Global Ecology and Conservation 15 (2018) e00430

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Rainfall and sea surface temperature: key drivers for occurrence of bull shark, *Carcharhinus leucas*, in beach areas

Jonathan M. Werry [a, b, *], Wayne Sumpton [c], Nicholas M. Otway [d], Shing Yip Lee [b, **, 1], Jodie A. Haig [b, e], David G. Mayer [c]

[a] Griffith Centre for Coastal Management, Griffith School of Engineering, Griffith University, Gold Coast, Queensland, 4222, Australia
[b] Australian Rivers Institute, Griffith School of Environment, Griffith University, Gold Coast, Queensland, 4222, Australia
[c] Queensland Department of Agriculture and Fisheries, Queensland Government, Queensland, Australia
[d] New South Wales Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach, New South Wales, Australia
[e] Fisheries and Conservation Science Group, School of Ocean Science, Bangor University, Wales, UK

ARTICLE INFO

Article history:
Received 20 August 2018
Accepted 20 August 2018

Keywords:
Weather
Climatic variables
Acoustic tags
Human interaction

ABSTRACT

Climate and weather-based drivers of shark movement are poorly known, yet vital for determining measures for effective conservation of shark populations and the management of shark-human interactions at different time scales. The bull shark, *Carcharhinus leucas*, an IUCN ‘Near-threatened’ species, is globally distributed in subtropical to tropical regions and is implicated in many attacks on humans because of its euryhaline habitat-use. However, drivers determining rapid transitions of this species among habitats along the freshwater-estuarine-marine continuum are yet to be fully understood. To identify triggers for movement by this species into beach areas we used conditional (binomial and gamma) generalised linear modelling (CGLM) of historical bull shark catches from the Queensland Shark Control Program (QSCP) collected from 1996 to 2007 across 1783 km of the Queensland coastline, Australia. We then compared catches before and after key weather events (such as floods) between 2006 and 2014 and used passive long-term acoustic telemetry to monitor movements of bull sharks into beach areas to test the model predictions. The CGLM showed that bull shark catch (occurrence) in beach areas is driven by rainfall and further influenced by sea surface temperature. Our model suggests that ≥100 mm total rainfall in the catchment associated with each beach area is significantly correlated with increased bull shark catch 1–8 days after the rainfall, a relationship also confirmed by the movements of acoustic tagged sharks between estuarine and beach areas. These trends provide the first predictive relationship for identifying increased risk of bull shark-human interactions in beach areas. They also suggest that the activity patterns of bull sharks are correlated with rainfall and this makes them particularly susceptible to localised, short-term changes in weather and long-term climate change.

* Corresponding author. Griffith Centre for Coastal management, Griffith School of Engineering, Griffith University, Gold Coast, Queensland, 4222, Australia.
** Corresponding author. Australian Rivers Institute, Griffith School of Environment, Griffith University, Gold Coast, Queensland, 4222, Australia.
E-mail addresses: j.werry@griffith.edu.au (J.M. Werry), joesylee@cuhk.edu.hk (S.Y. Lee).
[1] Present address: Simon F S Li Marine Science Laboratory, The Chinese University of Hong Kong, Shatin, Hong Kong.

https://doi.org/10.1016/j.gecco.2018.e00430

1. Introduction

Understanding how large shark movements change in response to meteorological variables is increasingly important as human populations grow and shark populations become increasingly threatened worldwide (e.g. Baum et al., 2003; Myers et al., 2007; Myers and Worm, 2003; Ferretti et al., 2008). Top level predator populations and their prey have been shown to be impacted by human disturbance, such as expanding coastal urban centres, overfishing and reduced biological productivity of food chains, and are likely to be effected by long term shifts in climate change and related shorter term factors, such as increased frequency of extreme weather events (e.g. Chin et al., 2010; Clarke et al., 2007; Curtis et al., 2013; Heupel et al., 2003; Hobday et al., 2011a; Matich and Heithaus, 2012; Udyaweri et al., 2013; Werry et al., 2012a). The risk of shark-human interaction is of increasing concern around the world, and in response mitigation programs have been put in place, though with little known impacts on shark populations (e.g. Haig et al., 2018; Meeuwig and Ferreira, 2014; Sumpton et al., 2011). To mitigate against negative shark-human interactions, whilst preserving vulnerable shark populations, it is vital to better understand the temporal changes in coastal habitat use (including those influenced by short-term seasonal weather patterns). Such data will enable predictive functions on bull shark behaviour to inform better conservation and management strategies. Sharks that rely on climate driven food chains, or short-term weather related fluctuations in food availability are likely to be highly susceptible to climatic variation (Chin et al., 2010; Meynecke et al., 2006). For example, important prey items for coastal sharks, such as mullet (*Mugil cephalus*) and barramundi (*Lates calcarifer*), have lifecycles correlated with short term weather patterns relating to rainfall and temperature and thus, have also been shown to be susceptible to long-term shifts in climate (Meynecke et al., 2006; Werry et al., 2011). In turn, these prey responses influence shark populations (e.g. Heupel and Simpfendorfer, 2014); however, few studies have related catch data to long- or short-term meteorological drivers for predicting the occurrence and movement patterns of sharks in specific habitats (Schlaff et al., 2014; Lee et al., 2018).

Recent studies indicate shark populations have undergone significant worldwide declines due to illegal and uncontrolled fishing practices; the magnitude of climate shifts can potentially obscure the effects of fishing and other anthropogenic activities (Walker, 2007). Shark species with reduced population sizes, slow population growth and existing anthropogenic pressures, are at increased risk to changes in climate and its associated drivers. Therefore identifying how climatic drivers influence sharks is critical for their conservation (Chin et al., 2010). Moreover, long-term climate-driven shifts in behaviour are mediated through responses to short-term weather events.

For ecosystem-based management to functionally operate, the environmental – behavioural interactions of coastal shark species must be approached, at least initially, on a species-by-species level. For example, sub-adult and adult tiger sharks (*Galeocerdo cuvier*) exhibit individual-based asynchronous occurrence in coastal habitats, but long-term residency on oceanic reefs (Meyer et al., 2009; Papastamatiou et al., 2013; Werry et al., 2014). Juvenile great whites (*Carcharodon carcharias*) make occasional across ocean excursions (Hillary et al., 2018) but primairly migrate along the 60–120 m contour on the east coast of Australia, and their occurrence in coastal habitats, such as beach areas, is related to the distance of a beach to this migration corridor (Bruce and Bradford, 2012; Bradford et al., 2012; Werry et al., 2012b). Sea surface temperature (SST) and lunar phase can also be used to predict white shark movement (Weltz et al., 2013; Werry et al., 2012b). Whereas, bull sharks (*Carcarhinus leucas*) appear to be driven by their link to the river-estuarine-marine continuum (Heupel et al., 2010; Werry et al., 2012a, 2011; Werry and Clua, 2013) and the amount of available estuarine habitat (Haig et al., 2018). The temporal use of critical habitats (such as beach areas) will vary between species, and also between ontogenetic stages of the same species. The predictability of spatial and temporal habitat use for sharks is further complicated by short-term weather events and long-term climate change.

Walker (2007) highlighted the components of weather and climate likely to impact sharks in coastal marine systems identified by Harley et al. (2006). These include increases in sea level, sea surface temperature, storm strength and frequency, coastal erosion, ultraviolet light (via reduced ozone); along with changes in ocean currents and upwelling events, rainfall, salinity and turbidity patterns, and reduced pH (e.g. Rosa et al., 2014). Sharks that rely on riverine, estuarine and inshore coastal habitats at the land and sea interface are probably the most at risk because these areas are likely to experience dynamic changes in food web viability and biological productivity through rainfall and temperature drivers. In turn, these will increase the vulnerability of certain shark species by altering their distribution and abundance patterns, compromising long-term survivorship (e.g. Bellwood et al., 2004; Chin et al., 2010; Martin, 2005). In contrast, Heupel and Simpfendorfer (2014) were unable to detect an influence of climate on the movement of grey reef whalers, *Carcharhinus amblyrhynchos*, in outer reef habitats and concluded that biological factors were the key drivers of the sharks' distribution and occurrence. Short and long term meteorological variables may therefore be better at providing predictions of the temporal and spatial occurrence of sharks in habitats at the land - sea interface (e.g. Knip et al., 2011), and clearly demonstrated by responses to weather events such as heavy rainfall.

Bull sharks have a lifecycle closely linked to the freshwater-estuarine-marine continuum; distributed between equatorial and subtropical coastal habitats (Werry et al., 2011; Werry and Clua, 2013). Bull sharks use upper river reaches for pupping (Werry et al., 2012a, 2011) and neonates and juveniles are physiologically adapted to occupy estuarine areas as nursery habitats (Heupel and Simpfendorfer, 2008; Pillans et al., 2005). Adult bull sharks readily occur in the nearshore and open marine environments (Brunnschweiler and Barnett, 2013; Cliff and Dudley, 1991; Werry et al., 2011; Werry and Clua, 2013) with large scale coastal migration (Espinoza et al., 2016; Heupel et al., 2015). These unique euryhaline abilities result in variable movement patterns for males and females and also for different age cohorts in coastal habitats. Adults readily move between fresh and oceanic waters (Heupel and Simpfendorfer, 2008; Pillans and Franklin, 2004; Thorson, 1971) where they occupy deeper marine areas to about 40 m (Brunnschweiler et al., 2010). The occupation of beach areas by bull sharks (Cliff and Dudley, 1991; Haig et al., 2018) has resulted in adverse shark–human interactions (West, 2011).

