Title Juvenile white sharks *Carcharodon carcharias* use estuarine environments in south-eastern Australia.

Authors: D Harasti, K Lee, B Bruce, C Gallen, and R Bradford

[1] Fisheries Research, NSW Department of Primary Industries, Locked Bag 1, Nelson Bay, NSW 2315, Australia.

[2] CSIRO Oceans and Atmosphere, G. P. O. Box 1538, Hobart, TAS, 7000, Australia.

Corresponding author: David Harasti, david.harasti@dpi.nsw.gov.au, +61 24916 3821

Abstract

Estuarine environments are known to provide important feeding, breeding, resting and nursery areas for a range of shark species, including some which are considered dangerous to humans. Juvenile white sharks (<3 m) are known to frequent inshore environments, particularly ocean beaches, but their presence in and use of estuaries and coastal embayments is unclear. Given that estuarine environments are often surrounded by highly populated areas, understanding how white sharks use these environments will not only assist with their conservation management, but also inform public safety policies. The use of estuarine environments by acoustic-tagged white sharks was investigated from 2009 to 2015 at Port Stephens, New South Wales and Corner Inlet, Victoria, both of which adjoin known nursery areas for the species. Juvenile white sharks were detected within both estuaries, with 20 individuals recorded within the Port Stephens estuary, including four on one day. Only one tagged shark was detected within Corner Inlet, however, monitoring effort and local tagging in the area was more restricted. Detections in Port Stephens were predominantly from October to January and peaked in November. This study demonstrates that the footprint of known nursery areas for white sharks in eastern Australia should be expanded to include their adjacent estuarine environments. Consequently, there is clear potential for them to be exposed to a range of anthropogenic estuarine impacts, and that human interactions are more likely over warmer periods (summer), when human use of such water-ways is more prevalent.

Keywords *Carcharodon carcharias*; Corner Inlet; Estuary; Marine; Port Stephens; Threatened species, nursery area.

Introduction

Many sharks use a range of habitat types which can vary depending on life-history stage (Froeschke et al. 2010; Knip et al. 2010). Inshore regions and estuaries are important pupping, nursery, feeding and resting areas for many species, including bonnethead *Sphyrna tiburo* (Heupel et al. 2006; Ubeda et al. 2009); leopard *Triakis semifasciatus* (Carlisle and Starr 2009); lemon *Negaprion brevirostris* (Yeiser et al. 2008), hammerhead *Sphyrna mokarran* (Roemer et al. 2016), and sevengill sharks *Notorynchus cepedianus* (Barnett et al. 2010). The use of estuaries and riverine environments is well documented for various life-history stages of the potentially dangerous bull shark, *Carcharhinus leucas* (Curtis et al. 2013; Heupel and Simpfendorfer 2008; Heupel et al. 2010; Werry et al. 2011). However, the use of estuarine habitats by other large, highly mobile and potentially dangerous species, such as the white shark, *Carcharodon carcharias*, is poorly documented. Estuaries and coastal environments are under increasing pressure from anthropogenic impacts due to urban and port developments (Curtis et al. 2013) and changes in land and water use (Verdonschot et al. 2013). Thus, a knowledge of the occurrence of sharks and their use of these habitats plays a key role in identifying threats and pressures, particularly for species of conservation concern (Castro 1993) and, increasingly, for public safety (Smoothey et al. 2016).

The white shark is globally listed as vulnerable (IUCN 2016), with protection provided under a variety of international treaties and national legislative instruments throughout its distribution. Accordingly, studies on the species are numerous and much is now known about its biology and ecology (Bruce and Bradford 2012; Cliff et al. 1989; Domeier 2012; Francis 1996), movements (Bonfil et al. 2010; Boustany et al. 2002; Domeier and Nasby-Lucas 2007; Domeier and Nasby-Lucas 2013; Weng et al. 2007a), predatory behaviour (Hammerschlag et al. 2006; Martin et al. 2005) and population structure (Blower et al. 2012; Gubili et al. 2012; Oñate-González et al. 2015; Pardini et al. 2000). However, most studies have focussed on sub-adult and adult white sharks because of their predilection to aggregate at readily accessible sites, such as pinniped colonies (Bruce et al. 2006; Chapple et al. 2011; Klimley et al. 2001; Robbins 2007; Towner et al. 2013). Comparatively less research has been directed at juvenile and young-of-year white sharks (Dewar et al. 2004; Klimley et al. 2002; Lyons et al. 2013; Weng et al. 2007b).

Recent evidence suggests juvenile white sharks spend a considerable amount of time in the near-shore environment (Dicken and Booth 2013; Lyons et al. 2013), including in discrete coastal nursery areas (Bruce and Bradford 2012; Harasti et al. 2016a). These locations can be close to estuaries, but the extent to which estuarine habitats are used by juvenile white sharks has not been specifically investigated. The growing number of records of juvenile white sharks from estuarine systems and semi-enclosed coastal bays suggests at least some level of occupancy and indicate that these environments could well provide important, and hitherto unrecognised, habitat. For example, juvenile white sharks have been caught in the artisanal seine-net, gillnet and longline fisheries operating inside Laguna Ojo de Liebre, Mexico (Cartamil et al. 2011; Santana-Morales et al. 2012). Similarly, a number of juvenile white sharks have been caught in Kaipara Harbour, New Zealand (Francis 1996; C. Duffy pers. comm.), and juvenile white sharks have been recorded near estuaries and river mouths in South Africa (Nel and Peschak 2006).

Within Australia, juvenile white sharks are broadly distributed along the east coast, with some individuals showing annual patterns of residency in two coastal nursery areas in waters surrounding Port Stephens in central New South Wales (NSW) and the southern section of 90 Mile Beach (Corner Inlet) in southeast Victoria (Bruce and Bradford 2012). Both of these nursery areas adjoin large estuarine or coastal inlet systems. To date, white sharks have not been reported from any research surveys of estuaries in eastern Australia despite such systems containing a variety of other shark species, including bull sharks (Smoothey et al. 2016). However, a growing number of media reports and public sightings of white sharks in Australian estuaries (SMH 2014; SMH 2015) suggest that these habitats are used more frequently than suspected.

Understanding the extent to which juvenile white sharks use estuarine systems will assist with assessing and managing the risk of exposure to additional anthropogenic pressures (i.e. pollution, fishing) that they may face. It will also improve our understanding of, and ability to manage, encounter risk with humans in these often heavily populated regions and widely used waterways, thereby providing a sound base to inform public safety policies. Using acoustic telemetry, this study demonstrates that juvenile white sharks use estuaries adjoining the known nursery areas in eastern Australia, particularly during summer.

MATERIALS AND METHODS

Study sites

This study was conducted from 2009 to 2015 in the Port Stephens estuary which adjoins one of two known juvenile white shark nurseries off the east coast of Australia (Bruce and Bradford 2012). Acoustic receivers were also deployed in Corner Inlet, Victoria and surrounding waters (adjacent to the second known juvenile white shark nursery). However, tagging effort and receiver coverage was too low in the Corner Inlet region to support rigorous statistical analyses.

