequent size/age structure in the nursery.

Acoustically tagged bull sharks displayed uncharacteristic movement patterns during the cold snap, with mass movements out of Tarpon Bay and into the Downriver region (where, even in past winters, there had been low detection frequencies), before disappearing into the Gulf of Mexico. Mass movements out of estuaries in response to atypical environmental conditions has been observed in juvenile blacktip sharks (*Carcharhinus limbatus*) in Terra Ceia Bay, central Florida, which left the bay in response to the drop in barometric pressure prior to the arrival of a tropical storm (Heupel et al. 2003). All individual blacktip sharks returned to Terra Ceia Bay within two weeks of their departure. Like blacktips, sea snakes (*Laticauda* spp.) in Lanyu, Taiwan vacated their normal coastal habitat in response to changes in barometric pressure prior to a typhoon, and returned less than two weeks later after its passage (Liu et al. 2010). In addition to the bull sharks that left during and only days after the cold snap (n = 14), three tagged sharks (75-107 cm TL) left the system a few weeks prior to the event in Dec 2009. One of these early-departing individuals was the only acoustically tagged shark to return to the estuary after the cold snap (in June 2010), and was one of the smallest individuals (75 cm TL) acoustically tagged at the time of the cold snap. The departure of sharks just before and during the cold snap was unusual, because unlike juvenile bull sharks within coastal estuaries in more northern portions of Florida (e.g. Heupel and Simpfendorfer 2008, Yeiser et al. 2008, Heupel et al. 2010), bull sharks in this nursery are typically year-round residents and do not seasonally or intermittently travel into or out of the estuary (Heithaus et al. 2009, P Matich & MR Heithaus *unpublished data*).

Despite water temperatures returning to normal (>18 °C) within three weeks of the cold snap, no acoustically tagged bull sharks returned to the estuary at this time, and only one individual returned during the study. Previous tag-recapture studies in Everglades National Park and along the Florida coast of the Gulf of Mexico revealed that some bull sharks will relocate to estuaries more than 100 km from initial capture locations (Wiley & Simpfendorfer 2007). Yet, the number of sharks making these long migrations (n = 3 of 302; 1%) was small, and tracking data from the Shark River Estuary suggest such movements are uncommon under normal conditions. Therefore, some individuals that left the estuary may have permanently emigrated, while others may have died.

The behavior resulting from the sudden drop in temperature caused reductions in the occurrence and concentration of bull sharks in the system by 70% and 40% respectively (i.e. approximately a 73% reduction in overall catch rates). This decline in shark abundance may have been due to temperature stress, increased predation, and/or permanent relocation. During the cold snap, two bull sharks (~100 cm total length) were found dead within the confines of the estuary, almost certainly from temperature-induced mortality. Finding even two dead sharks is notable, however, because sharks are negatively buoyant and sink upon death (Helfman et al. 1997), and the Shark River Estuary is turbid. Indeed, to our knowledge dead sharks have not been found in the system previously, despite considerable research effort in the study area. In addition, six (43%) of the acoustically tagged bull sharks were last detected by receivers in the southeastern part of the Shark River sampling region, suggesting they died within the estuary, but outside of the detection range of any individual receiver. Prior to the cold snap, only two of 23 (9%) acoustically tagged individuals (82 and 83 cm TL at capture in Jan 2009 and Nov 2008, respectively) may have died of natural causes (e.g. stress, starvation) in Mar and Apr 2009 in Tarpon Bay, suggesting the survival rate of juvenile bull sharks is relatively high in the Shark River Estuary (Heupel & Simpfendorfer 2011). There are virtually no predators of bull sharks within the estuary (MR Heithaus & P Matich *unpublished data*), and because all of the sharks that died during the cold snap died within days of each other, and movements during detection did not reveal abnormal movement patterns attributed to predation (i.e. faster rate of movement of a large predator that had consumed a smaller shark; Heupel & Simpfendorfer 2002), all of these individuals likely succumbed to the low temperatures. Temperature-related mortality may also be responsible for the low rate of return of individuals that left the system - in more northern estuaries in Florida, bull sharks (Indian River Lagoon) and smalltooth sawfish (*Pristis pectinata*; Ten Thousand Islands) also died due to thermal stress attributed to the 2010 cold snap (J Imhoff personal communication; D Bethea personal communication, respectively; see Fig. 1), suggesting the effects of the cold snap extended beyond the Shark River Estuary, and sharks that emigrated towards or into other estuaries or coastal areas during this time may not have been able to locate thermal refugia. However, three sharks did remain in the proximity of the DR region until Jan 22, 24, and 25 (54801, 58258, and 54802, respectively). By the dates of their final detection, water temperatures were comparable to previous years (mean = 20.3 °C from 22-25 Jan 2010 at DR), suggesting that some sharks that did not succumb to temperature stress.

Juvenile bull sharks that left the estuary may also have experienced increased mortality from predation. Small sharks in Florida's coastal waters are at considerable risk of predation from large predatory sharks (e.g. *C. leucas, Negaprion brevirostris*; Compagno 1984, Snelson et al. 1984, Castro 2011, P Matich & MR Heithaus *unpublished data*). During typical years, juvenile bull sharks almost exclusively remained in areas at least 10-15 km upstream from the DR region, probably to avoid larger sharks that live at the mouth of the estuary (Heithaus et al. 2009, P Matich *unpublished data*). However, in escaping their rapidly chilling estuarine habitat during the cold snap, juvenile bull sharks entered high-risk coastal habitats where predation may have reduced the number of sharks that returned to the estuary afterwards. It is also possible that despite temperatures returning to normal relatively quickly, departing bull sharks may have remained within coastal waters or traveled to other estuaries where they took up residence (Wiley & Simpfendorfer 2007, Yeiser et al. 2008, Heupel et al. 2010).

Regardless of whether departing sharks died from temperature stress, were eaten by predators, or relocated to another estuary, the abundance and size range of juvenile bull sharks was altered within the Shark River Estuary. Prior to the event, the size range of bull sharks in the system was relatively wide (66-200 cm TL). But for 12 months after the event, all sharks caught (n = 9) were less than 90 cm TL (68-86 cm TL), and most (n = 6; 67%) had umbilical scars indicating they were only weeks old. The variability in the size of captured sharks was very small, further suggesting they were from the same cohort, and that virtually all individuals of several age classes were lost from the nursery. Although nine individuals is a relatively small sample, the sampling effort in 2010 was comparable to previous years, and these nine individuals are reflective of the abundance and sizes of bull sharks in the estuary. Unless there is immigration, it will likely take several years for bull shark densities in the Shark River Estuary to recover and resemble the size structure present before the cold snap. Indeed, if the largest individuals in 2010 were 80-90 cm TL (the largest individual caught in 2010 was 86 cm TL), and exhibited fast growth rates for bull sharks (e.g. 20 cm TL per year; Neer et al. 2005), then these sharks will attain total lengths similar to the third quartile of sharks found in the estuary before the cold snap (130 cm TL) in at least 2-3 years.

