

Reproductive periodicity, localised movements and behavioural segregation of pregnant *Carcharias taurus* at Wolf Rock, southeast Queensland, Australia

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ABSTRACT: We examined grey nurse shark *Carcharias taurus* utilisation of Wolf Rock (which is located within a marine sanctuary zone and is the most northern known aggregation site on the eastern Australian seaboard) between December 2002 and February 2008 using underwater censuses, photo-identification and acoustic tracking of individual sharks. Photo-identification surveys identified 181 individual *C. taurus* (161 mature females, 1 immature female and 19 mature males). Eighty-one of these were re-identified at least once at Wolf Rock (77 females and 4 males) between December 2002 and February 2008. A biennial reproductive cycle was indicated for 18 out of 28 females for which re-identifications spanned at least 2 mating and/or pregnancy events. Re-identifications of 9 out of 28 female sharks suggest that, on occasion, there may be 3 yr between pregnancy events. Male *C. taurus* were observed between July and January, but were absent between February and April. Fresh mating scars on female sharks were observed in late November and December and pregnancies were visible from late-February. Many pregnant sharks remained at Wolf Rock until August or September (9 to 10 mo post-mating) and demonstrated strong site attachment with 78 to 90% of their time spent within 500 m of the Wolf Rock aggregation site. *C. taurus* is listed as critically endangered along the east coast of Australia and there is concern about their population's resilience globally. The improved knowledge of the reproductive periodicity of *C. taurus* and their behaviour during pregnancy will provide valuable information to assist with management throughout their distribution.

KEY WORDS: Aggregation · Site fidelity · Acoustic telemetry · Photo identification · Visual survey

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INTRODUCTION

Globally, *Carcharias taurus* (Rafinesque, 1810) (Lamniformes, Odontaspidae) is listed as Vulnerable on the International Union for Conservation of Nature's Red List of Threatened Species (Pollard et al. 2003) and the population along the eastern seaboard of Australia is listed as Critically Endangered (Cavanagh et al. 2003, Pollard et al. 2003). In Australia this population is also listed as critically endangered under the Environmental Protection and Biodiversity Conservation Act 1999 (Environment Australia 2002, Cavanagh et al. 2003). Wolf Rock is the northernmost identified

aggregation site for *C. taurus* on the eastern seaboard of Australia (Bennett & Bansemer 2004). The Queensland government acknowledged the importance of Wolf Rock as both a mating and aggregation site for pregnant *C. taurus* (Queensland Government 2003), and banned all forms of fishing within a 1.2 km radius in December 2003 (Queensland Government 1994).

Carcharias taurus is known to use an ovoviviparous reproductive strategy, in which the embryos feed on ova produced by the mother (oophagy) after the yolk sac is absorbed and, subsequently, also use intra-uterine cannibalism (adelphophagy). Cannibalisation of siblings results in a maximum of 2 pups per litter

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(one from each uterus) that are born at about 1 m total length (L_t) after a 9 to 12 mo gestation period (Gilmore et al. 1983, Compagno 2001, Pogonoski et al. 2002). However, considerable uncertainty and contradiction exists about temporal and spatial aspects of mating, gestation and parturition in *C. taurus*. Studies on the reproductive periodicity and associated migrations of mature female *C. taurus* suggest that considerable variation occurs within and between populations. While a biennial reproductive cycle (1 rest-year between pregnancy events) has been reported for *C. taurus* in the southwest Atlantic (Lucifora et al. 2002) and off the coast of southern Africa (Dicken et al. 2006a, 2007), both annual (i.e. pregnant each year) and biennial reproductive cycles have been suggested for *C. taurus* populations in the northwest Atlantic (Gilmore 1993, Branstetter & Musick 1994) and off the southeast coast of Australia (Gordon 1993, Compagno 2001, Otway et al. 2003).

In the NW Atlantic, SW Atlantic and South Africa pregnant *Carcharias taurus* are thought to aggregate in warmer waters (Bass et al. 1975, Branstetter & Musick 1994, Lucifora et al. 2002) which may enhance embryo development (Bass et al. 1975). Near-term pregnant female sharks in South African waters migrate to cooler waters in July and August prior to parturition which may occur in August or September (Bass et al. 1975) or between November and February (Dicken et al. 2006a, 2007). Pregnant sharks in the SW Atlantic occur in subtropical waters from April until parturition. After parturition, the SW Atlantic post-partum sharks may migrate south to cooler waters to rest for a year (Lucifora et al. 2002). In the NW Atlantic the situation appears more variable. Mature female sharks may remain in warmer southern waters (Gilmore et al. 1983, Gilmore 1993) and reproduce annually. Alternatively, they may migrate north to cooler waters after parturition to rest for a year (biennial reproductive cycle) (Branstetter & Musick 1994) or they may give birth anywhere in their range and reproduce biennially (Compagno 2001).

Migratory movements of *Carcharias taurus* along the east coast of Australia may be associated with reproduction (Pollard et al. 1996), but the pattern of movement for both males and females differs to that observed in South Africa. The east Australian *C. taurus* population is thought to migrate north in autumn and winter and south in spring and summer (Pollard et al. 1996, Otway et al. 2003, Bruce et al. 2005). Divers have reported mating scars on *C. taurus* in March and April and recently born pups in winter and early spring (Otway et al. 2003). These anecdotal reports are consistent with observations by Gilmore (1993) for mating and parturition in the NW Atlantic, but contrast with observations in South Africa (Bass et al. 1975, Dicken

et al. 2006a) and in the SW Atlantic (Lucifora et al. 2002).

Current knowledge about the reproductive periodicity and movements of mature female *Carcharias taurus* of the Australian east coast population is incomplete. Information on temporal and spatial distributions of *C. taurus*, particularly in relation to reproduction in this population, will assist in their conservation management. The outcomes of the present study may also provide a framework for interpretation of the reproductive behaviours of other populations of *C. taurus*. The present study investigated the aggregation of pregnant *C. taurus* at Wolf Rock, and their temporary segregation from the rest of the population. The goals were to provide information on the reproductive periodicity and behaviour of pregnant sharks to address the current uncertainties in the literature using the following methods: (1) visual diver surveys, (2) photo-identification (PID) surveys, and (3) passive and active acoustic telemetry to describe fine-scale movements and site utilisation during pregnancy.

MATERIALS AND METHODS

Study site. Wolf Rock (153° 11.800' E, 25° 54.630' S) is located 6 km northeast of Rainbow Beach off the Queensland coastline on the eastern seaboard of Australia (Fig. 1) and comprises 4 pinnacles that are aligned in a northeast direction, 2 of which are exposed under all tidal conditions. The pinnacles are characterised by steep walls and a series of gutters (Ford et al. 2003). *Carcharias taurus* commonly occurs around the formation at depths of 5 to 35 m (Bennett & Bansemer 2004). In addition to the prohibition of all fishing within a 1.2 km radius of Wolf Rock, a further 300 m buffer zone only allows for trolling for pelagic fishes. Ecotourism and, specifically, diving is also restricted within the 1.2 km radius marine sanctuary zone (Queensland Government 2006).