The Port Stephens estuary (32.71 S, 152.20 E) is approx. 930 km north of Corner Inlet (38.46 S, 146. 28 E), along the central coast of New South Wales and is 230 km north of Sydney (Fig. 1). It is the largest drowned river valley in NSW (Roy et al. 2001), covering an area of approximately 134 km^2, and comprises distinct eastern (49 km^2) and western (85 km^2) basins linked by a channel 1.1 km wide formed by the narrow peninsula of Soldiers Point. The eastern basin, where the acoustic monitoring took place, is a predominantly marine dominated environment with strong tidal currents influenced by deep narrow channels and shallow sand shoals (Vila-Concejo et al. 2007). The entrance to the estuary is 1.2 km wide with a shallow bar varying in depth from 4 – 8 m. The depth in the eastern basin varies considerable with shallow tidal flats dominated by seagrass, whilst a deep channel extends along the southern shore line reaching a maximum depth of 30 m (between HA1 and NB2: See Fig. 1). The widest section in the eastern basin is approximately 4 km. Salinity in the eastern basin is very similar to oceanic waters (34-35 ppt); however, salinity varies greatly depending on tidal state and amount of rainfall present in the catchment. Following large rainfall events, salinity in the western port has been recorded as low as 5 ppt, and on an outgoing tide the salinity in the eastern port around Nelson Bay has been recorded down to 17 ppt (NSW DPI unpublished data).

The Port Stephens estuary contains a diverse range of habitats, including sponge and soft coral habitats (Poulos et al. 2015; van Lier et al. accepted), and extensive seagrass meadows. The northern section of the eastern basin contains large sections of seagrass (*Zosterea capricornia* and *Posidonia australis*), as does Shoal Bay (Davis et al., 2015). The Port Stephens region is dominated by temperate fish assemblages with tropical species prevalent over summer (Davis et al. 2016; Harasti et al. 2016b), including various threatened and protected species (Harasti and Malcolm 2013; Harasti 2016). The estuary is an important region for tourism and is popular with a variety of water-users, including scuba divers, fishers, kayakers and swimmers, as well as various marine tourism ventures. Mean annual rainfall is 1350 mm per annum (BOM 2015b). Outside of the estuary are a number of rocky headlands, bays, small islands and three main ocean beaches. Stockton Beach commences 11 km south of the estuary and then runs a further 30 km southwest to the city of Newcastle. Bennett's Beach extends approximately 15 km to the northeast from the northern headland of the estuary (Yacaaba Head) and Mungo-Fiona Beach, separated from Bennett's Beach by a rock outcrop, extends a further 29 km northeast to Sugarloaf Point. The footprint of the Port Stephens white shark nursery extends about 35 km north of the Port Stephens estuary, 30 km south and about 25 km seaward (Bruce et al. 2013).

Corner Inlet (38.78 S, 146.48 E) is a submerged coastal plain, covering an area of about 600 km^2 at the southern end of Ninety Mile Beach in Victoria, Australia (Molloy et al. 2005). It is characterised by five permanent openings (Fig. 1). The largest opening, and main shipping channel, is 2 km wide and ~40 m deep (Victoria 2015). The inlet is characterised by large mudflats and sandbanks intersected by a series of channels ranging in depth from 1 to 20 m. Mean annual rainfall varies across the system from 880 to 1100 mm per annum (BOM 2015a). To the north of the Corner Inlet system is an uninterrupted 130 km beach ('90 Mile Beach') running northeast to Lakes Entrance. Satellite tracking data shows the footprint of the Corner Inlet white shark nursery to be more extensive, but less well defined than at Port Stephens, extending at least 15 km southwest, 100 km northeast, and up to 40 km seaward of the main entrance channel (Bruce and Bradford 2012).

Acoustic monitoring

A series of 12 VR2W acoustic receivers (Vemco-Amirix Systems Inc.) was deployed in the Port Stephens estuary, extending from the mouth to approx. 8 km inside the estuary (see Fig. 1). These receivers were deployed on a combination of fixed and temporary moorings. The fixed moorings were navigational pylons; temporary moorings were used where no such structures were available. Temporary moorings were typically constructed from a short length (~5 m) of 12 mm nylon rope with a steel plate (~20 kg) for an anchor and a 250 mm subsurface polystyrene float to keep the mooring rope vertical and clear of vessel traffic. Within the Port Stephens estuary ('the estuarine array'), acoustic receivers were deployed from 8 November 2010 to 11 November 2015, although the spatial coverage varied throughout this time as a result of occasional receiver loss, and receiver change over (Table 1). These receivers were complemented by a more extensive array of receivers in the coastal waters surrounding the Port Stephens estuary (the 'coastal array') designed to examine the residency patterns within the entire nursery area (Bruce et al. 2013).

The detection range of receivers in the estuarine array was assessed using Vemco V13 and V16 acoustic range test tags attached to several different moorings (Heupel et al. 2006). A VR100 acoustic receiver (Vemco) was used to detect acoustic pulses at fixed distances from the range test tags under a variety of environmental conditions. The maximum detection range for the receivers varied from ~ 400 m in the poorest sea conditions (ebb tide, poor visibility and large swell) to 500 m during conditions of high tide and no swell.

Tagging sharks

Juvenile white sharks were caught and tagged following the procedures of Bruce and Bradford (2013). In brief, sharks were captured using 12 mm rope fitted with a short wire trace and baited hook that had its barb partially removed to allow for easy removal. Baits (primarily sea mullet – *Mugil cephalus*) were presented to sharks after they were visually located from a small vessel operating near the surf zone along coastal beaches outside of the estuary. After capture, sharks were restrained in a purpose-built, in-water stretcher and supplied with a flow of oxygenated water via a submersible bilge pump. An acoustic tag (Vemco, V16-6x, 69 kHz) was surgically implanted into the peritoneal cavity via a 20-25 mm incision which was sutured close using PDS II Z195T sutures (Ethicon^{TM}). A conventional dart tag (HallPrint™) was applied to the dorsal musculature near to the first dorsal fin (to assist with future identification). Total length was measured to the nearest cm, the hook removed and the shark released. In some cases, sharks were also fitted with a satellite-linked radio tag (SLRT) attached to their first dorsal fin; these data are reported elsewhere (Bruce and Bradford 2012). Typically, a shark would be restrained within the stretcher for approximately 10 minutes prior to its release.

Environmental data

Half-hourly rainfall data for the Nelson Bay region was obtained from the Australian Bureau of Meteorology (www.bom.gov.au) weather station located at Nelson Head (32.71° S, 152.16° E). Only intermittent water temperature records were available (taken as part of other studies) inside the Port Stephens estuary and this lack of continuity precluded the use of these data in our analyses. As juvenile white sharks are commonly encountered in the coastal waters outside the Port Stephens estuary, we used the water temperature recorded at a nearby coastal reef at a depth of 18 m (NSW Fisheries *unpublished data* – Vemco Minilog II) to test if the occurrence of sharks in the estuary was correlated with coastal water conditions – herein 'coastal temperature'. Tidal state for Port Stephens was obtained using XTide (Flater 2014), provided as the mean estimated height every 30 minutes for the period of the array deployment. The fraction of moon illuminated (hereafter referred to as moon illumination) per day was obtained from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/MoonPhase).