Although rare, fatal and non-fatal shark-human interactions, partly attributed to bull sharks, have increased in Australian waters (West, 2011) and are thought to be attributed to an increase in human population, along with more people visiting beaches, a rise in the popularity of water-based fitness and recreational activities and people accessing previously isolated coastal areas (West, 2011). Between 1900 and 2015, 123 bull shark-human interactions were recorded in the Australian Shark Attack File (ASAF) along the east coast of Australia, with 43 fatalities (West, 2011). Bull shark attacks in Queensland prior to 1962 contributed to the implementation of the Queensland Shark Control Program (Sumpton et al., 2011; Werry et al., 2012b) at specific beaches in Queensland to reduce shark attack. Bull shark attacks have occurred in beach and connected coastal and canal habitats around Australia (ASAF; Werry et al., 2012a). While the risk of human fatality from shark-human interaction in Australian waters is low (less than 1.1 per year), these rare events can have serious personal consequences for humans, attract a high level of public and media interest (Hillary et al., 2018) with potential economic side effects and may lead to human responses (e.g. culls) that can impact on fragile marine ecosystems (Ruppert et al., 2013; West, 2011). Recently, the importance of environmental factors and climate variables in driving shark movement has been recognised, providing the opportunity to predict shark presence (Schlaff et al., 2014; Lea et al., 2018; Lee et al., 2018). Predicting the presence of dangerous species and enacting proactive mitigation in advance will become increasingly important in the future with increased human use of coastal waters and the need to conserve sharks for their important role in maintaining ecosystems (Myers et al., 2007; Meeuwig et al., 2015; Ruppert et al., 2013).

Understanding the influence of weather/climatic variables on bull sharks in coastal habitats, including beach areas, is essential for managing fisheries and shark-human interactions and achieving conservation outcomes in the face of global climate-change. In this study, we aimed to determine the influence of weather/climatic variables on occurrence of the euryhaline bull shark in the nearshore environment of Queensland, Australia, and specifically tested the hypothesis that rainfall is a key predictive driver for occurrence and movement of bull sharks into beach areas.

2. Materials and methods

2.1. Ethics statement

This research was done in accordance with QLD Fisheries permit 90306 and 143005 and a Griffith University animal care and ethics approval EAS 0505 AEC and ENV 1709 AEC.

2.2. Study sites

Our study focussed on three spatial scales in Queensland (QLD), Australia. Firstly, the largest spatial scale covered ten locations between Cairns (17° S) and the Gold Coast (28° S) spread over 1783 km along the east coast of QLD (Fig. 1a). This coastal area is dominated by surf and still water beach areas subject to oceanic conditions and terrestrial influence, with tropical conditions in the north and sub-tropical in the south. High and variable rainfall occurs across the catchments with numerous rivers ($n = 73$) draining into extensive mangrove stands in the nearshore environment (Meynecke et al., 2006). Nearshore waters vary in SST from an average of 15 °C in July to 28 °C in January (Suthers et al., 2011). The Great Barrier Reef lagoon occurs from Cairns and south to Bundaberg (24.85° S) and urban centres occur at each of the ten locations.

Secondly, we focussed on Moreton Bay Marine Park that is adjacent to Brisbane in southern QLD (Fig. 1b) and spans 3400 km^2 of the open and sheltered coastal waterways. This area is subject to riverine influx from the Brisbane River (and other smaller rivers) with extensive mangrove, shallow sand banks and seagrass beds in the west. Deeper open water areas and channels occur near the outer Moreton and North Stradbroke Islands (Fig. 1b), which possess surf beaches regularly used by bathers and surfers. We included this area because of a serendipitous opportunity to sample (i.e. before, during and after) the front of a flood plume that entered Moreton Bay in 2011 a major flood event following 209 mm of rainfall over the entire Brisbane River catchment in December 2010.

Lastly, we focussed on Southern Moreton Bay and the beach areas of the Gold Coast (GC); which span 54 km of the southern QLD coast (Fig. 1c). The GC is a highly urbanised area with extensive canal developments (i.e. artificial habitat *sensu* Werry et al., 2012a) attached to the natural causeway of the Nerang River/Broadwater that is connected to the natural mangrove-dominated southern Moreton Bay Marine Park. The GC Seaway provides a direct connection between estuarine areas and the GC beaches. The GC beaches are a major drawcard for tourism attracting over 40 million beach visits in some years and substantial tourism-related revenue (Raybould and Lazarow, 2009). The GC canals, Nerang River and associated waterways and adjacent beaches provide a range of habitats used consistently by bull sharks (see Werry et al., 2012a, 2011).

2.3. Historical catch records

Historical catch data (January 1996 to July 2007) from the Queensland Shark Control Program (QSCP) were used to examine the influence of climatic variables that may act as drivers of bull shark occurrence at the ten locations from Cairns to the Gold Coast along the eastern QLD coast (Fig. 1). At these locations the QSCP deployed a series of gillnets and baited

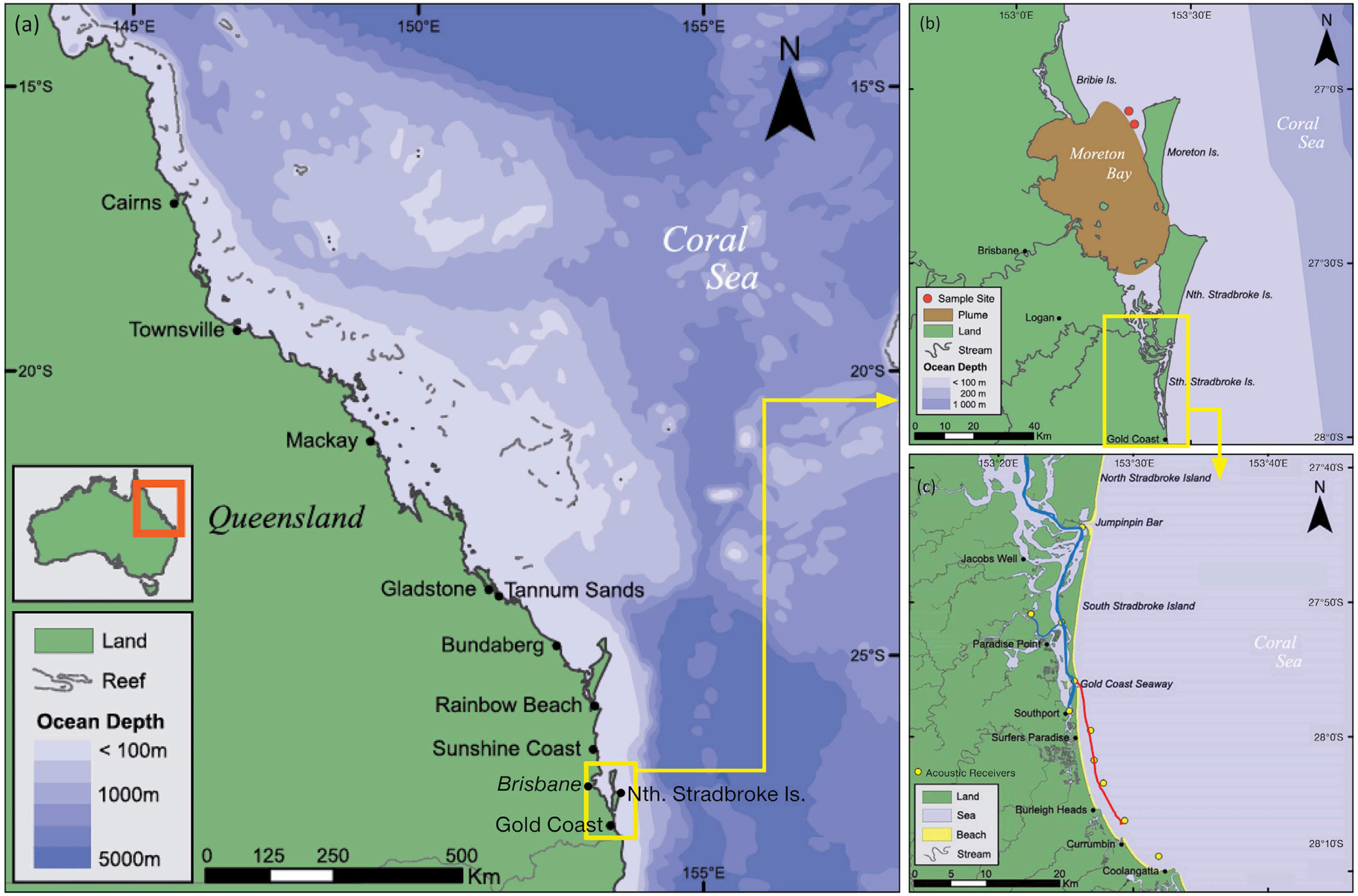

Fig. 1. The study area in Queensland, Australia, (a) showing the ten locations of the Queensland Shark Control Program and tropical north (Bundaberg to Cairns) and subtropical southeast Queensland. Greater Moreton bay (b) with the estimated position of the plume from the 2011 flood when sampling (red dots) at the front of the plume was done. Southern Moreton Bay and the Gold Coast (c) showing approximate locations of acoustic receivers (yellow dots) in estuarine and beach with red lines illustrating the movement of tagged bull sharks into beach areas and blue lines in estuarine areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

drumlines (fishing methods) specifically designed to target bull sharks and other large shark species (see Noriega et al., 2011 for a description). While drumlines were present at all ten locations, gillnets were only deployed at five locations: Cairns, Mackay, Rainbow Beach, Sunshine Coast and the Gold Coast. The QSCP maintained these standardised fishing methods and locations for the period of the study.

