Mar Biol (2010) 157:575–591
DOI 10.1007/s00227-009-1343-6

ORIGINAL PAPER

Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: depth behaviour, temperature experience and movements

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Received: 3 March 2009 / Accepted: 5 November 2009 / Published online: 20 November 2009

Abstract Satellite telemetry was used to study the movements and behaviour of ten blue sharks and one individual each of shortfin mako, thresher and bigeye thresher off eastern Australia. The tracks showed latitudinal movements of up to 1,900 km, but none of the sharks travelled away from the eastern Australian region. Tracking periods did not exceed 177 days. All species showed oscillatory dive behaviour between the surface layers to as deep as 560–1,000 m. Blue sharks spent 35–58% of their time in <50 m depths and 10–16% of their time in >300 m. Of these four species, the bigeye thresher spent the least time in the surface layers and the most time at >300 m depth. All four species showed clear diel behaviour generally occupying shallower depths at night than during the day. Blue sharks were mainly in 17.5–20.0°C water, while the thresher sharks showed a more bimodal temperature distribution.

Introduction

Pelagic sharks are taken by a wide range of commercial and recreational fisheries but are a particularly common bycatch of pelagic longline fisheries targeting tuna and billfish. With rising prices and demand in the international shark fin trade, together with the lack of high-seas fisheries management, these catches are likely to increase in the future. There is increasing concern over the status of pelagic shark populations and an urgent requirement for better catch data collection and information on their biology and behaviour to aid management and ensure sustainable use of these resources (Dulvy et al. 2008).

The oceanic and pelagic blue shark (*Prionace glauca*) is one of the most heavily fished sharks in the world and is captured in huge numbers by a wide range of fisheries, but particularly as a target or bycatch species of high-seas longliners (Nakano and Watanabe 1992; Bonfil 1994; Stevens 2000). It is the most widely distributed shark and is found in tropical and temperate areas of all oceans from about 60°N to 50°S (Last and Stevens 2009). While not particularly sought after for its meat, it is a major component of the international shark fin trade. It has been reported that blue sharks comprise 17% of the Hong Kong fin trade which represents a global trade-based estimate of about 10.7 million individuals or around 440, 000 tonnes (Clarke et al. 2006a, b). Despite featuring so prominently in fisheries, the catch data are often of poor quality and, despite several recent attempts, are not really adequate to assess population status. This is largely due to their highly migratory behaviour (related to reproduction and to the distribution of prey), complex population structure and lack of effective measures of catchability. Blue sharks are relatively productive for a chondrichthyan species with sexual maturity reached in 4–6 years for males and 5–7 years for females and usual litter sizes being 30–40 (although annual fecundity is uncertain; Nakano and Seki 2003; Nakano and Stevens 2008). Conventional tagging studies have demonstrated numerous trans-oceanic migrations and genetic studies show mixing between major ocean basins (Stevens 1976, 1990; Kohler et al. 1998).

Recent population assessments from a number of different regions have painted a confused picture of global population trends in this species (see summary in West et al. 2004).

Communicated by S. Garthe.

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In Australia, some preliminary studies have shown relatively recent declines in longline catch rates off the east coast, although the reasons for this are unclear (West et al. 2004). Despite the blue shark's relatively productive biology, there is a growing concern over the impact of fisheries on this species and the effects on the oceanic ecosystem of major reductions in their numbers. Blue sharks were assessed as Near Threatened for the IUCN (International Union for the Conservation of Nature) Red List by the Shark Specialist Group (SSG) following a meeting of the SSG in February 2007; however, it was noted at the time that data were not currently adequate for assessing population trends (Dulvy et al. 2008).

Shortfin mako (*Isurus oxyrinchus*) and thresher sharks (*Alopias* spp.) are, or have been, targeted in some areas for their valuable fins and meat and are also a relatively frequent catch of pelagic longline fisheries. These species are less productive than blue sharks, and there are concerns about their population status (Dulvy et al. 2008) with the shortfin mako and all thresher shark species listed as Vulnerable on the IUCN Red List.

