CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2011, **62**, 607–620

Pop-up archival satellite tagging of *Carcharias taurus*: movements and depth/temperature-related use of south-eastern Australian waters

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Abstract. Knowledge of migratory movements and depth/temperature-related use of coastal waters by sharks can lead to more sustainable fisheries and assist in managing the long-term conservation of those species now considered threatened. Pop-up archival satellite tags (PATs) provide an alternative to conventional tagging for documenting migratory movements. This study focussed on the migratory movements of *Carcharias taurus*, a critically endangered shark found along the east coast of Australia. From October 2003 to July 2008, 15 *C. taurus* individuals were tagged with PATs with varying deployments (60–150 days) and acoustic tags linked to an acoustic monitoring system providing accurate geo-location. Distances moved by *C. taurus* individuals ranged from 5 to 1550 km and varied according to sex and season. Migrations north and south were punctuated *en route* by occupation of sites for varying periods of time. The deepest depth recorded was 232 m off South West Rocks on the New South Wales mid-north coast. On average, *C. taurus* males and females spent at least 71% of their time in waters <40 m and 95% of their time in waters 17–24°C. By mainly occupying inshore waters, *C. taurus* is exposed to potentially adverse fishing-related interactions that may be difficult to mitigate.

Additional keywords: acoustic tagging, tag performance.

Introduction

Knowledge of migratory movements is fundamental to understanding a species' large-scale spatial and temporal patterns of abundance, reproduction, demography and capacity to withstand exploitation through directed fisheries or when captured as by-catch in another fishery. This is particularly true for many sharks, whose life-history characteristics, comprising slow growth, late onset of sexual maturity and low fecundity (Hoenig and Gruber 1990; Cortés 2000; Mollet and Cailliet 2002), make them extremely susceptible to targeted fishing (McAuley *et al*. 2007) and incidental capture in non-elasmobranch fisheries (e.g. Marín *et al*. 1998; Moyes *et al*. 2006; Campana *et al*. 2009). Fishing mortality, even at relatively low levels, can have severe consequences and results in dramatic population declines (Baum *et al*. 2003; Myers and Worm 2003; Baum and Myers 2004), especially for species with extremely low fecundity such as the grey nurse shark, *Carcharias taurus* Rafinesque, 1810.

In the past, *C. taurus* had a broad, albeit disjunct, distribution on inshore continental shelves in cool temperate to subtropical waters off the main continental landmasses (Compagno 2002; Last and Stevens 2009). With extensive overfishing and resulting population declines over much of its global range (Musick *et al*. 1993; Lucifora *et al*. 2002; Otway *et al*. 2004), it is doubtful that *C. taurus* still exists in the Mediterranean Sea (Fergusson *et al*. 2002). Its main remaining populations are now likely restricted to the east coasts of North and South America, South Africa and the east and west coasts of Australia. Globally, *C. taurus* is listed as 'Vulnerable' in the IUCN Red List of Threatened Species (Cavanagh *et al*. 2003).

In Australia, *C. taurus* occur as two separate and genetically distinct populations on the east and west coasts (Cavanagh *et al*. 2003; Stow *et al*. 2006). The species has been caught occasionally in the Arafura Sea, but has not been found in Tasmanian waters (Read and Ward 1986; Last and Stevens 2009). The range of the population off west Australia is less well known, but analysis of by-catch of commercial shark fisheries indicates that *C. taurus* may occupy sites from North-West Cape (21°46.00′S, 114°09.00′E) to the coastal waters off Cocklebiddy (32°15.00′S, 126°12.00′E) in the Great Australian Bight (Cavanagh *et al*. 2003). In contrast, the eastern Australian population has, over the past century, been subjected to many fisheries (Caldwell and Ellison 1939; Cropp 1964; Pepperell 1992; Reid and Krogh 1992), causing a markedly reduced population that extends from Yeppoon, Queensland (Qld) to Eden, New South Wales (NSW) (Fig. 1). *C. taurus* is now listed as critically endangered along the east coast of Australia under the IUCN (Cavanagh *et al*. 2003), NSW, Qld and Federal legislation.

The species is a relatively placid, strong-swimming shark that aggregates in rocky gutters, caves or under overhangs around inshore rocky reefs and islands. The shark is mainly piscivorous (Bass *et al*. 1975; Smale 2005) and has been recorded to depths of 191 m (Pollard *et al*. 1996; Compagno

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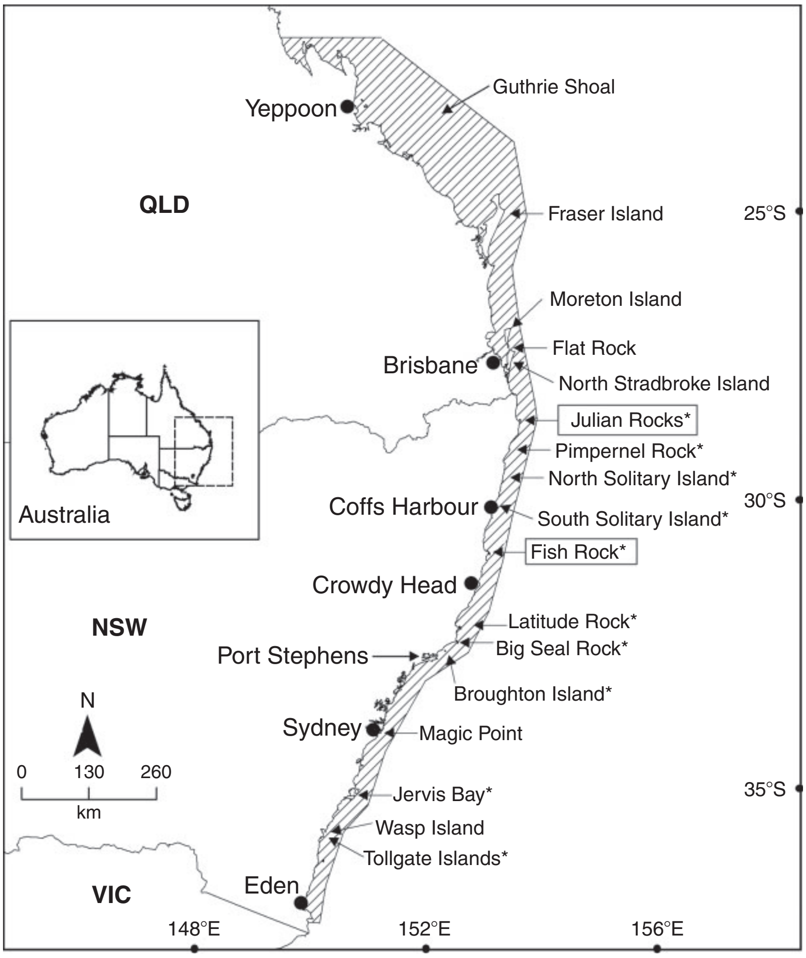

Fig. 1. Map of the SE coast of Australia showing the current range of *Carcharias taurus*, location of tagging sites (in boxes) and sites occupied during migratory movements of sharks tagged with pop-up archival satellite tags. Asterisks denote sites with SEACAMS acoustic listening stations.