2.4. Weather/climatic variables

Daily records for sea surface temperature (SST; Bureau of Meteorology and Environmental Protection Agency), rainfall (Bureau of Meteorology), Southern Oscillation Index (SOI; http://www.bom.gov.au/climate/current/soihtm1.shtml) and lunar phase (as fractions of the mood; http://aa.usno.navy.mil/data/docs/MoonFraction.php) were obtained for QSCP locations for the period January 1996 to July 2007. Rainfall was analysed in two ways: (1) as daily records; and (2) cumulative total rainfall for periods of one to eight days prior to when a bull shark was captured in the QSCP (hereafter referred to as prior 1–8 d rain or week rain). Wind direction and wind speed were recorded at 0900 and 1500 h. SST was recorded by QSCP fishing contractors when animals were captured. Daily rainfall for the Coomera and Nerang River catchment for 2009 to 2011 was also used to correlate the movement of bull sharks fitted with internal acoustic tags in the Gold Coast.

2.5. Size composition of catches

The QSCP fishing contractors recorded species, total length (TL), gear type (gillnet or drumline), prevailing weather, water temperature, and sea condition. Shark TL was measured as the straight-line length in centimetres from the tip of the snout to tip of the tail (top lobe). The presence of claspers (in males only) was used to determine gender for all sharks and the number (gender) of pups for all pregnant females was noted (Last and Stevens, 2009). Catch per unit effort (CPUE, number of sharks per unit of gear per day) and the catch statistics for each fishing method were divided into ontogenetic groups based on size; sharks < 2 m TL were classed as juvenile and ≥2 m TL were classed as adults.

The java or pig-eye shark, *Carcharhinus amboinensis*, is similar to the bull shark in its morphology and both species occur in Queensland waters (Last and Stevens, 2009). In 1992, a training program was implemented for QSCP fishing contractors with an emphasis on the identification of whaler sharks (Family Carcharhinidae). We then allowed several years to pass after initial identification training, during which time biologists were able to confirm consistent and correct whaler identification by the contractors. Consequently, analyses in this paper extend from 1996 onwards; using quality assured data for 1044 bull sharks.

2.6. Acoustic tagging

Bull sharks were captured using setlines at the sites distributed across the estuarine and nearshore areas of Southern Moreton Bay in early 2009 (see Werry et al., 2011). Setlines comprised one or two 8/0 sized, offset tuna hooks (Mustad, Gjovik, Norway) baited with freshwater eel and mullet and attached to 1 m long stainless wire trace suspended from a surface float. All sharks caught were restrained in a harness (as per Werry et al., 2012a). Bull sharks (1.15–1.6 m TL, $n = 6$) and (1.6–2 m TL, $n = 6$) were tagged with Vemco V16, R-coded 69-kHz acoustic tags (Amirix Systems Inc., Nova Scotia, Canada) via surgical implantation in the abdominal cavity. Each tag transmits a unique identification number, has a battery life of 60 months and acoustic ranges of 400–800 m given average coastal, sea conditions and wind strengths do not exceed 11–16 knots or 20–29 km/h (www.vemco.com/education/range.php). Following acoustic tagging, the TL of each shark was measured to the nearest cm after which the hook was removed and the shark released. Capture-stress was monitored as per Werry et al. (2012a).

2.7. Movements into beach areas

The movements of the acoustically-tagged sharks and their duration of occupation of estuarine and beach habitats were quantified over 32 months from January 2009 to December 2011 using an array of 10 Vemco VR2/VR2W omni-directional acoustic receivers (Amirix Systems Inc., Nova Scotia, Canada) strategically deployed at various sites (Fig. 1c; Table 1). Five

Table 1
Locations of estuarine and beach acoustic receivers during the period of study.

Habitat	Receiver	Description	Latitude	Longitude
Beach Area	1	Main beach	2759′24″	15326′12″
	2	Mermaid Beach	2802′05″	15326′39″
	3	Palm Beach	2806′45″	15328′40″
	4	Tugun	2708′06″	15329′49″
	5	Greenmount	2709′31″	15332′32″
Estuary	6	GC Seaway	2756′12″	15325′29″
	7	Nerang River	2758′27″	15325′22″
	8	Broadwater	2751′55″	15324′30″
	9	Coomera River	2709′31″	15324′30″
	10	Jumpinpin Seaway	2744′50″	15325′51″

receivers were deployed in the southern Moreton Bay at deep holes and/or junctions between river/estuarine and nearshore areas. One receiver was deployed at the Jumpinpin seaway between North and South Stradbroke Island, a second at the entrance to Coomera River in the Broadwater, a third at the entrance to the GC Seaway and a fourth at the entrance to the Nerang River and the GC canal system (Fig. 1c). Each receiver in the estuarine habitat was attached to a navigation marker or jetty piling approximately 1–3 m below mean low water mark. Five receivers were also deployed in the beach area of the GC approximately 800–1500 m from the shore. These were attached to a 12 mm rope and deployed mid-water, approximately 5 m from the sea floor, between a large plough anchor and marked float. These receivers were deployed at Narrow Neck (Main Beach), Mermaid Beach, Palm Beach, Tugun and Greenmount beach (see Fig. 1c). Retrieval, data download and replacement of the acoustic receivers was done at ~ 3-monthly intervals. Following data download, the detections were sorted by shark ID, ontogenetic stage, site, date and time. As this study focused on the usage of this system at larger spatial scales, the acoustic detection data were then pooled across replicate acoustic telemetry sites within the estuarine and nearshore beach habitats of the GC, as more in-depth analysis of movement will be reported elsewhere. Sharks were acoustically-tagged in 2009; however, their movements were only monitored in 2010 and 2011 as acoustic receivers were first deployed in beach areas in 2010. Daily rainfall data (Bureau of Meteorology) was collected for the Coomera/Nerang River and Tallebudgera Creek catchments and compared to the movements of the tagged bull sharks among the estuarine and beach habitats and to GC QSCP catches of bull sharks.

In situ range tests are important for determining environmental interference on receiver detection range (Mathies et al., 2014; Simpfendorfer et al., 2011; Welsh et al., 2012). In situ range tests were done in beach and estuarine habitat to account for acoustic tag detection variations with rainfall. Control tags were used to determine the detection range for receivers in estuarine and beach areas under non-rainfall conditions and during periods of prior 1-8d rain (i.e. the same as the historical catch model predictions). Detection range varied little between receivers and was slightly reduced in beach areas during significant rainfall periods.

2.8. Major rainfall events

Total catches of bull sharks from July 2008 to 2014 were examined at specific locations in the QSCP and compared with prior 1–8 d rain events to provide independent tests of the predictive rainfall model. Catches were examined at three representative locations across the largest spatial scale of the study and included Cairns, Mackay and the Sunshine Coast in the northern, central and southern regions of the QSCP, respectively. In addition, opportunistic sampling for bull sharks using baited lines at the front of the 2011 Brisbane flood plume in Moreton Bay was done to quantify whether bull sharks were using the plume front as a temporary feeding hotspot.

2.9. Statistical analyses

Daily CPUE data for bull sharks caught in the QSCP were analysed by stepwise forward conditional generalised linear modelling (CGLM, McCullagh and Nelder, 1989), using the program GenStat™ 9.2 (GenStat, 2008). To overcome analytical problems arising from numerous zero values, we used a binomial model for presence/absence, and a conditional gamma model for the numbers actually caught. Combining the means and standard errors of these binomial and conditional gamma models (Taylor et al., 2011) enabled more accurate and meaningful estimation of the main effects and interactions of statistical significance. The distributions of residuals were approximately normal. Variables that explained the greatest amounts of variance were plotted. Binomial and gamma (truncated zero) models were screened to select the dominant variables to retain in the final models. If a main effect or interaction term was significant in one model, then it was retained in the other model. This was done because the gamma model is conditional to the binomial model and the two models need to contain identical main effects and interactions when combined to estimate the overall adjusted means. The term “fishing gear” was always included in the initial CGLM analyses and further models were run separately for gillnets and drumlines as the combined models indicated that these fishing methods were not directly comparable. Significance of results was considered at $\alpha \leq 0.05$.

Rainfall on the day of capture and prior 1-8d rain were screened for significance and direction, and pooled as appropriate. Daily wind speed data were analysed separately using circular statistics to detect any potential relationships.

3. Results

3.1. Historical catch models

CGLM relationships between climatic variables and bull shark catch were evident for drumlines and gillnets, but these relationships varied for <2 m TL and ≥2 m TL bull sharks (Table 2). Rainfall had interesting effects and was negative for the day of capture, but positive for all days prior to capture. For this reason, and to lessen the degree of auto-correlation, rainfall for days one to eight prior to capture was pooled into ‘weekly rain’, which was fitted in the models as a single term (prior week rainfall). Week or prior rainfall was the only significant variable for bull shark catch with gillnets and drumlines for which correlations were evident across different ontogenetic stages. Patterns indicated a large, relative increase in catch after periods of ≥100 mm of rain, with the increased catch evident for 1–8 days after the rainfall event.