Several papers have recently reported on the results of satellite tagging of pelagic sharks; however, these have mainly focused on white (*Carcharodon carcharias*), basking (*Cetorhinus maximus*), whale (*Rhincodon typus*) and salmon (*Lamna ditropis*) sharks (e.g. Sims et al. 2003; Weng et al. 2005; Wilson et al. 2006; Domeier and Nasby-Lucas 2008). While a number of satellite-tagging studies on blue and shortfin mako sharks have been carried out recently, or are currently underway, few results have yet appeared in the primary literature. Most of our knowledge on the movements and behaviour of these sharks comes from conventional tagging (Stevens 1976, 1990; Kohler et al. 1998) or telemetry studies (Sciarrotta and Nelson 1977; Carey and Scharold 1990; Holts and Bedford 1993; Klimley et al. 2002; Nakano et al. 2003; Weng and Block 2004; Sepulveda et al. 2004). Satellite tracking can inform on habitat occupancy, residency times and migratory pathways as well as providing behavioural data on temperature experience and swimming depth that can be useful in refining catchability estimates. Much of this information is not currently available for pelagic sharks in the western Pacific, and so satellite tags were deployed off eastern Australia, mainly on blue sharks, between 2004 and 2007.

Methods

The satellite tags used were Wildlife Computers (Redmond, USA) smart position or temperature transmitting tags (SPOT4 or SPOT5). These provide ARGOS locations together with water temperature reported as time-at-temperature histograms in twelve user-defined bins. The histograms are constructed by counting the number of temperature readings (taken at 10 s intervals) which fall inside the bins. Temperature is measured from −40°C to +60°C, with a resolution of 0.2°C and accuracy of ±1°C.

Tags were attached by two 5-mm diameter bolts which passed through the first dorsal fin and were secured on the other side by two washers and nuts, or a plastic plate and nuts. Tags were secured so that the antenna extended out of the water when the fin broke the surface. Transmissions were detected and processed by the ARGOS data collection and location system. The accuracy of ARGOS position estimates is coded by location class (LC) 3, 2, 1, 0, A or B, with LC3 being the most reliable with a root mean square error of <150 m. The other numeric LC codes decline in reliability and can be within several kilometres of true (ARGOS 2008).

One satellite tag incorporated a Sirtrack transmitter and saltwater switch powered by two lithium AA cells. The components were fitted in a plastic cylindrical housing 112 mm long and 40 mm in diameter designed by CSIRO. The housing incorporated three stainless steel threaded bolts that passed through the first dorsal fin and were secured on the other side by a stainless steel plate fastened by an aluminium nut on the central bolt.

We also used Pop-up satellite archival tags (PAT 4.0, Wildlife Computers) that archive data on pressure (depth), temperature and light levels and transmit summarised data (depth-temperature profile, time-at-depth and time-at-temperature histograms in twelve user-defined bins, and light curves) through service ARGOS on release from the fish. Depth is recorded down to 980 m (resolution = 0.5 m; accuracy ±1, 0–100 m, 1% 100–1,000 m), temperature in the range of −40 to 60°C (resolution = 0.05°C; accuracy ±0.1°C) and light level is measured as irradiance (W/cm^2) at 550 nm wavelength. If the tags are recovered, the raw archived data can be retrieved. We programmed the tags to archive data at 30 or 60 s intervals into 2, 8 or 12 h bins with release times of 125, 180 or 250 days. The tags were attached using a combination of leader wire and monofilament trace. An 8 cm length of 182 kg (1.8 mm diameter) monofilament fitted with an RD1800 (Wildlife Computers) cut-off was attached with crimps to the burn-pin of the PAT. The RD1800 acts as a mechanical guillotine severing the monofilament tether when depth exceeds 1,800 m, preventing the PAT from being crushed. To prevent the RD1800 from rotating on the monofilament and prematurely releasing the PAT, the ends of the monofilament overlapped the RD1800. Attached to the monofilament trace was a 12 cm length of 82 kg (1.0 mm diameter) nylon-coated stainless steel wire trace leading to a stainless steel Floy tag-anchor (32 mm × 8.5 mm × 1 mm). The anchor was embedded to a depth of approximately 5 cm in the dorsal musculature level with the trailing edge of the first dorsal fin. In some cases, when a shark was landed on the deck of the vessel, a second anchor incorporating a loose-fitting monofilament loop around the body of the PAT was embedded in the dorsal musculature in-line with the first anchor to prevent excessive movement of the PAT. The PAT light-based geolocation estimates were refined using a sea surface temperature (SST) model (Patterson et al. 2008).

All sharks (except one) were captured from commercial longline vessels in the East Coast Tuna and Billfish Fishery (ETBF) that were operating offshore from southern Queensland or northern New South Wales. The vessels were either engaged in their normal fishing operations, or they were chartered for the tagging work. For the SPOT and some PAT, the sharks were landed on deck using a lifting cradle operated from a HIAB crane. The hook was left in place after cutting the trace. Other PAT were attached using a pole spear while the fish was in the water. The trace was cut as close to the hook as possible. One blue shark was SPOT-tagged in Storm Bay, southeast Tasmania, after capture on a handline from a recreational fishing vessel. The barbless hook was removed before release. Sex of the sharks was recorded and their fork length (FL) or total length (TL) measured.