Community- and Ecosystem-level Effects

Within Florida, acute cold events of at least eight straight days occur about every five years in south Florida; there were 12 such events from 1950-2009 (Flamingo Ranger Station). However, the last recorded occurrence of a cold snap with a duration of 12 days or longer prior to 2010 was in 1940 (Flamingo Ranger Station, Rehage et al. 2010), and there have been no published reports of massive fish kills in south Florida since the winter of 1976-77 (Gilmore et al. 1978, Snelson & Bradley 1978), and even this event was not as extreme as that in 2010. Considering the rare nature of these extended extreme events (occur every 30-40 years) with the low proportion of acoustically tagged bull sharks returning to the Shark River Estuary (n = 1; 6% of tagged individuals), and the probable ages of all bull sharks caught in 2010 (age-class 0), it suggests there has not been strong selection for the ability to withstand such events within this nursery.

The resulting change in bull shark density and sizes could have important consequences. Prior to the cold snap, bull sharks in the Shark River Estuary showed a relatively high degree of individual specialization in trophic interactions, with some large and small juveniles exclusively feeding from marine food webs and others from food webs based in the estuary or upstream marshes, in spite of being captured in the same location in the estuary (Matich et al. 2011). This specialization appeared to be driven by high levels of intraspecific competition (Matich et al. 2011), which combined with the risk of cannibalism and predation might have driven spatial size structuring of the sharks in the estuary (Simpfendorfer et al. 2005, Heithaus et al. 2009). As a result of the cold snap, and subsequent changes in shark abundance and size structure, intraspecific competition and the risk of cannibalism likely decreased considerably. Based on theory and studies of other taxa (e.g. Estes et al. 2003, Svanback & Persson 2004, Keren-Rotem et al. 2006, Bolnick et al. 2010), this would be predicted to result in an expansion of bull shark activity areas for small size classes and more generalized diets until the nursery recovers. Lower competition also could permit more juvenile bull sharks to feed in low-risk (upstream) areas, and thus avoid the high-food, high-risk areas that include marine-based food webs at the mouth of the estuary. Since bull sharks are the only sharks that regularly use estuaries and freshwater areas in Florida, this shift in habitat use could at least temporarily interrupt the role bull sharks play in linking marine and freshwater food webs (Matich et al. 2011). If structural changes like those that occurred in the Shark River Estuary occurred in other shark populations throughout South Florida, it could alter the dynamics of coastal ecosystems across a large spatial area for several years (e.g. Finstad et al. 2009, Holt & Barfield 2009), unless changes in immigration and/or density-dependent recruitment and survival increase the rate of recovery. Based on the relatively low rate of departures of sharks from the Shark River Estuary prior to the cold snap, studies in other bull shark nurseries (e.g. Steiner et al. 2007, Heupel & Simpfendorfer 2008,), and the presence of almost exclusively new cohorts since the cold snap, it appears that juvenile bull sharks tend to remain within their natal nurseries, and the rate of immigration into the Shark River from other nurseries is low and is unlikely to speed the recovery of densities and age structure.

Our study suggests that rare, but extreme environmental fluctuations can lead to marked localized changes in population size and structure, even in relatively large-bodied, highly mobile species. However, the importance of extreme events to long-term population and ecosystem dynamics remains unclear. To understand the long-term effects of these events, we must better understand how individual shark nurseries contribute to adult populations, the importance of density-dependence within shark nurseries, and how shark populations affect these estuarine ecosystems.

Acknowledgements

This work was made possible by the Florida Coastal Everglades LTER, and funding for this project was provided by the National Science Foundation (DBI0620409, DEB9910514, DRL0959026) and Florida International University's Marine Sciences Program. We thank the many volunteers who assisted with shark fishing, especially Cynthia Aceves, Derek Burkholder, Richard Chang, Bryan Delius, Meagan Dunphy-Daly, Kirk Gastrich, Cate Pritchard, Jeremy Vaudo, and Aaron Wirsing. Special thanks to Adam Rosenblatt for establishing the array of acoustic receivers and temperature loggers, and helping with downloading data from receivers and loggers. Andrew Fritz developed GATOR. Thanks to Joel Trexler for providing logistical support for this project. Thanks to Philip Stoddard for comments on the manuscript. Thanks to

NSF LTER database from Flamingo Ranger Station, Everglades National Park for providing annual temperature data. Research was conducted under Everglades National Park permits EVER-2009-SCI-0024, EVER-2007-SCI-0025, and EVER-2005-SCI-0030 and with Florida International University IACUC approval.

References

Aebischer NJ (1986) Retrospective investigation of an ecological disaster in the shag, *Phalacrocorax aristotelis*: a general method based on long-term marking. J An Ecol 55: 613-629

Anderson GW, Pillans RD, Hyodo S, Tsukada T, Good JP, Takei Y, Franklin CE, Hazon N (2006) The effects of freshwater to seawater transfer on circulating levels of angiotensin II C-type natriuretic peptide and arginine vasotocin in the euryhaline elasmobranch, *Carcharhinus leucas*. Gen Comp Endocrinol 147: 39-46

Bennets RE, Kitchens WM, Dreitz VJ (2002) Influence of an extreme high water event on survival, reproduction, and distribution of snail kites in Florida, USA. Wetlands 22: 366-373

Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proc R Soc Lond B 277: 1789-1797

Branstetter S, Stiles R (1987) Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ Biol Fish 20: 169-181

Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrooks SJ, Schmitts RJ (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. Global Change Biol 17: 2513-2524

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

Chapman DD, Babcock EA, Gruber SH, DiBattista JD, Franks BR, Kessel SA, Guttridge T, Pikitch EK, Feldheim KA (2009) Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. Mol Ecol 18: 3500-3507

Chan K-S, 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 (2006) A synthesis of long-term research by the Florida Coastal Everglades LTER Program. Hydrobiologia 569:531–544