Visual diver surveys. Five hundred and twenty-five visual diver surveys, each of about 30 min duration, were conducted between 2002 and 2007. The local dive operator (Wolf Rock Dive) conducted 488 surveys with the remainder conducted by C.S.B. (2002 to 2007), staff from the Queensland Parks and Wildlife Service (2002 and 2003), and the recreational diving community (2002 to 2007). Data recorded during each survey included the number of *Carcharias taurus* observed, their sex, and observations of mating scars or pregnancy. If the sex of any shark could not be determined it was recorded as unknown. When 2 dives were conducted on a single day the maximum number of sharks in each category was used (i.e. counts were not averaged between the 2 dives). To minimise the risk of

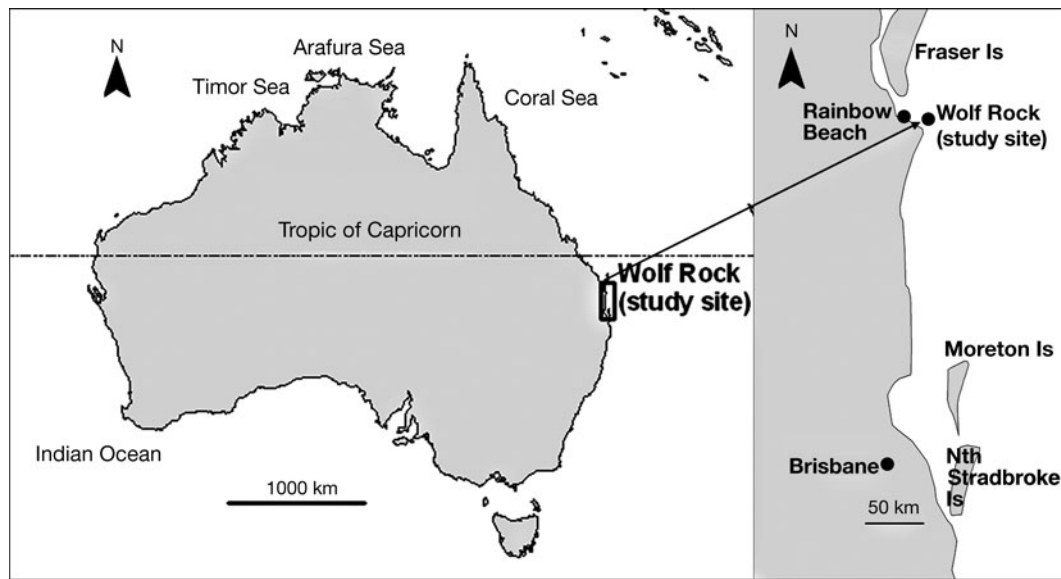


Fig. 1. Study site, Wolf Rock in southeast Queensland, Australia

double counts, divers were instructed to record the maximum number of sharks observed in their field of view at any one time. The risk of double counting individuals was considered low as the majority of surveys were conducted by experienced individuals who had a good knowledge of the local topography and the behaviour and movements of *C. taurus* at Wolf Rock. Visual survey data were analysed using a 1-way ANOVA to explore differences in the survey effort between years and a Tukey test was applied post hoc. Significance was accepted at $p < 0.05$ (as for all other tests). A 2-way ANOVA with year and month as the 2 factors was used to examine maximum shark numbers observed in these surveys. A Student-Newman-Keuls post hoc test was used to identify where differences lay.

Photo-identification (PID) surveys and size estimates. High-resolution images of *Carcharias taurus* at Wolf Rock were collected over a 6 yr period to construct a photographic database of individually identifiable sharks based on the spot-patterns on their flanks (Bansemer & Bennett 2008). Photographic 'recaptures' of individuals were determined by matching spot-patterns in the initial image with subsequent images (see Bansemer & Bennett 2008).

Thirty-two PID surveys were undertaken by the primary author (2002 to 2008), 17 by the local dive operator (2005 to 2007), and 11 by the diving community (2004 to 2007). With the exception of October, at least one PID survey was conducted in each calendar month over the duration of the study. A PID survey was defined as two 30 min dives conducted in a single day at the study site. Images of *Carcharias taurus* from

Wolf Rock were catalogued by aspect (left or right flank), sex, and date of image capture. Specific information recorded in relation to each image of a shark flank included whether the contralateral flank was known for this individual, its sex, maturity, presence of mating scars, and visible pregnancy.

Fresh mating scars comprised tooth puncture wounds and lacerations where white subcutaneous tissues were visible (Fig. 2a). Pregnancy could be determined from 3 to 4 mo post-mating, based on the elapsed time from the first appearance of mating scars. Pregnant sharks had a noticeably distended abdominal region with particularly distinct lateral bulges (Fig. 3).

Female sharks were considered mature at ≥ 2.2 m L_t and male sharks at ≥ 2.0 m L_t based on the known sizes at maturity for this species (Bass et al. 1975, Lucifora et al. 2002). The size (L_t) of individual sharks was estimated by eye in PID surveys and in subsequent analysis of high resolution images of identified individuals. In addition, 4 dives were conducted and 25 individual female sharks were measured with a laser measurement system which provided a scale by projecting 2 laser-light spots (50 cm apart) onto the flank of the shark as it was photographed. The projection system comprised 2 underwater lasers mounted on a rigid stainless steel frame attached to an underwater video camera housing. Each laser projected a beam parallel to the focal axis of the camera. The accuracy of this system relies on a shark being perpendicular to the focal axis with no lateral body flexion, and still images captured from the video footage were only analysed if the shark in frame fulfilled

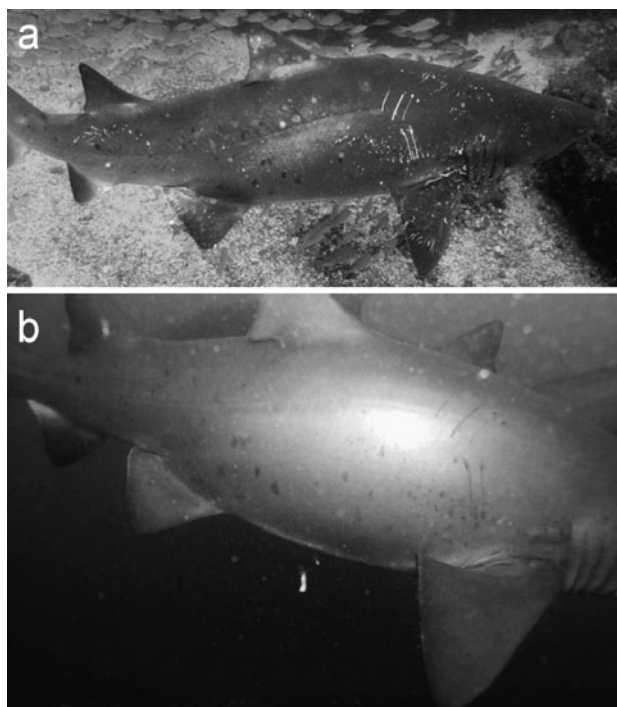


Fig. 2. *Carcharias taurus*. Healing rate of mating scars (white lines and dots) (a) Female *C. taurus* with fresh mating scars on 26 November 2007, (b) same female on 29 February 2008 with fewer visible mating scars (most healed)

these criteria. Image distortion due to the wide angle lens resulted in potential underestimates of L_t by about 5%.