For calculation of movement rates, we used the SPOT tag data with location classes of 1, 2 or 3 and calculated speeds between successive satellite fixes. Data from telemetry studies of blue sharks suggest that they rarely swim faster than 5 km/h even when assisted by currents (Sciarrotta and Nelson 1977; Carey and Scharold 1990). We rejected any movement rates greater than 6 km/h (1.67 m/s). The tracks from SPOT tags were filtered to remove positions with location class *Z*, any on the land, and those exceeding movement rates of 6 km/h.

Sea surface temperature (SST) measured using AVHRR (Advanced Very High Resolution Radiometer) and chlorophyll *a* (Chl *a*) from SeaWiFS satellite imagery (NOAA TIROS-N satellites) were extracted for every available position (location classes 3, 2, 1, 0, A, B) each day. The SST and Chl *a* values were then averaged to give a daily value on each track, and the frequency of these environmental variables was examined for any preference by each shark.

Two blue sharks were double-tagged with PAT and SPOT. For one of these sharks, the PAT was subsequently found washed up on a beach and the full archive of data, collected at one minute intervals, was recovered. We compared the daily geolocation longitudes derived from the PAT archive using Wildlife Computers GPE program with the average daily longitude from the satellite tag, only using location classes ≥ 1 (Teo et al. 2004). SST based latitudes matching the geolocation longitudes were also compared with the daily average latitudes transmitted by the SPOT tag. The differences between the satellite fixes and the geolocation longitudes and SST latitudes were changed to absolute values and the average difference calculated.

Results

Tag deployments

Nine blue sharks were tagged with either SPOT or PAT, and one with a Sirtrack tag. Two of these sharks were double-tagged with both SPOT and PAT (Table 1). The PAT from one of these double-tagged fish (B1) was recovered, and provided the full archival record. One shortfin mako, one thresher shark (*Alopias vulpinus*) and one bigeye thresher (*Alopias superciliosus*) were also tagged with PATs (Table 1).

Tag performance

SPOT or Sirtrack tags on blue sharks transmitted for periods of between 0 and 159 days (average 71 days). The total transmission period summed for all sharks was 494 days. Transmissions were received on 277 of these days and positions were calculated for 226 days. One double-tagged blue shark (B2) apparently died soon after tagging (based on the depth record from the PAT) and two others transmitted for less than 12 days (Table 1). Only three tags transmitted for more than 4 months. Only one PAT tag (T1) remained attached, and collected data, until the pre-set pop-off period of 180 days. All other PAT collected data for periods of between 0 and 88 days (Table 1). The PAT remained attached to sharks for a total of 428 days out of the programmed total of 1,455 days (29.4%). Not all of these days provided valid data that passed Wildlife Computer's checksum procedures. Valid data were obtained for 335 days; 23% of the total programmed days. In addition, the tag from one blue shark was recovered providing the full 82 days of archived data (this tag had transmitted 81 days of summarised data).

Depth behaviour and temperature experience

Blue sharks spent considerable time at the surface but were also recorded down to 980 m, the limit of the PAT4 depth sensor. They were recorded in temperatures from 22.5°C at or near the surface to 4.8°C at depth (Table 2). The percentage of time spent at different depths and temperatures for three PAT-tagged blue sharks are shown in Fig. 1. They spent between 35 and 58% of their time in depths of less than 50 m, between 52 and 78% of their time in less than 100 m and between 10 and 16% in depths greater than 300 m (Fig. 1). These same sharks spent between 52 and

Table 1 Satellite tag releases of pelagic sharks off eastern Australia

Shark no.	Sex	Length (cm)	Date tagged	Tag type	Position	Data period[a]	Notes
B1	M	240 FL	10.7.04	SPOT4/PAT4	34°13′S 152°52′E	52/82 (125)	DT PAT recovered
B2	M	271 FL	10.8.04	SPOT4/PAT4	34°48′S 152°54′E	0/0 (250)	DT
B3	M	251 FL	23.9.04	Sirtrack	28°23′S 160°08′E	11	
B4	M	202 FL	23.9.04	SPOT4	28°27′S 160°17′E	129	
B5	F?	228 FL	24.9.04	SPOT4	28°11′S 160°39′E	137	
B6	F	224 TL	28.7.05	SPOT4	34°04′S 153°12′E	6	
B7	F	c 200 TL	26.3.07	SPOT5	43°06′S 147°29′E	159	
B8	F?		19.9.05	PAT4	33°43′S 151°44′E	32 (180)	
B9			20.9.05	PAT4	36°01′S 151°50′E	35 (180)	
B10		250 FL	20.9.05	PAT4	36°00′S 151°50′E	0 (180)	
T1			27.9.04	PAT4	28°41′S 155°42′E	177 (180)	
BT1	F	170 FL	14.8.05	PAT4	34°43′S 152°01′E	14 (180)	
SFM1			28.7.05	PAT4	33°54′S 153°02′E	88 (180)	