Data analysis

A Generalised Additive Mixed Model (GAMM) was used to determine if size (total length), sex or month influenced the occurrence of juvenile white sharks in the Port Stephens estuary. The proportion of days per month that each shark was detected in the estuary was used as the response variable. This was calculated as the number of days per month that a shark was detected, divided by the number of days in that month/number of days receivers were deployed. A seasonal pattern in juvenile white shark detections is evident in waters surrounding the Port Stephens estuary, with sharks generally departing the region by February-March (Bruce et al. 2013). To account for this in our analyses we only included months when sharks were detected (i.e. the number of days detected per month > 0). Since the proportion of days per month that each shark was detected had values between 0 and 1, a beta error distribution and logit link were used. The unique shark identity code was used as a random effect to account for repeated measures on the same sharks. Smooth terms were used for the size of the shark and month to test for a non-linear relationship. The number of receivers deployed during each month was used as an offset to account for the varying spatial coverage of the array. The GAMM was applied using the '*gam*' function in the mgcv package (Wood 2006; Wood 2011) in R (R Core Team 2009) and the maximum likelihood smoothness selection was used. The 'best' model structure was determined using a backwards selection whereby non-significant predictor variables (determined by the *p*-value for smooth terms or if the confidence interval for an estimated parametric term included zero) were sequentially dropped from the model and the model re-fitted until all terms were significant. Prior to modelling, data exploration was conducted following the general protocol of Zuur et al. (2010) using Cleveland dot plots, boxplots, and scatterplots to identify patterns and any outliers. A variance inflation factor (VIF) was used to determine if the explanatory variables were correlated and no collinearity was evident (all VIF values < 3). This data exploration was used prior to all modeling unless otherwise stated.

A generalised linear mixed model (GLMM), with a binomial link function, was used to determine if juvenile white sharks used the estuary more at certain times of the day. The proportion of detections in each hourly bin was calculated and used as the response variable with hour of the day as the predictor variable. Only data from days where the receivers had been deployed the whole day were included so that the number of receivers deployed was the same for each hour. To account for the correlation between values from the same shark, the unique tag code was used as a random effect. A backwards selection process using likelihood ratio tests (LRTs) was used to find the 'best' model.

The influence of moon illumination, month, mean hourly tide height (average tide height from half hourly data), coastal temperature, and cumulative hourly rainfall on the number of sharks within the Port Stephens estuary was examined using a generalised linear model (GLM). The number of individual sharks detected for each hour of each day throughout the study period was used as the response variable, including hours when no sharks were detected (i.e. number of sharks = 0). Because of the high number of zeros, a zero-inflated GLM was applied using the *'zeroinfl'* function in the pscl R package (Zeileis et al. 2008). A zero-inflated model combines both a binomial component to model the presence-absence of the sharks and a Poisson component to model the count data (number of sharks). Both Poisson and negative binomial error distributions (with logit link functions) were tested and compared using Akaike's Information Criterion (AIC). The model with a Poisson error distribution had the lowest AIC (ΔAIC = 2.0) suggesting the number of sharks was best modelled using the Poisson distribution. A generalized additive model was also tested to account for a non-linear relationship between the response and explanatory variables, but the GLM had a lower AIC (ΔAIC = 44.4). The number of receivers deployed for each hour of each day was used as an offset to account for the differing spatial coverage of the receivers. Again, a backwards selection process using LRTs was used to find the 'best' model structure.

As only a single shark was detected inside the Corner Inlet system, our analyses unless otherwise stated focus on sharks in Port Stephens.

RESULTS

From 2009-2014, a total of 34 juvenile white sharks were tagged with internal acoustic tags; 30 tagged in the Port Stephens region and four in the Corner Inlet region. A further eight sharks were tagged prior to the installation of acoustic receivers in 2010. These have been included in this study because seven of them were detected in either the estuaries or nursery areas during the course of this study. At the time of tagging, sharks ranged in size from 170 to 320 cm total length (225 ± 0.31 cm; mean ± SD) with a sex bias of 4:1 in favour of females. Of the 34 juvenile white sharks tagged, 20 were subsequently detected either within or at the mouth of the Port Stephens estuary, with one of these sharks also detected inside Corner Inlet. Seven of the 20 sharks were detected in the Port Stephens estuary in two or more years (seasons), whilst some individuals were detected in the beach nursery area but did not enter the estuary in that year (Fig. 2). All but two of the 34 sharks were detected on acoustic receivers outside of the Port Stephens estuary. One of these two sharks (T10.31), fitted with a SLRT, provided satellite data over a two-year period, including several crossings of the Bondi Line (~33.93°S, 151.36°E), a cross-shelf line of acoustic receivers administered by the Integrated Marine Observing System Animal Tracking Facility (IMOS ATF). Shark T10.31 was never acoustically detected along the coast during the two-year track, suggesting the acoustic tag had failed. The other shark (T13.11) was re-captured in commercial fishing operations on the southern NSW coast, approximately 400 km north and 28 days after it was tagged near Corner Inlet.

Sharks detected within the Port Stephens estuary, ranged in size from 170 to 280 cm TL (221 ± 25 cm; mean ± SD), with a sex bias of 2:1 towards females (Table 2). Only one tagged shark (T11.02) was detected within Corner Inlet on 23 days over a 66 day period between mid-December 2011 through to mid-February 2012. This shark was also detected in the Port Stephens estuary during October – November 2011 and again in October – December 2012. The lack of detections of other sharks, however, precluded further analyses of occupancy in the Corner Inlet system..

Juvenile white sharks were detected on all receivers deployed within each of the two estuarine systems. Individually, sharks were detected within the Port Stephens estuary over periods ranging from a single day, up to 104 non-consecutive days (Table 2) during the study. There were only 12 days on which multiple sharks were detected on the estuarine array, with four being the highest number detected on any given day (Fig. 3). When multiple sharks were detected on the estuarine array, they were separated in time by at least 30 minutes on all but six occasions. Furthermore, on only two occasions were different sharks detected on the same station within 30 minutes of each other.

Several juvenile white sharks appeared to be present for extended periods indicating repeated use over several consecutive days (Fig. 3). One shark (T12.03) was detected on 25 out of a possible 42 days between 26 October and 7 December 2012 and it recorded the most number of detections for any shark within the Port Stephens estuary. Of the 25 days it was detected in the estuary, it was also detected on the array off Bennett's Beach on 20 of these days indicating frequent movement in and out of the estuary. This individual was recorded in the estuary on a total of 104 days during the study period with most daily detections occurring in 2014 (n =48).

The presence of sharks was seasonal, occurring predominantly in the Port Stephens estuary between October and January with a seasonal peak in detections occurring in November (Fig. 4). No tagged sharks were detected entering the estuary between March and May. Juvenile white sharks used the area closer to the entrance than the rest of the estuary, with only one shark being detected in the western section of the eastern basin (Fig. 5).

