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Population distribution, aggregation sites and seasonal occurrence of Australia's western population of the grey nurse shark *Carcharias taurus*

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ABSTRACT: Western Australia (WA) is host to a genetically discrete population of grey nurse sharks *Carcharias taurus*, listed by the IUCN as Near Threatened based on mean annual catch rates prior to protection within Australian waters in 1997. Only one small aggregation has been documented in WA to date with little data available on population dynamics, or spatial and temporal distribution along the WA coastline. We analysed *C. taurus* data from 16 years (2006–2021) of diver observations (2347 sightings) and commercial fisheries bycatch records (574 sharks), finding evidence of 4 new aggregation sites. Sightings at Shark Cave, a popular dive site near Perth, were related to water temperature and time of year (non-linear), with sightings per unit effort generally higher during the warmer months of summer and autumn (20–22°C). Evidence of fishing injuries was found on 17% of all *C. taurus* photo-tagged at Shark Cave. Strong site philopatry was apparent at most sites, and included a male shark that returned for 12 consecutive years to the Exmouth Navy Pier. This study confirms the range of Australia's western population of *C. taurus* from near the South Australia/WA border, north to Shark Bay, with distribution extending further north along the coast when sea temperatures are lower (May–December). The beneficial role of citizen science in large observation studies such as this one is supported. However, while this research greatly increases the *C. taurus* knowledge base in WA, a large information deficit still exists. The identification and assessment of further aggregation sites is recommended, underpinning future management and protection measures for this iconic species.

KEY WORDS: *Carcharias taurus* · Aggregation · Site philopatry · Population distribution · Seasonality · Western Australia

1. INTRODUCTION

The grey nurse shark *Carcharias taurus* occurs around the world in subtropical and temperate waters, with its global conservation status recently upgraded to Critically Endangered (Rigby et al. 2021). The species is vulnerable to anthropogenic pressures owing to its reproductive biology and propensity to aggregate in specific locations in nearshore environments (Dicken et al. 2007, Hoschke & Whisson 2016, Haulsee et al. 2018). It displays adelphophagous reproduction, with embryos feeding on ova and subsequently cannibalising each other until only 1 pup remains in each uterus. Consequently, a maximum of only 2 pups are born every 2 yr at approximately 1 m total length (TL) (Gilmore et al. 1983, Branstetter & Musick 1994, Last & Stevens 2009). Lifespans of this species reach at least 40 yr for females and 34 yr for males (Passerotti et al. 2014, Harry 2018). The longest records for wild *C. taurus* in mark and recapture studies are 22 yr (male) off the south coast of WA (Jakobs & Braccini 2019) and 26 yr (female) off the

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coast of South Africa (https://issuu.com/saambr/docs/tagging_news_2020_interactive). While *C. taurus* is documented to reach sexual maturity at 6–7 yr and 190–195 cm TL for males, and 9–10 yr and 218–235 cm TL for females (Gilmore et al. 1983, Lucifora et al. 2002, Goldman et al. 2006), different populations may display varying rates of growth and maturity (Bass et al. 1975, Gordon 1993, Otway & Ellis 2011, Passerotti et al. 2014, Hoschke & Whisson 2016).

Although reported from water depths up to 168 m (McAuley 2004) and 230 m (Otway & Ellis 2011) on the western and eastern continental shelves of Australia, respectively, *C. taurus* is more commonly observed in small groups around inshore rocky reefs in water depths of 15 to 40 m. These locations are known as aggregation sites (Otway et al. 2003, Hoschke & Whisson 2016), and when combined with a low reproductive rate, this aggregatory behaviour in shallow water makes the species vulnerable to overfishing, with severe declines reported in the northwest and southwest Atlantic Ocean (Musick et al. 2000, Lucifora et al. 2002) and eastern Australia (Otway et al. 2004). In other documented populations of *C. taurus*, adult sharks migrate north and south along coastlines to mate and breed (Smale 2002, Dicken et al. 2006, 2007, Haulsee et al. 2018) and studies on Australia's eastern population indicate a varied migration pattern depending on sex and maturity of sharks (Bansemer & Bennett 2009, 2011). More than 20 aggregation sites have been described off Australia's east coast (Bansemer & Bennett 2010), with the majority now protected from fishing (Lynch et al. 2013, DEE 2014), following their identification as habitat critical to survival of the species (DEWHA 2009). The northernmost site — Wolf Rock off southern Queensland — is the only location where mature sharks are known to aggregate for mating and gestation. Sites further south on the east coast host a mixture of mature and immature sharks depending on the time of year. Mature males travel north up the coast in winter to mate between October and December, and are thought to then head offshore before reappearing further south from February onwards; the cycle repeats the following year (Bansemer & Bennett 2011). Females migrate north in November/December for mating then gestate at Wolf Rock before slowly migrating south to pup the following August/September. They are thought to remain in the southern or central areas until the cycle is repeated every 2 to 3 yr (Bansemer & Bennett 2009, 2011). Immature and juvenile sharks on the east coast tend to stay at the same sites over consecutive seasons and years (Bansemer & Bennett 2011).

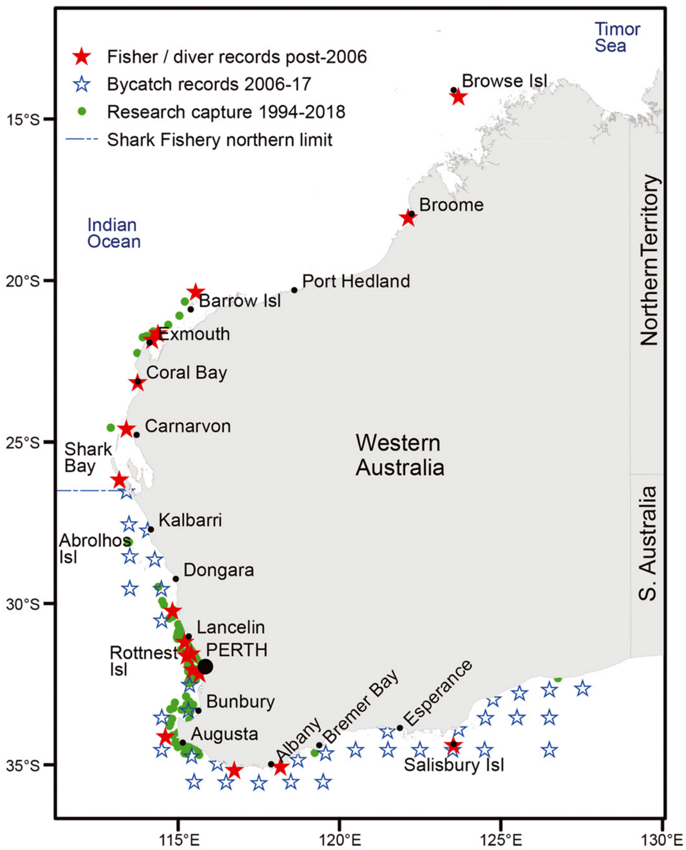

Fig. 1. *Carcharias taurus* occurrences in Western Australia. Red stars: records from divers/fishers; blue stars: commercial fishing bycatch representing at least one shark caught within the corresponding graticule block; green dots: Department of Primary Industries and Regional Development historical research capture data

DNA diversity studies have revealed that the population of *C. taurus* occurring along the western and south-western part of the Australian continent is genetically discrete from the eastern Australian population, as well as from other populations around the world (Stow et al. 2006, Ahonen et al. 2009). The range of the western population has previously been documented extending westwards from near the Western Australia (WA)–South Australia (SA) border, around the south-west, to just north of Exmouth (Chidlow et al. 2006, Hoschke & Whisson 2016) (Fig. 1). Occasional records further north in WA have included 7 specimens caught offshore in 55–195 m depth between Exmouth and Barrow Island by the WA Department of Primary Industries and Regional Development (DPIRD unpubl. data, 2001–2004), and 4 sharks caught by Indonesian fishers near Browse Island in 2013 (Momigliano & Jaiteh 2015). Further, 2 sharks were caught by longline fishers off Bali (White et al. 2006), and in Northern Territory waters observations have been recorded from the Arafura Sea

(Last & Stevens 2009) and a seamount in 130–160 m depth in the Timor Sea (www.abc.net.au/news/2019-04-06/grey-nurse-shark-population-discovered-nt-tiwi-conocophillips/10978352).