Active and passive acoustic tracking. Transmitters, receivers and tag attachment methods: For the active tracks of *Carcharias taurus* we used two V16TP-3H-01 (–5 to 35°C) tags transmitting at 54 and 63 kHz, and a V10 directional hydrophone connected to a VR100 deck unit receiver (Vemco). Passive tracks used four V16 4H-69KHz-R64K coded transmitters with min/max off times of 15/40 sec, and four VR2 underwater acoustic receivers (Vemco). Each acoustic transmitter was encased in a small float and connected by a corrodible galvanic link (Ocean Appliances) to a small M-tag that was inserted into the dorsal musculature below the first dorsal fin (see Bruce et al. 2005) of mature free-swimming female *C. taurus*. Tags were attached to sharks that had been seen with fresh mating scars in the preceding few months and were presumed pregnant.

Active tracking: Two active tracks of 24 h duration were planned for February 2006; however, due to weather constraints the tracks were restricted to 7 h 45 min and 16 h 52 min respectively. The shark's depth and bottom depth (depth under the boat), VR100 signal strength, the position of the boat (using the VR100's inbuilt GPS), and bearing of the boat to the location of

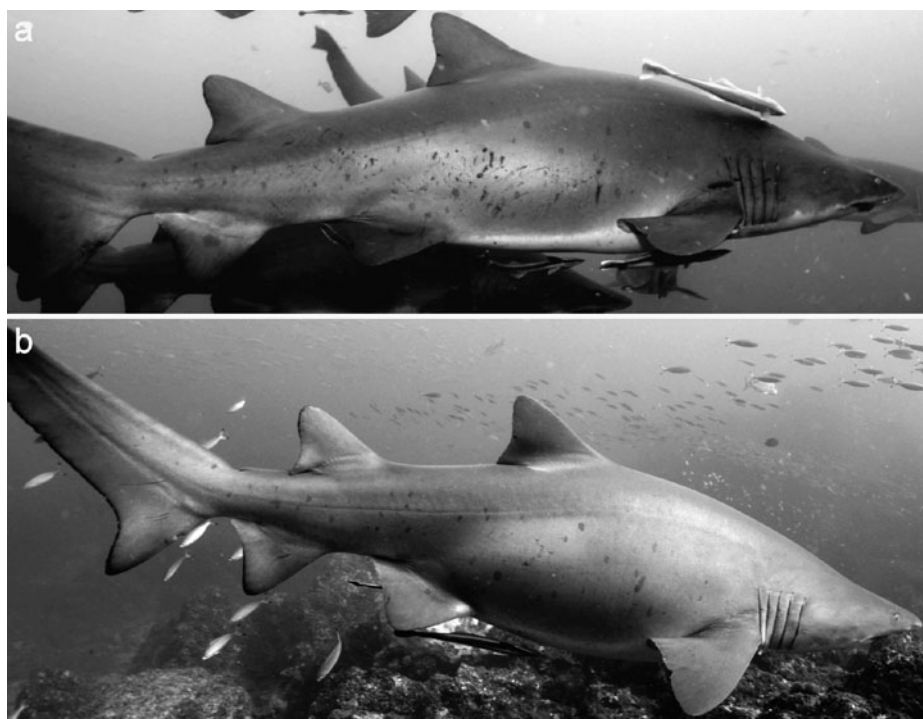


Fig. 3. *Carcharias taurus*. Visibility of pregnancy in (a) female with mostly healed mating scars on 3 February 2007, but with few signs of pregnancy and (b) same female on 2 June 2007, more clearly pregnant

the shark were recorded every 5 min, with the tracking vessel kept as close to the shark as possible. The position of the tracking vessel ($\approx$ the shark's position) was plotted using Arcview 9.2 to determine the movement of sharks throughout the tracking period.

Passive tracking: Four VR2 receivers, each covered in PVC tape to protect them from biofouling (the sensor and indicator light were not covered), were positioned approximately 30 cm above the sea floor by attachment to temporary moorings that were specifically deployed for the present study. Range tests were conducted from a small boat and by divers using acoustic tags that were subsequently deployed on sharks. Two V16 tags attached to a rope 15 and 25 m from a lead weight were lowered from the boat until the weight made contact with the seafloor at various distances (0 to 1800 m) and bearings from each of the 4 receivers, the time, and GPS coordinates were recorded. Range testing was also undertaken by 2 divers, each of whom carried a V16 transmitter. Divers swam around Wolf Rock and recorded the time, their depth, and described their position on an underwater slate approximately every 5 min. Upon completion of range testing the 4 listening stations were retrieved for data download and analysis. The locations of the 4 receivers and range test results were plotted (ArcView 9.2) and overlaid on a geo-referenced map (produced by UniDive; Ford et al. 2003) that contained information on bathymetry and underwater features. The receivers were redeployed in the same positions at Wolf Rock prior to attachment of acoustic tags to 4 female sharks. The presence of each of the 4 tagged sharks within the range of the 4 VR2 receivers was determined for one hour blocks for between 8 and 15 d. A paired *t*-test was used to determine whether a difference in tag detection occurred between the (log-transformed) proportion of time that each shark was detected in the day and night.

RESULTS

Visual diver surveys

The only significant difference in survey effort was between 2003 and 2007 ($p < 0.05$) which had relatively low and high effort, respectively. The maximum number of sharks observed was significantly different between years (2-way ANOVA, $p < 0.001$) (Fig. 4) after allowing for the effects of month, but was not significantly different between months ($p = 0.115$). More sharks were seen in 2007 compared to 2002, 2003, and 2004. The maximum number of female sharks observed during any survey for each month and year was significantly different between years ($p < 0.001$)

(Fig. 4) and between months ($p = 0.001$), although the post hoc test was unable to determine where these differences lay. A 2-way ANOVA indicated that there was no difference in the number of males observed between years ($p = 0.272$), but there was a significant difference between months after allowing for the effect of year ($p < 0.001$). More sharks were seen in both October and December compared to February through June ($p < 0.05$), although the power of the test was low. The male:female ratio peaked in the September to December period (at up to 6:1). No male sharks were observed at Wolf Rock in any year during February, March, or April (Fig. 4). Mating scars were only observed on sharks at Wolf Rock from mid-October to December (Fig. 5a). Pregnancy was first evident in April with pregnant sharks observed at Wolf Rock until late September/early October (Fig. 5b).

Photographic identification

A minimum of 181 individual *Carcharias taurus* were identified at Wolf Rock over 5 yr (December 2002 to February 2008), consisting of 162 females (161 adults and 1 immature shark based on visual and laser measurement of L_t) and 19 adult males (based on clasper size and L_t). One hundred and sixty-nine individuals were identified by the spot-patterns on their right flank (150 females and 19 males) and 163 by the spot-patterns on their left flank (147 females and 16 males). Twenty-five sharks were identified by the spot-patterns on both their left and right flanks. A total of 171 photographic re-captures for individually identified females and 5 re-captures for males were obtained.