2002). Like many elasmobranchs, *C. taurus* exhibits late onset of sexual maturity (USA, males: 6–7 years, females: 9–10 years), low fecundity (two pups born biennially after intrauterine cannibalism and oophagy – Springer 1948; Gilmore *et al*. 1983) and longevity of ≈35 years (Branstetter and Musick 1994; Goldman *et al*. 2006). Their biology and specific habitats make them extremely vulnerable to over-exploitation, with reduced populations requiring decades to recover (Smith *et al*. 1998; Mollet and Cailliet 2002; Otway *et al*. 2004).

An understanding of the migratory movements of *C. taurus* and its associated reproductive cycle (Bass *et al*. 1975; Gilmore *et al*. 1983; Smale 2002) has emanated from conventional tagging in the USA (Kohler *et al*. 1998) and South Africa (Davies and Joubert 1966; Dicken *et al*. 2007). However, the emergence of patterns from these studies has required tagging over decades and the long-term commitment of the recreational anglers involved. In contrast, preliminary data on the migration of east Australian *C. taurus* have been obtained using underwater visual censuses (Otway *et al*. 2003), conventional (cattle-ear) tagging (Otway and Burke 2004) and acoustic tagging (Bruce *et al*. 2005). These studies all inferred a northerly migration over autumn–winter months and a southerly migration during spring–summer months.

In 2003, conventional tagging of *C. taurus* off the east Australian coast was stopped by the Federal government over concerns that tag bio-fouling and associated abrasions could be detrimental to the sharks (Department of the Environment and Heritage 2003). Pop-up archival satellite tags (PATs) provide an alternative to conventional tagging and have yielded detailed information on the migratory movements and post-release survival of a range of sharks (e.g. Weng *et al*. 2007; Campana *et al*. 2009; Stevens *et al*. 2010). As fishing is a key threatening process for *C. taurus*, it is important to identify the frequency and spatial extent of fishing-related interactions. To do so requires an understanding of the shark's migratory movements and depth/temperature-related use of coastal waters. Moreover, demographic modelling (Otway *et al*. 2004) has shown that mitigating these anthropogenic threats, particularly with immature females, is critical to the recovery and long-term survival of the east coast *C. taurus* population. Hence, this study used PATs to quantify the migratory routes, distances travelled and the depth/temperature-related occupation of east Australian waters

Table 1. Biological attributes, planned and realised periods of deployment, and data recovery for 15 *Carcharias taurus* individuals tagged with pop-up archival satellite tags (PATs) and acoustic (AC) tags at Fish Rock (*n* = 14) and Julian Rocks (*n* = 1, Shark 11) between October 2003 and July 2008

TL, total length (m); M, mature; I, immature; R, recovery of PATs

Shark No. (Maturity)	TL (m)	Tags attached	Tagging date	PAT deployment (days)		Pop-up and recovery	Data recovery (%)
				Planned	Realised		
Male							
1 (M)	2.25	PAT, AC	29.04.05	150	150	Yes	96.20
2 (M)	2.20	PAT, AC	22.05.07	77	77	Yes, R	100.00
3 (M)	2.45	PAT, AC	22.05.07	70	70	Yes	96.11
4 (M)	2.40	PAT, AC	22.05.07	84	84	Yes	94.03
5 (M)	2.40	PAT	23.10.03	180	180	No	0.00
6 (M)	2.26	PAT	11.11.03	120	120	Yes	94.30
7 (M)	2.15	PAT, AC	01.12.06	120	117	Yes, R	100.00
8 (I)	1.80	PAT, AC	01.12.06	120	120	Yes	100.00
Female							
9 (I)	2.40	PAT, AC	22.05.07	98	68	Yes, R	100.00
10 (I)	2.10	PAT, AC	22.05.07	91	59	Yes	100.00
11 (M)	2.97	PAT	16.07.08	90	38	Yes	100.00
12 (I)	2.40	PAT	11.11.03	90	90	Yes, R	100.00
13 (I)	2.25	PAT, AC	01.12.06	120	115	Yes, R	100.00
14 (I)	2.37	PAT, AC	01.12.06	120	51	Yes, R	100.00
15 (I)	2.38	PAT, AC	01.12.06	120	–	No	0.00

by *C. taurus*. A serendipitous event also enabled an assessment of the survival and movements of a sexually mature female after the removal of a fishing gaff embedded in the animal's oesophagus.

Materials and methods

Study sites

Tagging was done at Fish Rock off South West Rocks (30°56.25′S, 153°06.05′E) and Julian Rocks off Byron Bay (28°37.00′S, 153°37.75′E) between October 2003 and July 2008 (Fig. 1). Fish Rock lies in 20–40 m of water, 2.1 km offshore of Smoky Cape, and the surrounding reef supports aggregations of *C. taurus* and a diverse temperate fish community with some tropical species present during the warmer months (Otway *et al*. 2003). In contrast, Julian Rocks is 3.5 km offshore of Byron Bay in 20 m of water. The site supports a diverse tropical and temperate fish community throughout the year (Harriott *et al*. 1997), with *C. taurus* aggregating in the gutters to the north of the site during winter months. Males are generally more abundant in June, while putatively pregnant females are present from July (Hayward 2003; Otway *et al*. 2003). Both sites are influenced by the East Australian Current (EAC) (Tranter *et al*. 1986), onshore winds and a prevailing 1–2-m south-easterly swell. Mean seawater temperatures range from ≈19.0°C in winter to ≈25.0°C in summer, with fluctuations occurring with EAC reversals, internal waves, upwellings and weather systems. The resulting daily variation in seawater temperature at both sites is greatest in summer and least in winter (N. M. Otway and M. T. Ellis, unpubl. data).

Pop-up archival satellite tags and geo-location of sharks

The pop-up archival satellite tags used included four PTT 100 PATs (Microwave Telemetry, Columbia, MD, USA) and eleven Mk 10 PATs (Wildlife Computers, Redmond, WA, USA). These tags archive data on temperature, pressure (depth) and light levels and transmit this information in different formats via the ARGOS system following release. Microwave Telemetry PATs transmit hourly readings, whereas Wildlife Computers PATs transmit summarised data comprising time at depth, time at temperature histograms and depth temperature profiles for 12 user-defined bins. If released tags are recovered, the archived data can be retrieved.

PATs were programmed with a range of deployment durations (Table 1) for two reasons. First, rough seas can greatly affect the transmission of archived data to the ARGOS system and differing deployment periods can help ensure that PATs deployed contemporaneously are not exposed to the same adverse sea conditions following release, thus enhancing data recovery. Second, using differing deployment periods hopefully permits the staggering of PAT releases along the route, enabling a better determination of the overall migratory path.

Sharks were also tagged with Vemco V16TP, R-coded, 69-kHz acoustic tags (Amirix Systems Inc., Nova Scotia, Canada) with randomised transmission delays of 60–183 s. The tags were detected on the SE Australian coastal acoustic monitoring system (SEACAMS), comprising a network of ≈60 Vemco VR2W acoustic listening stations deployed at numerous sites along the NSW coast (Fig. 1).