Compagno LJV (1984) FAO Species Catalogue. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. II. Carcharhiniformes. FAO Fisheries Synopsis, Rome

Cortes F, Jaureguizar AJ, Menni RC, Guerrero RA (2011) Ontogenetic habitat preferences of the narrownose smooth-hound shark, *Mustelus schmitti*, in two Southwestern Atlantic coastal areas. Hydrobiologia 661: 445-456

Daufresne M, Bady P, Fruget J-F (2007) Impacts of global changes and extreme hydrolclimatic events on macroinvertebrate community structures in the French Rhone River. Oecologia 151: 544-559

Doan TM (2004) Extreme weather events and the vertical microhabitat of rain forest anurans. J Herpetol 38: 422-425

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

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. Science 289: 2068-2074

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes, and implications. J An Ecol 72: 144-155

Finstad AG, Einum S, Ugedal O, Forseth T (2009) Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon. J An Ecol 78: 226-235

Flamingo Ranger Station NOAA. Florida Coastal Everglades Meteorological Stations. Climate and Hydrology Database Projects. Long Term Ecological Research network and U.S. Department of Agriculture. Accessed 5 Nov 10. http://climhy.lternet.edu/plot.pl

Fletcher D, Mackenzie D, Villouta E (2005) Modeling skewed data with many zeroes: a simple approach combining ordinary and logistic regression. Environ Ecol Stat 12: 45-54

Foster KA, Foster G, Tourenq C, Shuriqi MK (2011) Shifts in coral community structures following cyclone and red tide disturbances within the Gulf of Oman (United Arab Emirates). Mar Biol 158: 955-968

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

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. J An Ecol 77: 1020-1029

Gabbert AE, Leif AP, Purvis JR, Flake LD (1999) Survival and habitat use by ring-necked pheasants during two disparate winters in South Dakota. J Wildl Manage 63: 711-722

Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Mar Biol 149: 189-199

Gilmore RG, Bullock LH, Berry FH (1978) Hypothermal mortality in marine fishes of South-Central Florida January 1977. Northeast Gulf Sci 2: 77-97

Helfman GS, Collette BB, Facey DF (1997) Chondrichthyes: sharks, skates, rays, and chimaeras. In: The diversity of fishes. Blackwell Science, Inc. Malden, MA

Heithaus, MR, D Burkholder, RE Hueter, LI Heithaus, HL Pratt Jr, and JC Carrier. 2007. Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. Canadian Journal of Fisheries and Aquatic Sciences 64: 1302-1313.

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, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In: Sibert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Dordrecht, p 217–234

Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Can J Fish Aquat Sci 59: 624-634

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

Heupel MR, Yeiser BG, Collins AB, Ortega L, Simpfendorfer CA (2010) Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. Mar Freshw Res 61: 1-10

Heupel MR, Simpfendorfer CA (2011) Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. Mar Ecol Prog Ser 433: 237-244.

Holdo RM, Holt RD, Fryxell JM (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. Am Nat 173: 431-445

Holt RD, Barfield M (2009) Trophic interactions and range limits: the diverse roles of predation. Proc R Soc Lond B 276: 1435-1442

IPCC (2007) Climate change 2007: The physical science basis. In: Qin, D, M Manning, Z Chen, M Marquis, KB Averyt, M Tignor, and HL Miller (eds) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Keren-Rotem T, Bouskila A, Geffen E (2006) Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behav Ecol Sociobiol 59: 723-731

Klimley PA, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environ Biol Fishes 63:117-135

Lea M-A, 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

Liu Y-L, Lillywhite HB, Tu M-C (2010) Sea snakes anticipate tropical cyclone. Mar Biol 157: 2369-2373

Mantzouni I, MacKenzie BR (2010) Productivity responses of a widespread marine piscivore, *Gadus morhua*, to oceanic thermal extremes and trends. Proc R Soc Lond B 277: 1867-1874

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

McIvor CC, Ley JA, Bjork RD (1994) Changes in Freshwater inflow from the Everglades to Florida Bay on biota and biotic processes: A review. In: Davis, SM and JC Ogden (eds) Everglades. The ecosystem and its restoration. St. Lucie Press, Boca Raton, FL

Meehl GA, Zwiers F, Evans J, Knutson T, Mearns L, Whetton P (2000) Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. Bull Am Meteorol Soc 81: 427-436

Mulholland PJ, Roberts BJ, Hill WR, Smith JG (2009) Stream ecosystem response to the 2007 spring freeze in the southeastern United States: unexpected effects of climate change. Global Change Biol 15: 1767-1776

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

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

Rehage JS, Loftus WF (2007) Seasonal fish community variation in headwater mangrove creeks in the southwestern Everglades: an examination of their role as dry-down 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/article314.html

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

Ruetz CR, Trexler JC, Jordan F (2005) Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance. J An Ecol 74: 322-332

Schoener TW, Spiller DA, Losos JB (2001) Predators increase the risk of catastrophic extinction of prey populations. Nature 412: 183-186

Serafy JE, Valle M, Faunce CH, Luo J (2007) Species-specific patterns of fish abundance and size along a subtropical mangrove shoreline: an application of the delta approach. Bull Mar Sci 80: 609-624

Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. Estuaries 28: 78-85.

Snelson Jr FF, Bradley Jr WK (1978) Mortality of fishes due to cold on the east coast of Florida, January 1977. Fla Sci 41: 1-12

Snelson Jr FF, 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

Speed CW, Field IC, Meekan MG, Bradshaw CJA (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408: 275-305

Steiner PA, Michel M, O'Donnell PM (2007) Notes on the occurrence and distribution of elasmobranches in the Ten Thousand Islands estuary, Florida. Am Fish Soc Symp 50: 237-250

Svanback R, Persson L (2004) Individual diet specialization, niche width, and population dynamics: implications for trophic polymorphisms. J An Ecol 73: 973-982

Swenson JE, Adamic M, Huber D, Stokke S (2007) Brown bear body mass and growth in northern and southern Europe. Oecologia 153: 37-47

Tabacchi E, Steiger J, Corenblit D, Monaghan MT, Planty-Tabacchi A-M (2009) Implications of biological and physical diversity for resilience and resistance patterns within highly dynamic river systems. Aquat Sci 71: 279-289

Thibault KM, Brown JH (2008) Impact of an extreme climatic event on community assembly. PNAS 105: 3410-3415

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91: 2833-2849

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

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

Yeiser BG, Heupel MR, Simpfendorfer CA (2008) Occurrence, home range and movement patterns of juvenile bull (Carcharhinus leucas) and lemon (Negaprion brevirostris) sharks within a Florida estuary. Mar Freshw Res 59: 489-501

Table 1: Number of longline sets, number of juvenile bull sharks caught on longlines, and average water temperatures with standard deviations for each sampling period.