Table 2
Probability binomial values for combined deviance (ANDEV) from conditional General Linear Models analysing the effects of climate variables on bull shark catch in drumlines and gillnets. Significant relationships are highlighted in bold.

Gear	Shark size	Rain	Prior rain	Southern Oscillation Index	Lunar phase	Sea Surface Temperature	Wind Speed 9:00	Wind Speed 15:00
Drumline	All	0.64	**<0.001**	**0.02**	0.92	**<0.001**	0.338	
	<2 m TL	0.323	**<0.001**	**0.001**	0.793	**<0.001**	0.609	0.98
	≥2 m TL	0.198	**0.015**	0.696	0.801	**0.028**	0.324	
	Pregnant F	0.953	0.173	0.463	0.245	0.274	0.133	**0.03**
Gillnet	All	0.012	**0.022**	0.103	**0.05**	0.094	0.549	0.648
	<2 m TL	0.026	**0.012**	0.667	**0.023**	0.488	0.566	0.909
	≥2 m TL	0.095	0.124	**0.035**	0.485	0.114	0.208	0.531
	Pregnant F	0.542	0.193	**0.033**	0.382	0.167	0.581	0.696

For drumlines, CGLM analyses showed a positive relationship to prior 1-8d rain and SST for <2 m TL and ≥2 m TL bull shark and catch increased exponentially for both ontogenetic stages of the bull shark after ≥100 mm of prior rainfall (Fig. 2a). Correlations with SST were significant for <2 m TL and ≥2 m TL bull sharks captured on drumlines and these patterns occurred with an interaction between years and locations for both ontogenetic groups ($p = 0.04$ and $p = 0.028$, respectively). CPUE increased with increasing SST for <2 m TL and ≥2 m TL shark (Fig. 2b).

CPUE of ≥2 m TL bull sharks caught in gillnets varied significantly between locations and years ($p = 0.024$), whereas there was an interaction between years and locations for < 2 m TL bull sharks ($p = 0.019$). Results of the CGLM indicated a significant relationship with the SOI and the passive capture of ≥2 m TL bull sharks in nearshore habitat with increase in catch during periods of positive SOI (Fig. 2c). Alternatively, the CGLM indicated <2 m TL bull shark CPUE was significantly correlated with rainfall on day of capture, prior 1-8d rain and moon phase (Table 1). In this case, < 2 m TL bull shark CPUE also increased after a

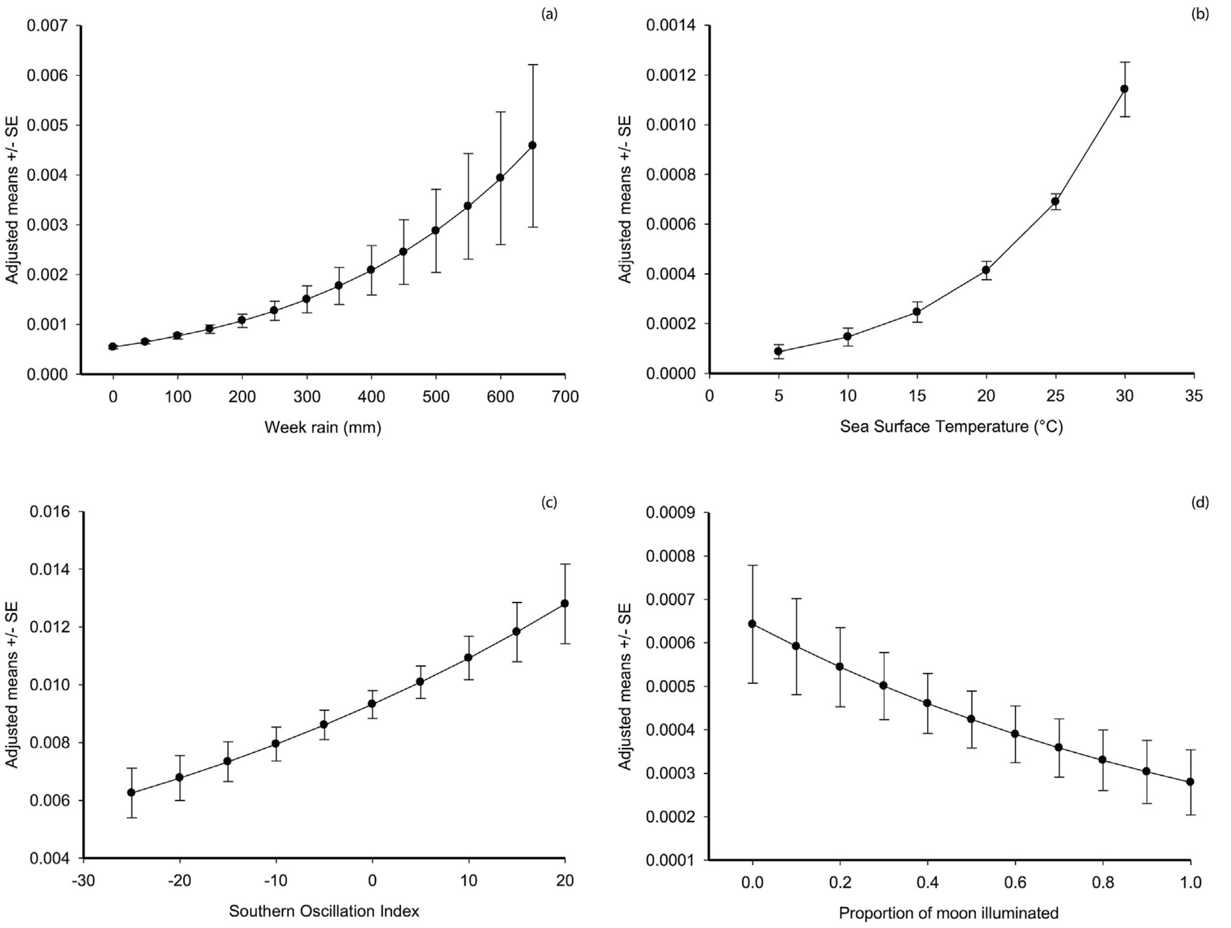

Fig. 2. Plots for results from CGLM mean CPUE (±SE) for rainfall 1–8 days prior to capture for (a) combined < 2 m TL and ≥2 m TL bull sharks captured on drumlines, (b) CGLM mean CPUE (±SE) for sea surface temperature (SST) and combined catch of <2 m TL and ≥2 m TL bull sharks caught on drumlines, (c) CGLM mean CPUE (±SE) of SOI for bull sharks caught in gillnets, and (d) CGLM for lunar phase and juvenile (<2 m TL) bull sharks caught in gillnets.

threshold of 100 mm of rainfall was exceeded. As shown in Fig. 2d, < 2 m TL bull shark CPUE decreased almost linearly in nearshore habitat from no exposed moon (0%) to full moon (100%).

No relationships between wind direction with any bull shark CPUE or gear type were determined with circular statistics (Rayleigh's tests, $P > 0.05$). However, CGLM indicated a positive relationship with decreasing wind speed at 15:00 for pregnant female CPUE (Table 1). Pregnant female CPUE also increased during periods of positive SOI.

3.2. After major rainfall

Local-scale patterns of increased number of bull sharks captured between 2006 and February 2014 on QSCP fishing gear before, during and after major rainfall indicated a pattern of increased catch after a combined 100 mm of rainfall or greater as per modelled predictions (Fig. 3). Many catches clearly occurred after periods of major prior rainfall in all locations.

3.3. Brisbane flood (2011)

Sampling at the interface of the Brisbane river flood indicated that bull sharks were present within and at the front of the turbid plume. Four sub-adult/adult bull sharks (1.6–2.2 m TL) were captured and tagged with acoustic tags for long-term movement studies, which will be reported elsewhere.

3.4. Movements among estuarine and beach habitat

Twelve bull sharks tagged with acoustic tags occurred frequently within southern Moreton Bay (81,818 detections) and infrequently in beach areas of the Gold Coast (150 detections) with 99.81% and 0.19% occurring across nine of the acoustic receiver sites in the Southern Moreton Bay and Gold Coast beaches, respectively (Fig. 4). After a prior 1-8d rain event, up to three individuals were simultaneously detected moving along the Gold Coast beach area for periods of 4 days. After an absence of between 3 and 7 days they were again detected on the estuarine array (Fig. 4). Further detections occurred within the beach area within the modelled prediction periods. Comparison with bull sharks caught in the GC QSCP from 2009 to 2011 also indicated a concordance with prior 1-8d rain.

4. Discussion

Understanding the drivers for temporal variation in large shark occurrence and movements is increasingly important for their management and conservation, as sharks play an important role in the functioning of ecosystems (Schlaff et al., 2014; Ruppert et al., 2013). Their wide-ranging and elusive behaviour, and difficulties in capture makes statistically relevant data difficult to obtain (Heithaus et al., 2002; Werry et al., 2014). This study utilised long-term historical catch records and short-term acoustic tracking to identify meteorological variables that directly influence the occurrence, catch and movements of bull sharks in beach areas.