The locations of PAT-tagged *C. taurus* individuals during their migrations were determined using a variety of methods. In order of decreasing accuracy, these included: SEACAMS; observations by recreational SCUBA divers with the shark's sex, total length (TL), tag position (left or right) and date sighted used for identification; and the geo-positioning algorithms associated with the light curves obtained from each PAT together with comparisons of measured depths and water temperature to charted bathymetry and sea-surface temperatures.

The final (pop-up) locations of PAT-tagged *C. taurus* individuals were determined using either SEACAMS or position fixes derived from the ARGOS system. When acoustic detections were obtained on SEACAMS at the time of the PAT's release, the known position of the particular listening station was used. Alternatively, the shark's final position was determined using the time of the first PAT transmission combined with positional fixes of the released PAT provided by the ARGOS system. The reliability of these satellite fixes is coded in location classes (LC) with increasing accuracy from B through A, 0, 1, 2 and 3, with the most accurate position (LC 3) having a root mean square error of <150 m ARGOS (2008). The time of the first PAT transmission, the first satellite fix classified as LC 3 or LC 2 following PAT release and the post-release surface track were then used to back-calculate the position of a PAT when released.

Tagging procedures

Prior to deployment, each tag was attached to ≈10 cm of monofilament line (100 kg breaking strain), which was, in turn, attached to an intra-muscular dart made of surgical plastic. The acoustic tags were then inserted into small floats to provide buoyancy and prevent abrasions of the shark's skin. As fouling organisms can reduce a PAT's buoyancy and prevent surfacing following release (Hays *et al*. 2007) and conventional tags on *C. taurus* have become fouled (Dicken *et al*. 2006; N. M. Otway, unpubl. data), the PAT and acoustic tags were painted with two coats of antifouling paint.

C. taurus individuals were captured at Fish Rock and Julian Rocks using a similar method that was modified at each site because of the different vessels used. While detailed descriptions can be found in Smith (1992) and Otway *et al*. (2009), briefly, the chosen *C. taurus* individual was caught by SCUBA divers using a lasso, taken to the surface and placed in a partially submerged stretcher on or next to the boat. This process took no longer than 10 min and resulted in minimal struggling by *C. taurus*. Each shark was then placed in dorsal recumbency to induce tonic immobility (Watsky and Gruber 1990; Henningsen 1994) and examined for evidence of injuries associated with its capture or prior fishing interactions. This was done as previous studies have shown that many *C. taurus* have hooks and associated nylon line and/or wire trace embedded in and around their jaws, buccal cavity and gills (Otway *et al*. 2003; Otway 2004; Bansemer and Bennett 2009). Immediately before tagging, the shark was rolled into left or right lateral recumbency to provide easier access to the tagging site. The PAT and acoustic tags were attached on either side of the first dorsal fin by inserting the plastic dart through a 5-mm incision in the skin covering the epaxial muscle mass using a stainless-steel applicator. The TL of each shark, with caudal fin in the depressed position (Francis 2006), was then measured to the nearest cm. Reproductive data from the east Australian *C. taurus* population obtained via tagging and necropsies ($n = 211$) over the past 10 years have shown that 50% of males and females are sexually mature at 2.101 (s.e. = 0.063) m TL and 2.587 (s.e. = 0.027) m TL, respectively (Otway *et al*. 2009). Consequently, the sex of the shark was determined via the presence of claspers in males, the length and calcification of which were used in combination with TL to determine sexual maturity. The sexual maturity of captured females was determined using TL together with the presence/absence of hymen. Finally, any embedded fishing gear was removed and the shark released.

Data processing and statistical analyses

Comparisons of the planned (programmed) and realised periods of PAT deployment and similar comparisons between the sexes were done using *t*-tests (Snedecor and Cochran 1967). Depth and temperature data from the PATs were examined and 6-hourly means calculated. The means were linked to known positions and used to provide depth and temperature profiles for individual legs in each migratory path. Kolmogorov–Smirnov (K-S) tests (Sokal and Rohlf 1969) were used to examine the percentages of time that *C. taurus* spent in waters of various depths during the hours of daylight and darkness for individual sharks and between the sexes using means for males and females. Similarly, the mean percentages of time that *C. taurus* spent in waters of various temperatures were compared between the sexes using K-S tests after pooling across individual males and females.

Results

Tagging

Fifteen *C. taurus* individuals were tagged with PATs between October 2003 and July 2008, with 11 individuals also tagged with an acoustic tag (Table 1). Fourteen *C. taurus* individuals were tagged at Fish Rock, with 87.5% of males sexually mature and 100% of females sexually immature. Despite this, the mean (±s.e.) TL of males (2.24 ± 0.073) and females (2.32 ± 0.049) did not differ significantly between the sexes ($t_{12} = -0.89$, $P = 0.39$) when pooled over the autumn–winter and spring–summer tagging periods. The last *C. taurus* tagged was captured at Julian Rocks to remove a 1.07-m long fishing gaff embedded in the animal's oesophagus. Following the gaff's successful removal, this sexually mature, 2.97-m TL female was tagged with a PAT to assess the shark's survival and subsequent movements.

None of the sharks caught using the lasso became overly stressed following capture and restraint, tagging, the associated measurements and the removal of fishing gear. Diver observations indicated that within minutes of release, the swimming behaviour of each tagged shark was indistinguishable from those of the surrounding *C. taurus* individuals. Additional reports including video footage of PAT-tagged sharks were provided by recreational SCUBA divers on numerous occasions throughout the tag deployments and also indicated that the sharks were swimming normally and unaffected by the presence of the tags.

Performance of PATs

Two PATs failed to transmit any data via the ARGOS system (Table 1). The first tag, deployed on a *C. taurus* male, was observed by SCUBA divers at Big Seal Rock on two occasions. On the first occasion (a week before the PAT's release), the tag had several barnacles, with basal diameters of ≈15 mm, growing on the float. On the second occasion (10 days after the tag's scheduled release), the PAT was absent. The second tag, deployed on a *C. taurus* female, was not detected on SEACAMS or observed by divers. A further seven PATs were washed ashore over a wide geographic range from Main Beach, North Stradbroke Island (Qld) to Cookies Beach, Durras (southern NSW) and six were recovered, enabling 100% of the archived data to be obtained (Table 1). Transmissions from the remaining PATs enabled varying amounts of data to be obtained (Table 1).

While the planned PAT deployment periods in autumn–winter and spring–summer varied (Table 1), the mean (±s.e.) planned deployment periods of *C. taurus* males (115.13 ± 13.33 days, $n = 8$) and females (101.50 ± 5.98 days, $n = 6$) did not differ significantly ($t_{12} = 0.93$, $P = 0.37$). In contrast, the mean realised PAT deployment period of *C. taurus* males was significantly greater than that of females ($t_{12} = 2.54$, $P = 0.026$) and this difference appeared to be unaffected by the timing of tag deployment (Table 1). The planned and realised PAT deployment periods also varied with sex. With males, the mean (±s.e.) planned (115.13 ± 13.33 days) and realised (114.75 ± 13.32 days) deployment periods did not differ significantly ($t_7 = 1.00$, $P = 0.35$). However, for females, the mean (±s.e.) planned (101.50 ± 5.98 days) and realised (70.17 ± 11.45 days) deployment periods differed significantly ($t_5 = 2.89$, $P = 0.034$), with the realised PAT deployment period reduced by 39%, on average.