B blue shark, *T* thresher shark, *BT* bigeye thresher, *SFM* shortfin mako, *DT* double tagged

[a] Transmission period for SPOT and data collection period for PAT; figures in parenthesis are programmed times to pop-off

Table 2 Extremes of depth and temperature recorded by PAT for blue (B), thresher (T), bigeye thresher (BT) and shortfin mako (SFM) sharks

Shark no.	Sex	Length (cm)	Max depth (m)	Min temp (°C)	Max temp (°C)
B1	M		980[a]	4.8	22.2
B8			768	7.7	21.6
B9			560	9.2	22.5
SFM1			620	8.8	23.4
T1			640	11.0	27.0
BT1	F	170 FL	600	11.1	21.6

[a] Limit of depth sensor

66% of their time in water temperatures of 17.5–20.0°C (Fig. 1). Of three SPOT-tagged blue sharks, two (B5 and B1) also spent most time in 17.0–20.0°C, while the other (B4) was mainly in 20.0–25.0°C water (Fig. 2a–c).

Shortfin mako, thresher and bigeye thresher sharks all spent time from at or near the surface down to 600–640 m depth and experienced temperature ranges of 8.8–27.0°C (Table 2; Fig. 3). The shortfin mako spent 63% of its time in less than 50 m depths, 82% in <100 m and 4% in depths greater than 300 m (Fig. 3a). The proportions of time spent in these depth zones by the thresher shark and bigeye thresher were 35, 42 and 18% and 10, 23 and 50%, respectively (Fig. 3b, c). The shortfin mako mainly occupied temperatures of 17.5–22.5°C, while the thresher shark spent most time in 15–17.5 and 22.5–25.0°C water and the bigeye thresher in 12.5–15.0 and 20.0–22.5°C water (Fig. 3a–c).

To more directly compare the depth distributions of the individual blue sharks with each other, and with the shortfin mako and thresher sharks, cumulative plots of percentage time-at-depth for these six sharks are shown in Fig. 4a, b.

We examined blue shark depth behaviour for any diel patterns. The summarised PAT histogram collection times allowed this for sharks B8 and B9 (Fig. 5a, b), but not for B1 where the 12-h bins gave too much overlap between night and day. Both sharks spent more time in the surface layers during the night with B8 spending 86% of its time at night and 79% during the day in less than 100 m depth, while B9 spent 93% of its time at night and 73% in the day in this depth zone. However, the PAT from double-tagged