The western population of *C. taurus* in Australia is listed as Near Threatened on the International Union for Conservation of Nature (IUCN) Red List (Pollard et al. 2003) based on a stable catch per unit effort between 1989 and 1997 (Cavanagh et al. 2003). In 1997 the species became protected in all Australian Commonwealth Waters and in 1999 was protected in WA waters, where it was listed as Vulnerable (EPBC Act 1999). Since it became protected in Australian waters, *C. taurus* bycatch data has been the only empirical indicator of population status. Unlike the eastern population of *C. taurus* in Australia, the western population has been the subject of minimal research. A pop-up archival tag study in 2003 tracked 3 juveniles and 1 mature female shark, with the juveniles travelling up to 489 km north from Rottnest Island or Ledge Point (south of Lancelin) before returning south, and the female remaining near her tagged location off the Abrolhos Islands (McAuley 2004) (Fig. 1). The tagged sharks spent most time in water depths of 20 to 60 m (range: 0–146 m) and water temperatures between 16 and 22°C (McAuley 2004). In 2005, the Department of Fisheries (now DPIRD) investigated several potential aggregation sites described by divers and fishers; however, the project failed to confirm any sites (Chidlow et al. 2006). Then, as part of its 2009–2016 shark monitoring project, DPIRD fitted 3 *C. taurus* with acoustic tags (McAuley et al. 2016). A male shark (2 m fork length) was recorded near its tagged location south of Augusta in late August 2012, then offshore from Rottnest in early September 2012, and again 1038 km further north near Coral Bay in mid-October 2012, providing the first evidence of male *C. taurus* migration in WA (Jakobs & Braccini 2019). One tagged female was detected 3593 times by receivers between the Perth Coast and Rottnest Island from October 2014 to May 2015 but not detected elsewhere. Most detections between October and January were in Cockburn Sound during the daytime when *C. taurus* are usually less active (Pollard et al. 1996); however, they coincided spatially and temporally with a snapper *Chrysophrys auratus* spawning aggregation (Crisafulli et al. 2019). The first *C. taurus* aggregation site confirmed in WA was the result of a 5 yr study (2007–2012) near Exmouth on WA's North West Cape, where a small aggregation was documented at the Exmouth Navy Pier, with sharks displaying strong site philopatry and residency between May and November each year (Hoschke & Whisson 2016).

This study aimed to compile all available data for Australia's western *C. taurus* subpopulation, including photographic records submitted via a Community Monitoring Program, DPIRD research data, commercial fisheries bycatch data, and updated results from WA's only documented aggregation site (Exmouth Navy Pier), to provide a more definitive assessment of range and population distribution, including additional aggregation sites and indicators of seasonal occurrence.

2. MATERIALS AND METHODS

2.1. Community Monitoring Program

In 2014, a Community Monitoring Program was established as part of the present study to observe and document *Carcharias taurus* occurrences at a site known as 'Shark Cave' near Rottnest Island, where sharks had been reported by recreational divers since at least 2006. The monitoring program was subsequently expanded to include all historic sightings of *C. taurus* throughout WA and was promoted by the authors via a mix of social media, information/education sessions to local dive/fishing organisations, presentations to marine scientists and the general public, and the publication of a feature article in *The Rottnest Island Fish Book* (Whisson & Hoschke 2017). The Community Monitoring Program involved the submission of photographs and videos of *C. taurus* dating back to 2006. All data (photographs, videos, accompanying information, etc.) were recorded in a database including date, location, number of sharks, water temperature and data source. Sex was determined by presence/absence of claspers (if visible), with the authors estimating maturity of females based on indications of mating scars or pregnancy, and/or published correlations with total length (TL) (Lucifora et al. 2002, Dicken et al. 2007). Given that the age at maturity of males in WA may be greater than in other populations of *C. taurus* (Hoschke & Whisson 2016), maturity estimates for males were based on clasper size and calcification. Clasper lengths extending >75% of the distance between the pelvic and anal fins, and appearing calcified, were classified mature. The number of sharks recorded from each dive was either the maximum number visible in a single photograph or video frame (MaxN); or if no footage was available, the maximum number observed by the diver at any one time. Only one MaxN value was recorded from each location per day, to avoid duplication.

2.2. Exmouth Navy Pier

Exmouth Navy Pier has been the subject of an ongoing monitoring programme since 2007 when an aggregation of *C. taurus* was first reported at the site (Hoschke & Whisson 2016). The pier is located just north of Exmouth (Fig. 1) and extends 175 m offshore in water depths up to 15 m and the area has been protected from fishing since 1964 as prohibited under the Commonwealth Defence (Special Undertakings) Act 1952. The present study combined all pre-existing *C. taurus* records (2007–2012) from this programme with subsequent monitoring data (2013–2021) to record site philopatry and the number, sex and maturity of *C. taurus* at the site over the entirety of the programme (2007–2021). Fixed position video records (Hoschke & Whisson 2016) were supplemented with a combination of handheld video footage and underwater photography, in addition to observations from a local dive company recorded on a daily log.

2.3. Photographic identification and shark measurements

C. taurus individuals were uniquely identified, or 'photo-tagged', by recording the pattern of spots on their flanks, which are present from birth (Bansemer & Bennett 2008). A photographic database combining the authors' data with the Community Monitoring Programme was established to record photographs of each flank with a unique photo-tagged ID number, shark sex and maturity, location and date of sighting, photographer, data source, and a photo quality rating. Additional information was recorded for fishing injuries, swelling in females indicating possible pregnancy, scoliosis and mating scars. Only the left flank of each shark was used for determining unique shark numbers to avoid duplication, as it was not always possible to match the left and right sides of the same shark (except at the Exmouth Navy Pier, where all sharks had left and right sides paired by the authors). Shark size was determined by measuring precaudal length (PL, from the tip of the snout to the precaudal pit) and TL using a stereo laser measuring system attached to a handheld camera (estimated error ± 0.1 m) or *in situ* tape measurement when sharks were motionless near the seafloor (estimated error ± 0.2 m) as per Hoschke & Whisson (2016). Given the inherent biases in measuring TL directly (e.g. variations in caudal fin posture/angle), PL is considered more accurate (Francis 2006); however, TLs measured with the caudal fin in its usual resting/natural position were included for comparison to published literature.

2.4. Fisheries bycatch data

Bycatch data for *C. taurus* was supplied by DPIRD and extracted from the Temperate Demersal Gillnet and Demersal Longline Fishery (TDGDLF) for the period 2006 to 2017 (these are the only commercial fisheries in WA with reportable *C. taurus* bycatch). This fishery comprises the West Coast Demersal Gillnet and Demersal Longline (Interim) Managed Fishery (operates between 26° S and 33° S) and the Joint Authority Southern Demersal Gillnet and Demersal Longline Managed Fishery (operates between 33° S and the WA/SA border). The area excludes the Abrolhos Islands and an area off the Perth metropolitan coast to the 250 m depth contour where shark fishing has been prohibited since 15 November 2007. Commercial shark fisheries further north have been closed between Steep Point and Exmouth since 1993, between Exmouth and Broome since 2005, and north of Broome since 2008. The limited shark catch reported by Australian commercial fishers north of Broome for the period 2005–2008 did not include any *C. taurus*. Each bycatch record of *C. taurus* from the TDGDLF was referenced to the one degree graticule block it occurred within, and the sum of all data points from 2006 to 2017 for each block was displayed on a map using Jenks Natural Breaks to summarise the spatial distribution of catches. Where comments on size/sex were included in the original bycatch record they were used to classify shark maturity/sex and plotted to show spatial distribution. Fishing effort data was accessed for an average of 25.8 vessels active within the fishery per year (range: 20–32) between 2008 and 2017. Data in the form of fishing day count (i.e. sum of the number of active days for all fishing vessels) for each year was used to determine bycatch per unit effort (BPUE) for *C. taurus* (fishing day counts not available for 2006 and 2007). The linear trend in BPUE over time was investigated using linear regression.

2.5. Ocean temperature measurement

Multiple temperature loggers (Onset Hobo model UA-001-64 data loggers) were deployed off Rottnest Island (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/n050p107_supp1.pdf) to measure *in situ* conditions near Shark Cave. The loggers were attached to ropes approximately 1 m above the seafloor with a float above and weight below, in water depths of 3 m (Parker Point), 8 m (South) and 12 m (Green Island). Ocean temperatures were recorded hourly from February 2010 to December 2021. There were periods with incomplete data due to loss or flooding of a logger, and no data was recorded for any location for the period January to May 2015 (Supplement 2 at www.int-res.com/articles/suppl/n050p107_supp2.xlsx). Recorded temperatures were averaged across the 3 sites to calculate a general temperature record for the region for comparison with shark sightings.

2.6. Statistical analysis

The extensive dataset arising from the *C. taurus* Community Monitoring Program at Shark Cave allowed for intra- and inter-annual variations in prevalence as determined by 'sightings per unit effort' (SPUE), which was calculated as the cumulative MaxN per month divided by the number of dives (aggregated by month). This normalization accounted for the variation in dive effort between months. Differences in SPUE among months were determined using a non-parametric Kruskal-Wallis rank sum test, with post hoc pairwise comparisons (corrected for multiple testing) analysed with Dunn's Test ($\alpha = 0.05$). Trends in SPUE across time were assessed using linear regression. As this discretised analysis revealed weak but non-significant intra- and inter-annual differences in SPUE (likely limited by sample size), we also tested for non-linear relationships between MaxN sightings, day of year (DOY), year, and *in situ* ocean temperature data from nearby loggers using a generalized additive model (GAM) (Hastie & Tibshirani 1990).