Eighty-one individuals (77 females and 4 males) were re-identified at Wolf Rock at least once following their initial identification, 23 of which matched for both their left and right flanks. Time from the initial identification to subsequent identifications ranged from 1 d to >4 yr. While some sharks were only seen once at Wolf Rock, the maximum number of re-identifications for an individual at this site was 10. The maximum number of sharks identified during any PID survey was 41, all of which were mature females.

The mean, minimum, and maximum sizes of female sharks measured with the twin laser system were 246 cm, 225 cm, and 269 cm L_t respectively. A single shark of 173 cm L_t with a spinal deformity that affected L_t was excluded from the analysis. No males were measured in this study. Fresh mating scars were concentrated on and in the vicinity of the pectoral fins, and were only observed in late November and December (Fig. 2a). Photographic recaptures indicated that, with the exception of relatively severe wounds, most mating scars healed within 2 to 3 mo (Fig. 2b).

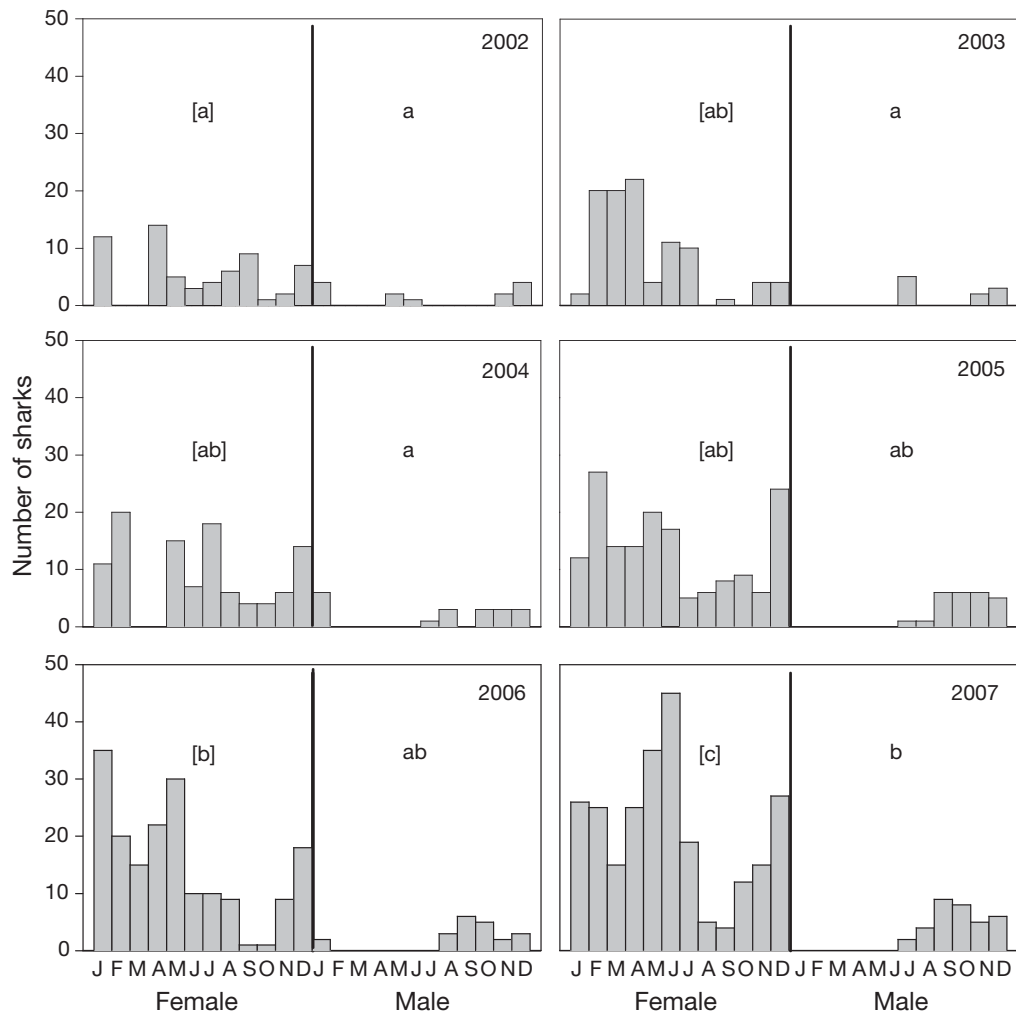


Fig. 4. *Carcharias taurus*. Maximum number of sharks counted during a single survey (dive) per month between 2002 and 2007. For years that share a common letter within square brackets the maximum number of females are not significantly different from each other. Similarly, for years that share a common letter with no brackets the maximum number of female and male sharks combined are not significantly different from each other

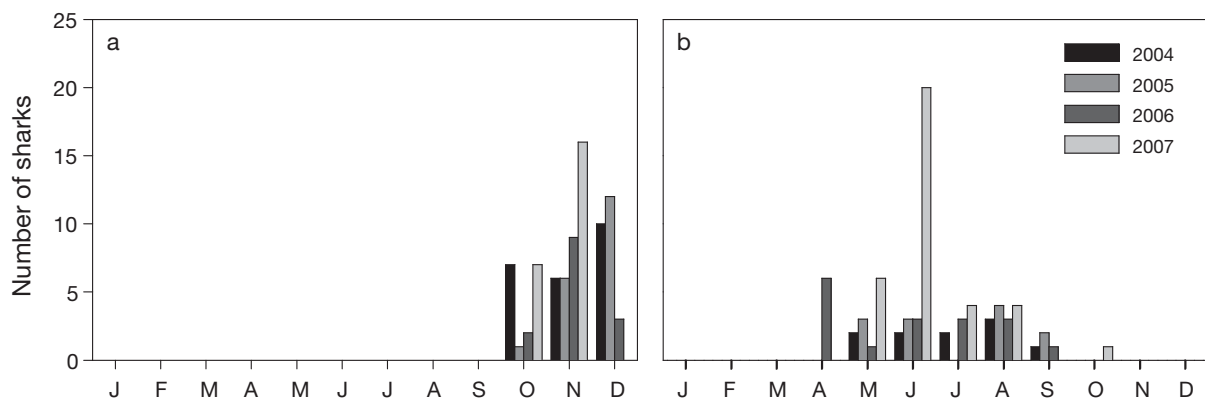


Fig. 5. *Carcharias taurus*. Maximum number of sharks counted during an individual survey for each month between 2002 and 2007 with (a) mating scars, and (b) visibly pregnant

Female *Carcharias taurus*: single identification only

Eighty-five sharks were identified based on observations of the right flank on a single occasion only. Thirty-three had mating scars, with fresh scars only seen in late November and December, and 14 were visibly pregnant (Table 1). Seventy-one sharks were identified based on their left flank spot-patterns, of

Table 1. *Carcharias taurus*. Number of female sharks with a single identification only. Total number of individuals identified during each month by their right flank (RF) and left flank (LF). I: no visible mating scars and not pregnant; M: mating scars; P: pregnant

	Summer			Autumn			Winter			Spring		
	D	J	F	M	A	M	J	J	A	S	O	N
RF (n = 85)												
I	0	3	25	3	3	1	1	1	0	0	0	2
M	3	3	19	1	1	0	0	0	0	0	0	7
P	0	0	0	0	1	2	7	0	3	1	0	0
LF (n = 71)												
I	1	3	14	4	2	2	0	0	0	1	0	4
M	2	3	16	0	0	0	0	0	0	0	0	4
P	0	0	0	0	6	0	7	0	3	0	0	0

which 26 had mating scars and 16 were visibly pregnant (Table 1). Spot-patterns were known for both flanks for 2 of these sharks.