The 'best' GAMM model of the proportion of days per month sharks were detected in the estuary included month of the year and the random effect (the unique shark identity code) as the predictor variables. Both sex and size were non-significant and were not included in the 'best' GAMM model, indicating that these are 'poor' predictors of the monthly occurrence of sharks within the estuary. The significance of the random effect indicates that there was high individual variation between sharks that was not explained by sex, size or month of the year. However, this 'best' GAMM only explained 22% of the model deviance indicating that other factors may be influencing how long sharks spend in the estuary every month.

There was a significant difference in the proportion of detections during different hours of the day (binomial GLMM: LRT p-value < 0.05), however this was driven by some sharks only being detected in the estuary for a short period of time and thus the majority of the detections occurred within one hourly bin. Overall, there was no clear diel pattern in the dataset (Fig. 6), although juvenile white sharks tended to be present more often at night than in the day. Despite this, juvenile white sharks were detected at all hours.

Moon illumination, rainfall, tide, month and coastal temperature were all significant (zero-inflated Poisson GLM: LRT p-values < 0.01) predictors when modelling the presence and number of juvenile white sharks in the Port Stephens estuary. However, the estimates for the binomial component of the model (modelling the presence-absence data) suggest that none of the predictors are good at predicting the presence of white sharks in the estuary (all standard errors span zero). For the count component of the model, there was a strong seasonal signal with sharks present only during the Austral summer. During these months juvenile white sharks were present more often on a full moon, mid tide, no rainfall, and with coastal water temperatures between 15 and 19 °C (Fig. 7).

DISCUSSION

Near-shore marine waters are known to support nursery areas for several large, potentially dangerous shark species, including bull shark (*Carcharinus leucas*) and white shark (*Carcharodon carcharias*) (Carlson et al. 2010; Curtis et al. 2014; Lyons et al. 2013; Werry et al. 2011). Along the eastern seaboard of Australia, two white shark nurseries have been identified (Bruce and Bradford 2012). Both of these nurseries are adjacent to large estuarine systems, however, the degree to which juvenile white sharks use estuarine habitats has not previously been documented. We found that a high percentage (~56%) of juvenile white sharks tagged on the east coast of Australia used the Port Stephens estuary. Furthermore, the Port Stephens estuary was used by multiple sharks over several years with some individuals returning to the estuary in consecutive years. A single tagged juvenile was also detected on receivers up to 15 km inside the Corner Inlet estuary in south east Victoria. However, the number of sharks tagged in SE Victoria and the time period over which acoustic monitoring took place was more limited than at Port Stephens, so the extent that juvenile white sharks enter the Corner Inlet system may well be higher than our data suggest.

It is well established that some large shark species use estuarine habitats during various stages of their life cycle. Bull sharks are perhaps best known of the large and potentially dangerous sharks that frequent estuarine habitats. Juvenile bull sharks occur in natural and artificial estuaries across their range (Cardeñosa et al. 2016; Heupel and Simpfendorfer 2008; Werry et al. 2011) where individuals may reside for periods of weeks to months (Heupel et al. 2010). In contrast, most juvenile white sharks that entered the Port Stephens estuary were present only for short periods, with some being detected only on a single day. Whilst a few sharks were detected more regularly (e.g. one shark (12.03) was detected on 25 out of consecutive 42 days), it is not known if these individuals remained in the estuary for extended periods or if they moved in and out without being detected. Shark 12.03 was recorded frequently moving between the beach environment and the estuary on the same day on numerous occasions indicating that movement between these two areas was occurring on a daily basis. Whilst there was good receiver coverage along Bennett's Beach to the north, if sharks headed into deep water on leaving the estuary or to the south, sharks may have eluded detection as no receivers covered these areas.

Juvenile white sharks were predominantly found inside the estuary within a few kilometres of the entrance, in particular on the northern side of the eastern basin. However, one shark was detected 8 km inside the estuary on receiver ANCH1. It is not known if this shark swam west into the western basin as this was the most western receiver deployed in the estuary. There is anecdotal evidence of a juvenile white shark travelling further into the estuary provided by a commercial fisher who reported the capture of a juvenile white shark in September 2015 in a mesh net approx. 13 km inside the Port Stephens estuary within the western basin in 2015 (NSW DPI *unpub data*). The shark was caught north-west of Soldiers Point, where there is a deep channel that extends down to 35 m. This is an area affected by strong tidal currents with extensive sponge dominated habitat (Davis et al. 2015) and has different characteristics to those of the eastern basin where sharks were found most frequently to occur. There have also been several observations by the public of juvenile white sharks inside other estuaries within NSW, particularly Lake Macquarie and Lake Illawarra (SMH 2014; SMH 2015). Thus it is likely that juvenile white sharks enter estuarine environments along the east Australian coast more frequently that previously considered.

Estuaries may provide juvenile sharks with abundant food resources or provides refuge from predation (Branstetter 1990; Castro 1993; Heupel and Hueter 2002; Heupel et al. 2010; Simpfendorfer and Milward 1993). However, it is unlikely given the relatively large size of juvenile white sharks (up to 3 m), and their higher propensity for ocean beach and coastal water residency in the area, that the estuary acts as a refuge for the individuals entering the system. The northern side of the estuary, where shark detections were most abundant, features a protective embayment that consists of extensive seagrass meadows (< 4 m depth) and sand habitats in depths 4-15 m (Davis et al. 2015). It is a highly productive area that potentially provides a wider range of prey species and thus foraging opportunities may explain sharks' preference for this area. Indo-Pacific bottlenose dolphins (*Tursiop aduncus*) are known to frequent this area of the estuary (Wiszniewski et al. 2009), and it is an area targeted by commercial fishers for species such as mulloway (*Argyrosomus japonicas*) (NSW DPI *unpub data*). Alternatively, as the waters in this area of the estuary are sheltered from wind and wave energy, it is possible that sharks use this area for resting after feeding in other areas of the nursery area; further investigation is required to assess this.

Research on other shark species indicates that environmental cues, such as temperature and salinity, can play an important role in a species' distribution within estuaries (Carlisle and Starr 2009; Castro 1993; Grubbs et al. 2007; Heupel 2007; Heupel and Simpfendorfer 2008), although the relationship to specific cues may vary between species or between estuaries even for the same species (Heupel et al. 2010). In the current study, the presence of sharks in the estuary was highly seasonal, corresponding to their peak presence on surrounding coastal waters over the spring and summer period (Bruce and Bradford 2012) and this drove a correlation with coastal water temperatures and the presence of juvenile white sharks in the Port Stephens estuary.