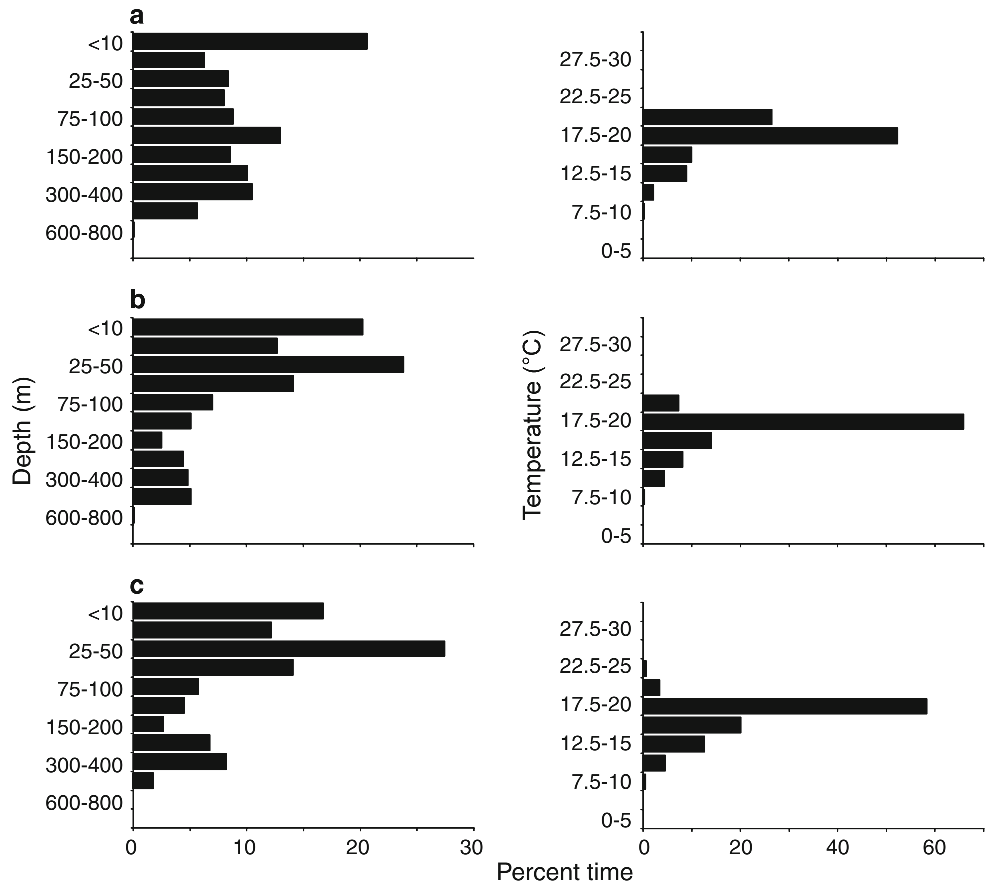


Fig. 1 *Prionace glauca.* Histograms of percentage time-at-depth and percentage time-at-temperature from PAT **a** shark B1, **b** shark B8, **c** shark B9

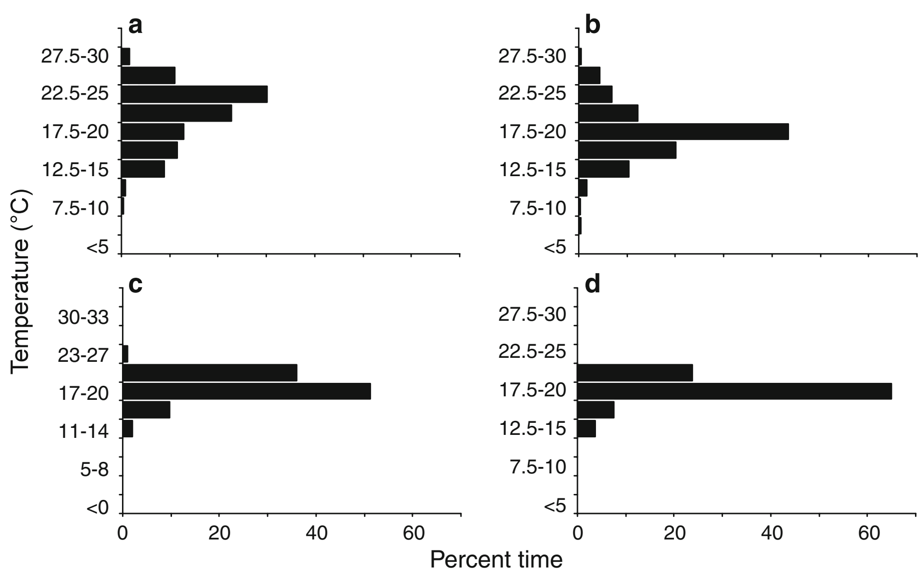


Fig. 2 *Prionace glauca.* Histograms of percentage time-at-temperature for SPOT tags **a** shark B4, **b** shark B5, **c** shark B1 and **d** for the PAT on shark B1 (restricted to the same time period as the SPOT with which it was double tagged)

shark B1 was recovered allowing examination of the full archival record. This shark showed clear diel behaviour for much of its track. For example, between 5 and 19 September, it made regular dives to about 480 m during the day, including two dives to 960 m on 6 and 7 September, while at night it mostly stayed in the top 100 m of the water column (Fig. 6b). While the same diel pattern was evident between 25 July and 8 August, this shark showed more irregular depth behaviour during this period (about 18% of its track-time) with less regular dives and more extended periods of time spent at the surface during the day (Fig. 6a). We examined the summarised time-at-depth data which the PAT transmitted during these two periods; however, they were not markedly different other than the shark spent more