Female *Carcharias taurus*: multiple identifications within 12 mo

Thirty-seven sharks were identified by their right flank spot-patterns, of which 24 were seen with mating scars. Sixteen of these were later seen when pregnant, 6 were not resighted after February (when pregnancy is generally visible) and 2 were resighted after February but did not appear pregnant (Fig. 6). Mating scars were not observed in 9 of the initial 37 sharks, but these sharks were later observed pregnant.

Forty-nine sharks were identified by their left flank spot-patterns, of which 33 had mating scars. Nineteen of these sharks were subsequently seen pregnant, 11 were not resighted after February, and 3 were resighted after February but did not appear pregnant (Fig. 6). Mating scars were not observed in 16 of the initial 49 sharks, but 13 of these sharks were later observed pregnant. Spot-patterns were known for both flanks for 11 of these sharks.

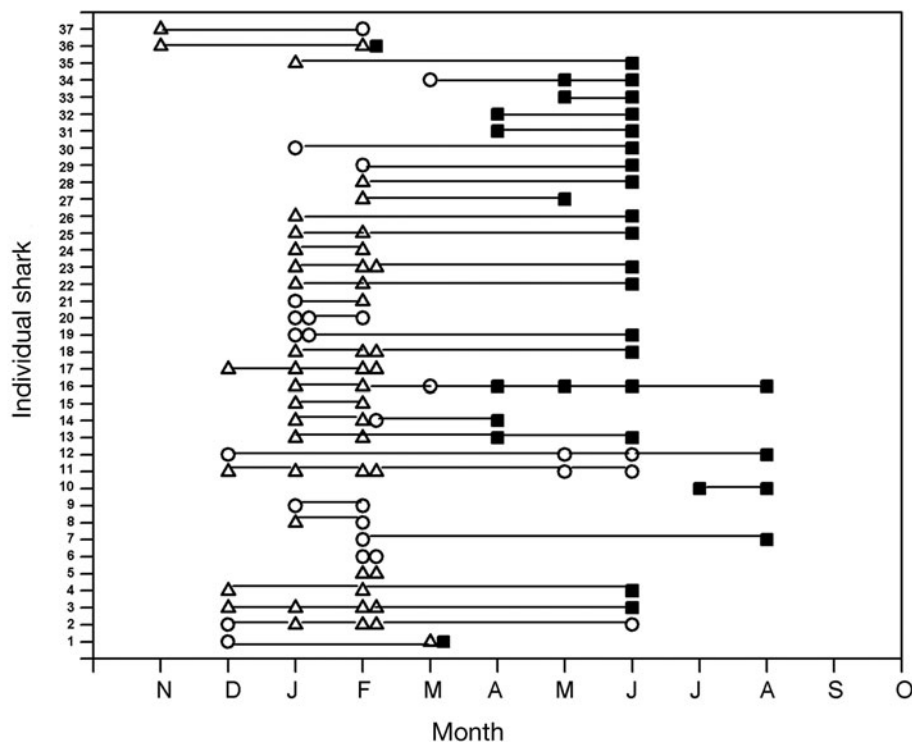


Fig. 6. *Carcharias taurus*. Multiple identifications of individual female sharks within a 12 mo period. (O) No mating scars visible, not visibly pregnant; (Δ) mating scars visible; (■) visibly pregnant; (—) links data points for individual sharks to improve readability

Female *Carcharias taurus*: multiple identifications across multiple years

Twenty-eight female *Carcharias taurus* were re-identified by their right flank spot-patterns on multiple occasions between 2 and >4 yr, capturing several mating and pregnancy events. Eighteen of these sharks were identified with mating scars and/or were visibly pregnant in one year. Approximately 12 mo after parturition was expected to occur (e.g. after 9 to 12 mo gestation), these 18 sharks were again identified at Wolf Rock with mating scars and/or were visibly pregnant. Nine sharks were identified with mating scars and/or were visibly pregnant in one year and then not subsequently identified at Wolf Rock until 2 yr after parturition would have been expected to occur. Two years after the expected parturition, these 9 sharks were identified with mating scars and/or were visibly pregnant. One shark was identified in 2 subsequent years at Wolf Rock; however, this shark was only identified as visibly pregnant in the second year (Fig. 7).

Twenty-seven sharks were identified by their left flank spot-patterns; 16 of these were identified with mating scars and/or were visibly pregnant one year and subsequently identified at Wolf Rock with mating scars and/or were visibly pregnant approximately 12 mo after parturition would have been expected to occur. Nine sharks were identified with mating scars

and/or were visibly pregnant one year and not subsequently identified at Wolf Rock for approximately 24 mo. However, these 9 sharks were identified again at Wolf Rock with mating scars and/or were visibly pregnant approximately 2 yr after parturition would have been expected to occur. One shark appeared to take 3 yr between mating events, and was then observed at Wolf Rock in the next consecutive year. However, this shark was not identified as pregnant at any time. A final shark was identified at Wolf Rock as pregnant one year, identified in the consecutive year not pregnant but with nylon tape fixed around its head and gill slits, and was then subsequently identified 3 yr later with mating scars. The spot-patterns were known for both flanks for 9 sharks.

Male *Carcharias taurus*: all identifications

Nineteen male *Carcharias taurus* were identified by their right flank spot-patterns and 16 by their left flank spot-patterns during the present study; the spot-patterns were known for both flanks for 2 of these sharks. Four sharks were re-identified at least once at Wolf Rock; one shark in December in 2 subsequent years, and the other 3 between September and December of the same year. Male sharks were only photographically identified between August and December across all years.