Using a GAM allowed for estimation of the complex non-linear relationships between the predictor variables and the response (MaxN). Predictor variables were tested for collinearity, which can confound interpretations of model outputs (Dormann et al. 2013). Owing to the strong correlation between DOY and ocean temperature ($R^2 = 0.73$, $p < 0.001$) using the circular-linear correlation functionality in R (*circlin.cor*{Directional}; Tsagris et al. 2022), models were therefore created to test for differences in explanatory power. Few records of 'zero sightings' within the dataset necessitated the construction of models that employed a Poisson distribution with a log-link function. Thin plate shrinkage smoothers (ts) were used to fit the relationship between MaxN and year and temperature, whereas a cyclic cubic regression spline was used for the circular variable DOY. Shrinkage smoothers penalize the effective degrees of freedom to 1 when they do not contribute meaningfully to the model performance (Marra & Wood 2011). We limited the number of knots (the maximum number of inflections possible for fitted models) to 6, which reduces model overfitting and caps the effective degrees of freedom at 5 (Wegmann et al. 2016). Model performance was evaluated by considering the reduction of Akaike's information criterion (AIC) and maximizing explained deviance as an indicator of increased model performance (Wood 2006). These models were only used to explore significant differences in sightings over time and in different ocean conditions and were not used to predict; therefore, no further cross-validation was conducted. All statistical analyses were conducted in R version 4.1.2 (R Core Team 2021).

3. RESULTS

3.1. Community monitoring

The Community Monitoring Program resulted in 4 new *Carcharias taurus* aggregation sites being identified between Rottnest and Lancelin in WA (Fig. 2). 'Shark Cave' is located approximately 100 m inside the south-west corner of the West End Demersal Sanctuary Zone within Rottnest Island Marine Park; 'Opera House' is a deeper dive site (~30 m) situated 5 km to the northeast of Rottnest Island within a large limestone reef cave system; 'Direction Bank' includes a number of caves in depths of 30–40 m approximately 30 km WSW of Two Rocks; and 'Key Biscayne' is a jack-up oil rig platform that sank in 42 m of water in 1983 while under tow approximately 20 km south-west of Lancelin. Data compiled from a total of 683 dives and 216 d of video footage in WA resulted in 2347 *C. taurus* records (Table 1) and the photo-tagging of 148 sharks using left flank spot patterns.

3.2. Shark Cave, Rottnest Island

Diver records (comprising photographs, video footage or dive logs) included 78 dives undertaken during the Community Monitoring Program (2014–2021), and a further 41 dives from historic records dating back to May 2006. Sharks were observed at the site year-round, although SPUE appeared to vary

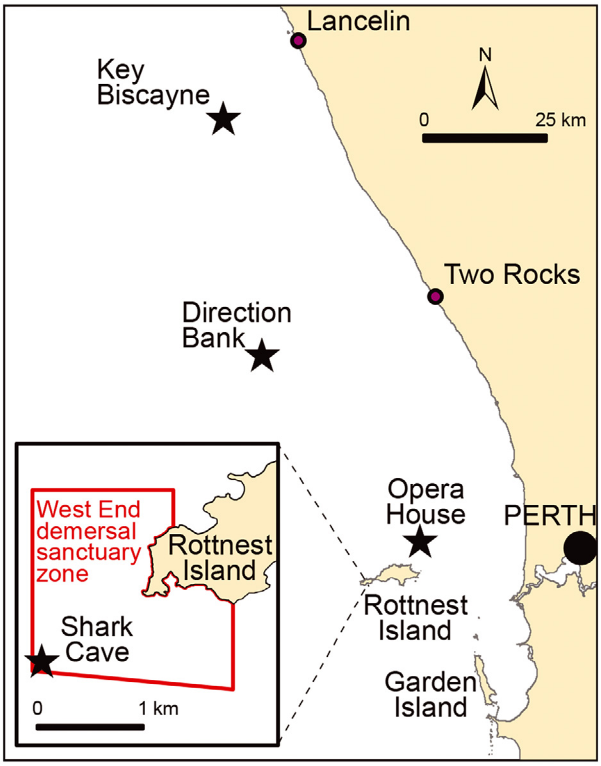

Fig. 2. Location of *Carcharias taurus* aggregation sites near Perth, Western Australia (stars)

seasonally (Fig. 3a). In general, SPUE was higher during the warmer months at the beginning of the year and decreased as water temperatures cooled (Fig. 3a), with water temperature ranging between 18 and 24°C (Fig. S2 in Supplement 1). The Kruskal-Wallis non-parametric test was not able to determine significant differences in SPUE by month ($\chi^2 = 17.85$, df = 11, p = 0.09); however, the relationship between time of year and *C. taurus* sightings was further explored using GAMs. Annual total sightings per unit effort did not show any significant change over time ($F(1,14) < 0.001$, p = 0.98), although some years recorded higher SPUE on average than others indicating variability may exist from year to year (Fig. 3b).

Two generalized additive models were fitted to determine the explanatory power of DOY, year, and water temperature on the MaxN of *C. taurus* at Shark Cave. DOY and ocean temperature were found to be highly correlated ($|r| = 0.73$) and were therefore not included in the same model. In Model 1, DOY and year were both significant predictors (p < 0.001) of *C. taurus* MaxN at Shark Cave (Table S1 in Supplement 1). In general, higher sightings of *C. taurus* can be expected between Days 60 and 180 (March–June) and peaking in April, with significantly fewer sightings centred around DOY 270 (September) (Fig. 4). Year was also a significant predictor of MaxN, with lower sightings of *C. taurus* early in the record (2010–2015), and higher sightings in general from 2016–2021 (Fig. 4). In Model 2, temperature and year were similarly significant predictors of MaxN (p < 0.001; Fig. 4). MaxN was generally higher between 19–22°C, with the relationship remaining unclear at higher temperatures (Fig. 4). Model 1 explained the most variability in the response variable ($R^2 = 0.26$; Table S1); however, Model 2 performed similarly ($R^2 = 0.23$; Table S1).

Classification of sex and maturity of sharks from photos was possible in 227 out of 777 sightings at Shark Cave. Due to the varying quality of photos and videos reviewed, it was only possible to photo-tag 66 sharks from the site (left flanks only), comprising 40 females (17 mature) and 26 males (11 mature).

Table 1. *Carcharias taurus* diver observation summary from Western Australia, 2006–2021. MaxN: maximum number of individual sharks seen on a given day. Photo-tagged *C. taurus* includes left flank-identified sharks only

Site	Site depth (m)	All *C. taurus* observations: Dives	MaxN: Count	MaxN: Mean	MaxN: Max	Photo-tagged *C. taurus*: Count	Mature: Male	Mature: Female
Shark Cave, Rottnest	20–25	119	776	6.5	22	66	11	17
Opera House, Rottnest	25–30	28	111	4.0	10	9	0	2
Other records off Perth / Rottnest	10–30	38	64	1.7	6	4	0	0
Direction Bank	30–40	11	87	7.9	30	10	1	1
Key Biscayne Wreck	25–40	23	78	3.4	8	11	2	2
Steep Point caves, Shark Bay	12–16	5	9	1.8	2	5	1	3
Navy Pier, Exmouth	10–16	652	1158	1.8	8	31	2	5
Other records north of Lancelin	12–52	11	13	1.2	2	4	0	1
Other records south of Garden Isl	15–35	12	51	4.3	12	8	0	4
		899	2347			148	17	35