Migratory movements

Sexually mature *C. taurus* males tagged at Fish Rock in autumn–winter (Sharks 1–4) migrated north (Fig. 2). Their northerly migration was punctuated via the occupation of various sites *en route* (Table 2). Whilst at these rocky reefs, the sharks were observed and photographed by SCUBA divers and detected by SEACAMS. The duration of occupation of these sites varied among sharks and sites, and ranged from less than a day to 2 weeks. Whilst at these sites, the sharks swam at shallower depths, on average, compared with when migrating north between sites (Table 2). The PATs on two *C. taurus* males (Sharks 2 and 3) were released near Henderson Rock (off Moreton Is., Qld) and Fraser Is. (Qld), having travelled at least 450 km and 700 km, respectively, from Fish Rock. Over the period of monitoring, both sharks spent at least 90% of their time in water depths <60 m and did not exceed a depth of 128 m. While seawater temperatures ranged from 18 to 23.6°C, the sharks spent ≈95% of their time in waters 19–23°C. The two remaining sharks (Sharks 1 and 4) swam north to Fraser Is. (Qld), then east of the coral reefs comprising the Capricorn and Bunker groups (Great Barrier Reef, Qld) and entered the Capricorn Channel (Table 2). After ≈14 days in the Capricorn Channel, the PAT on Shark 4 was released ≈6 km to the east of Guthrie Shoal (Table 2) The remaining shark (Shark 1) spent ≈42 days in the Capricorn Channel before its southward journey to Shag Rock (off North Stradbroke Is., Qld), where its PAT was released (Table 2). This shark then migrated further south and was detected at Fish Rock over 17 days in November 2005 by SEACAMS. During their northerly migration, Sharks 1 and 4 travelled at least 1000 km and 1550 km, respectively, and did not exceed a depth of 136 m. They spent ≈49% and ≈91% of their time, respectively in water depths <60 m and mainly occupied deeper waters when swimming north of Fraser Island and in the Capricorn Channel (Table 2). While seawater temperatures ranged from 17.4 to 25.2°C, both sharks spent at least 90% of their time in waters 20–24°C.

Sexually mature *C. taurus* males tagged at Fish Rock in spring–summer (Sharks 5–7) migrated south (Fig. 2). As discussed earlier, one PAT (on Shark 5) failed to surface. However, SCUBA divers observed the animal for 7 days before leaving Fish Rock, then at Big Seal Rock just before the PAT's scheduled release. Assuming the PAT was released at Big Seal Rock, this shark would have travelled at least 180 km during its migration south. The southerly migration of the two remaining sharks (Sharks 6 and 7) was punctuated by the occupation of various sites *en route* for varying durations where they swam at shallower depths, on average, compared with when migrating south between sites (Table 2). Whilst at these sites, the sharks were observed and photographed by SCUBA divers and/or detected by SEACAMS. After tagging, one shark (Shark 6) remained at Fish Rock for ≈4 weeks, then swam to North Solitary Island, where it remained for 9 days. The shark then swam south to a site off Jervis Bay and then to the Tollgate Islands where it remained until its PAT was released (Table 2). The other shark (Shark 7) left Fish Rock, swam south and occupied at least three sites for short periods before reaching Wasp Island where its PAT was released (Table 2). During their migration south, Sharks 6 and 7 travelled at least 720 km and 640 km, respectively, spent over 90% of their time in water depths <60 m and did not exceed a depth of 125 m. While both sharks occupied waters with a wide range of temperatures (i.e. 13.8–25°C), they spent at least 84% of their time in waters 18–25°C.

The single sexually immature *C. taurus* male (Shark 8) tagged at Fish Rock in spring–summer remained at the site until the PAT was released on 2 April 2007. While at Fish Rock, the shark swam at an overall mean (±s.e.) depth of 21.61 (0.41) m (range = 0.00–41.70 m), was detected almost continuously by the four SEACAMS listening stations and was regularly observed by SCUBA divers. During its occupation of the site, it spent 100% of its time in water depths <45 m and 100% of its time in waters 18–25°C.

The single sexually mature *C. taurus* female (Shark 11) tagged at Julian Rocks in autumn–winter survived following the removal of the embedded fishing gaff as indicated by the absence of PAT release within 96 h (via the tag's constant depth option) and its subsequent migratory movements (Fig. 3). The shark remained at Julian Rocks for ≈6 h, swam south for 9 days and then north until reaching Lennox Head where its PAT was released (Table 3). Over the period of monitoring, the shark travelled at least 400 km and did not exceed a depth of 100 m. It spent ≈37% of its time in water depths <30 m and ≈61% of its time in waters 40–80 m in depth. While seawater temperatures ranged from 18 to 23°C, the shark spent ≈92% of its time in waters 19–22°C.

The two sexually immature *C. taurus* females tagged at Fish Rock in autumn–winter (Sharks 9 and 10) exhibited very different patterns of movement, with only one individual migrating (Fig. 3). The first shark (Shark 9) remained at Fish Rock for 1 day, was detected by SEACAMS and then spent 16 days undertaking two offshore excursions (Table 3). During the first excursion, lasting 7 days, the shark swam offshore and