This study has demonstrated that estuarine habitats adjacent to known coastal nursery areas are frequently used by juvenile white sharks with 56% of tagged sharks being recorded within these systems. Individuals were recorded revisiting these estuarine habitats in successive years and one individual was recorded moving between the widely geographically separated Port Stephens and Corner Inlet systems. These patterns of estuarine use by multiple individuals for extended periods of occupancy and repeated over consecutive years are consistent with the nursery area definition proposed by Heupel et al. (2007) and indicates that the eastern basin of the Port Stephens estuary and broad areas of the Corner Inlet system form part of the overall nursery area habitat for white sharks in eastern Australia expanding the nursery areas footprints described by Bruce and Bradford (2012). The extent to which juvenile white sharks use other estuarine systems along eastern Australia or in deed other areas across their global range remains unclear, but both anecdotal and research-based observations suggest a more wide-spread use of estuaries than previously considered. The reason for their occurrence within these estuarine habitats is not clear, but is most likely in response to foraging opportunities provided by the local abundance of potential prey and this warrants further investigation. These findings suggest that juvenile white sharks may be exposed to estuarine-based anthropogenic impacts previously not considered as representing significant threats (Mull et al. 2013). In addition, given the eastern section of the Port Stephens estuary is very popular with tourist activity, particularly swimming in the eastern basin between Nelson Bay and Shoal Bay, there is a higher potential for interaction between juvenile white sharks and humans than previously considered, especially over the warmer months when white sharks are more prevalent and human water use increases. This study provides a better understanding of the nature of estuarine use by white sharks, raising awareness of encounter risk within these highly utilised waterways and can inform management of potentially adverse human-shark interactions.

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Compliance with Ethical Standards

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Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval: This research was carried out under approval of the New South Wales Animal Care and Ethics Committee (permit ACEC REF 12/07-CSIRO) and the Tasmanian Department of Primary Industries, Parks, Water and Environment Animal Ethics Committee (AEC 1/2013-14).

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Tables

Table 1 Details of receiver deployments within Port Stephens estuary.

Site Name	Depth (m)	Date first deployed	Date last retrieved	Total days
YAC1	10	11 October 2012	29/04/2013	200
YAC2	9	12 July 2012	29/04/2013	291
JMY1	7	30 August 2011	30/09/2014	1127
JMY2	6	26 September2013	30/09/2014	369
SB1	7	4 September 2012	30/04/2013	238
SB2	5	12 July 2012	23/04/2014	650
NB1	4	12 July 2012	9/07/2015	1092
NB2	5	4 September 2012	23/04/2014	596
HA1	15	8 November 2010	18/11/2015	1836
HA2	4	12 July 2012	23/04/2014	650
ANCH1	4	1 November 2011	26/04/2013	542
TM1	17	8 November 2010	29/04/2013	903

Table 2 Details of the 20 juvenile white sharks detected within the Port Stephens estuary, New South Wales and/or Corner Inlet, Victoria.

Shark	Tagging date	Tagging location	Total length (cm)	Sex	First date detected in estuary	Last date detected in estuary	Number days detected
T09.01	28/10/09	Bennett	240	Female	12/01/11	17/12/11	4
T09.02	29/10/09	Bennett	210	Female	11/11/10	18/11/12	6
T09.21	30/10/09	Bennett	240	Female	11/01/11	21/01/11	3
T09.22	30/10/09	Bennett	220	Female	21/11/10	26/08/11	9
T09.23	30/10/09	Bennett	210	Female	13/11/10	1/12/10	4
T10.25	27/10/10	Stockton	190	Male	13/11/11	23/11/11	2
T10.26	27/10/10	Stockton	220	Male	10/09/11	10/09/11	1
T10.28	27/10/10	Stockton	220	Female	12/01/11	14/05/11	3
T11.01	25/10/11	Bennett	210	Female	2/11/11	26/11/12	4
T11.02 (Port Stephens)	25/10/11	Bennett	220	Female	30/10/11	3/12/12	22
T11.02 (Corner Inlet)	25/10/11	Bennett	220	Female	16/12/111	30/03/12	43
T11.03	25/10/11	Bennett	230	Male	26/10/11	29/10/12	8
T11.10	25/10/11	Bennett	240	Male	29/10/11	26/11/11	8
T11.11	25/10/11	Bennett	170	Male	29/10/11	6/11/11	3
T11.14	25/10/11	Bennett	230	Female	28/10/11	5/02/12	33
T12.02	19/12/12	Bennett	220	Female	21/12/12	20/07/14	4
T12.03	10/10/12	Bennett	280	Female	9/10/12	5/10/15	104
T12.04	10/10/12	Bennett	230	Male	6/11/12	6/12/13	7
T12.05	19/12/12	Bennett	260	Female	10/10/12	29/12/12	2
T13.09	31/10/13	Bennett	190	Male	4/11/14	4/11/14	1

T14.03	24/11/14	Bennett	190	Female	8/11/15	8/11/15	1

Table 3 Estimated coefficients (and back-transformed estimates) of linear and categorical predictors for the zero-inflated Poisson GLM model and their standard errors (S.E.).

	Poisson (count) with log link		Binomial with logit link	
Explanatory variable	Estimate	SE	Estimate	SE
Moon illumination	-0.29 (0.74)	0.21 (0.55)	-6.71 (0.00)	1.55 (0.83)
Rainfall	-0.05 (0.95)	0.12 (0.53)	-15.49 (0.00)	8.50 (1.00)
Tide	0.31 (1.36)	0.12 (0.53)	-0.31 (0.43)	0.41 (0.60)
Month	0.23 (1.25)	0.02 (0.50)	0.10 (0.52)	0.06 (0.51)
Water temperature	-0.54 (0.58)	0.04 (0.51)	-0.43 (0.39)	0.21 (0.55)