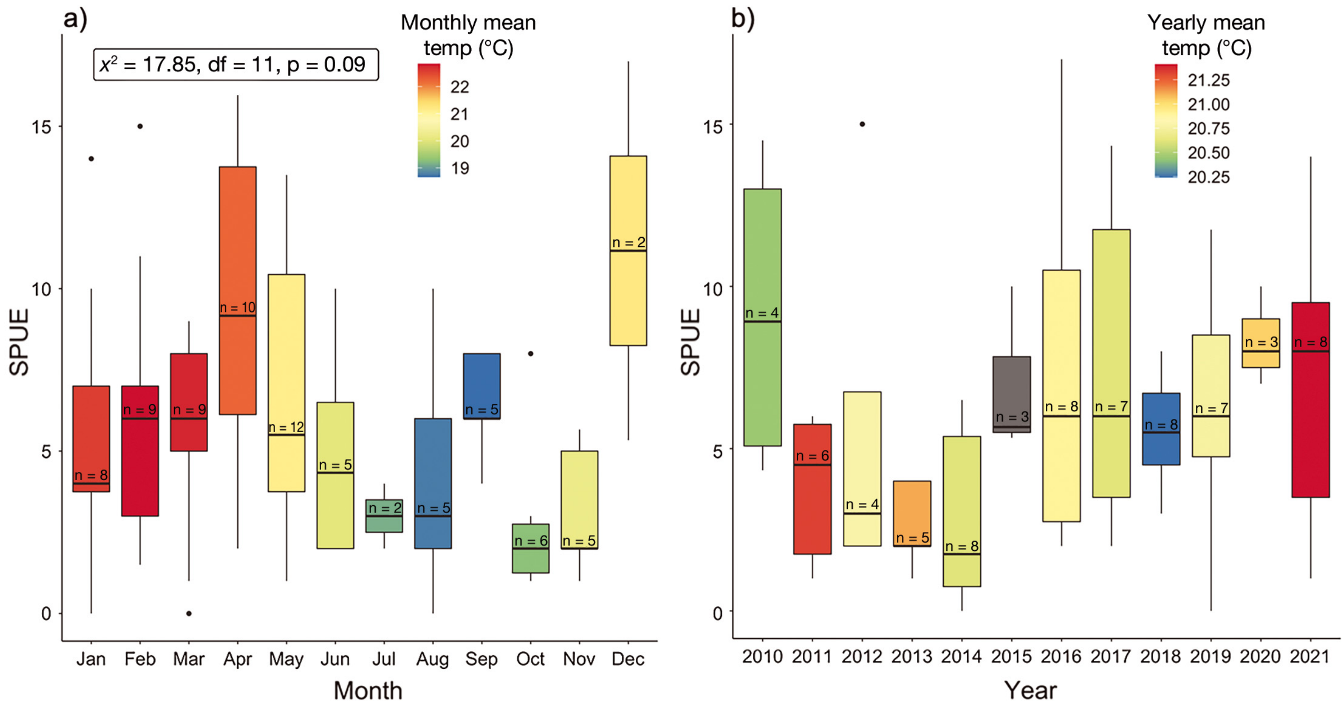

Fig. 3. Monthly sightings (MaxN) per unit effort (SPUE) of *Carcharias taurus* at Shark Cave, Rottnest Island, 2006–2021. MaxN: maximum number of individual sharks seen on a given day). (a) Boxplot showing intra-annual variation of SPUE, with sample size (n = number of monthly values within box) indicated and boxes coloured by monthly mean water temperature measured by nearby temperature loggers in 2010–2021. Kruskal-Wallis test statistics indicate no significant difference in SPUE by discrete month across years ($p > 0.05$). (b) Boxplot shows inter-annual variations of SPUE, with the sample size indicated (*n*) and boxes coloured by yearly mean water temperature measured by nearby loggers. Temperature logger coverage did not span the entire year in 2015 and the average temperature therefore is not presented (grey box)

Mature sharks appeared to exhibit more seasonality, and were most common between March and June (Fig. 5). Mature males were rarely seen outside of this 4 mo period (2 records in August, 1 in September; Fig. 5). Immature sharks exhibited less seasonality, and were observed almost all year round (Fig. 5).

Of the 66 *C. taurus* photo-tagged from Shark Cave, 20 sharks were recorded at the site in more than 1 yr, including both male and female, mature and immature sharks. One immature female shark was observed on 11 separate occasions (in 9 different months) between November 2015 and October 2017, and the longest record of an individual shark was a female that was photographed at Shark Cave 7 times (in 6 yr) between 2006 and 2017. During the study, 11 photo-tagged sharks from Shark Cave (17% of all photo-tagged sharks recorded from the site) were identified at some time with retained fishing tackle or injuries thought to have been sustained by fishing. Two sharks, an immature male and female, had large gaping wounds beneath the gills. Most minor injuries were either hooks in the jaw or tackle protruding from the mouth or gills.

Mature female *C. taurus* were observed all year round at Shark Cave (although none were photo-tagged in August or December); however, there were only minor indications of mating activity or pregnancy. Four mature females photographed in April or May had old scarring around the pectoral fins and gills, which could be attributed to mating activity, and two of these had enlarged bellies (possible pregnancy). Two additional females had fresher scarring, possibly due to mating — one was photographed with a heavily ripped pectoral fin and scratches in May 2010, and the other had fresh scars on the flanks when photographed in November 2016.

3.3. Opera House, Key Biscayne, Direction Bank

Between February 2012 and November 2021, the Community Monitoring Program resulted in 28 dives documented from the Opera House site (average 3 dives yr^{-1}; range: 0–5). A MaxN of 5 or more sharks was recorded in 6 out of 9 yr (excluding 2014 when no dive records were received) (Fig. 6) and an average

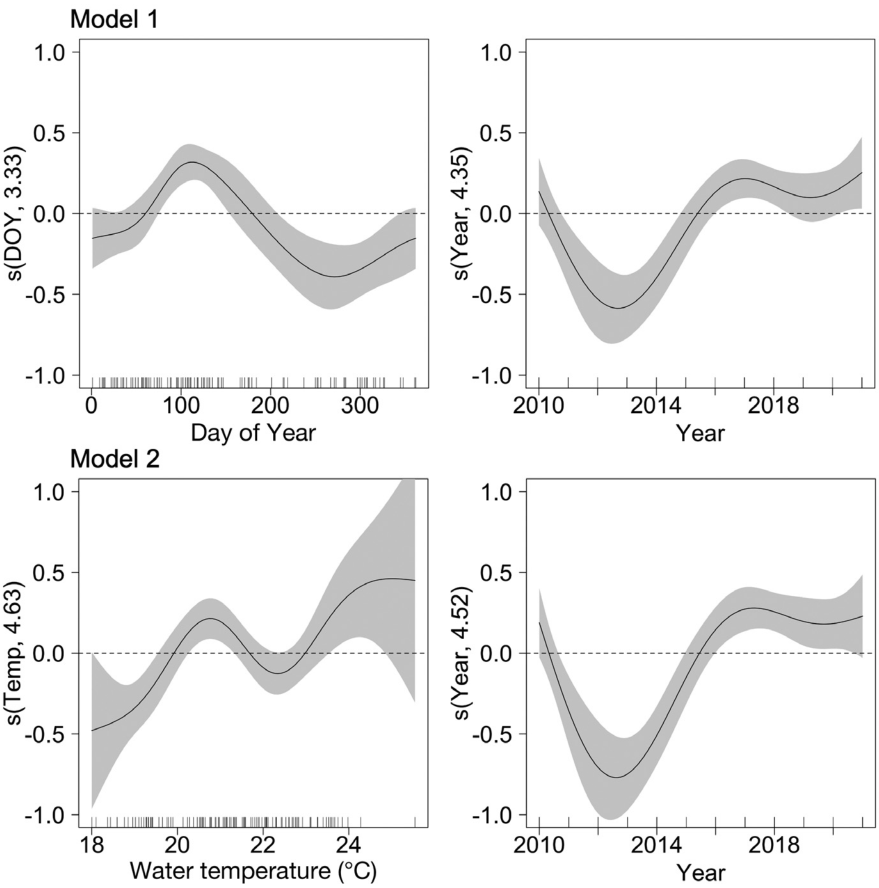

Fig. 4. Predictor variable response functions for generalized additive models predicting sightings (MaxN) of observed *Carcharias taurus* at Shark Cave, Rottnest Island, 2006–2021. Black lines: smoothed curve of partial additive variable effect MaxN; grey shading: 95% confidence interval. Partial variable responses >0 are predictive of increased *C. taurus* MaxN, while partial variable responses <0 are predictive of decreased *C. taurus* MaxN. Short vertical lines (rug) on the *x*-axis of single variable plots represent the distribution of variable observations upon which the model's response was built. MaxN: maximum number of individual sharks seen on a given day; DOY: day of year

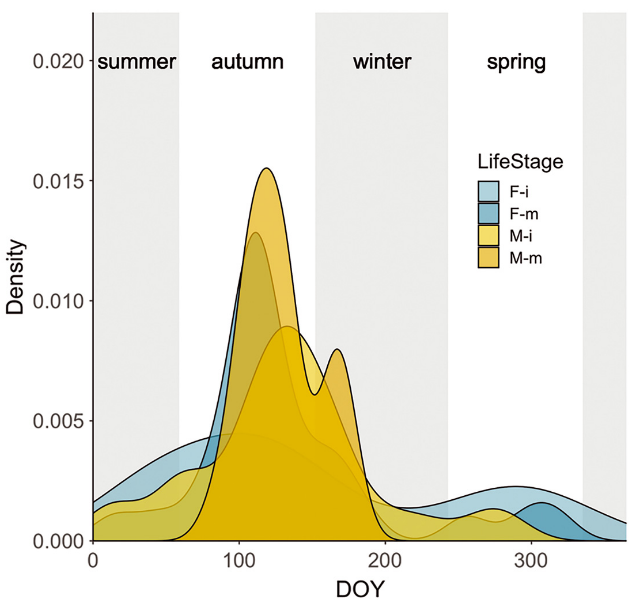

Fig. 5. Density of photo-tagged *Carcharias taurus* at Shark Cave, Rottnest Island by sex and maturity, 2006–2021. F-i: immature female; F-m: mature female; M-i: immature male; M-m: mature male. DOY: day of year. Data represents density of observations of left flank photo-tagged sharks with a maximum of one record for each shark per DOY, cumulated over the study period