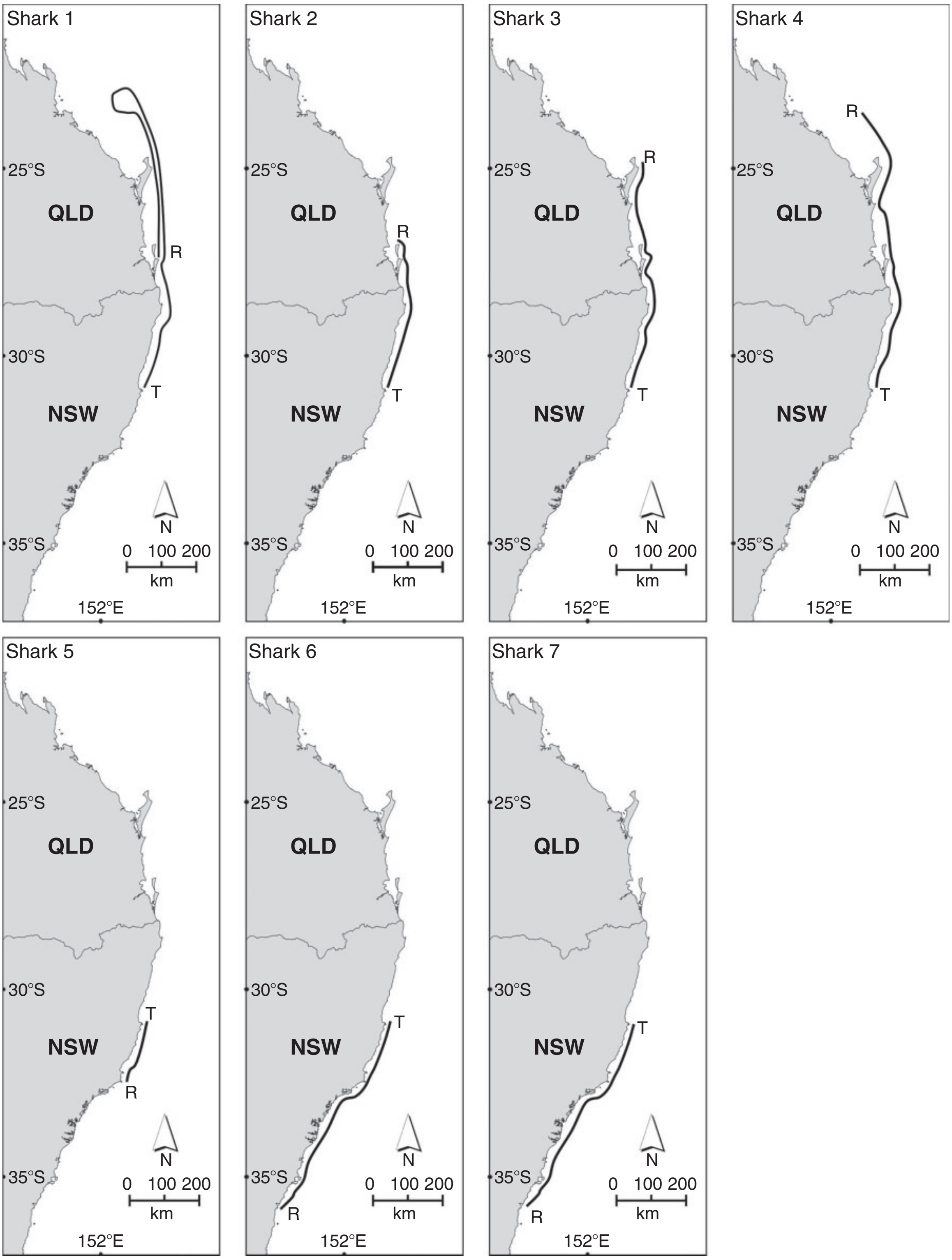

Fig. 2. Map showing migratory movements of *Carcharias taurus* males tagged with pop-up archival satellite tags at Fish Rock during autumn–winter (Sharks 1–4) and spring–summer (Sharks 5–7) over 2003–2008.

Table 2. Mean (s.e.) swim depth and range (in metres) of *Carcharias taurus* males tagged with pop-up archival satellite tags between 2003 and 2008

B_I, Broughton Island; C_C, Capricorn Channel; F_R, Fish Rock; F_L, Flat Rock; F_I, Fraser Island; J_B, Jervis Bay; J_R, Julian Rocks; L_R, Latitude Rock; N_S, North Solitary Island; P_R, Pimpernel Rock; S_R, Shag Rock; S_S, South Solitary Island; T_I, Tollgate Islands

Shark 1		Shark 2		Shark 3		Shark 4		Shark 6		Shark 7	
Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range
At F_R	19.97 (0.24) 4.03–40.35	At F_R	21.42 (0.53) 5.50–35.46	At F_R	22.40 (0.41) 15.50–35.24	At F_R	20.80 (0.25) 16.24–30.00	At F_R	12.49 (0.34) 0.00–28.29	At F_R	24.81 (0.23) 15.29–29.90
Travel N	38.20 (0.85) 22.86–32.30	Travel N	45.62 (0.53) 36.94–61.08	Travel offshore	48.80 (3.28) 37.46–55.54	Travel N	58.80 (1.92) 40.69–65.50	Travel N	26.38 (0.39) 22.33–34.25	Travel S	14.98 (1.93) 5.50–65.00
At S_S	25.50 (0.17) 28.86–32.30	At S_S	25.97 (0.24) 25.50–26.26	Travel N	13.64 (1.39) 5.50–28.92	At S_S	15.48 (0.69) 6.04–25.50	At N_S	22.42 (0.28) 16.38–29.78	At L_R	5.91 (0.82) 5.50–7.14
Travel N	41.20 (0.53) 10.76–79.35	Travel N	41.81 (3.87) 32.75–50.67	At J_R	5.76 (0.55) 5.50–7.25	Travel N	18.89 (2.16) 5.50–25.50	Travel S	45.44 (1.57) 17.87–86.36	Travel S	14.98 (2.38) 5.50–29.34
At N_S	27.13 (0.44) 17.48–36.31	At N_S	26.35 (0.34) 25.50–27.64	Travel N	15.64 (0.76) 5.50–23.86	At P_R	20.66 (1.21) 15.38–25.50	At J_B	18.98 (0.42) 13.40–43.18	At B_I	6.69 (1.13) 5.50–10.07
Travel N	41.02 (1.17) 37.66–43.04	Travel N	38.05 (1.15) 27.60–45.40	At F_L	12.83 (0.98) 5.50–18.88	Travel N off F_I	27.13 (0.44) 17.48–36.31	Travel S	66.88 (1.83) 25.31–98.27	Travel S	17.17 (1.82) 5.50–55.63
At P_R	25.73 (1.72) 10.76–36.31	At P_R	20.50 (1.10) 20.05–21.50	Travel N	36.07 (1.75) 5.83–89.56	Travel to C_C	75.99 (0.54) 46.50–92.24	At T_I	9.61 (0.26) 0.00–32.76	At J_B	8.19 (0.71) 5.50–15.50
Travel N	39.77 (1.23) 13.45–53.97	Travel N	33.33 (1.34) 23.47–53.97	Pop-up – 31.07.2007 at Fraser Island, Qld		Pop-up – 14.08.2007 at Guthrie Shoal, Qld		Pop-up – 11.03.2004 at Tollgate Islands, NSW		Travel S	6.68 (0.17) 5.50–15.50
At F_L	21.40 (0.20) 16.14–24.21	At F_L	22.35 (0.65) 15.46–26.65							Pop-up – 27.03.2007 at Wasp Island, NSW	
Travel N off F_I	52.35 (0.62) 34.97–73.97	Travel N	49.95 (3.33) 37.46–55.54								
Travel in C_C	40.06 (0.23) 14.79–68.59	Pop-up – 07.08.2007 at Henderson Rock, Qld									
Travel S	61.84 (1.01) 33.62–82.04										
At S_R	21.89 (0.70) 17.48–26.90										
Pop-up – 29.09.2005 at Shag Rock, Qld											

Fig. 3. Map showing migratory movements of *Carcharias taurus* females tagged with pop-up archival satellite tags at Fish Rock and Julian Rocks during autumn–winter (Sharks 9 and 11) and spring–summer (Sharks 12–14) over 2003–2008.