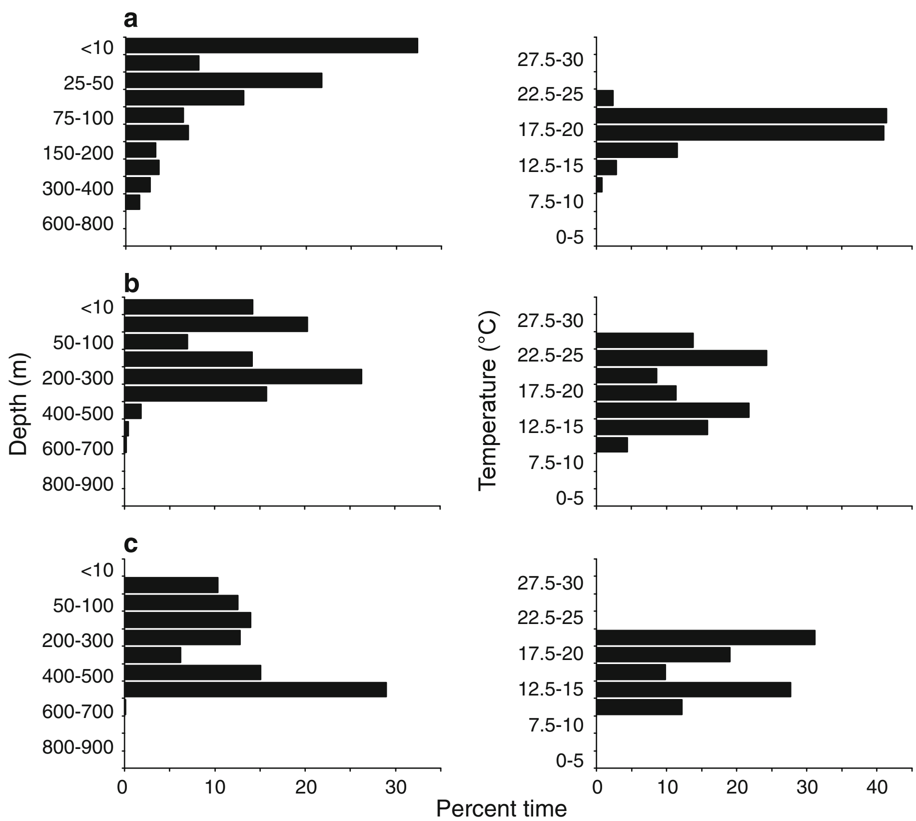


Fig. 3 Histograms of percentage time-at-depth and percentage time-at-temperature from PAT for **a** *Isurus oxyrinchus*, **b** *Alopias vulpinus*, **c** *Alopias superciliosus*

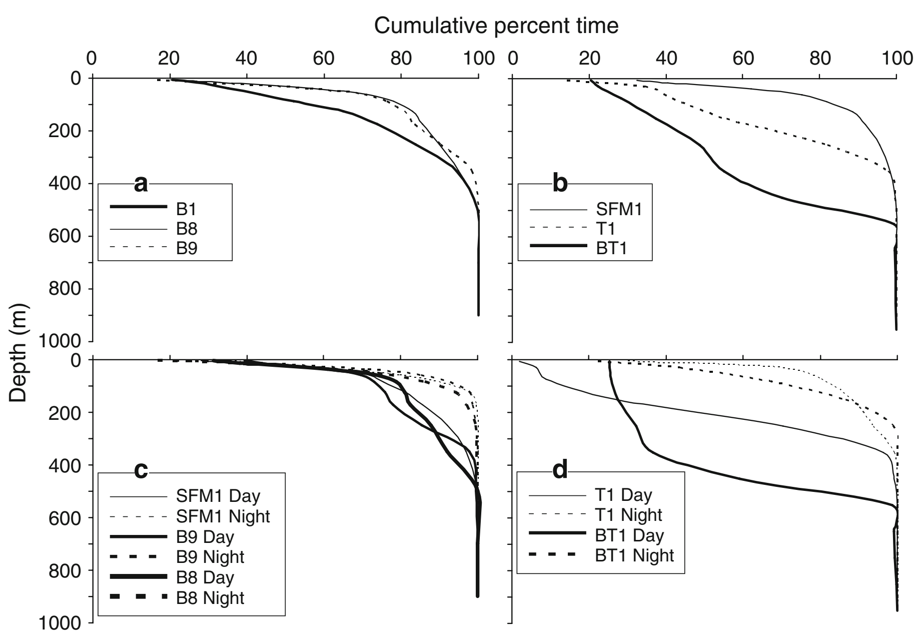


Fig. 4 Cumulative plots of percentage time-at-depth from PAT for **a** *Prionace glauca*, **b** *Isurus oxyrinchus*, *Alopias vulpinus* and *Alopias superciliosus*, **c** day and night periods for *Prionace glauca* and *Isurus oxyrinchus*, **d** day and night periods for *Alopias vulpinus* and *Alopias superciliosus*

time (31%) at 50–150 m and less time (13%) deeper than 200 m from 25 July to 8 August than in the September period (15 and 32%, respectively). Because of the 12-h bins, we could not examine diel differences without some overlap in the data (day 1000–2200 h, night 2200–1000 h). From 25 July to 8 August, shark B1 spent 56% of the day and 42% of the night at 0–50 m, compared to 43 and 56%, respectively in the September period. By comparison, both shark B8 and B9 spent 61% of time in this depth zone in the day, and shark B8 spent 62% and shark B9 71% at night.