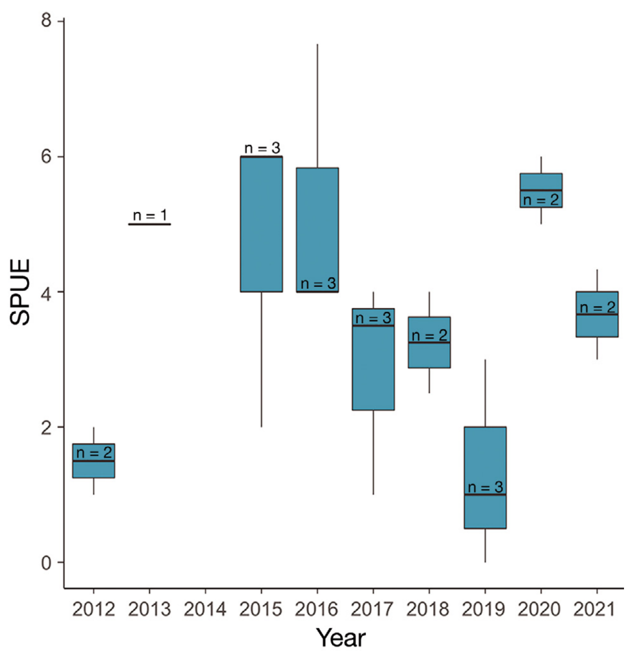

Fig. 6. Combined yearly sightings (MaxN) per unit effort (SPUE) of *Carcharias taurus* at Opera House, Rottnest Island, 2012–2021. Number of monthly SPUE values per year summarized by boxplot is indicated. MaxN: maximum number of individual sharks seen on a given day

of 3.96 (range: 0–10) sharks seen per dive (Table 1). Sharks were photographed in all months except March, June, and August (no dives were recorded in these months), and all were immature apart from one mature female photographed in May 2017, and a smaller female with possible mating scars photographed in August 2012. Most sharks were seen in November (MaxN = 10 in 2015 and 2016), and 11 out of 23 dives at the site recorded at least 5 sharks. The intermittent and opportunistic nature of this dataset prevents further exploration of the seasonality and interannual variability at this site, however sightings remained relatively consistent over time (Fig. 6)

Of the 23 dives undertaken at the Key Biscayne site (Table 1), 9 were in March and 7 in April, with averages of 3 and 5 sharks photographed or videoed per dive, respectively. Sharks were also recorded in February (MaxN = 2), August (MaxN = 5) and October (MaxN = 2); however, mature sharks were only observed in March. There was no evidence of site philopatry at either Opera House or Key Biscayne. A mature female *C. taurus* was photographed in caves at Direction Bank in May and another in October, and a mature male photographed in May; all other observations at the site were immature sharks (Table 1), 3 of which were recorded at the site in more than one year.

3.4. Exmouth Navy Pier

Individual *C. taurus* were previously documented at the Exmouth Navy Pier from 2007 to 2012 (Hoschke & Whisson 2016). The present study extended this monitoring record by 9 yr to 2021, during which time an additional 15 *C. taurus* were recorded, bringing the total number of photo-tagged sharks to 31, with an average of 5.5 unique sharks (range: 2–10) observed at the site every year (Fig. 7a). Sharks were recorded at the site every year from late May or early June through until mid to late November (except for 2021 when 2 young female sharks stayed until December 17) and were absent for the rest of the year (Fig. 7b). Most sharks at the site were immature (~1.5–2.5 m TL), with only 1 mature male and female usually appearing each year. Sharks displayed strong site philopatry, with nearly all returning to the site over at least 2 yr, with some long-term records of sharks maturing: a male shark (M16) first photographed as a juvenile in 2009 was recorded at the site every year for the next 12 yr (up to and including 2021), only maturing in 2017/18 (measured at 1.89 m PL (2.81 m TL) in 2018 with full length calcified claspers). A mature female (F13) was recorded in 2012–14 and 2017–19 (measured at 2.06 m PL, 2.94 m TL in June 2019).

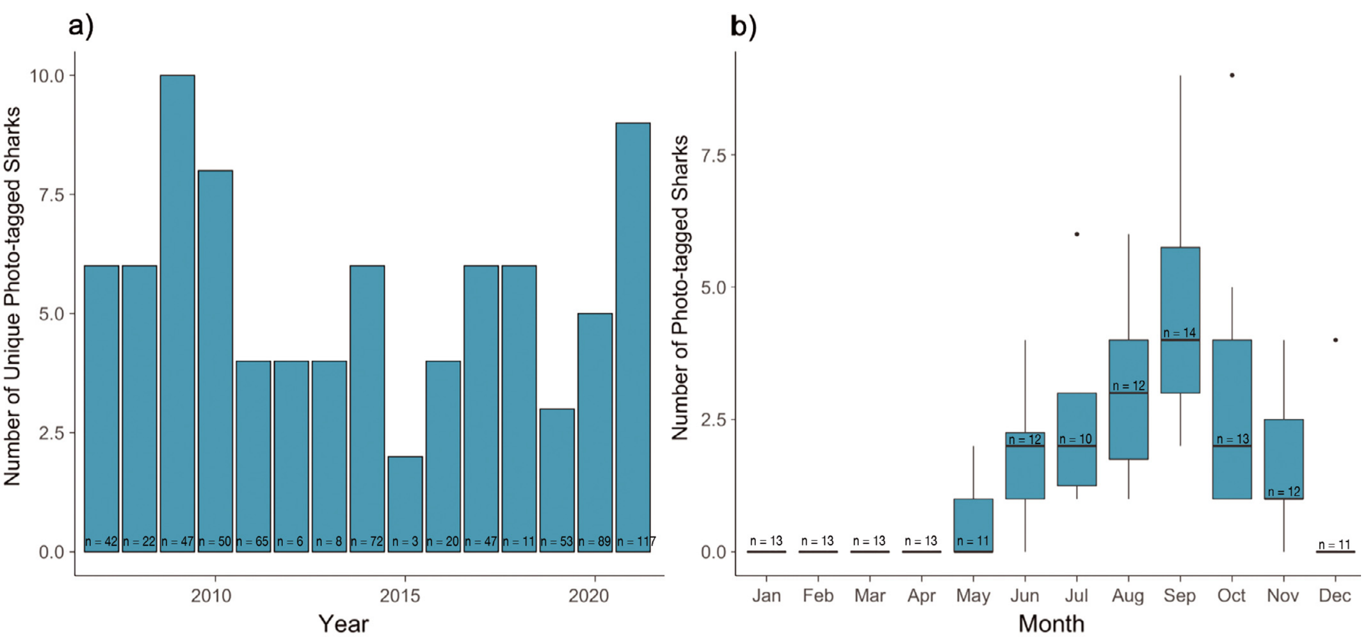

Fig. 7. (a) Number of unique photo-tagged *Carcharias taurus* recorded at Exmouth Navy Pier each year from 2007–2021. n: number of days with dives and/or video footage during the shark residency period from May to December each year. (b) Monthly observations of photo-tagged *C. taurus* at Exmouth Navy Pier, 2007–2021. Data represents mean (±SE) and maximum number of photo-tagged sharks seen per month (each shark only counted once per month each year) over the study period. Number of observation months across years (n) summarized by boxplot is indicated

3.5. Additional *Carcharias taurus* sightings in Western Australia

Numerous other records emanated from the Community Monitoring Program for *C. taurus* (Table 1, Fig. 1). Sightings off the Perth Coast were common, particularly near Garden Island (Fig. 2) and other caves around Rottnest Island, with most reports away from the aggregation sites relating to single sharks. Ten *C. taurus* (5 mature females, 1 immature female and 4 immature males) were photo-tagged from caves off Mandurah (50 km south of Perth) in December 2020 and 2021, with MaxN of 12 sharks in December 2020; 5 *C. taurus* including a mature male were recorded from drop camera footage at 141 m depth west of Augusta (Langlois et al. 2021); spearfishers near Walpole (120 km west of Albany) reported at least 12 *C. taurus* in April 2018, including a near-mature male (S. Marns pers. comm.), with unconfirmed reports of up to 50 *C. taurus* off Walpole and Bremer Bay. Three pregnant females were videoed off Salisbury Island, Recherche Archipelago in June 2016 (D. Riggs pers. comm. 2020). North of Lancelin diver records are scarce: 1 *C. taurus* was reported from a wreck in 52 m water depth, 100 km south of Dongara in January 2011; 2 or 3 (MaxN = 8) *C. taurus* frequent caves around Steep Point, Shark Bay between October and January each year; and 1 or 2 sharks are occasionally recorded from Coral Bay, Exmouth Gulf and the Muiron Islands (located 35 km northeast of Exmouth) between May and November, including 1 immature female photo-tagged shark seen at Coral Bay several times between 2008 and 2013. Spearfishers have reported between 6 and 10 pregnant females near the coast in 20 m depth 40 km NW of Carnarvon in late July/early August each year (unconfirmed), and occasional confirmed sightings off Broome, also during the winter months.