	Longlines (n)	Sharks (n)	Temperature (°C)
Jan-Mar			
2006	19	16	23.3 ± 3.5
2007	7	8	24.5 ± 0.8
2009	39	12	21.0 ± 3.1
2010	31	0	17.2 ± 3.9
Apr-Jun			
2006	18	11	28.2 ± 1.7
2007	30	5	24.3 ± 1.1
2009	56	18	28.0 ± 2.2
2010	33	5	27.6 ± 2.3
Jul-Sep			
2006	8	4	29.6 ± 1.1
2007	21	6	30.8 ± 1.4
2009	39	12	30.7 ± 1.2
2010	25	2	30.1 ± 1.0
Oct-Dec			
2006	38	14	25.7 ± 1.8
2007	4	3	19.8 ± 1.4
2009	43	3	25.1 ± 2.0
2010	30	2	23.1 ± 4.9

Table 2: Results from logistic regression investigating the factors influencing bull shark occurrence and concentration (longline sampling) and the probability of detecting at least one shark [P(1 shark)] and all sharks [P(all sharks)] on acoustic receivers. Significant factors are in bold. Non-significant interactions (P>0.10) were excluded from final models.

	Region	Month	Year	Region*Month	Region*Year	Month*Year	N	Adj. R^2
Longlines								
Occurrence	**6.83, 3 (<0.01)**	2.53, 3 (0.06)	**11.45, 3 (<0.01)**	0.69, 9 (0.71)	0.60, 9 (0.79)	**3.65, 9 (<0.01)**	105	0.40
Concentration	0.52, 3 (0.67)	0.57, 3 (0.64)	**5.86, 3 (<0.01)**	**2.38, 9 (0.04)**	0.47, 6 (0.82)	1.27, 8 (0.31)	48	0.40
Acoustic tracking								
P (1 shark)	**30.40, 3 (<0.01)**	**2.51, 11 (0.01)**	**56.60, 2 (<0.01)**	0.69, 33 (0.84)	**11.71, 6 (<0.01)**	0.67, 8 (0.72)	88	0.81
P (all sharks)	**34.50, 3 (<0.01)**	**2.55, 11 (<0.01)**	**7.73, 2 (<0.01)**	0.72, 33 (0.81)	**3.50, 6 (<0.01)**	0.89, 8 (0.53)	88	0.71

Figure Legends

Figure 1: Longline and acoustic telemetry sampling regions (DR: Downriver, SR: Shark River, TB: Tarpon Bay, and UR: Upriver) within the Shark River Estuary of Florida, USA. Locations of acoustic receivers are indicated by white circles, squares, and stars. Acoustic receivers with Hobo temperature loggers are white squares. White stars are the locations of receivers that last detected sharks the six sharks lost within the system during the cold snap (i.e. last detected within the SR region). Note that those locations are in relatively close proximity to receivers both upstream and downstream and exiting the system without a detection on another receiver would have been unlikely. Although there appear to be unmonitored exits from the estuary (general area indicated by white arrows), sharks moving into this portion of the system cannot exit into the Gulf of Mexico without passing by one of the monitored exits (i.e. all exits to the Gulf of Mexico are monitored by acoustic receivers). Locations of the Indian River Lagoon (IRL) and Ten Thousand Islands (TTI) are indicated on the inset map.

Figure 2: A) Mean daily system water temperature, and b) regional variation in the probability of detecting at least one acoustically tagged bull shark. Bars indicate the number of sharks with transmitters active within the study area.

Figure 3: Acoustic receiver detections of tagged sharks from 1 Nov 2009 until departure from the system (black line or dot represents detection in system; * indicates shark last detected within Shark River region (i.e. was not detected on any of the most downstream monitors before disappearing permanently); # indicates the shark that was detected in the system after 23 Jun 2010). Gaps in detections include days in which sharks were in areas within the system but

outside the detection range of acoustic receivers. Mean system water temperature is displayed in gray.

Figure 4: Proportion of acoustically tagged sharks that left (i.e. emigrated) from the estuary and the proportion of sharks that were ‘lost’ (i.e. last detected by an acoustic receiver within the array that was not adjacent to an exit point of the estuary) from Nov 2008 - Jan 2010.

Figure 5: Bull shark occurrence varied across regions (a) and with an interaction of season and year (b). The number of sharks captured on longlines with sharks (concentration) varied across years (c) and with an interaction of months and region (d). Bars are SE and bars with different letters are significantly different based on post hoc Tukey’s test.

Figure 6: Annual differences in a) mean bull shark total length in cm, b) mean probability of a caught bull sharks being less than 90 cm TL, and c) mean probability of a caught bull shark having an umbilical scar, for sharks caught from May 22 - December 16. Bars are SE and bars with different letters are significantly different based on post hoc Tukey’s test.