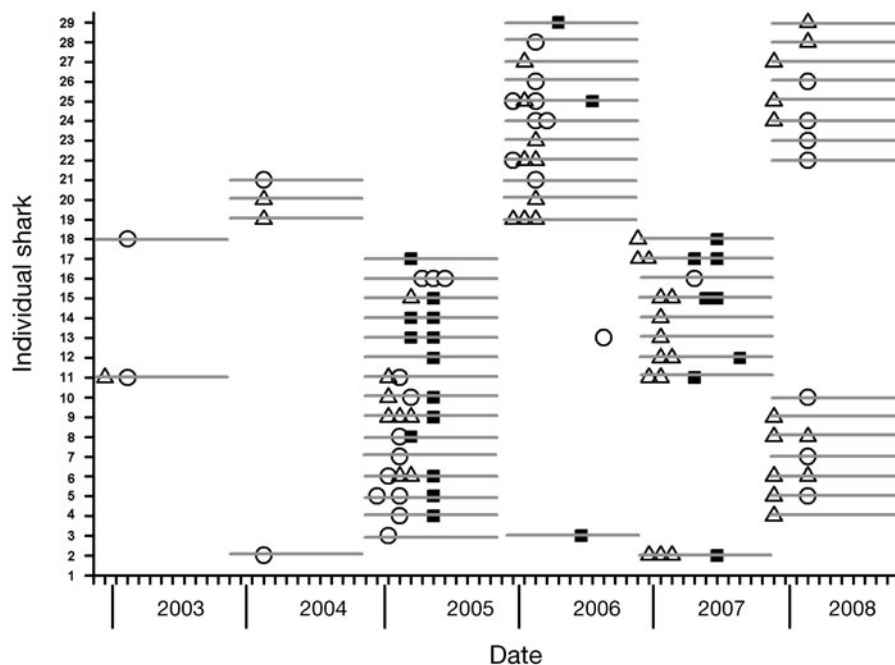


Fig. 7. *Carcharias taurus*. Multiple identifications of individual female sharks over multiple years. (O) No mating scars visible, not visibly pregnant; (Δ) mating scars visible; (■) visibly pregnant; (—) approximate duration of expected pregnancy

Active and passive acoustic tracking

Active tracking

One mature female shark was tracked for 7 h 45 min from 08:40 to 16:25 h on 3 February 2006, but the tracking was unable to continue due to unsafe sea conditions. The second mature female shark was tracked for a total of 16 h 52 min, with the first track from 08:56 to 23:45 h on 13 February 2006 stopped due to unsafe sea conditions. A second track was resumed when the shark was relocated at 06:37 h on 14 February 2006, and continued until 08:40 h when it was again stopped due to unsafe sea conditions. Both sharks remained in close proximity (within 200 m) to the main rock formation throughout the duration of the track (Fig. 8).

Passive tracking

Range-testing indicated that while the acoustic signal from a tag could be detected up to 860 m from one listening station, the detection ranges were generally restricted to 200 to 500 m. Four mature female sharks observed with mating scars prior to the present study were successfully tagged and the presence/absence of each shark at Wolf Rock was monitored from 2 to 16 February 2007. These sharks spent $83.0 \pm 6.2\%$ (mean $\pm$ SD; range 78 to 90%) of their time within close proximity to Wolf Rock (Table 2). On average, there was no significant difference between the proportion

of time that sharks were detected during day or night ($p = 0.99$). Short apparent absences of sharks were considered to represent signal detection failures when individuals were in acoustic blind spots rather than excursions from the site. On 2 occasions no signal was received from 2 of the tagged sharks for over 24 h, which suggested that temporary emigration beyond the detection envelope had occurred. The final loss of the acoustic signal from each shark probably occurred when each tag detached from the shark and floated out of range of the receivers. Two of the 4 sharks were resighted, minus their tags, within 3 wk of the termination of the present study.

DISCUSSION

There is general consensus that *Carcharias taurus* displays a biennial reproductive cycle (Bass et al. 1975, Lucifora et al. 2002, Dicken et al. 2006a, 2007), although Gordon (1993) and Gilmore (1993) have suggested that an annual reproductive cycle occurs for the east Australian and NW Atlantic populations, respectively. Gordon (1993) studied a captive population of *C. taurus* in which males and females were housed together, providing the opportunity for annual mating encounters. Data were not provided on whether mating events resulted in pregnancies. Gilmore (1993) stated that *C. taurus* 'mate synchronously each year in the late winter and spring after parturition' (p. 111), based on observations of pregnant females captured

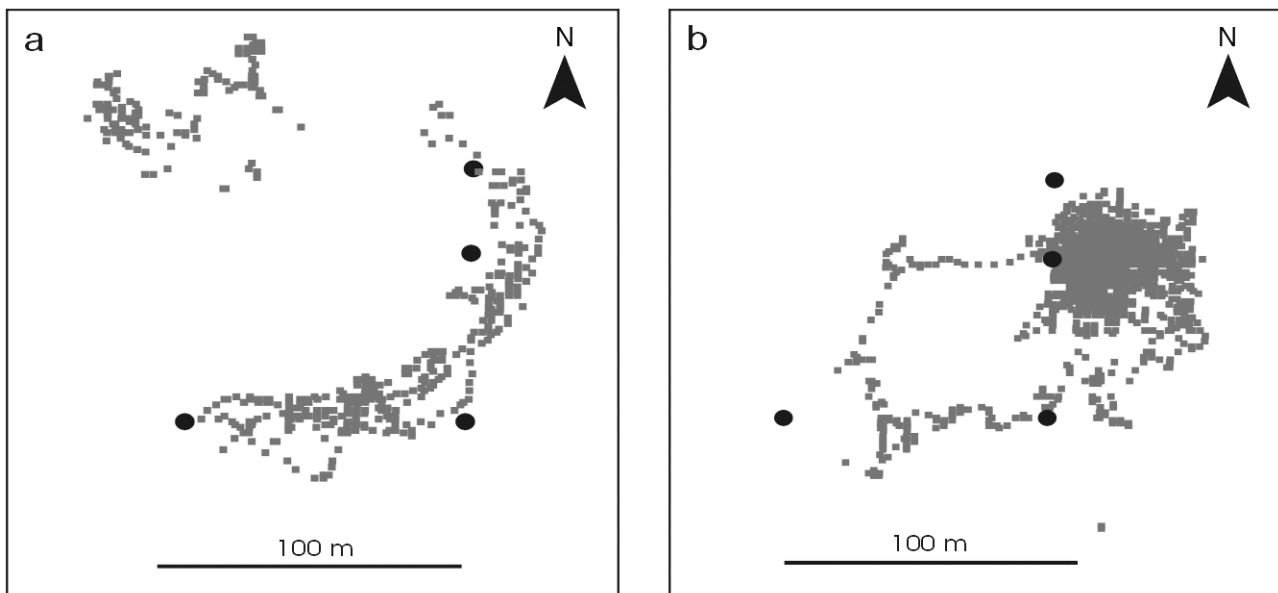
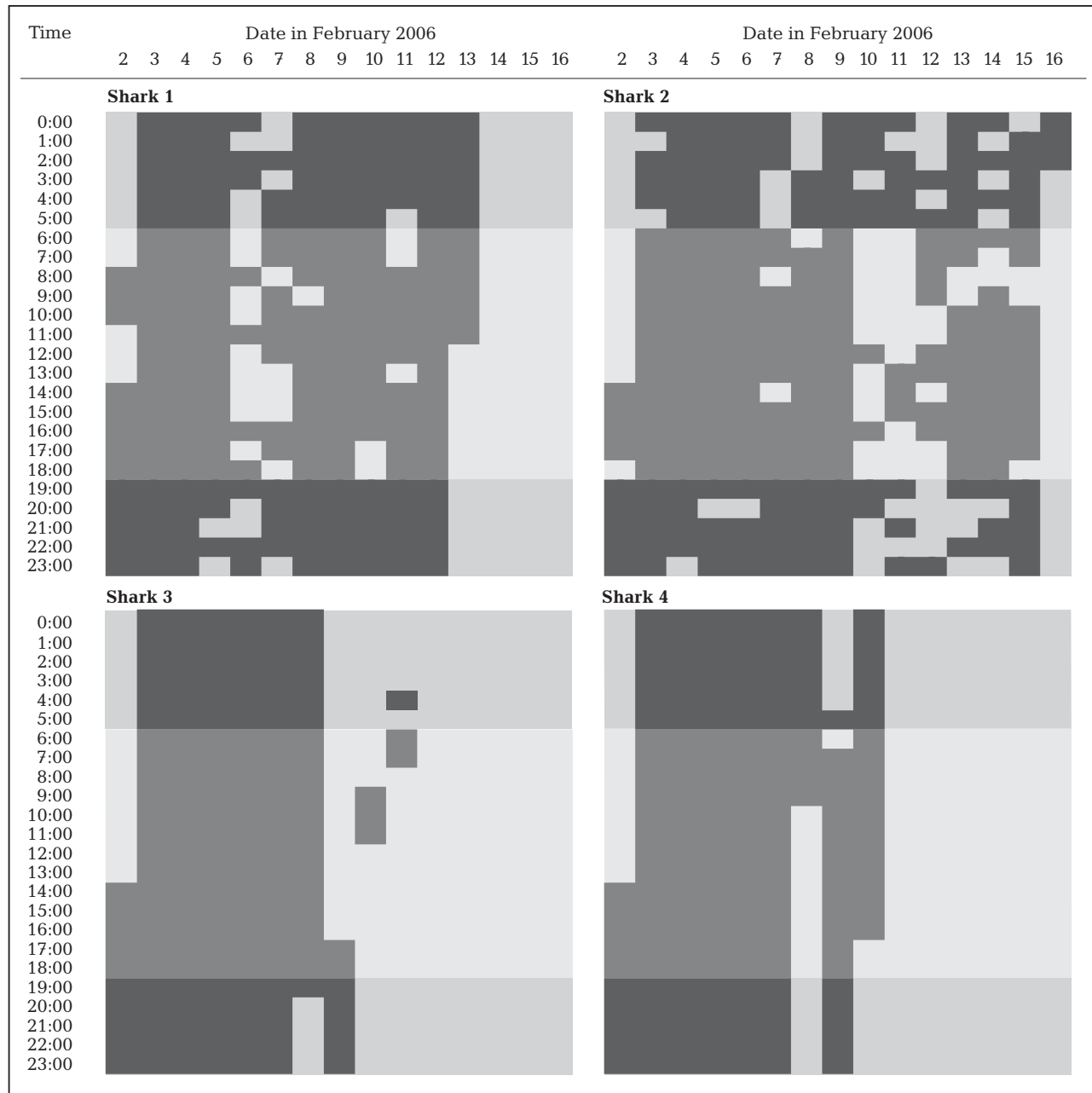