3.6. Fisheries bycatch data

A total of 574 *C. taurus* were reported as bycatch in the west/south coast demersal fisheries between 2006 and 2017. Eleven sharks were caught in water depths over 100 m (average 50 m, maximum 183 m). Of these records, only 14% included an indication of maturity or sex, with 24 mature or 'large' sharks, 23 immature or 'small' sharks and 35 juveniles or 'very small' sharks reported. Most sharks were caught on the south-west coast of WA from Bunbury to Bremer Bay, with other higher concentration catch areas from south of Dongara to west of Kalbarri, and approximately 250 km east of Esperance (Fig. 8). Bycatch of juvenile sharks was concentrated in a single block 200 km east of Esperance, and in 2 blocks to

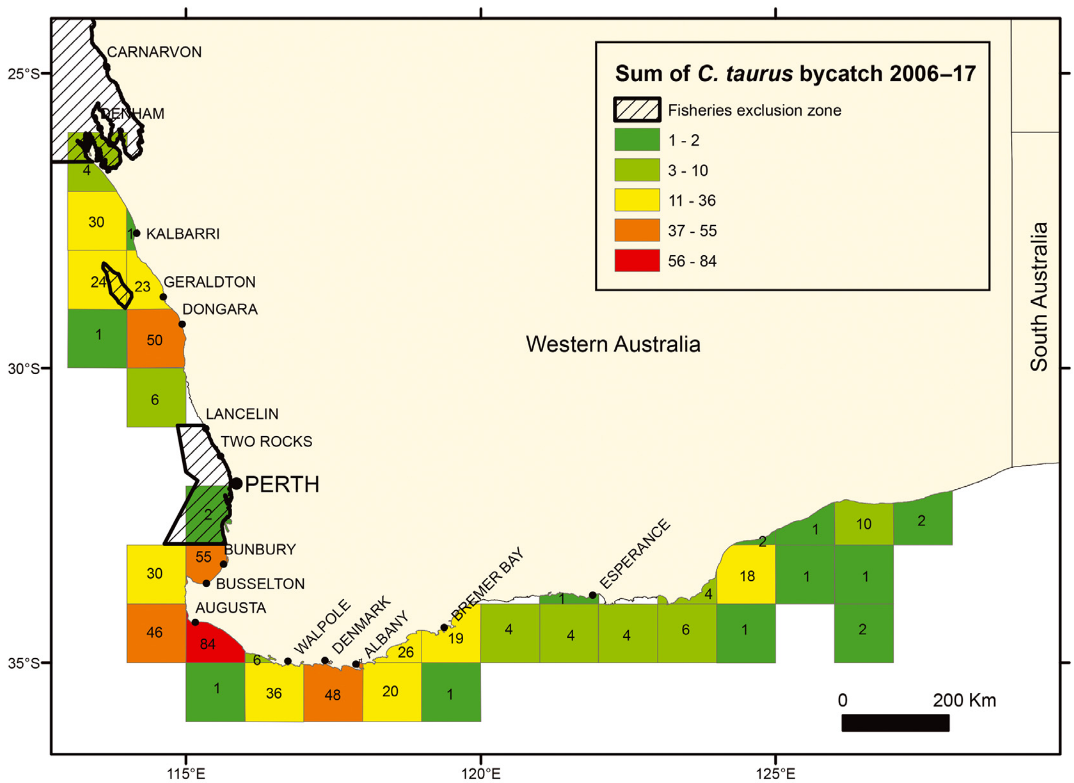

Fig. 8. Western Australian *Carcharias taurus* bycatch data from the west and south coast demersal fisheries between June 2006 and December 2017

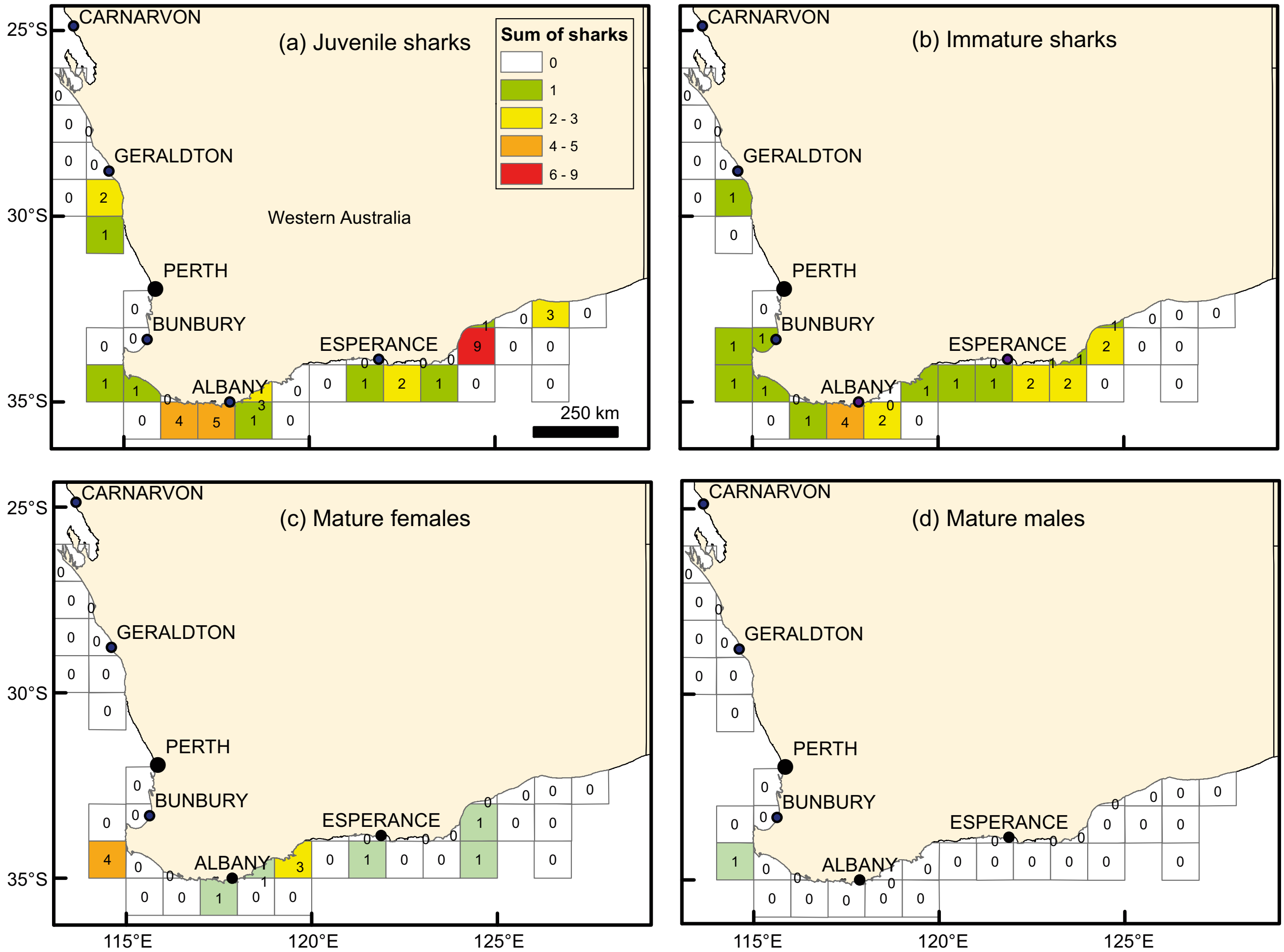

Fig. 9. Sum of bycatch data for (a) juvenile, (b) immature, (c) mature female and (d) mature male *Carcharias taurus* from the west and south coast demersal fisheries (Western Australia) between June 2006 and December 2017 per graticule block

the south-west of Albany, with immature sharks also more abundant in these regions (Fig. 9). Mature sharks were rarely recorded, with only 1 large male and a small number of mature female sharks near Augusta and east along the south coast (Fig. 9).

The total annual reported bycatch of *C. taurus* for the west and south coast demersal fisheries for the years 2007 to 2017 averaged 49.91 (range: 24–75) individuals; note: 2006 was excluded from this calculation as it only contained data from the last 7 months of the year. Bycatch of *C. taurus* appeared to decrease over the reported period, with 0.14 fewer sharks per 100 fishing days caught each year (Fig. 10); however, the linear regression model was not significant at $p < 0.05$ ($F(1,8) < 0.001$, $p = 0.07$, $R^2 = 0.35$). Additional reporting years will help determine if this trend becomes significant over time.