Catches of both juvenile and adult sharks increased in the week following rainfall (≥100 mm), and was positively correlated with SST and SOI, though negatively with increased light during lunar phase. Identifying the drivers of movement between habitats helps to elucidate the role sharks play in linking separate habitats along continental margins and between the land and sea interface (e.g. Heupel et al., 2015; Werry et al., 2011). The response of different ontogenetic stages to these weather/climatic drivers reflects the range of habitat-use of this species throughout its life cycle. Bull shark distribution is closely tied to fresh and low-salinity environments as juveniles and this is followed by a transition into nearshore marine habitat; which accompanied with a shift in diet to larger vertebrate prey (Cliff and Dudley, 1991; Werry et al., 2011). The relationship between rainfall and catch did not vary with gear type (drumlines and gillnets) or combined catches (i.e. all TL combined). However, catches varied between ontogenetic stages (size cohorts). The significant relationship of bull sharks caught by baited drumlines with prior 1-8d rain suggests frequent occurrence and active feeding in nearshore areas after rainfall. A relationship with prior rainfall and catch in gillnets was only significant for <2 m TL bull sharks, suggesting that ≥2 m TL bull sharks may be moving into these areas specifically for feeding (i.e. captured primarily on drumlines) or may be able to avoid the gillnets in these conditions.

The mechanisms that drive increased catch of bull sharks after rainfall may be due to two interacting mechanisms. As an increased movement of freshwater drains from a catchment into nearshore areas via rivers may physically push juveniles further towards marine waters; additionally the murky freshwater plumes interact with seawater to create localised in-water fronts. Such fronts aid plankton blooms, supporting baitfish populations, which feed juvenile and adult bull sharks. The size composition of bull shark catch in the QSCP comprises juvenile and adult sharks ranging from 0.6 to 3.1 m TL, with relative frequent occurrence of animals between 1.6 and 2.2 m TL (Haig et al., 2018). This size range corresponds with the known estuarine-marine transition period in the life cycle of the bull shark from QLD waters (Werry et al., 2011) and reflects the size range and movement of the acoustic-tagged sharks in moving into beaches from estuarine areas in this study.

The increased intensity of storm events under climate change predictions (The Climate Council, 2017) will have implications for bull shark movements along the freshwater-estuarine-marine continuum (Chin et al., 2010; Werry et al., 2011). As the spatial and temporal scales and intensity of rainfall events increase, the pattern of bull shark occurrence and movements are likely to respond accordingly. For example, increased and sustained rainfall/flooding will dramatically alter the salinity

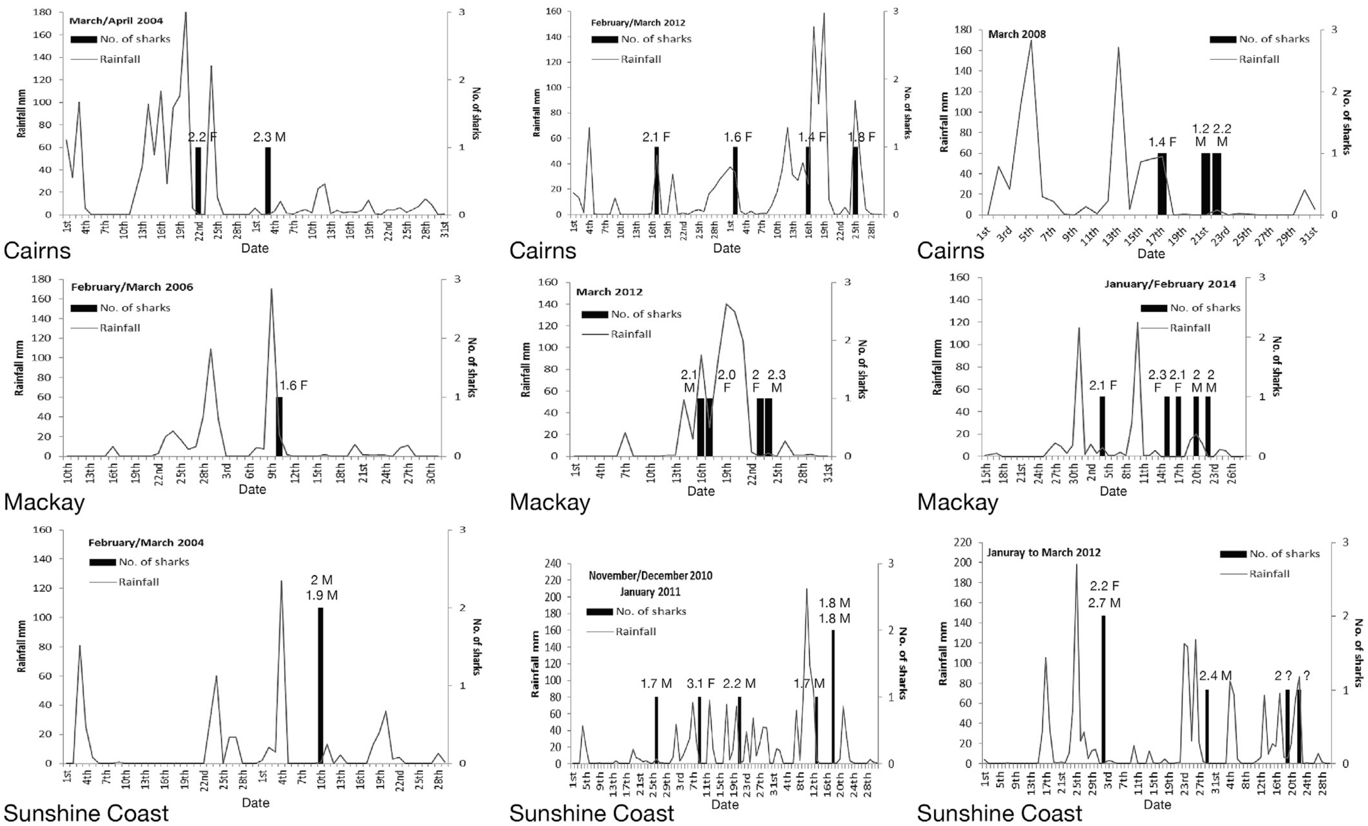

Fig. 3. Snapshots in time of number of bull sharks captured at three locations along the Queensland coastline, Australia, (Cairns, Mackay, Sunshine Coast) after accumulated periods of rainfall ≥ 100 mm. Numbers above vertical lines refer to size in TL and sex (M: male, F: female) for captured bull sharks. These data include time periods outside the modelled period (1996–2007) not presented here to further illustrate the relationship between prior weekly rainfall and shark occurrence.

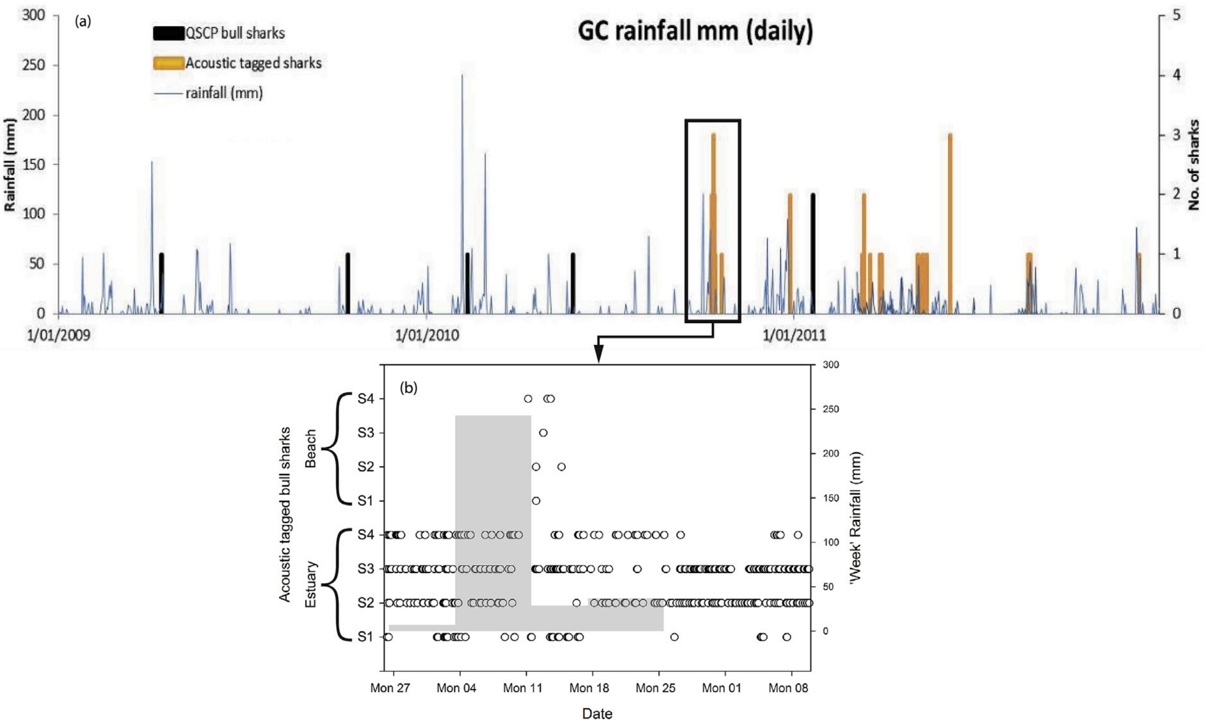

Fig. 4. Capture of bull sharks in QSCP gears on the Gold Coast, Australia, and occurrence of bull sharks with acoustic tags in beach areas in relation to prior rainfall (a), and a (b) highlighted example of movement of bull sharks with acoustic tags from estuarine areas into beach areas after a period (8 days) of accumulated rainfall. Grey area denote prior 1-8d rain. S1 to S4 refers to acoustic tagged sharks detected on estuarine and beach receivers separately. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

gradients in river and estuarine systems disrupting normal size segregation. Abnormal and increased mixing of juveniles and adults may have negative impacts for bull shark populations as large bull sharks cannibalize smaller conspecifics (Vorenberg, 1962). Alternatively, bull sharks may exhibit flight behaviour and leave estuarine and/or coastal areas and occupy deeper (offshore) waters prior to extreme weather events as has been demonstrated for *Carcharhinus limbatus*, *C. tilstoni, C. sorrah* and *C. amboinensis* (Chin et al., 2010; Udyaweri et al., 2013).