Figures

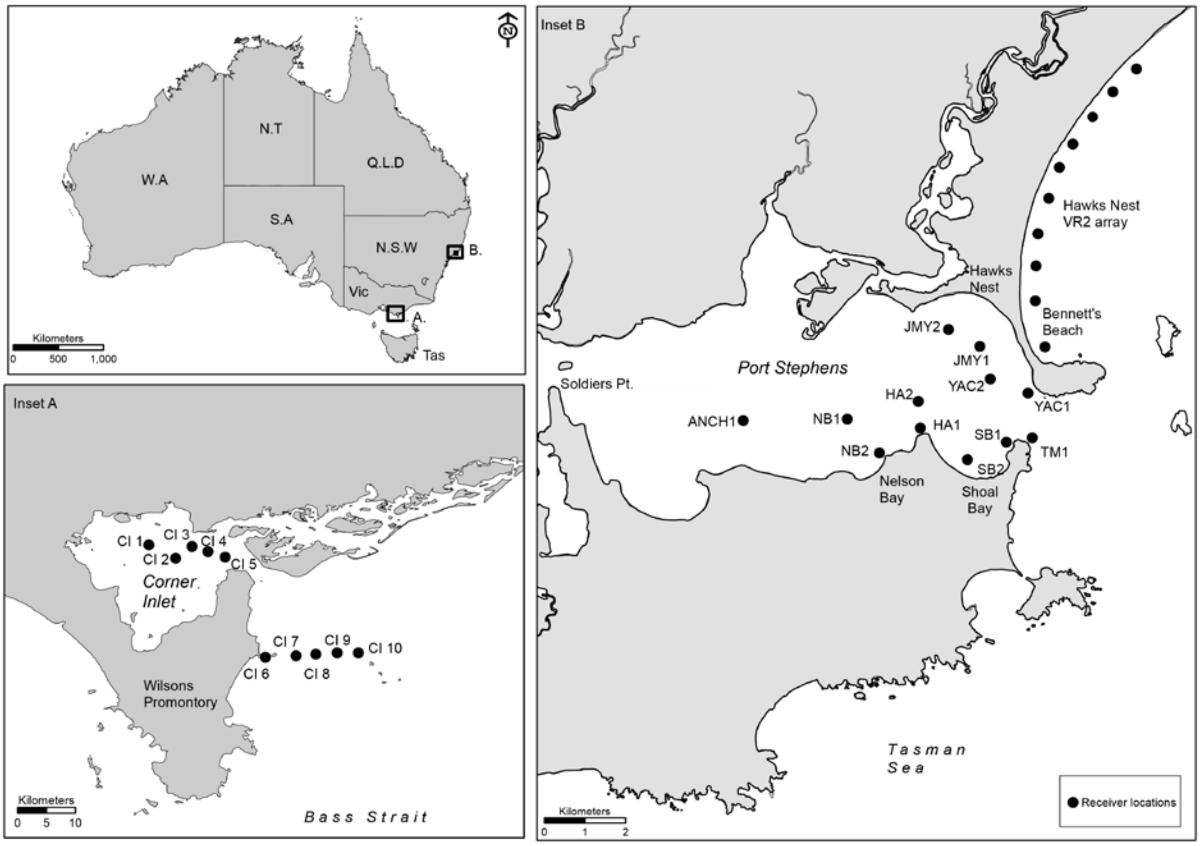

Fig. 1 Location of study sites and inset boxes indicating the positioning of acoustic receivers in Corner Inlet, Victoria (Inset A) and Port Stephens, New South Wales (Inset B).

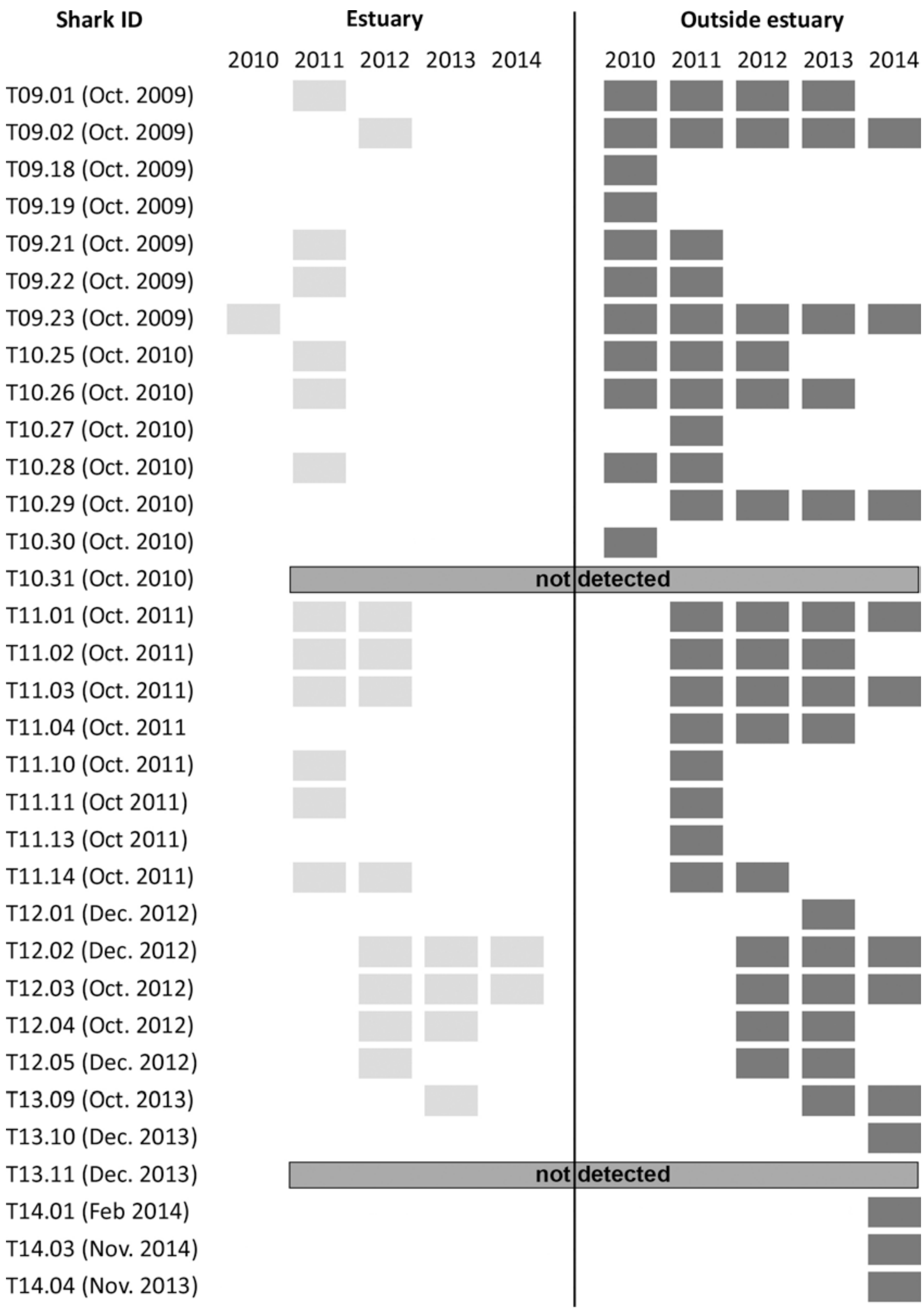

Fig. 2 Detection pattern for tagged juvenile white sharks (month, year of tagging) in Port Stephens. Light grey boxes indicate detections inside the estuary; dark grey boxes indicate detections outside of the estuary; grey bars with black outline indicate sharks which were never acoustically detected.