Table 3. Mean (s.e.) swim depth and range (in metres) of *Carcharias taurus* females tagged with pop-up archival satellite tags between 2003 and 2008
C_H, Crowdy Head; F_R, Fish Rock; J_R, Julian Rocks; N_S, North Solitary Island; P_S, Port Stephens; S_S, South Solitary Island

Shark 9		Shark 11		Shark 12		Shark 13		Shark 14	
Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range	Activity	Swim depth range
At F_R	19.97 (1.21) 16.76–24.76	At J_R	35.33 (2.64) 15.00–45.00	At F_R	24.76 (0.52) 23.82–32.76	At F_R	25.06 (0.51) 7.99–35.46	At F_R	13.55 (0.26) 8.93–16.38
Travel offshore	41.79 (2.38) 37.70–48.25	Travel S	56.58 (1.49) 40.77–72.03	Travel offshore	56.60 (0.30) 26.80–68.49	Travel N	13.36 (0.63) 5.50–31.08	Travel S	53.10 (0.49) 43.18–61.05
Offshore	81.95 (2.55) 69.38–99.75	Travel N	47.78 (1.23) 35.54–68.78	At F_R	21.80 (0.24) 7.44–47.65	Travel S	47.50 (2.51) 13.72–70.17	At C_H	12.04 (1.08) 4.47–17.87
Mid shelf	69.62 (1.21) 65.50–74.79	Travel N	7.87 (0.53) 5.50–23.00	Travel S	53.31 (0.60) 28.29–62.54	Off P_S	6.33 (0.21) 5.50–26.01	Pop-up – 27.01.2007 at Crowdy Head, NSW	
Offshore	108.80 (2.32) 94.50–122.40	Pop-up – 23.08.2008 at Lennox Head, NSW		At C_H	16.08 (0.38) 1.49–32.76	Pop-up – 26.03.2007 at Morna Point, NSW			
Travel N	42.03 (2.80) 24.24–51.31			Pop-up – 11.02.2004 at Crowdy Head, NSW					
At S_S	20.13 (0.46) 15.46–53.43								
Travel N	53.98 (3.77) 17.95–65.50								
At N_S	11.82 (0.98) 5.50–15.83								
Pop-up – 26.07.2007 at N. Solitary Island, NSW									

on one occasion (27 May 2007) spent ≈5 min in waters 150–200 m in depth and 17.6°C. During the second excursion, lasting 9 days, the shark moved further offshore and (on 3 June 2007) descended over the shelf break for ≈17 min, swimming to a maximum depth of 232 m. On returning to near-shore waters, the shark swam north to South Solitary Island where it remained for 40 days (SEACAMS detections). The shark then swam to North Solitary Island where it remained until its PAT was released. Whilst at these sites, the shark swam at shallower depths, on average, compared with when migrating between the sites (Table 3). During the period of monitoring, this *C. taurus* female travelled at least 150 km north and spent ≈75% of its time in water depths <60 m. While seawater temperatures ranged from 15 to 26°C, the shark spent ≈91% of its time in waters 19–24°C. The second shark (Shark 10) remained at the site for the entire PAT deployment (released 19 July 2007) and was detected almost continuously by the four SEACAMS listening stations. Whilst at Fish Rock, it swam at an overall mean (±s.e.) depth of 17.81 (0.52) m (range = 5.50–35.46 m) and was regularly observed by SCUBA divers. During its occupation of the site, it did not exceed a depth of 60 m, spent ≈94% of its time in water depths <40 m and ≈99% of its time in waters 20–24°C.

Sexually immature *C. taurus* females tagged at Fish Rock in spring–summer (Sharks 12–14) migrated south (Fig. 3). Two individuals (Sharks 12 and 14) spent some time at Fish Rock, with one individual also swimming offshore for a short period. Both sharks migrated south in deeper waters, then moved inshore and occupied shallower waters off Crowdy Head where their PATs were released (Table 3). During the period of monitoring, these sharks travelled at least 100 km, did not exceed 80 m depth and spent at least 78% of their time in water depths <60 m. The sharks occupied waters with a wide range of temperatures (i.e. 15–26°C) and spent at least 74% of their time in waters 18–25°C. The remaining shark (Shark 13) remained at Fish Rock for 15 days then swam north to a site off Coffs Harbour. It then swam south, reaching the waters off Port Stephens where its PAT was released (Table 3). Over the period of monitoring, this shark travelled at least 400 km (100 km north and then 300 km south). During its migration, it did not exceed a depth of 100 m, spent ≈96% of its time in water depths <60 m and ≈90% of its time in waters 19–26°C.

Depth-related occupation of coastal waters

The percentages of time spent at various depths by individual *C. taurus* males (Table 4) did not differ significantly between

Table 4. Comparison of the percentage of time spent at various depths during the daylight and at night by *Carcharias taurus* males (*n* = 7) and females (*n* = 6) tagged with pop-up archival satellite tags between 2003 and 2008

Depth (m)	Male shark							Mean (%)	Female shark						Mean (%)
	1	2	3	4	6	7	8		9	10	11	12	13	14	
Day															
10	4.53	2.16	31.23	2.04	35.56	54.77	0.71	18.71	0.11	11.09	25.83	7.91	56.89	88.29	31.69
20	7.72	14.55	32.47	17.19	32.99	13.96	24.26	20.45	42.35	33.46	11.11	32.23	15.47	9.15	23.96
30	23.41	62.29	7.76	12.26	18.49	24.77	73.00	31.71	27.08	43.98	0.24	31.94	20.16	2.56	20.99
40	37.13	10.99	7.44	11.67	2.57	2.32	2.04	10.60	1.60	11.47	10.41	3.74	3.13		5.06
50	17.16	6.45	10.71	6.53	3.59	2.20		6.66	4.48		25.63	1.08	0.003		5.20
60	5.39	3.52	2.79	2.95	1.41	1.17		2.46	3.75		9.83	15.32	4.14		5.51
70	3.68	0.04	5.05	6.00	2.05	0.81		2.52	6.54		15.20	7.77	0.21		4.95
80	0.86		1.06	33.90	1.16			5.28	4.07		1.75				0.97
90	0.12		0.90	5.77	1.28			1.15	5.33						0.89
100			0.61	1.68	0.90			0.46	2.89						0.48
125									1.65						0.28
150									0.15						0.03
200															
Night															
10	3.46	12.26	30.92	3.15	40.60	57.57	6.98	22.13	1.70	18.02	27.21	23.35	63.93	66.27	33.41
20	6.91	14.83	21.37	17.15	33.55	10.01	59.22	23.29	44.40	47.49	10.02	32.975	12.82	31.86	29.93
30	21.73	51.85	14.25	13.56	10.68	24.36	33.70	24.31	22.98	32.30	1.21	16.13	15.37	1.85	14.97
40	36.05	10.52	13.53	9.55	1.92	5.27	0.10	10.99	3.04	2.18	11.29	3.85	2.28	0.02	3.78
50	21.61	4.87	11.41	5.32	4.27	1.70		7.03	3.19	0.01	24.56	3.73	0.70		5.37
60	7.65	4.95	4.96	5.44	1.92	0.79		3.68	4.73		13.00	16.49	3.11		6.22
70	1.98	0.73	2.56	12.27	3.42	0.30		3.04	5.57		11.89	3.49	1.77		3.79
80	0.62		0.65	19.97	2.56			3.40	4.33		0.71		0.02		0.84
90			0.22	13.11	0.64			2.00	4.02		0.10				0.69
100			0.09	0.46	0.43			0.14	2.55						0.43
125			0.04	0.02				0.01	3.06						0.51
150									0.23						0.04
200									0.21						0.03
K-S tests															
D	0.20	0.20	0.30	0.25	0.20	0.20	0.10	0.18	0.23	0.10	0.20	0.20	0.20	0.10	0.15
P	0.98	0.98	0.68	0.83	0.98	0.98	1.00	0.99	0.83	1.00	0.98	0.98	0.98	1.00	0.99

day and night (K-S tests, $D = 0.100$–0.300, $P = 0.68$–1.00). The immature *C. taurus* male (Shark 8) spent 100% of its time in a narrower depth range (0–45 m) compared with the sexually mature males. The percentage of time spent at various depths averaged across all *C. taurus* males, all females and by the individual female (Table 4) did not differ significantly between day and night (K-S tests, $D = 0.182$, $P = 0.988$; $D = 0.153$, $P = 0.995$; $D = 0.100$–0.231, $P = 0.83$–1.00, respectively). The sexually mature female (Shark 11) occupied a similar range of depths during the day and at night to the sexually immature females (Table 4).