The shortfin mako and both thresher shark species showed diel behaviour in swimming depth occurring shallower at night (Figs. 5c, d, 7a). The shortfin mako and bigeye thresher spent 90 and 42% of their time at night in less

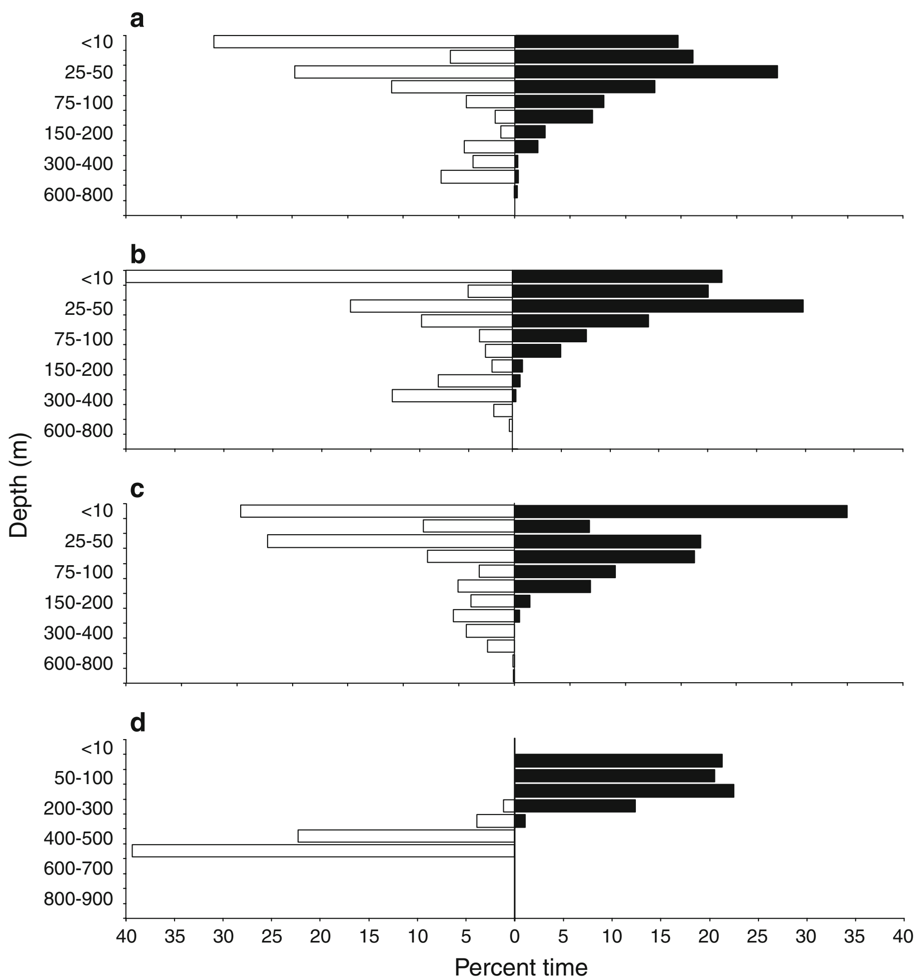


Fig. 5 Histograms of percentage time-at-depth during the day and night from PAT for **a** *Prionace glauca* B8, **b** *Prionace glauca* B9, **c** *Isurus oxyrinchus*, **d** *Alopias superciliosus*. Day 1000–1800 h; night 1800–0200 h. Day *open histograms*, night *solid histograms*

than 100 m depths, while in the day they spent 76 and 0%, respectively in this depth zone (Fig. 5c, d). For the thresher shark, we were able to separate the periods into day, night, dusk and dawn because of the 2-h histogram collection times. The thresher shark spent much more time in the top 100 m of the water column at night (80.3%) than during the day (8.9%), while dusk was more similar to the night pattern, with 51% in this depth layer, and dawn more similar to the day pattern with 31% in this depth layer (Fig. 7b). The bigeye thresher spent all day at depths greater than 200 m with 62% of its time spent below 400 m, while the thresher shark spent some time in the surface layers during the day. The two species were more similar in their depth behaviour at night, although the bigeye thresher did not venture into the top 10 m of the water column.

Cumulative plots of diel variations in depth distribution for individual blue sharks, and for the shortfin mako and thresher sharks, are shown in Fig. 4c, d to allow more direct comparison of inter and intra-species depth behaviour.