Fig. 8. *Carcharias taurus*. Active tracks of 2 mature females relative to VR2 receivers. (a) First track, between 08:40 and 16:25 h on 3 February 2006; (b) second track, between 08:56 and 23:45 h on 13 February 2006 and 06:37 and 08:40 h on 14 February 2006. (■): Shark location at 5 min intervals. (●) VR2 receiver

Table 2. *Carcharias taurus*. Site occupancy of 4 mature female sharks with fresh mating scars present in November or December 2005. Dark shaded cells represent a shark detected by a receiver, blank cells mean the shark was not detected by any receivers. Dark bands: night; light bands: daylight hours



off the Atlantic coast of Florida and in the northern Gulf of Mexico. The data from the present study did not provide support for an annual reproductive cycle in this species, as there was no evidence of a sequential annual pregnancy in any individual shark.

However, about two-thirds of the identified individuals seen over multiple years appeared to exhibit a biennial cycle (mating scars and/or pregnancy observed every second year), and one-third of the sharks

appeared to take an extra year between mating and/or pregnancy events (e.g. 3 yr from their previous mating or pregnancy event) (Fig. 7). However, an important assumption of the present study is that in years that sharks were not identified at Wolf Rock they were not pregnant at other locations. Additional PID surveys were undertaken by the primary author and the diving community at numerous aggregation sites along the east coast of Australia (south of Wolf Rock) between

2004 and 2008. During these surveys, sharks that were identified as pregnant at Wolf Rock in the present study were also identified at other locations in 'resting years'; to date, none of these sharks have been identified as visibly pregnant or with mating scars in a 'resting year' (authors' unpubl. data).

The present study and studies on *Carcharias taurus* populations in the SW Atlantic (Lucifora et al. 2002), South Africa (Dicken et al. 2006a, 2007), and the NW Atlantic (Branstetter & Musick 1994) indicate that very recent post-partum females may behave differently to female sharks that are about to mate. These post-partum females undertake a resting period in cooler waters and do not migrate to warmer waters with the other females to mate, they migrate for the mating season in the following year. The suggestion of an annual reproductive cycle by Gilmore (Gilmore et al. 1983, Gilmore 1993) can be explained if all of the sharks were sampled (26 ind. reported) from 'pregnancy sites' that lacked representation of non-pregnant, resting-phase individuals.

Similarly, in South Africa it was thought that near-term pregnant sharks captured in the shark control program off central Natal in July to August were on their way south to pup, whereas the non-pregnant mature female sharks captured at the same sites in October to November were on their northward migration directly after pupping in the Eastern Cape (Bass et al. 1975). However, given that a biennial reproductive cycle is now accepted for the population off South Africa (Dicken et al. 2006a, 2007), it is likely that those non-pregnant females captured in the shark control program in late spring were individuals returning north for the October to December mating season (Bass et al. 1975) after a resting year. The recent post-partum females may remain in cooler southern waters until the following mating season, as was observed in the present study.

A particular benefit of a PID approach, as used in the present study, is its potential to provide information on individual animals from multiple observations in time and space. Its use can avoid the misinterpretation of results, such as has occurred in many previous studies that have relied on catch data or other tagging methodologies (Bass et al. 1975, Gilmore et al. 1983, Gilmore 1993). *Carcharias taurus* is a good case study in which sequential sighting of a particular shark, as identified by its unique spot-patterns (Bansemer & Bennett 2008), can be used to follow its reproductive status (Figs. 6 & 7). Without this ability to recognise individual sharks it is far harder to gather unequivocal evidence to support (or refute) a biennial reproductive cycle in the wild.