An exponential increase was observed in bull shark CPUE in beach areas with increasing temperature, suggesting that this is also an important environmental driver for this species. Bull sharks move along the QLD and New South Wales coastline without distinct seasonality (Heupel et al., 2015). Studies have shown that the distribution of several estuarine shark species are influenced by temperature (Heupel and Hueter, 2002; Simpfendorfer et al., 2005). Species that are able to exploit warming conditions are likely to move pole-ward in their range (Chin et al., 2010). However, some cartilaginous fishes have been shown to feed in higher water temperatures and rest in cooler waters and may seek out optimal temperatures rather than habitats (Matern et al., 2000). Increases in SST may alter current coastal migration patterns, and results in increased CPUE at latitudes with optimal SST. A more thorough understanding of how water temperature affects the localised and migratory movements of bull sharks is required to better elucidate their movements towards beach areas and provide predictive consequences with shifting global temperatures. This is particularly pertinent for improved conservation of the species and management of shark-human interactions as the number and activity of beach goers also increase during warm periods.

Recent literature suggests that sharks and rays occupying freshwater/estuarine habitats and rocky/coral reefs are most vulnerable to climate change, and that this will be determined by case-specific interactions of multiple factors and species attributes (Chin et al., 2010). This is because changes in temperature, freshwater input and ocean circulation will have the most widespread effects on such species (Chin et al., 2010). That the bull shark lifecycle is linked to the freshwater-estuarine-marine continuum (Werry et al., 2011); and that a positive relationship exists between catch and nearshore beach areas in relation to rainfall and SST, suggests this species is highly responsive to short-term climate conditions and susceptible to seasonal and also long term climate change. Altered weather and climate patterns in response to climate change are likely to lead to shifts in bull shark behaviour, movement, recruitment (pupping), transitions between nursery and adult foraging habitats, migratory behaviour and interactions with humans. These will have important ramifications for species conservation and management on local, continental and global scales (e.g. Heupel et al., 2015; Myers et al., 2007). These factors coupled with coastal habitat destruction and/or modification (e.g. Curtis et al., 2013; Werry et al., 2012a) suggests that bull shark populations may continue to decline globally in the future (Baum et al., 2003; Ferretti et al., 2008; O'Connell et al., 2007; Myers et al., 2007). Reducing mortality, preserving coastal catchments and estuarine habitats, and addressing fisheries sustainability are means to alleviate the impacts of shifting climate on bull shark populations.

Mechanisms underpinning relationships of climate variables and shark catch are likely influenced by changes in distribution from altered habitats and changes in population dynamics, i.e. recruitment, growth, survival, abundance, (Chin et al., 2010). Adult and juvenile bull sharks in nearshore habitats are influenced by rainfall and sea surface temperature as suggested by the analyses, and these patterns of catch reflect ontogenetic activity and movement responses to these climate variable drivers. We suggest that adult bull sharks are moving into nearshore areas, possibly from deeper coastal waters (>25 m deep) (Brunnschweiler et al., 2010;, Werry et al., 2011; Heupel et al., 2015), to feed in the freshwater plumes extruding from river mouths. Lagged responses of shark catch to rainfall reflect changes in availability of food and foraging effectiveness with changes in salinity after sufficient rainfall (>100 mm). Lagged responses to rainfall have been recorded on scales of days to years for other nearshore species such as mud crabs (*Scylla serrata*), mullet (*Mugil* spp.) and barramundi (*Lates calcarifer*) (Hill et al., 1982; Williams, 2002; Staunton-Smith et al., 2004).

A significant impact of rainfall on fish catch is reflected in a significant relationship with the Southern Oscillation Index (SOI). El Niño or dry years in eastern Australia lead to reduced fish catch and La Nina or wet years translated to higher catches (Meynecke et al., 2006) and these patterns were also consistent for bull shark in the current study. Pregnant bull shark catch also increased significantly with a positive SOI (wetter conditions), suggesting better neonate recruitment during wet years when nearshore fisheries catch is higher. While it is difficult to prove underlying climate-recruitment correlations, rainfall and temperature are known to affect fish species throughout their lifecycle (Bergenius et al., 2005; Sissenwine, 1984; Uphoff, 1989). In addition, disruption of ecological processes that drive biological productivity and prey availability modulated by climate (e.g. rainfall) are likely to influence bull shark catch and long-term trends in populations. Many sharks are 3rd or 4th trophic level consumers and as such regulate lower trophic levels (Cortés, 1999). Increased frequency and severity of drought periods in Queensland is likely to affect a number of trophic cascades, in both an upwards direction (changing fish populations effecting bull shark behaviour) and downwards (ontogenetic and physiologically driven shark behaviour in response to changing environmental conditions resulting in altered fish demographics) (O'Connell et al., 2007).

Lunar phases have been shown to play a role in food availability, activity, stress, temperature and salinity ‘choices’, for lemon sharks (Brown and Gruber, 1988) and diving behaviour of whale sharks (Graham et al., 2006). Moonlight avoidance has been recorded in other marine predators; for example the Galápagos fur seal, *Arctocephalus galapagoensis* experiences variable feeding efficiency from altering its behaviour in high light conditions in order to avoid predators (namely sharks) (Trillmich and Mohren, 1981). We hypothesis that juvenile bull sharks may be moving into beach areas with greater frequency during periods of reduced moonlight to avoid predation from adult conspecifics. In addition, poor light conditions during the new moon may increase catch by nets for all shark sizes, while the same pattern was not evident for the drumlines.

This study has demonstrated specific links of bull shark catch and movement to components of climate through short-term responses to weather events. Predictions of future rainfall and SOI trends are possible and can be monitored for informed adaptive management in fishing and shark control measures. Positive effects of rainfall, such as availability of food, and negative effects such as higher mortality of juvenile bull sharks through a reduction in nursery habitat, from changes in salinity and turbidity, infer linked mechanisms between productivity, rainfall and catchability. Therefore, management policies that ensure sustainability of shark populations under conditions of extreme climate pressure, such as reduced rainfall patterns from more frequent El Niño, should be implemented. Differences in catch for bull sharks <2 m and ≥2 m TL highlight the importance of individual management and conservation strategies for juvenile and adult bull shark populations. Shark fisheries are sustainable when enough long-lived adults remain in populations to ensure sufficient recruitment (Prince et al., 2005). Adequate protection of habitats vital for each ontogenetic stage of a species' life cycle is necessary (Gillanders et al., 2003; Prince et al., 2005; Punt et al., 2005; Werry et al., 2012a). Management strategies that incorporate protection of rivers and estuaries in addition to nearshore habitats will ensure conservation of ‘near threatened’ bull shark populations (IUCN, 2008) in the face of predicted climate change (Hobday and Lough, 2011b; Werry et al., 2011).

Fishing methods deployed by the QSCP target bull shark in nearshore waters, as such catches of adult and pregnant females in nearshore areas are increased in the days following a rainfall event (>100 mm). Further, understanding stock-recruitment relationships in elasmobranchs is important for fisheries management and these relations have been suggested to be linear (e.g. dogfish; Holden, 1977) or density−dependent, with constant recruitment over a range of high parental stock levels (e.g. gummy shark; Walker, 1994). However, limited studies have identified climatic variables as drivers. Sufficient rainfall may be an important element in the parturition process of bull sharks. The significant relationship between SOI and pregnant bull shark catch in gillnets suggests pupping may coincide with appropriate climatic conditions for neonates and this warrants further investigation.

We recommend management agencies inform beach goers of heightened risk of bull shark interaction in beach areas after periods of heavy rainfall. Beach closures, and/or public education during higher risk periods would help to reduce adverse incidents and allay fear of shark attack more generally (Curtis et al., 2012). Shark incident response planning would ensure that during high-risk periods local authorities would be prepared for emergency medical response (Curtis et al., 2012).

Estuarine and coastal systems are likely to exhibit earlier regional changes in species loss from shifts in climate as many species in these habitats live near their tolerance levels (Carlton, 1996; Curtis et al., 2013). Given the ability of bull sharks to tolerate a wide range of salinities and climate conditions, this species may be capable of sustaining greater fluctuations in climate extremes. Measuring the movement of bull sharks <2 m TL and >2 m TL is critical to better understand the responses of bull sharks to climate variables in nearshore habitat and to determine the connectivity between nursery habitats and those utilised by adults. Bull sharks are highly adaptable (Ortega et al., 2009) and acoustic and satellite telemetry will better determine the movement and depth preferences of adults in shelf environments and the importance of connectivity of nearshore habitats to the shark's life cycle (Brunnschweiler and Barnett, 2013; Daly et al., 2014; Heupel et al., 2015; Werry et al., 2011). Determining which specific habitats or sites contribute more per unit area to the production of individuals that recruit to adult populations will enable management efforts to focus on connected habitats that make the largest contribution to adult populations and potentially have these sites set aside as marine protected areas (Gillanders et al., 2003; Haig et al., 2018; Espinoza et al., 2015). Conserving these habitats may provide buffers for bull shark populations in the face of climate change.