4. DISCUSSION

4.1. Citizen science

The identification of individual *Carcharias taurus* using spot patterns (photo-tagging) has allowed citizen scientists to contribute to ongoing monitoring programmes such as the present study by greatly increasing geographical coverage, total effort, time span (including retrospective observations) and volume of data available to researchers. There are, however, limitations associated with the extensive use of observations provided by recreational divers, including the potential to underestimate shark numbers at a given site based on photographic records, and the likelihood that *C. taurus* numbers may be negatively affected by high diver visitation rates at popular sites (Barker et. al 2011). When combined with historic by-

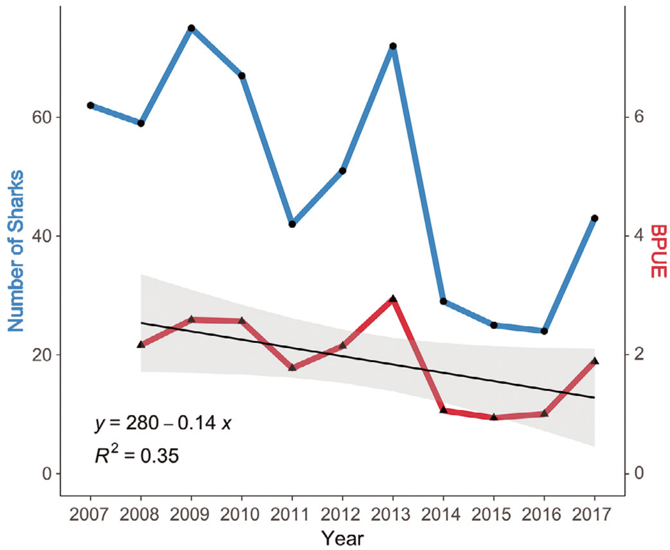

Fig. 10. Total annual reported bycatch (blue/circle) and BPUE (red/triangle) of *Carcharias taurus* for the west and south coast demersal fisheries in Western Australia, 2007–2017. Black line represents linear regression with confidence intervals (grey shading). BPUE: bycatch per unit effort including all reported *C. taurus* bycatch during the given year per 100 fishing days, excluding 2007, which did not have fishing days reported

catch data, the Community Monitoring Program included in this study has provided invaluable baseline knowledge to underpin future research and inform the management and conservation of WA's population of *C. taurus*.

4.2. Distribution, range and migration of *Carcharias taurus* in Western Australia

While marine scientists and commercial fishers have known for many years that *C. taurus* is found along much of the WA coastline, this study, for the first time, provides an evidence-based distribution of the western population of *C. taurus* in Australia (Fig. 11). This information was compiled from a range of robust sources, including bycatch records from commercial fisheries, photographic records from an in-depth Community Monitoring Program, and other verified/published occurrences (Fig. 1). Fisheries bycatch data combined with diver records off the Perth Coast maps the *C. taurus* population from near the South Australia border north to Shark Bay; diver records extend that range to Exmouth and

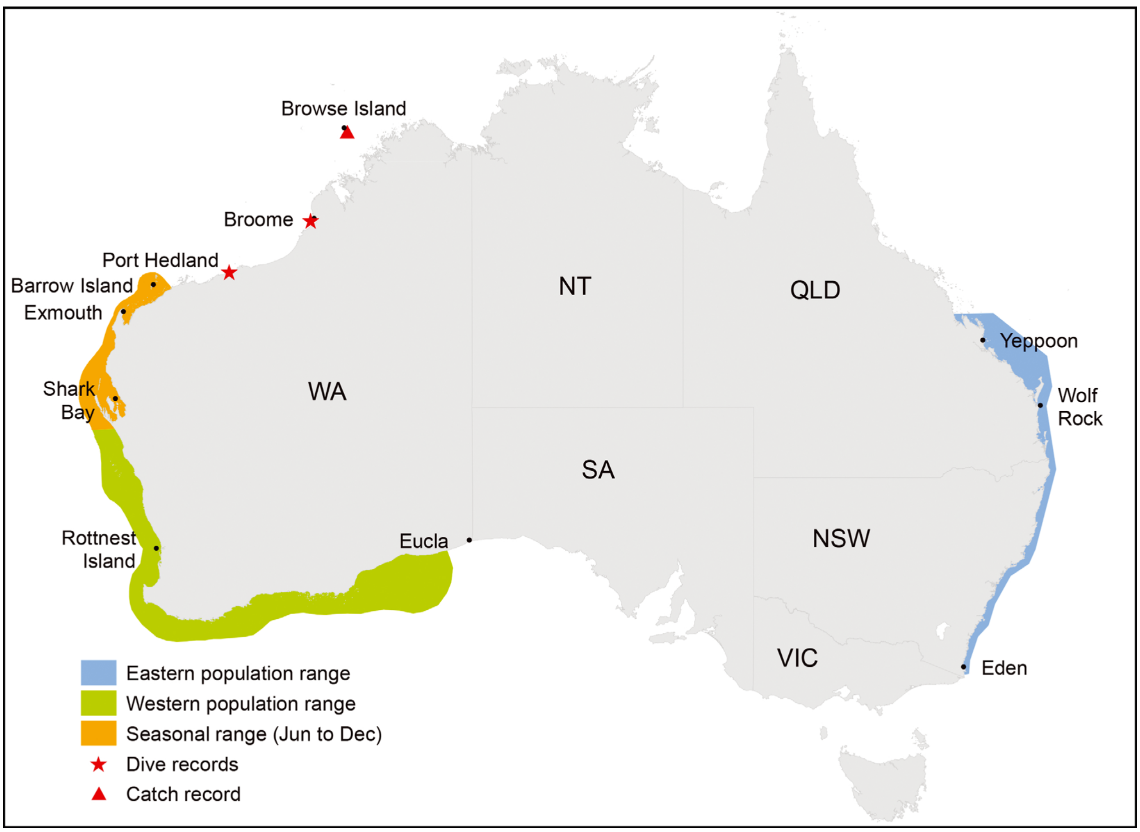

Fig. 11. Distribution of *Carcharias taurus* in Australia. Note: Occurrence data beyond Barrow Island are limited, so it is conceivable that the population extends further to the north

the Muiron Islands; research capture data (DPIRD unpubl. data) extends it from Exmouth to Barrow Island (Fig. 11), and occasional fisher and diver observations further to the north indicate that the species occurs as far north as the Timor Sea.

4.3. Aggregation sites and photo-tagging

This study follows the publication of the first confirmed *C. taurus* aggregation site in WA at the Exmouth Navy Pier (Hoschke & Whisson 2016) by providing evidence of an additional aggregation at Shark Cave, Rottnest Island and evidence of a further 3 aggregation sites in deeper waters: Opera House (northeast of Rottnest Island); Direction Bank (offshore from Two Rocks); and the Key Biscayne Oil Rig (offshore from Lancelin) (Fig. 2). All locations meet the criteria for a *C. taurus* aggregation site, with at least 5 sharks present on a recurrent basis each year (Hoschke & Whisson 2016).

Shark Cave, Rottnest Island, shows similarities to the more central/southern aggregation sites on the east coast with a mixture of mature and immature sharks (Bansemer & Bennett 2011). Few small juveniles or YOY sharks were recorded, and there is little evidence of mating or gestation (i.e. fresh scarring, mating activity or obvious pregnancy), so the site is not considered to be a nursery or mating/gestation site. The presence of mature males between March and June each year is comparable to the east coast cycle where they are assumed to come in from further offshore around this time and remain until migrating north for mating later in the year (Bansemer & Bennett 2011). Three photo-tagged mature males returned to Shark Cave in the March–June period in consecutive years suggesting an annual pattern to their movements; however, this also coincides with the annual run of large salmon *Arripis truttaceus* schools along the Perth Coast, which may be an influencing factor.

The depths and locations of the Key Biscayne, Direction Bank and Opera House aggregation sites result in a lower level of diver visitation and corresponding *C. taurus* data than Shark Cave. While mature male and female sharks have occasionally been observed at all 3 sites, they are predominantly host to immature sharks; however, no YOY juveniles (1–1.5 m TL) have been observed.

The small *C. taurus* aggregation at the Exmouth Navy Pier typically features a single mature male, a single mature female (only observed occasionally), and several immature sharks, only present during the cooler months (May to December) but showing strong site philopatry. The presence of juvenile sharks (1.52, 1.53 and 1.63 m TL) this far north suggests that pupping is not restricted to waters in the more southern and central parts of their range, in contrast to observations along the east coast (Bansemer & Bennett 2011). A single resident mature male during the winter months demonstrates a different residency pattern to other known aggregation sites further south in WA where mature males are rarely seen more than once in a year, and usually earlier (between March and June). The Exmouth Navy Pier is an unusual habitat for a *C. taurus* aggregation: it is further north (latitude 21.68°S) than all 20 documented aggregation sites on the east coast; is situated only 175 m off the mainland coast; and is shallow (10–15 m water depth). However, given the site's high biodiversity (Whisson & Hoschke 2013), it is tenable that the aggregation is linked to the abundant food supply.

C. taurus aggregation sites recorded during this study lie between Perth and Exmouth in areas where recreational diving is more common, with 3 of the sites in depths bordering recreational dive limits (>25 m). It is highly likely that numerous other aggregation sites occur along the WA coast in caves >30 m depth that are yet to be discovered. Examples include caves off Bremer Bay, Walpole, Mandurah and Carnarvon, where anecdotal evidence collected during this study from divers and spearfishers indicate aggregations of between 10 and 50 *C. taurus*, including mature sharks. This indication is reinforced by the commercial fisheries bycatch data, where the average catch depth was 50 m.