Figure 1

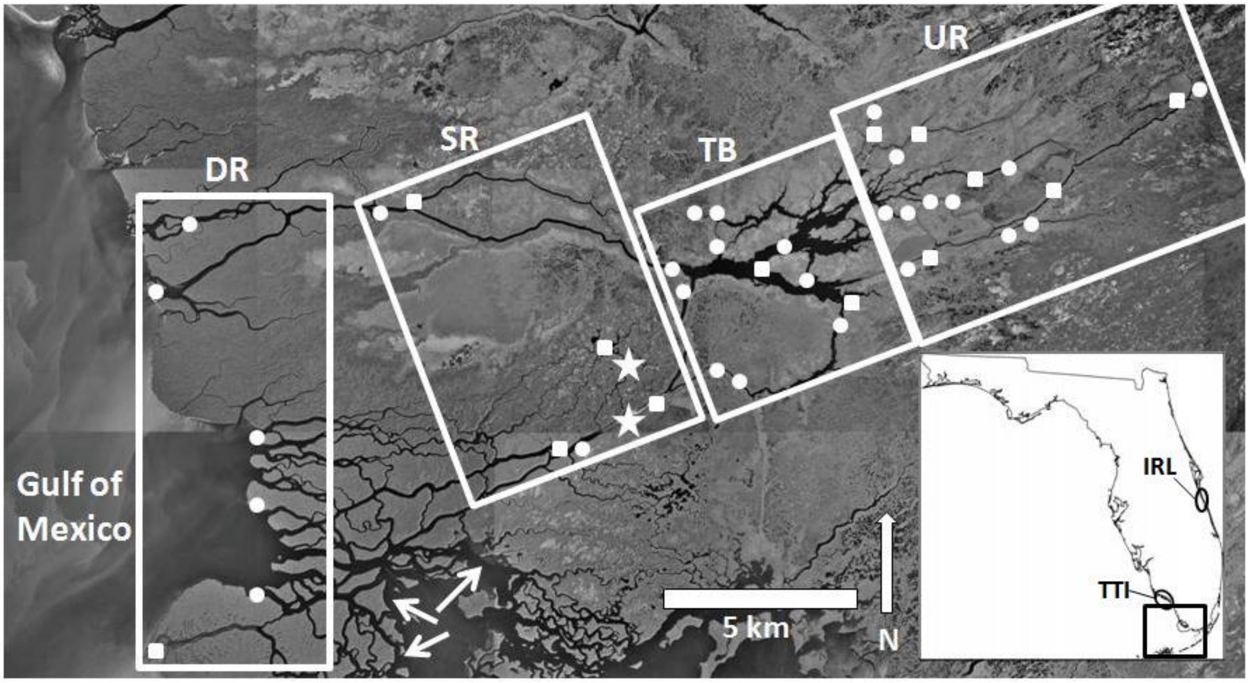


Figure 2

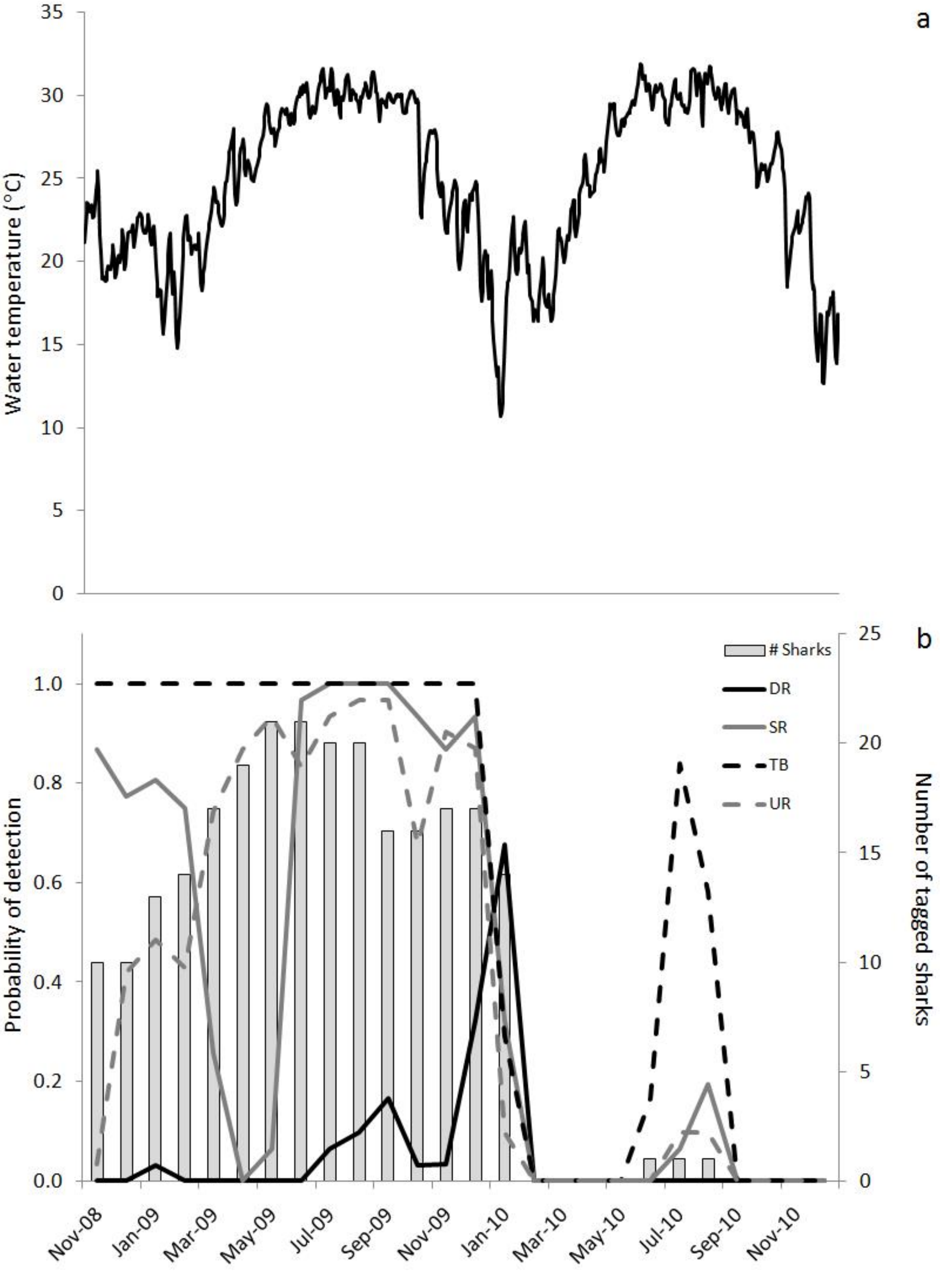

a
Water temperature (°C)
35
30
25
20
15
10
5
0
b
Probability of detection
1.0
0.8
0.6
0.4
0.2
0.0
Number of tagged sharks
25
20
15
10
5
0
Sharks
DR
SR
TB
UR
Nov-08
Jan-09
Mar-09
May-09
Jul-09
Sep-09
Nov-09
Jan-10
Mar-10
May-10
Jul-10
Sep-10
Nov-10