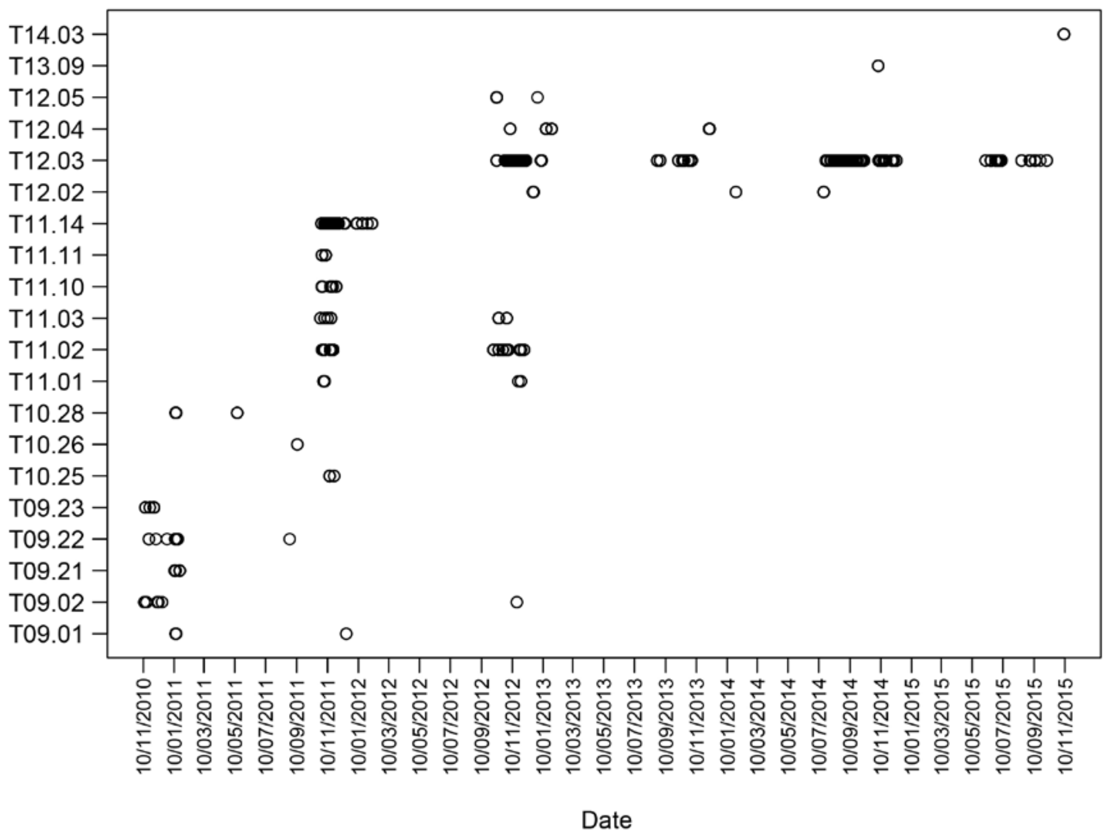

Fig. 3 Time series of detections across all VR2W receivers in Port Stephens estuary from 2010-2015 for 20 juvenile white sharks.

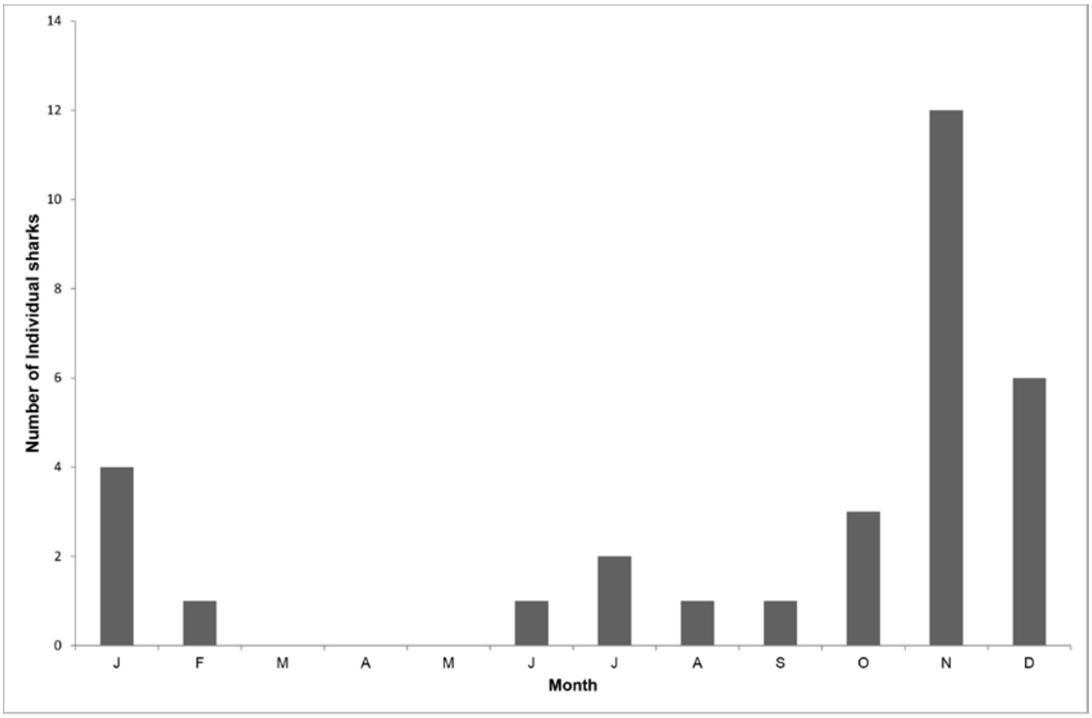

Fig. 4 Number of individuals sharks detected monthly (1=January, 12 = December) on acoustic receivers within the Port Stephens estuary from 2010-2015.

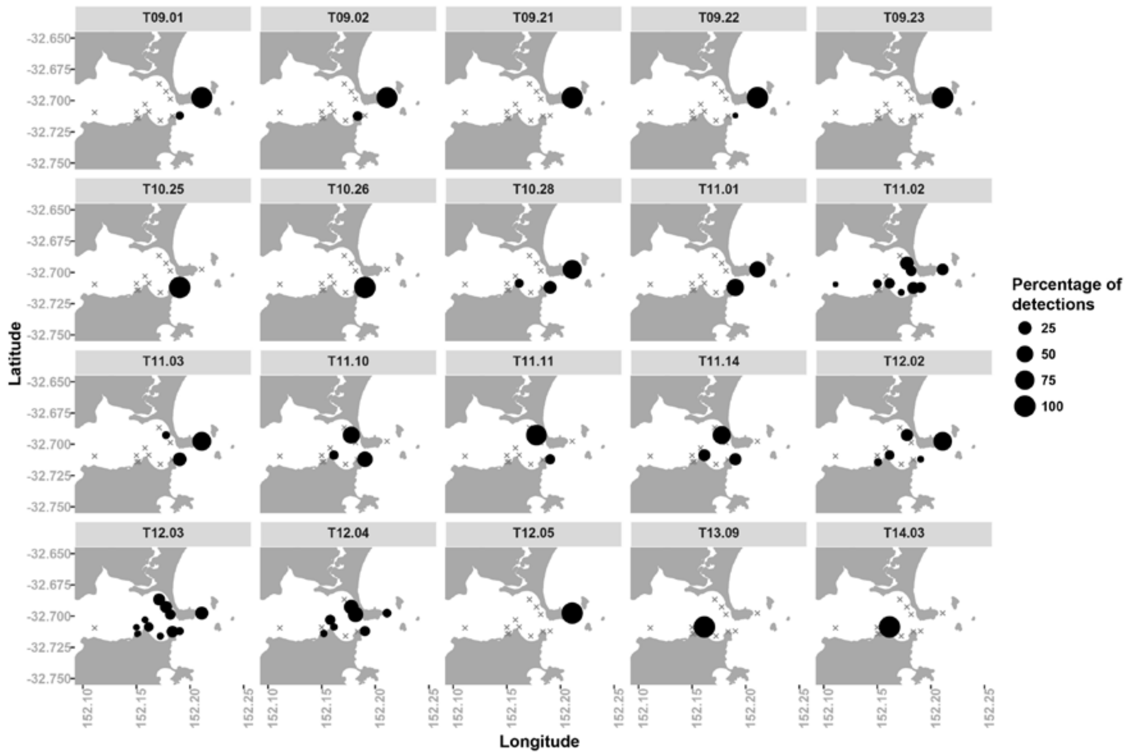

Fig. 5 Percentage of detections per day that receiver was deployed for individual sharks (n=20) at each VR2W receiver ("x") deployed within the Port Stephens estuary.