5. Conclusion

The life history characteristics and habitat requirements of a shark determine its ability to respond and adapt to changes in climate. Consequently, understanding how sharks use coastal habitats is imperative to conserving sharks in the face of climate change. Our study has shown rainfall and SST are key drivers affecting the occurrence and movement of bull sharks into beach areas and highlights the significance of identifying how sharks respond to climate cues. We have provided the first predictive trigger for periods of increased risk of shark-human interaction; which will hopefully lead to reduce attacks via bather education and in turn help safe guard the important ecological role sharks play in marine ecosystems.

Acknowledgements

We thank Sea World, Australia, for providing a support vessel and mother ship for the acoustic tagging component of this study. We also thank the Sea World dive team for deployment and retrieval of acoustic receivers in estuaries and the Gold Coast QSCP contractors for assistance with deployment and monitoring of receivers in beach areas. Acoustic tagging was made possible with a grant from the Sea World Research and Rescue Foundation (SWRRFI). Receivers in beach areas were made possible by a QLD DAAF grant for the QLD Large Shark Tagging Program (QLSTP). The Authors gratefully acknowledge Tangalooma Resort, Moreton Island, for assistance as a research base during work carried out in Moreton Bay.

References

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the northwest Atlantic. Science 299, 389–392.
Bellwood, D.R., Hughes, T.P., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833.
Bergenius, M.A.J., McCormick, M.I., Meekan, M.G., Robertson, R.D., 2005. Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish. Mar. Biol. 147, 291–300.
Bradford, R.W., Hobday, A.J., Bruce, B.D., 2012. Identifying juvenile white shark behaviour from electronic tag data. In: Global Perspectives on the Biology and Life History of the White Shark. CRC Press, New York, 551–270.
Brown, C.A., Gruber, S.H., 1988. Age assessment of the lemon shark, Negaprion brevirostris, using tetracycline validated vertebral centra. Copeia 1988, 747–753.
Bruce, B.D., Bradford, R.W., 2012. Habitat use and spatial dynamics of juvenile white sharks, Carcharodon carcharias. In: Eastern Australia in: Global Perspectives on the Biology and Life History of the White Shark. CRC Press, New York, pp. 225–254.
Brunnschweiler, J.M., Barnett, A., 2013. Opportunistic visitors: long-term behavioural response of bull sharks to food provisioning in Fiji. PLoS One 8 (3).
Brunnschweiler, J.M., Queiroz, N., Sims, D.W., 2010. Oceans apart? Short-term movements and behaviour of adult bull sharks *Carcharhinus leucas* in Atlantic and Pacific oceans determined from pop-off satellite archival tagging. J. Fish. Biol. 77, 1343–1358.
Carlton, J.T., 1996. Biological invasions and cryptogenic species. Ecology 77, 1653–1655.
Chin, A., Kyne, P.M., Walker, T.I., McAuley, R.B., 2010. An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. Global Change Biol. 16, 1936–1953.
Clarke, S., Milner-Gulland, E.J., Bjorndal, T., 2007. Social, economic, and regulatory drivers of the shark fin trade. Mar. Resour. Econ. 22, 305–327.
Cliff, G., Dudley, S.F.J., 1991. Sharks caught in the protective gill nets of Natal, South Africa. 4. The bull shark (*Carcharhinus leucas*) (Valenciennes). S. Afr. J. Mar. Sci. 10, 253–270.
Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. ICES J. Mar. Sci. 56, 707–717.
Curtis, T., Bruce, B., Cliff, G., Dudley, S., Klimley, P., Kock, A., Lea, R., Lowe, C., McCosker, J., Skomal, G., Werry, J.M., West, J., 2012. Responding to the risk of white shark attack: updated statistics, prevention, control methods and recommendations. In: Domeier, Michael L. (Ed.), Global Perspectives on the Biology and Life History of the Great White Shark. CRC Press, Boca Raton, FL.
Curtis, T.H., Parkyn, D.C., Burgess, G.H., 2013. Use of human-altered habitats by bull sharks in a Florida nursery area marine and coastal fisheries. Dynam. Manag. Ecosys. Sci. 5, 28–38.
Daly, R., Smale, M.J., Cowley, P.D., Froneman, P.W., 2014. Residency patterns and migration dynamics of adult bull sharks (Carcharhinus leucas) on the east coast of southern Africa. PLoS One 9 (10), e109357.
Espinoza, M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2016. Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? PLoS One 11 (2), e0147608. https://doi.org/10.1371/journal.pone.0147608.
Espinoza, M., Ledee, J.I.E., Simpfendorfer, C.A., Tobin, A.J., Heupel, M.R., 2015. Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. Ecol. Appl. 8, 2101–2118.
Ferretti, F., Myers, R.A., Serena, F., 2008. Loss of large predatory sharks from the Mediterranean Sea. Conserv. Biol. 22, 952–964.
GenStat, 2008. GenStat for Windows, Release 11.1, eleventh ed. VSN International Ltd, Oxford.
Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser. 247, 281–295.
Graham, R.T., Roberts, C.M., Smart, J.C.R., 2006. Diving behaviour of whale sharks in relation to a predictable food pulse. J. R. Soc. Interface 3, 109–116.
Haig, J.A., Lambert, G.I., Sumpton, W.D., Mayer, D.G., Werry, J.M., 2018. Habitat features influence catch rates of near-shore bull shark (*Carcharhinus leucas*) in the Queensland Shark Control Program, Australia 1996-2012. Estuar. Coast Shelf Sci. 200, 289–300.
Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.
Heithaus, M., Dill, L., Marshall, G., Buhleie, B., 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Mar. Biol. 140, 237–248.