Figure 3

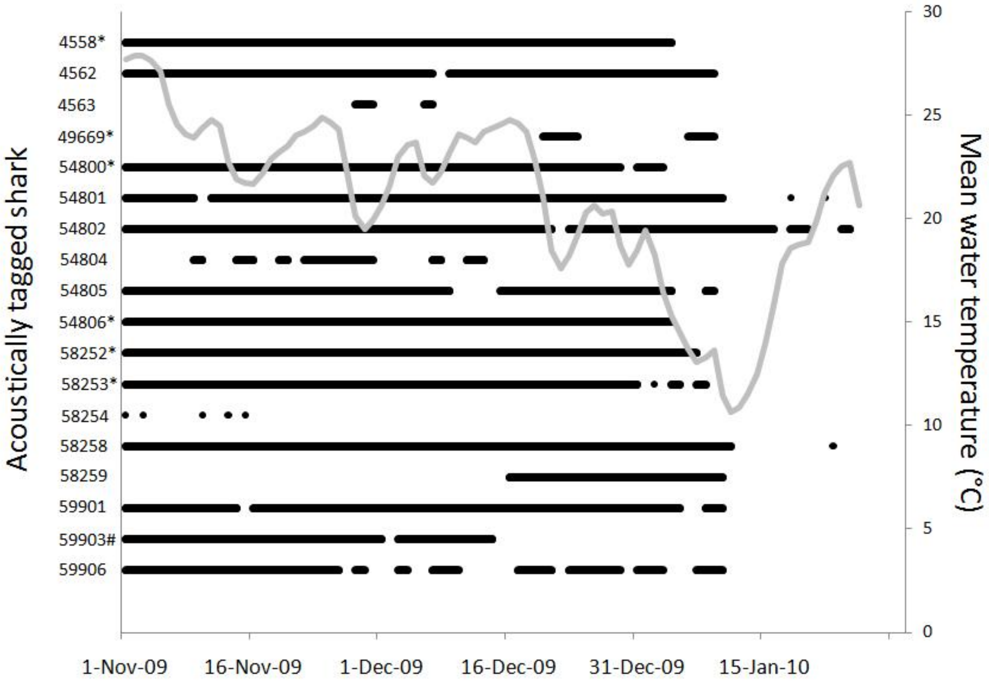

Acoustically tagged shark
4558*
4562
4563
49669*
54800*
54801
54802
54804
54805
54806*
58252*
58253*
58254
58258
58259
59901
59903#
59906
Mean water temperature (°C)
30
25
20
15
10
5
0
1-Nov-09
16-Nov-09
1-Dec-09
16-Dec-09
31-Dec-09
15-Jan-10

Figure 4

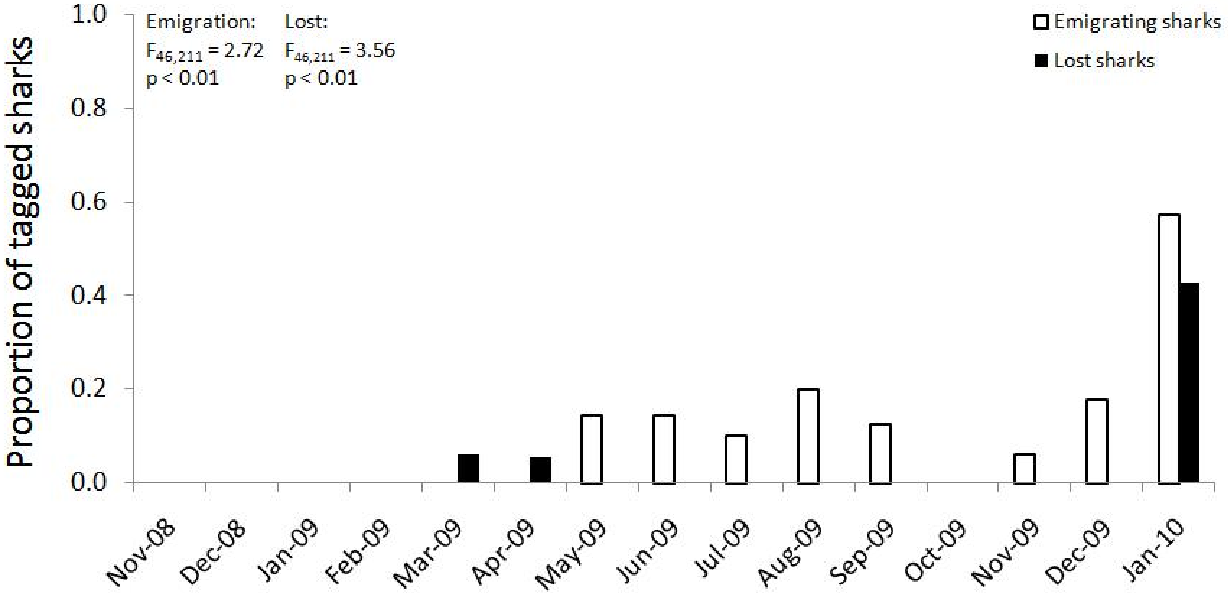

1.0
0.8
0.6
0.4
0.2
0.0
Proportion of tagged sharks
Emigration:
$F_{46,211} = 2.72$
$p < 0.01$
Lost:
$F_{46,211} = 3.56$
$p < 0.01$
☐ Emigrating sharks
■ Lost sharks
Nov-08
Dec-08
Jan-09
Feb-09
Mar-09
Apr-09
May-09
Jun-09
Jul-09
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-10