Results from the present study indicate that mating occurred at Wolf Rock between mid-October and late

December with a peak in late November/early December. Many females that arrived at Wolf Rock in January and February had probably mated 1 to 2 mo prior to their arrival based on the partially healed state of their mating scars (their appearance was consistent with the state of healing exhibited on sharks that were identified with fresh mating scars in late November and December). The similarity in appearance of mating scars in January and February suggests that the mating season normally spans about 2 mo, and is supported by observations of mating from October to December in captive sharks (housed at UnderWater World, Mooloolaba, about 200 km south of Wolf Rock, and is supplied with seawater at ambient ocean temperature) (C. S. Bansemer unpubl. data). Anecdotal reports of *Carcharias taurus* mating in winter on the east coast of Australia (Otway et al. 2003) have not been independently verified.

Although a migration of pregnant sharks to warmer waters for pregnancy has been suggested for the South African and SW and NW Atlantic *Carcharias taurus* populations (Bass et al. 1975, Branstetter & Musick 1994, Lucifora et al. 2002, Dicken et al. 2006a, 2007), this has not been suggested in relation to the Australian east coast population. Previous analyses of the movement of sexually mature female sharks suggest that they move southwards in spring and early summer and the return movement to northern sites occurs in the autumn and winter months (Otway & Parker 2000, Otway et al. 2003, Otway & Burke 2004). However, these studies failed to recognise that mature female sharks show different patterns of migration depending on whether they are pregnant or are in a resting year. Unpublished observations from additional visual and PID surveys linked to the present study found that in their mating year mature female *C. taurus* migrate northwards from June (winter), arrive at Wolf Rock from September to late January, remain at this northern site for much of their pregnancy before their subsequent southward migration (beginning around June). Most pregnant sharks had left Wolf Rock by October, presumably for their migration to southern pupping sites. Pregnant sharks seen initially at Wolf Rock have been identified, still visibly pregnant, at sites south of Wolf Rock in July to September en-route to pupping grounds (authors' unpubl. data).

The duration of gestation for *Carcharias taurus* is thought to be between 9 and 12 mo within all populations (Bass et al. 1975, Gilmore 1993, Lucifora et al. 2002, Otway et al. 2003, Dicken et al. 2006a). Observations of *C. taurus* made in Otway et al. (2003) on the eastern Australian coast suggest that they give birth during winter at aggregation sites (Otway et al. 2003), although the authors cautioned that 'the timing of pupping, mating, and the duration of gestation will need to

be verified' (p. 6). While there are reports of recently born pups in the wild during winter (Otway et al. 2003), there is no certainty that these anecdotal reports by divers are correct. In contrast, there is evidence to support a late spring/summer parturition period; for example, a shark caught in Queensland waters (possibly from Wolf Rock) in July 1992 was pregnant at the time of capture and gave birth (in captivity) to 2 full-term pups in November 1992 (A. Fischer pers. comm.).

In the present study, mating occurred in late November/early December, pregnancies were first visible in late February, and the latest a pregnant shark was present at Wolf Rock was early October (most of them left by the end of September). As the closest site to Wolf Rock where young of the year (YOY) or juvenile sharks have been observed is about 500 km to the south, and the most southerly site is about 1200 km south (authors' unpubl. data), it seems likely that parturition occurs a considerable time after pregnant sharks leave their gestation grounds in the north. In South Africa, a pregnant *Carcharias taurus* travelled 1897 km from her northern gestation area to the southern parturition area, and another tagged pregnant shark travelled 383 km in 13 d or 29.5 km d⁻¹ (Dicken et al. 2006a, 2007). Swimming continuously at this speed it would take about 40 d for a pregnant shark to travel from Wolf Rock to the most southerly known pupping site on the east coast of Australia. However, transit times are likely to be extended as pregnant sharks first observed at Wolf Rock have been subsequently identified at more southerly Queensland sites in July where they have remained for 7 to 22 d. These locations are 300 km north of the most northerly site that juvenile *C. taurus* are occasionally observed, and 500 km north of the areas where YOY and juvenile *C. taurus* start to become more prevalent (authors' unpubl. data). Given the time of mating, the time of departure of pregnant sharks from Wolf Rock, and the fact that post-departure interruptions in the southwards migration do occur, it is likely that the pupping season extends from November to February for this population, rather than during the winter as previously suggested (Otway et al. 2003). The pattern of mating and pupping reported in the present is consistent with the reproductive behaviours exhibited by *C. taurus* in South African (Dicken et al. 2006a, 2007) and SW Atlantic waters (Lucifora et al. 2002).

Previous acoustic tracks of *Carcharias taurus* at sites on the eastern seaboard of Australia demonstrated that nocturnal absences from sites occurred more frequently than absences during the day, and were thought to reflect feeding activities out of range of the receivers during the night (Bruce et al. 2005). In contrast, the acoustically-tagged sharks at Wolf Rock showed no such day–night variation: either these sharks were not feeding during the period of the study

(hydroid growth on the teeth of pregnant sharks has been reported from South Africa and was interpreted to indicate a period of fasting) or ample food resources were present within the receivers' envelope of detection at this site. In a study of 4 mature females at 3 different locations over a 12 mo period, Bruce et al. (2005) found that sharks spent 0.5 to 6.9% of their time within range of the receivers at the site where they were tagged. This contrasts with the 78 to 90% of time that mated (and presumed pregnant) females spent at Wolf Rock in the present study, which suggests that gestating sharks, prior to their southerly migration, may be more strongly site-affixed than non-gestating sharks. It is important to note that the present study was conducted over 15 d and provides a relatively short snapshot of behaviour. A longer-term acoustic monitoring program was considered, but rejected due to concerns about tag-induced injury caused by long-term tag attachment (Department of Environment & Heritage 2003, Dicken et al. 2006b, Bansemer & Bennett 2008). Bruce et al. (2005) also actively tracked 2 mature female sharks that both remained within 200 m of an aggregation site for the duration (4 h and 12 h) of their study. A similar behaviour was observed at Wolf Rock and further active tracks of pregnant female *C. taurus* may be of limited value if they are strongly site-affixed.

This is the first detailed study to monitor individual mature female *Carcharias taurus* over multiple years and reproductive cycles using PID (Bansemer & Bennett 2008) and visual survey techniques to determine their reproductive periodicity. The present study revealed that mature female *C. taurus* along the eastern Australian seaboard gestate in northern warmer waters and are segregated from the rest of the *C. taurus* population. Furthermore, while the majority of females likely exhibit a biennial reproductive cycle, about one-third of the observed sharks may take 3 yr between some pregnancy events (this observation has implications for population modelling). Pregnant sharks remained within protected waters in close vicinity of the rock formation. The reproductive periodicity and timing of associated migrations of mature female *C. taurus* along the eastern seaboard of Australia is similar to that observed in South Africa, and not as has been suggested previously (Otway et al. 2003).

In conclusion, Wolf Rock is the only known site where female *Carcharias taurus* segregate and aggregate during pregnancy along the eastern seaboard of Australia. The total number of mature females currently identified across all known aggregation sites on the Australian east coast is 240 ind. (authors' unpubl. data). Considering that 161 mature females have been identified at Wolf Rock throughout the course of the present study, it is highly likely that at least one other gestation area exists on the east coast of Australia,

probably further north of Wolf Rock. Given the critically endangered status of *C. taurus* on the east coast of Australia, the identification and protection of other *C. taurus* gestation sites is warranted.

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