On average, the percentages of time spent at various depths by *C. taurus* males and females did not differ significantly during the day (K-S test, $D = 0.317$, $P = 0.556$) or at night (K-S test, $D = 0.279$, $P = 0.663$). *C. taurus* males spent $\approx$71% of their time in waters <40 m and $\approx$94% of their time in waters <80 m (Table 4). On average, *C. taurus* females spent $\approx$78% of their time in waters <40 m and $\approx$97% of their time in waters <80 m, respectively (Table 4). Combined, both sexes spent $\approx$74% of their time in waters <40 m and $\approx$95% of their time in waters <80 m.

Temperature-related occupation of coastal waters

Males and females of *C. taurus* were similar in their occupation of waters of varying temperatures (Table 5). On average, the percentages of time spent in waters of various temperatures did not differ significantly between the sexes (K-S test, $D = 0.133$, $P = 0.998$). Combined, *C. taurus* males and females spent $\approx$96% of their time, on average, in waters 17–24°C (Table 5).

Discussion

This is the first study to use PATs to provide detailed information on the autumn–winter and spring–summer migratory movements of sexually mature *C. taurus* males and sexually immature *C. taurus* females, the distances travelled, and depth- and temperature-related use of continental shelf waters off eastern Australia. Double-tagging *C. taurus* with acoustic tags substantially enhanced positional accuracy and enabled various legs of the migratory paths to be documented.

Patterns of movement

Over autumn–winter months, sexually mature *C. taurus* males migrated north from Fish Rock (NSW waters) to the Capricorn

Table 5. Mean (±s.e.) percentage of time spent by *Carcharias taurus* individuals in waters of differing temperatures for males ($n = 7$), females ($n = 6$) and sexes combined ($n = 13$)

Temperature (°C)	Percentage of time spent at temperature		
	Males	Females	Sexes combined
12	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
13	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
14	0.09 (0.06)	0.20 (0.20)	0.14 (0.10)
15	0.95 (0.60)	1.35 (0.88)	1.13 (0.52)
16	0.81 (0.58)	2.34 (1.69)	1.52 (0.86)
17	1.74 (1.15)	3.07 (1.81)	2.35 (1.05)
18	3.01 (1.48)	12.52 (6.45)	7.40 (3.37)
19	4.89 (1.05)	15.98 (4.70)	10.01 (2.77)
20	16.83 (5.38)	21.61 (6.72)	19.04 (4.28)
21	24.32 (4.53)	16.95 (4.15)	20.92 (3.29)
22	24.62 (2.88)	16.39 (5.62)	20.82 (3.24)
23	13.28 (1.39)	7.39 (3.95)	10.56 (2.14)
24	6.56 (3.65)	2.00 (1.38)	4.46 (2.18)
25	2.68 (1.84)	0.18 (0.13)	1.53 (1.07)
>25	0.22 (0.22)	0.02 (0.02)	0.13 (0.12)

Channel in the southern Great Barrier Reef, Qld and this was followed by a return journey in spring–summer. The migration north was consistent with previous studies (Otway *et al*. 2003; Otway and Burke 2004; Bruce *et al*. 2005) and punctuated by the occupation of sites *en route* for periods of up to 14 days. When travelling north, the males mainly swam in shallower waters (i.e. <50 m) until Fraser Island, after which they moved into deeper waters (i.e. 60–80 m). The northward distances ranged from 450 to 1550 km and represented various stages along the migratory route and included a partial return south to North Stradbroke Island by one individual. This same shark was subsequently detected by SEACAMS at Fish Rock in November 2005, having travelled an overall distance of at least 3100 km in 6 months. In contrast, the maximum distance travelled by *C. taurus* individuals tagged off the east coast of the USA as part of National Marine Fisheries Service Cooperative Shark Tagging Program is 1187 km (Kohler *et al*. 1998). In South Africa, little is known about the movements of sexually mature *C. taurus* males. A recent study (Dicken *et al*. 2007) only documented four males in 177 recaptures. The female recaptures included a pregnant individual that was tagged at a gestation site off northern KwaZulu-Natal and travelled 1897 km south to a parturition site.

Over the spring–summer months, sexually mature *C. taurus* males migrated to southern NSW waters, travelling unidirectional distances of 650 km over 3–4 months. When migrating south, the sharks often swam in deeper waters (i.e. 60–80 m) and their movements were likely assisted by the EAC. This southerly migration was also punctuated by the occupation of sites *en route* for periods lasting up to several weeks. Previous catches in the shark meshing program (Reid and Krogh 1992) and more recent underwater visual censuses (Otway *et al*. 2003) have shown that over the summer–autumn months, the *C. taurus* population south of Port Stephens is significantly biased towards females and comprises mainly sexually mature females and juveniles of both sexes. These observations suggest that on returning from their northerly migration, only some sexually mature males migrate to sites such as Wasp Island and the Tollgate Islands in southern NSW waters. It is likely that the remainder disperse over various sites between Fish Rock and Port Stephens. Combining the northerly and more extensive southerly movements, this suggests that a proportion of sexually mature males may migrate 4500 km annually.

Sexually immature *C. taurus* females migrated over smaller distances compared with sexually mature males. Over the spring–summer period, sexually immature females migrated south over distances ranging from 100 to 400 km and swam in deeper waters, presumably to gain assistance from the EAC. The movements south were also punctuated by the occupation of sites *en route* for periods lasting several days. In South Africa, *C. taurus* females >1.8 m TL travelled a mean distance of 324 km (Dicken *et al*. 2007) and these distances are similar in magnitude to the juveniles documented in this study. However, it is likely that the movements of sexually mature, gestating females are substantially greater. Evidence for this is provided from the necropsies of *postpartum* females caught during spring between Sydney and Port Stephens (N. M. Otway and M. T. Ellis, unpubl. data) together with a study of putatively, gestating females at Wolf Rock, Qld (Bansemer and Bennett 2009). Combined, the data suggest that a southerly migration to parturition sites in NSW waters likely occurs over winter–spring, with females covering unidirectional distances of 1000–1500 km. In contrast, *C. taurus* females <1.8 m TL have been estimated to travel a mean distance of only 17.3 km in South African waters (Dicken *et al*. 2007). However, along the east coast of Australia, an earlier tagging study using cattle ear tags (Otway and Burke 2004) showed that a sexually immature female, 1.53 m TL when tagged, migrated north from the Tollgate Islands to Fish Rock (Fig. 1) over autumn–winter and travelled 650 km over 2 months. Thus, it is likely that the distances travelled by South African *C. taurus* <1.8 m TL have been underestimated, primarily as a direct consequence of the very seasonal fishing effort underpinning the tagging and recapture events in the summer fishing season, a situation acknowledged by Dicken *et al*. (2007).