Figure 5

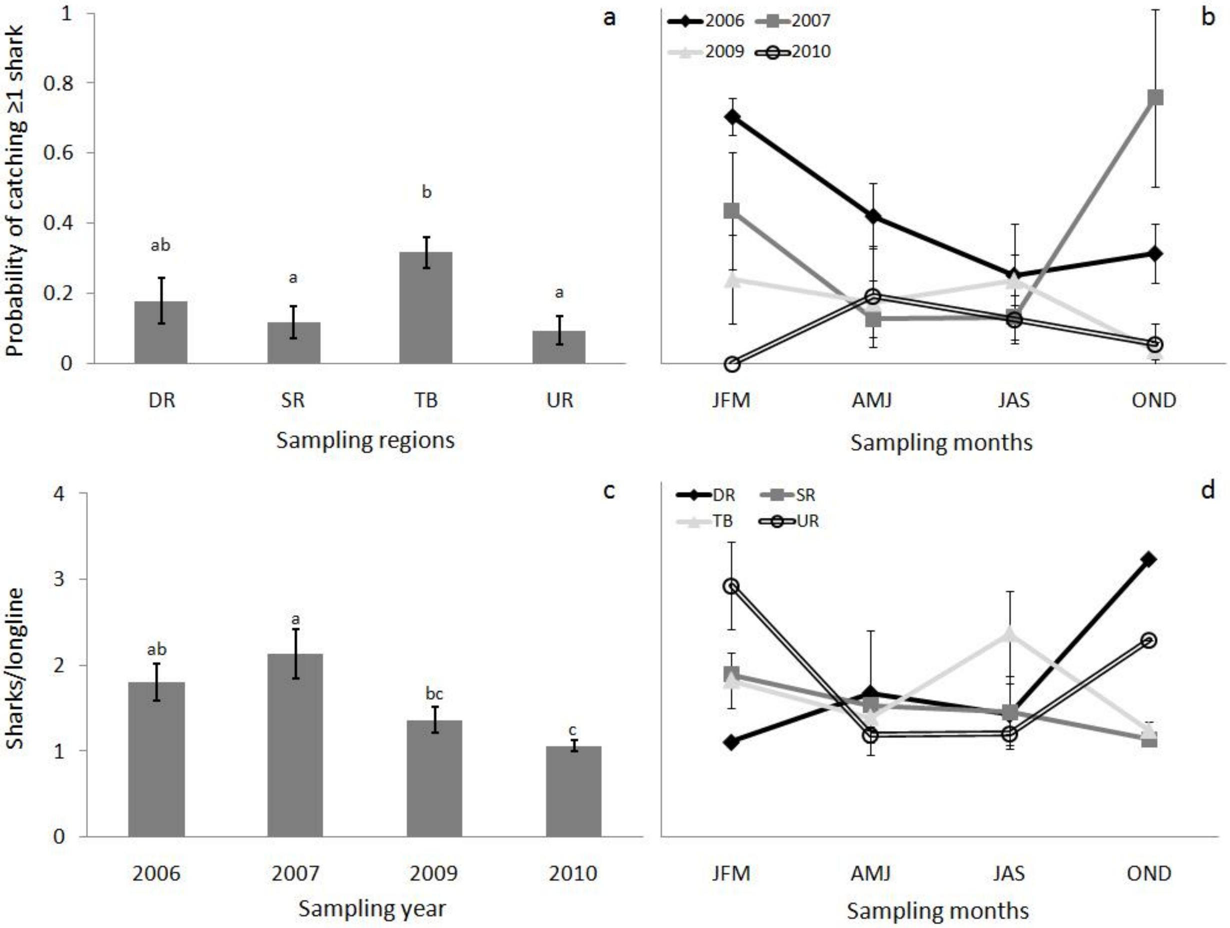
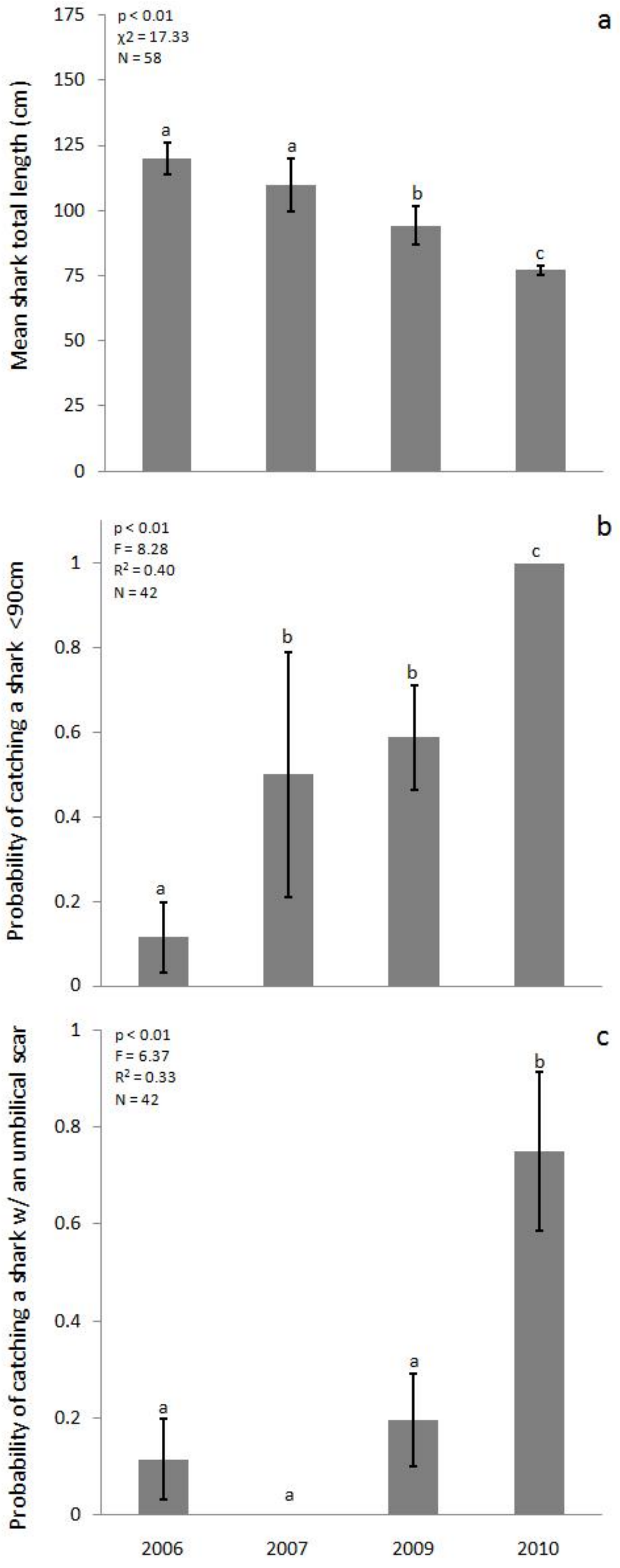

a
Probability of catching ≥1 shark
1
0.8
0.6
0.4
0.2
0
ab
a
b
a
DR
SR
TB
UR
Sampling regions
b
2006
2007
2009
2010
JFM
AMJ
JAS
OND
Sampling months
c
Sharks/longline
4
3
2
1
0
ab
a
bc
c
2006
2007
2009
2010
Sampling year
d
DR
SR
TB
UR
JFM
AMJ
JAS
OND
Sampling months

Figure 6


a
p < 0.01
χ2 = 17.33
N = 58
Mean shark total length (cm)
175
150
125
100
75
50
25
0
a
a
b
c
b
p < 0.01
F = 8.28
R² = 0.40
N = 42
Probability of catching a shark <90cm
1
0.8
0.6
0.4
0.2
0
a
b
b
c
c
p < 0.01
F = 6.37
R² = 0.33
N = 42
Probability of catching a shark w/ an umbilical scar
1
0.8
0.6
0.4
0.2
0
a
a
a
b
2006
2007
2009
2010

Appendix 1: Table 1: Number of longline sets, number of juvenile bull sharks caught on longlines, and average water temperatures with standard deviations for each sampling region for each sampling period. Note that sample effort was consistently high throughout the study in the region with the highest catch rates.