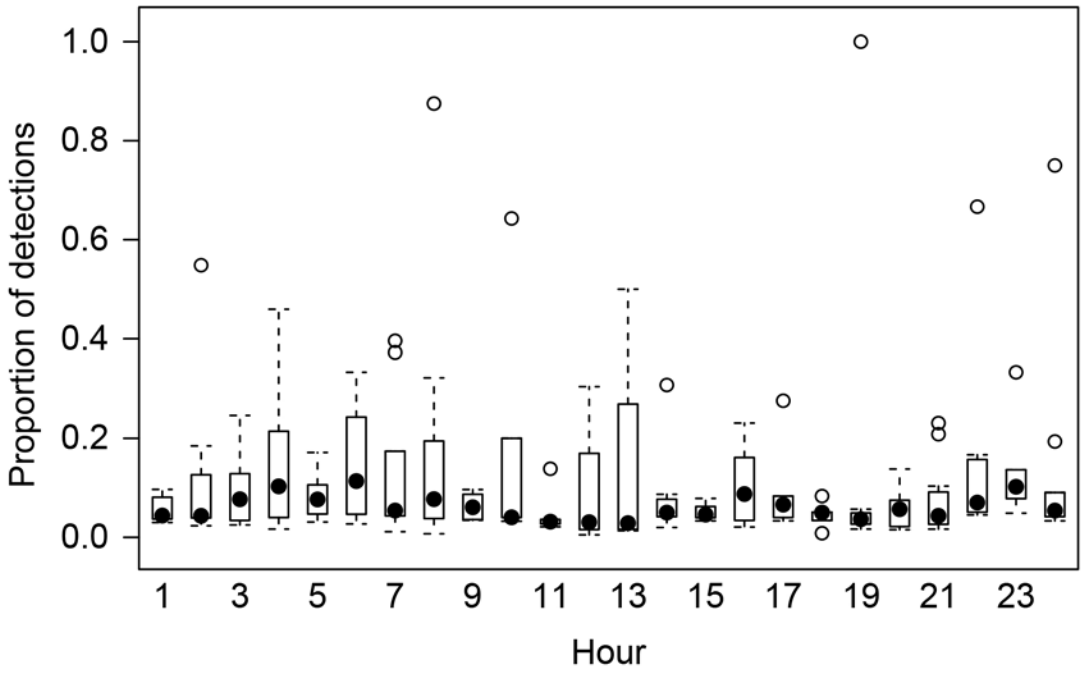

Fig. 6 Proportion of detections per hour of the day for 20 sharks detected within Port Stephens estuary.

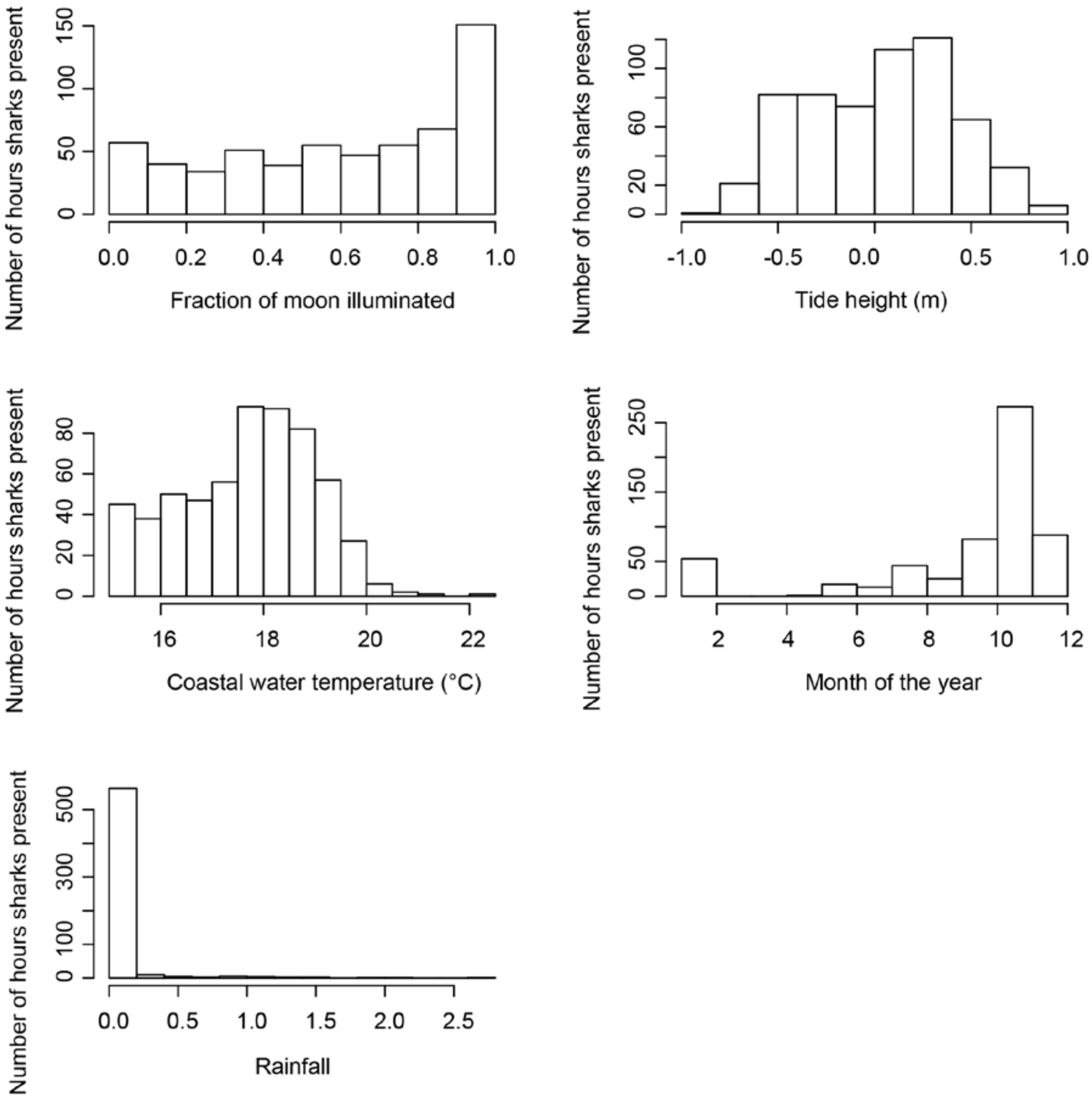

Fig. 7 The number of hours a shark was detected within Port Stephens estuary against environmental variables.