Depth and temperature related use of coastal waters

Three *C. taurus* individuals tagged at Fish Rock moved offshore for periods of 3–16 days and occupied mid-shelf waters with depths of 60–80 m and abnormally higher temperatures (i.e. 19–21°C). Their offshore movements were likely in response to an episodic incursion of the EAC or the intrusion of a warm-core eddy onto the continental shelf at Smoky Cape as such events have been documented in previous oceanographic studies (Rochford 1984; Tranter *et al*. 1986). Similar swimming behaviour associated with the Leeuwin Current, has been hypothesised for *C. taurus* off west Australia (McAuley 2004).

Overall, *C. taurus* males and females exhibited similar patterns of depth and temperature-related use of coastal waters. Combined, both sexes spent ≈95% of their time in waters 17–24°C, ≈74% of their time, on average, in waters <40 m and ≈95% of their time in waters <80 m. The occupation of deeper depths and cooler temperatures was mainly evident when migrating north or south. The large proportion of time spent in waters <40 m indicates that *C. taurus* mainly occupies the inshore coastal waters of the east Australian continental shelf. This same area is also used by many vessels in the commercial and recreational fishing fleets.

The similar depth-related use of the continental shelf waters, together with the extensive migrations documented here, further reinforce results of genetic studies (Stow *et al*. 2006; Feldheim *et al*. 2007) showing that the east coast *C. taurus* individuals comprise a single, well mixed population with very low genetic variation. Moreover, a recent study (Ahonen and Stow 2009) has confirmed the results in Stow *et al*. (2006) and modelled present-day genetic variation (measured as allelic richness) in the east coast population. The modelling showed that processes preventing migration can result in further erosion of genetic variation, the rate of which would accelerate as population size decreases. Importantly, the occupation of inshore waters means that *C. taurus* will continue to be captured, albeit accidentally, by commercial and recreational fishers (Otway *et al*. 2004; Bansemer and Bennett 2010) and caught in the shark meshing programs off the NSW and Qld coasts (Reid and Krogh 1992). This continuing fishing-related mortality provides the most likely process capable of causing disruptions to migratory movements and losses in genetic variation over future generations.

The variation in depth-related use of coastal waters by individual sexually mature *C. taurus* males during their northerly migration over autumn–winter and the contrasting, contemporaneous movements of sexually immature females obtained in this initial study demand that additional PATs are deployed to ensure that the emerging migratory patterns are truly representative. The migratory movements of sexually immature males and sexually mature females in their gestational and resting phases were not documented in this study. Such studies are needed and would likely provide information on possible parturition sites and the timing and duration of the southward migration of pregnant females. Quantifying the movements of sexually mature females during the year-long reproductive resting phase (Branstetter and Musick 1994; Smale 2002; Dicken *et al*. 2007) is also fundamental to understanding possible fishing-related interactions. During the resting phase, *C. taurus* females likely feed continuously to replace the energy reserves expended during the previous pregnancy. By doing so, the resting-phase females may increase their risk of adverse fishing-related interactions, leading to greater rates of mortality in this demographic stage and a reduction in the population growth rate (Otway *et al*. 2004).

More generally, studies using PATs and acoustic tags can provide substantial, much-needed data on the migratory movements of many shark species that are targeted or caught as by-catch in various fisheries of the world (e.g. Marín *et al*. 1998; Baum and Myers 2004; Stevens *et al*. 2010). The detailed information arising from the use of PATs can also substantially increase our understanding of shark mortality rates (Moyes *et al*. 2006; Campana *et al*. 2009) and ecology (Dewar *et al*. 2004; Weng *et al*. 2007), and lead to better demographic models and estimates of sustainable harvest (Cortés 2000; Mollet and Cailliet 2002; McAuley *et al*. 2007). The detailed information from such studies can also assist management efforts to ensure the long-term conservation of the ever-increasing list of threatened shark species in the world's oceans and seas.

PAT performance

Of the 15 PATs deployed, one was not sighted by SCUBA divers and failed to transmit data. Of the 14 remaining PATs, eight tags reached their programmed pop-up dates and two tags attained 97.5% and 95.8% of their planned deployments, respectively. The remaining four PATs were all attached to females and realised deployments of between 42.2 and 69.3% of the programmed deployments, resulting in a significantly reduced mean deployment period on *C. taurus* females. In previous studies on sharks (e.g. Weng *et al*. 2007; Campana *et al*. 2009; Stevens *et al*. 2010), a significant proportion of PATs did not reach their programmed pop-off dates. While the performance of the PATs used in this study was generally equivalent to that reported previously, a sex-based difference has not been identified in earlier studies. This difference may be peculiar to *C. taurus* and more attributable to the different life-history stages (i.e. sexually mature males and sexually immature females) examined in this study. Additional PAT deployments on other life-history stages of *C. taurus*, including sexually immature males and sexually mature females in gestational and resting phases, will be required to identify any further differences, and possible causes of differences, in PAT performance.

Of the two PATs that failed to transmit data, one tag was released, but SCUBA divers had reported observing several barnacles attached to the tag's float 1 week before the end of its programmed 6-month deployment. It is highly likely that the PAT failed to reach the surface owing to the reduced buoyancy attributable to the bio-fouling, a factor that has been identified in a study investigating why ARGOS satellite tags on marine organisms stop transmitting (Hays *et al*. 2007). It is unclear why the second tag failed to transmit and while there are several possible reasons for the failure, including aerial damage (Hays *et al*. 2007), scavenging by predators (Kerstetter *et al*. 2004) and tag destruction, bio-fouling appears to be the most likely reason given the barnacles on the other PAT and the substantial bio-fouling documented previously on conventional tags used with *C. taurus* in South Africa and Australia (Davies and Joubert 1966; Otway and Burke 2004; Dicken *et al*. 2006).

Acknowledgements

We are grateful to B. Louden, J. Gilligan, P. and K. Hitchins, T. Long and Sea World staff, M. Gray, P. and S. Byrne, J. and B. Nelson, J. Cavazzini, and the Cape Byron Marine Park staff for help with tagging. The functioning of SEACAMS would not continue without the efforts of H. Malcolm, J. and K. Duggan, R. and J. Duncan, and the staff of Sydney Aquarium and Oceanworld Manly. We thank the numerous divers who reported the locations of tagged sharks, the people who found and returned the PATs and J. Mumby, who spent many days preparing the PAT data for analysis. Comments from R. Creese, M. Lowry, the editor, guest editors and referees were constructive and improved the paper. Funds were provided by Industry and Investment NSW, the Sea World Research and Rescue Foundation Inc., the Northern Rivers CMA, and the Department of the Environment, Water, Heritage and the Arts. The work was done under scientific research permit (P01/0059[A]) and in accordance with an Animal Care and Ethics Committee approval (ACEC 99/14 Port Stephens).

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Manuscript received 15 June 2010, accepted 13 December 2010