DR	Jan-Mar			Apr-Jun			Jul-Sep			Oct-Dec		
	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.
2006	0	0	NA	0	0	NA	4	1	30.1 ± 0.1	2	0	24.4 ± 0.4
2007	0	0	NA	9	2	24.5 ± 1.2	3	0	31.6 ± 0.4	1	2	20.8
2009	9	2	22.6 ± 2.0	7	1	26.0 ± 1.9	8	2	30.5 ± 1.1	4	0	23.6 ± 2.8
2010	11	0	18.0 ± 2.5	3	0	27.3 ± 3.5	5	0	30.9 ± 1.1	7	0	25.8 ± 2.6

SR	Jan-Mar			Apr-Jun			Jul-Sep			Oct-Dec		
	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.
2006	6	5	18.9 ± 1.8	7	5	26.6 ± 1.3	2	0	30.1 ± 0.6	8	2	25.8 ± 1.8
2007	0	0	NA	6	0	24.7 ± 0.5	5	2	31.6 ± 0.6	1	0	21.2
2009	5	0	22.7 ± 0.7	6	0	27.9 ± 1.7	6	1	30.5 ± 0.4	7	0	24.5 ± 1.9
2010	8	0	15.3 ± 3.2	6	0	27.8 ± 2.6	9	0	29.7 ± 1.0	5	0	25.1 ± 3.0

TB	Jan-Mar			Apr-Jun			Jul-Sep			Oct-Dec		
	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.
2006	8	6	25.2 ± 2.1	7	5	29.2 ± 0.5	2	3	28.0 ± 0.0	18	10	25.5 ± 2.2
2007	4	5	24.6 ± 0.8	8	2	23.7 ± 1.2	5	3	31.3 ± 0.9	2	1	18.5 ± 0.6
2009	19	10	20.7 ± 3.3	29	13	28.6 ± 1.9	19	9	30.8 ± 1.2	22	3	25.0 ± 3.0
2010	9	0	20.0 ± 3.9	15	5	27.6 ± 2.2	7	2	30.5 ± 1.1	10	2	22.5 ± 5.5

UR	Jan-Mar			Apr-Jun			Jul-Sep			Oct-Dec		
	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.	Longlines	Sharks	Temp.
2006	5	5	25.7 ± 0.8	4	1	29.1 ± 0.9	0	0	NA	10	2	25.9 ± 1.1
2007	3	3	24.4 ± 0.8	7	1	24.4 ± 1.0	8	1	29.8 ± 1.7	0	0	NA
2009	6	0	18.7 ± 2.2	14	4	27.9 ± 1.7	6	0	31.1 ± 0.5	10	0	26.5 ± 2.9
2010	3	0	10.6 ± 0.2	9	0	27.7 ± 2.2	4	0	29.3 ± 0.4	8	0	19.8 ± 4.9

Appendix 2: Acoustically tagged sharks with dates of capture and last date detected in the array of acoustic receivers, cause of tracking termination, sex, and total length in cm. Individuals with identification numbers in bold were present in the Shark River Estuary during the cold snap.

ID	Capture date	Date of last detection	Tracking outcome	Sex	Total length (cm)
2064	6 Mar 2009	23 Mar 2009	Transmitter malfunction	M	142
4558	18 Dec 2007	4 Jan 2010	Lost	M	90
4562	7 Nov 2008	9 Jan 2010	Emigrated	F	105
4563	31 Jan 2008	7 Dec 2009	Emigrated	F	77
4564	8 Jan 2008	13 Jul 2009	Emigrated	F	107
49663	10 Oct 2008	4 May 2009	Emigrated	M	105
49664	10 Oct 2008	5 May 2009	Emigrated	M	124
49665	10 Oct 2008	4 Jun 2009	Emigrated	F	71
49667	10 Oct 2008	2 Sep 2009	Emigrated	M	110
49668	10 Oct 2008	9 Aug 2009	Emigrated	F	123
49669	10 Oct 2008	9 Jan 2010	Lost	F	131
49670	7 Nov 2008	14 Apr 2009	Lost	F	83
49671	31 Jan 2009	29 Jul 2009	Emigrated	F	116
49672	11 Jan 2009	26 Aug 2009	Emigrated	M	93
49673	11 Jan 2009	9 Mar 2009	Lost	M	82
54799	14 Mar 2009	8 Aug 2009	Emigrated	F	75
54800	4 Apr 2009	3 Jan 2010	Lost	M	110
54801	15 Feb 2009	22 Jan 2010	Emigrated	M	75
54802	4 Apr 2009	25 Jan 2010	Emigrated	M	112
54803	14 Mar 2009	21 Aug 2009	Emigrated	M	75
54804	14 Mar 2009	13 Dec 2009	Emigrated	F	105
54805	8 May 2009	9 Jan 2010	Emigrated	F	129
54806	5 Apr 2009	4 Jan 2010	Lost	F	125
54807	4 Apr 2009	7 May 2009	Transmitter malfunction	F	82
54808	8 May 2009	Never detected	Never detected	M	149
58250	8 May 2009	14 Jun 2009	Emigrated	F	86
58251	30 May 2009	21 Jun 2009	Emigrated	M	132
58252	8 May 2009	7 Jan 2010	Lost	M	81
58253	12 Jun 2009	8 Jan 2010	Lost	F	125
58254	12 Jun 2009	15 Nov 2009	Emigrated	M	75
58255	25 Jul 2009	1 Aug 2009	Died	F	77
58256	24 Jun 2009	18 Dec 2009	Died	M	77
58257	24 Jun 2009	17 Oct 2009	Transmitter malfunction	M	69
58258	4 Aug 2009	24 Jan 2010	Emigrated	M	115
58259	16 Dec 2009	10 Jan 2010	Emigrated	F	75
59901	25 Jul 2009	10 Jan 2010	Emigrated	M	79

59902	30 Jul 2009	Never detected	Never detected	F	73
59903	31 Oct 2009	29 Aug 2010	Emigrated	F	75
59906	24 Oct 2009	10 Jan 2010	Emigrated	F	136
59907	17 Sep 2009	20 Sep 2009	Emigrated	F	67