Records of *C. taurus* over a 15 yr period at both Shark Cave (Rottnest Island) and Exmouth Navy Pier provide some evidence of a stable population, with long-term site philopatry, a relatively high number of immature sharks, and no significant change in observed shark numbers, despite increased diver visitation and/or incidental fishing impacts. Although 148 sharks were photo-tagged in WA during this study, no individual sharks were seen at more than one site, even though many were seen over different months and years at the same site. This is not surprising given the findings from eastern Australia, where immature and juvenile sharks tend to stay at the same sites over consecutive seasons and years (Bansemer & Bennett 2011). No mating, gestation or pupping sites have been identified in WA, and it is likely that mature sharks are usually further offshore except when they enter shallower waters to feed on smaller schooling prey, e.g. snapper *Chrysophrys auratus* spawning inshore from Garden Island in November (Crisafulli et al. 2019) and the annual run of large salmon *Arripis truttaceus* schools along the Perth Coast in March–June. This is supported by a pop-up archival satellite tagging study of *C. taurus* in the western South Atlantic, where the average depth of males was found to be positively correlated with shark size (Teter et al. 2015).

4.4. Fishing and diving impacts

The proportion of *C. taurus* showing evidence of fishing injuries at Shark Cave, Rottnest Island (17%), is high compared to data for the east coast *C. taurus* population, where on average 7.5% of sharks (range 0–15%) were identified with retained fishing gear across 14 aggregation sites (Bansemer & Bennett 2010). Although Shark Cave lies within a demersal Sanctuary Zone, it is situated close to the edge of the boundary (~100 m), and this may not be a sufficient buffer to limit incidental hooking. Bansemer & Bennett (2010) recommended closure of a 1 km radius to all fishing at a comparable site on the east coast (Fish Rock) where 14% of sharks were impacted by fishing gear. Fishing injuries or retained fishing gear have not been observed in *C. taurus* at the Exmouth Navy Pier, where the fishing buffer around the site is a minimum of 800 m.

Shark Cave, Rottnest Island, is increasing in popularity as a recreational dive site with as many as 6 boats anchored around the cave at one time. Anecdotal feedback from dive company operators indicates the number of sharks present on a given day decreases as more divers arrive at the site. These observations are supported by Barker et. al (2011), where close diver proximity (3 m distance) and group size (12 divers) negatively affected the short-term behaviour of *C. taurus* at an aggregation site in eastern Australia.

4.5. Fisheries bycatch data

Bycatch data provided indications of a broad *C. taurus* pupping/nursery area off the south coast of WA with juvenile and immature sharks more prevalent in catch records. Utilisation of the data was limited by the lack of additional information, including size (TL and PL), sex, and maturity (clasper length). This information would greatly assist research into the life cycle and migration patterns of *C. taurus* in WA. The majority of records (86%) had no additional information apart from whether the shark was released dead or alive. For example, for the 50 sharks caught in the graticule block to the south of Geraldton (Fig. 8), only 3 had any sex or size data recorded (Fig. 9). Improving data reporting could assist in identifying areas important for mating, gestation, and pupping for this species in WA.

4.6. Seasonality in *C. taurus* occurrences in Western Australia

All *C. taurus* sightings and captures compiled in this study from Shark Bay and further north occurred during the cooler sea temperature months from May to December (Table S2 in Supplement 1), conforming with the findings of Otway & Ellis (2011) in eastern Australia, and Teter et al. (2015) in the western North Atlantic, where tagged *C. taurus* spent 95% of the time in ocean temperatures of 17–24°C and 17–23°C, respectively. In addition, all records of *C. taurus* at the Exmouth Navy Pier since monitoring began in 2007 have been between May and December, with shark occurrence at the site highly correlated with ocean temperature (point biserial correlation coefficient, $r_{pb} = 0.28$; $p < 0.01$, $n = 1290$), and no sharks observed when sea temperatures exceed 25.5°C at the site (Hoschke & Whisson 2016). This evidence points to the occurrence of *C. taurus* being seasonal in the warmer waters of WA (Fig. 11) and is most likely correlated with water temperature, with observations only reported north of Shark Bay between May and December each year. It is likely that the sharks are either migrating south or moving into deeper, cooler water offshore for the warmer summer months. Temperature-driven migration and/or residency would concur not only with other *C. taurus* findings in Australia (e.g. Otway & Ellis 2011) but also with studies of *C. taurus* populations in other parts of the world (e.g. Kneebone et al. 2012, Teter et al. 2015, Haulsee et al. 2018) and indeed other migratory shark species (Brooks et al. 2013, Baremore et al. 2021, Rider et al. 2021).

In contrast, at the comparatively lower ocean temperature at Shark Cave off the Perth Coast, sharks were present throughout the whole year, albeit in fluctuating numbers. Season and ocean temperature were highly correlated and predictive of *C. taurus* prevalence, with sightings per unit effort most likely driven by the presence of optimal water temperature (19–22°C) in the autumn. Furthermore, mature sharks appeared to exhibit greater seasonality than immature individuals, with mature males rarely seen outside of the March–June period. Partial migration, with only sharks over a certain size undergoing large migrations, has previously been documented both in *C. taurus* (Dicken et al. 2006, Bansemer & Bennett 2009) and other shark species (Lea et al. 2015, 2018, Hammerschlag et al. 2022). It is plausible that mature males have a similar migration pattern to the eastern Australian population, where northerly migration occurs during winter (June onwards) for mating at more northern sites between October and December, after which they are thought to head offshore until they reappear further south from late February onwards and remain until the cycle is repeated the following winter (Bansemer & Bennett 2011, Otway & Ellis 2011). In WA, inshore records of males near the Perth Coast occur between March and June, with several individuals returning to Shark Cave, Rottnest Island, within this period over consecutive years. Records of male sharks north of Shark Bay only occur between May and December, and a mature male travelled 1294 km from south of Augusta to Coral Bay in 2012 (Jakobs & Braccini 2019).

Insufficient evidence exists to determine whether female *C. taurus* migrate in a similar pattern to those along the eastern coast of Australia. A photo-tagged mature female (TL 2.94 m in June 2019) at the Exmouth Navy Pier was recorded at the site for 21 d between June and August 2014, 2 d in September 2017, 3 d in August 2018, 1 d in June 2019 and was absent in 2020 and 2021, which could tie in with the triennial reproductive cycle observed on the east coast (Bansemer & Bennett 2009). Fisheries bycatch data indicates juvenile sharks are common along the WA south coast, where heavily pregnant females have also been recorded (D. Riggs pers. comm. 2020), and near the Abrolhos Islands (Fig. 8). However, we have measured juvenile sharks (1.5–1.6 m TL) in the Exmouth Navy Pier aggregation, indicating that at least some females at the northern end of the *C. taurus* range in WA are pupping in these warmer waters, rather than migrating to the lower temperatures further south for parturition, as is the case in eastern Australia (Bansemer & Bennett 2009) and South Africa (Dicken et al. 2006, 2007). The WA population may therefore have more similarities to the populations in the SW and NW Atlantic, where mature female sharks gestate and give birth in warmer subtropical waters but may migrate south to cooler waters after parturition (Gilmore et al. 1983, Lucifora et al. 2002). Whether or not female *C. taurus* migrate, and if so at what stage in their life cycle, remains unclear for the WA population.

5. CONCLUSIONS

This study documented a considerable number of *Carcharias taurus* along the WA coastline, and it is highly probable that many additional aggregation sites exist in the region based on the gathered data, including extensive anecdotal evidence of this species in areas visited by recreational divers. The organised collection of data through community monitoring programmes should be embraced within the environmental management sector, particularly where observational data are critical to the development of robust biodiversity measures.

The seasonal occurrence and prevalence of *C. taurus* at nearshore locations in the northern half of WA is likely a function of ocean temperature, with shark observations sharply declining during the onset of the warmer months. It follows that climate change and future ocean warming could impact the range of this genetically discrete, near-threatened population.

While this study has significantly increased the knowledge base of *C. taurus* in WA, there is still a large information deficit that requires redressing by a continued research effort; in particular:

- migratory behaviour along the western coast of Australia
- destination of sharks in northern WA during warmer months
- growth rates of males compared to other global populations
- reduction of fishing-related injuries
- identification/protection of additional aggregations.

Finally, the authors recommend a continued effort to locate, assess and protect additional *C. taurus* aggregation sites that incorporates citizen science input, which, by its nature, includes the primary users of these locations, thus embedding a sense of importance and community investment in the management and conservation of this vulnerable species.

Availability of data and material. The datasets developed and/or analysed during the present study are available from the corresponding author on reasonable request. For access to the fisheries bycatch data supporting this study's findings, contact should be made with the Western Australian Department of Primary Industries and Regional Development.

Author contributions. A.H. and G.W. developed the project and collected data. D.H. and A.H. performed data analysis. All authors contributed to writing the manuscript in the order listed.

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