Heupel, M., Simpfendorfer, C.A., Espinoza, M., Smoothey, A.F., Tobin, A., Peddemors, V., 2015. Conservation challenges of sharks with continental scale migrations. Front. Mar. Sci. 24.
Heupel, M.P., Simpfendorfer, C.A., 2014. Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. Mar. Ecol. Prog. Ser. 496, 47–57.
Heupel, M.R., Yeiser, B.G., Collins, A.B., Ortega, L., Simpfendorfer, C.A., 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, M.R., Simpfendorfer, C.A., 2008. Movement and distribution of young bull sharks Carcharhinus leucas in a variable estuarine environment. Aquat. Biol. 1, 277–289.
Heupel, M.R., Simpfendorfer, C.A., Hueter, R.E., 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with tropical storm Gabrielle. J. Fish. Biol. 63, 1357–1363.
Heupel, M.R., Hueter, R.E., 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Mar. Freshw. Res. 53, 543–550.
Hill, B.J., Williams, M.J., Dutton, P., 1982. Distribution of juvenile, subadult and adult *Scylla serrata* (Crustacea: portunidae) on the tidal flats in Australia. Mar. Biol. 69, 117–120.
Hillary, R.M., Bravington, M.V., Patterson, T.A., Grewe, P., Bradford, R., Feutry, P., Gunasekera, R., Peddemors, V., Werry, J.M., Francis, M.P., Duffy, C.A.J., Bruce, B.D., 2018. Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. Sci. Rep. 8, 2661.
Hobday, A.J., Smith, A.D.M., Stobutzki, I.C., Bulman, C., Daley, R., Dambacher, J.M., Deng, R.A., Dowdney, J., Fuller, M., Furlani, D., Griffiths, S.P., Johnson, D., Kenyon, R., Knuckey, I.A., Ling, S.D., Pitcher, R., Sainsbury, K.J., Sporcic, M., Smith, T., Turnbull, C., Walker, T.I., Wayte, S.E., Webb, H., Williams, A., Wise, B. S., Zhou, S., 2011a. Ecological risk assessement for the effects of fishing. Fish. Res. 108, 372–384.
Hobday, A.J., Lough, J.M., 2011b. Projected climate change in Australian marine and freshwater environments. Mar. Freshw. Res. 62, 1000–1014.
Holden, M.J., 1977. Elasmobranchs. In: Gulland, J.A. (Ed.), Fish Population Dynamics. Wiley, UK, pp. 187–215.
IUCN, 2008. *Carcharhinus leucas* IUCN (international union for conservation of nature) red list of threatened species. Available: www.iucnredlist.org. (Accessed 1 May 2015).
Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., Tobin, A.J., Moloney, J., 2011. Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshorenearshore region. Mar. Ecol. Prog. Ser. 425, 233–246.
Last, P.R., Stevens, J.D., 2009. Sharks and Rays of Australia. CSIRO Division of Fisheries, Australia, 513pp.
Lea, J.S.E., Wetherbee, B.M., Sousa Choy Aming, L.L., Humphries, N.E., Queiroz, N., Harvey, G.M., Sims, D.W., Shivji, M.S., 2018. Ontogenetic partial migration is associated with environmental drivers and influences fisheries interactions in a marine predator. ICES J. Mar. Sci. 75 (4), 1383–1392. https://doi.org/10.1093/icesjms/fsx238.
Lee, K.A., Roughan, M., Harcourt, R.G., Peddemors, V.M., 2018. Environmental correlates of relative abundance of potentially dangerous sharks in nearshore areas, southeastern Australia. Mar. Ecol. Progr. Ser. 599, 157–179.
Martin, A.R., 2005. Conservation of freshwater and euryhaline elasmobranchs: a review. J. Mar. Biol. Assoc. U. K. 85, 1049–1073.
Matern, S.A., Cech Jr., J.J., Hopkins, T.E., 2000. Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioural thermoregulation? Environ. Biol. Fish. 58, 173–182.
Mathies, N.H., Ogbum, M.B., McFall, G., Fangman, S., 2014. Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. Mar. Ecol. Prog. Ser. 495, 27–38.
Matich, P., Heithaus, M.R., 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.
McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, second ed. Chapman and Hall, London.
Meeuwig, J.J., Harcourt, R.G., Whoriskey, F.G., 2015. When science places threatened species at risk. Con. Lett. 8, 151–152.
Meeuwig, J.J., Ferreira, L.C., 2014. Moving beyond lethal programs for shark hazard mitigation. Anim. Conserv. 17, 297–298.
Meyer, C.G., Clark, T.B., Papastamatiou, Y.P., Whitney, N.M., Holland, K.N., 2009. Long-term movements of tiger sharks (*Galeocerdo cuvier*) in Hawaii. Mar. Ecol. Prog. Ser. 381, 223–235.
Meynecke, J.O., Lee, S.Y., Duke, N.C., Warnken, J., 2006. Effect of rainfall as a component of climate change on estuarine fish production in Queensland, Australia. Estuar. Coast Shelf Sci. 69, 491–504.
Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423, 280–284.
Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H., 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315, 1846–1850.
Noriega, R., Werry, J.M., Sumpton, W., Mayer, D., Lee, S.Y., 2011. Trends in annual CPUE and evidence of sex and size segregation of *Sphyrna lewini*: management implications in coastal waters of northeastern Australia. Fish. Res. 110, 472–477.
O'Connell, M., Shepherd, T., O'Connell, A., Myers, R., 2007. Long-term declines in two apex predators, bull sharks (*Carcharhinus leucas*) and alligator gar (*Atractosteus spatula*), in Lake Pontchartrain, an oligohaline estuary in southeastern Louisiana. Estuar. Coast 30, 567–574.
Ortega, L., Heupel, M., Beynen, P., Motta, P., 2009. Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. Environ. Biol. Fish. 84, 361–373.
Papastamatiou, Y.P., Meyer, C.G., Carvalho, F., Dale, J.J., Hutchinson, M.R., Holland, K.M., 2013. Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. Ecology 94, 2595–2606.
Pillans, R.D., Good, J.P., Anderson, W.G., Hazon, N., Franklin, C.E., 2005. Freshwater to seawater acclimation of juvenile bull sharks (Carcharhinus leucas): plasma osmolytes and $Na+/K+$-ATPase activity in gill, rectal gland, kidney and intestine. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 175, 37–44.
Pillans, R.D., Franklin, C.E., 2004. Plasma osmolyte concentrations and rectal gland mass of bull shark, *Carcharhinus leucas*, captured along a salinity gradient. Comp. Biochem. Physiol. 138A, 363–371.
Prince, J.D., 2005. Gauntlet fisheries for Elasmobranches – the secret of sustainable shark fisheries. J. Northwest Atl. Fish. Sci. 35, 407–416.
Punt, A.E., Pribac, F., Taylor, B.L., Walker, T.I., 2005. Harvest strategy evaluation for school and gummy shark. J. Northwest Atl. Fish. Sci. 35, 387–406.
Raybould, M., Lazarow, N., 2009. Economic and Social Values of beach Recreation on the Gold Coast. Cooperative Research centre for Sustainable Tourism, Australia. Technical report.
Rosa, R., Baptista, M., Lopes, V.M., Pegado, M.R., Paula, J.R., Trübenbach, K., Leal, M.C., Calado, R., Repolho, T., 2014. Early-life exposure to climate change impairs tropical shark survival. Proc. R. Soc. B. 281 (1783).
Ruppert, J.L.W., Travers, M.J., Smith, L.L., Fortin, M.J., Meekan, M.G., 2013. Caught in the Middle: combined Impacts of Shark Removal and Coral Loss on the Fish Communities of Coral Reefs. PLoS One 8 (9), e74648.
Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev. Fish Biol. Fish. 24, 1089–1103.
Simpfendorfer, C.A., Freitas, G., Wiley, T., Heupel, M.R., 2005. Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida estuary. Estuaries 28, 78–85.
Simpfendorfer, C.A., Heupel, H.M., White, W.T., Dulvy, N.K., 2011. The importance of research and public opinion to conservation management of sharks and rays: a synthesis. Mar. Freshw. Res. 62, 518–527.
Sissenwine, M.P., 1984. Why Do Fish Populations Vary? Springer, Berlin, Heidelberg.
Staunton-Smith, J., Robins, J.B., Mayer, D.G., Sellin, M.J., Halliday, I.A., 2004. Does the quantity and timing of fresh water flowing into a dry tropical estuary affect year-class strength of barramundi (*Lates calcarifer*)? Mar. Freshw. Res. 55, 787–797.
Sumpton, W., Taylor, S., Gribble, N., McPherson, G., Ham, T., 2011. Gear selectivity of large-mesh nets and drumlines used to catch sharks in the Queensland Shark Control Program. Afr. J. Mar. Sci. 33, 37–43.

Suthers, I.M., Everett, J.D., Roughan, M., Young, J.W., Oke, P.R., Codie, S.A., Hartog, J.R., Hobday, J.A., Thompson, P.A., Ridgeway, K., Baird, M.e., Hassler, C.S., 2011. The Strengthening East Australian Current, its eddies and biological effects – an introduction and overview. Deep Sea Res. Part II 58, 538–546.
Taylor, S.M., Webley, J.A.C., Mayer, D.G., 2011. Improving the precision of recreational fishing harvest estimates using two-part conditional general linear models. Fish. Res. 110, 408–414.
The Climate Council, 2017. Tropical Cyclones and Climate Change: Factsheet, 8pp.
Thorson, T.B., 1971. Movement of bull sharks, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia 1971, 336–338.
Trillmich, F., Mohren, W., 1981. Effects of the lunar cycle on the Galápagos Fur seal, *Arctocephalus galapagoensis*. Oecologia 48, 85–92.
Udyaweri, V., Chin, A., Knip, D.A., Simpfendorfer, C.A., Heupel, M., 2013. Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. Mar. Ecol. Prog. Ser. 480, 171–183.
Uphoff Jr., J.H., 1989. Environmental effects on survival of eggs, larvae, and juveniles of striped bass in the Choptank River, Maryland. Trans. Am. Fish. Soc. 118, 251–263.
Vorenberg, M.M., 1962. Cannibalistic tendencies of lemon and bull sharks. Copeia 1962, 455–456.
Walker, T.I., 1994. Stock assessments of the gummy shark, *Mustelus antarcticus Günther*, in bass strait and off south Australia. In: Hancock, D.A. (Ed.), Population Dynamics for Fisheries Management. Australian Society for Fish Biology Workshop Proceedings, Perth, Australia.
Walker, T.I., 2007. The state of research on chondrichthyan fishes. Mar. Freshw. Res. 58, 1–3.
West, J.G., 2011. Changing patterns of shark attacks in Australian waters. Mar. Freshw. Res. 62, 744–754.
Weltz, K., Kock, A.A., Winker, H., Attwood, C., Sikweyiya, M., 2013. The Influence of Environmental Variables on the Presence of White Sharks, C*archarodon carcharias* at Two Popular Cape Town Bathing Beaches: a Generalized Additive Mixed Model. PLoS One 8 (7), e68554.
Welsh, J.Q., Fox, R.J., Webber, D.M., Bellwood, D.R., 2012. Performance of remote acoustic receivers within a coral reef habitat: implications for array design. Coral Reefs 31, 693–702.
Werry, J.M., Planes, S., Berumen, M.L., Lee, K.A., Braun, C.D., Clua, E., 2014. Reef-Fidelity and Migration of Tiger Sharks, *Galeocerdo cuvier,* across the Coral Sea. PLoS One 9 (1), e83249.
Werry, J.M., Clua, E., 2013. Sex-based spatial segregation of adult bull sharks, *Carcharhinus leucas*, in the New Caledonian great lagoon. Aquat. Living Resour. 26, 281–288.
Werry, J.M., Lee, S.Y., Lemckert, C.J., Otway, N.M., 2012a. Natural or Artificial? Habitat-Use by the Bull Shark, *Carcharhinus leucas*. PLoS One 7, e49796.
Werry, J.M., Bruce, B.D., Sumpton, W., Reid, D., Mayer, D.G., 2012b. Beach areas used by juvenile white sharks, *Carcharodon carcharias*, in eastern Australia. In: Global Perspectives on the Biology and Life History of the White Shark. CRC Press, New York, pp. 271–286.
Werry, J.M., Lee, S.Y., Otway, N., Hu, Y., Sumpton, W., 2011. A multi-faceted approach for quantifying the estuarine-nearshore transition in the lifecycle of the bull shark, *Carcharhinus leucas*. Mar. Freshw. Res. 62, 1421–1431.
Williams, L.E., 2002. Queensland's Fisheries Resources Current Condition and Recent Trends 1988-2000. Information Series QI02012. Queensland Department Primary Industries and Fisheries, Brisbane.