Depth-data collection times for PAT for user-defined periods of day, night, dusk and dawn can vary from actual day lengths experienced by a fish over the course of its track. For the shortfin mako, bigeye thresher and two blue sharks in this study, day was defined as 1000–1800 h and night as 1800–0200 h. The latest sunsets experienced by the shortfin mako, bigeye thresher and blue sharks B8 and B9 were at 1822, 1726, 1751 and 1814 h, respectively. The thresher shark (defined periods for dawn of 0400–0600, day 0600–1800, dusk 1800–2000 and night 2000–0400 h) experienced variations in sunrise times of 0448–0530 h and in sunset of 1757–1815 h.

Blue sharks have been reported to show tropical submergence, swimming deeper in tropical waters. We tried to evaluate this by examining depth behaviour at the extremes of latitude in our tracks. Unfortunately, the tracks from PAT, where we had associated depth data, did not show much latitudinal variation, and because of the light-based geolocation, we were less certain of their positions. The tracks from SPOT showed more latitudinal variation, and are potentially more accurate, but we could only infer swimming depths from the temperature data. We examined the temperature data for shark B5 from 6 to 8 November, when it was at 35°S in a SST of 18°C (from satellite imagery) and again from 25 December to 5 February, when it was at 21°S

Fig. 6 *Prionace glauca.* Periods from the full archival depth and light-level record of the PAT on shark B1 showing **a** more irregular depth behaviour between 25 July and 8 August with less regular dives and often considerable periods spent at the surface during the day and **b** normal diel behaviour (shallower at night) from 5 to 19 September

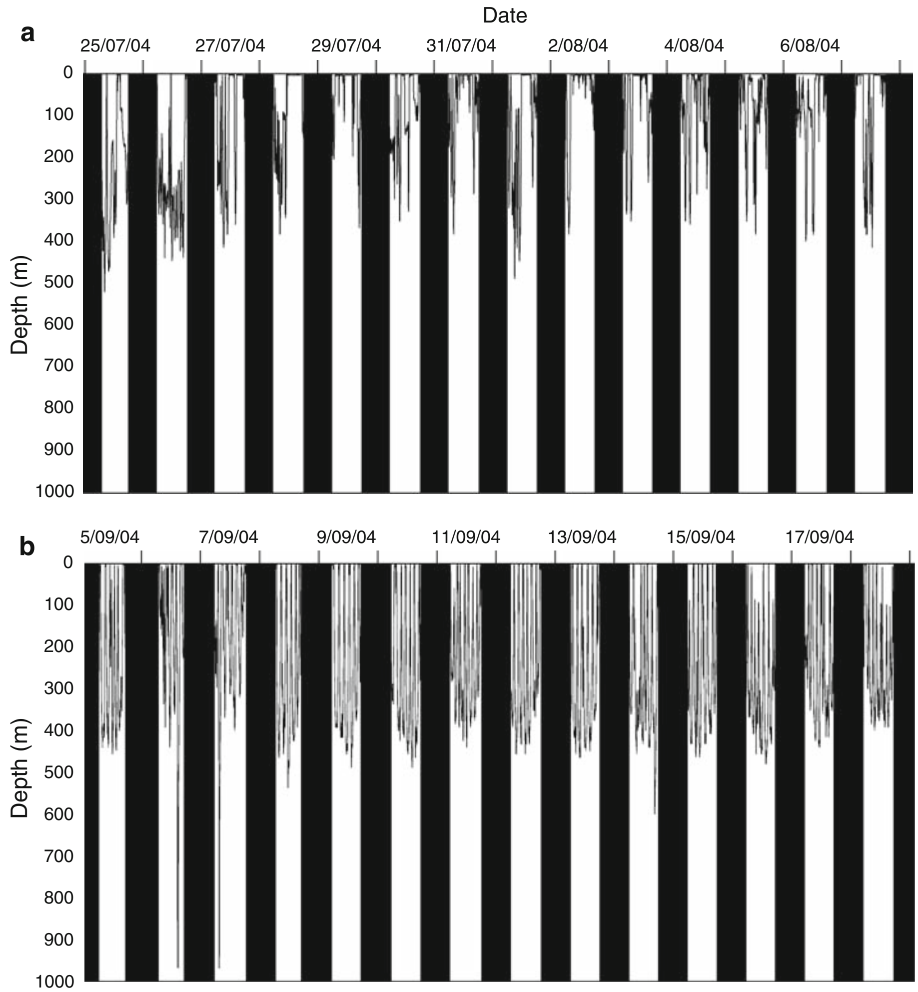
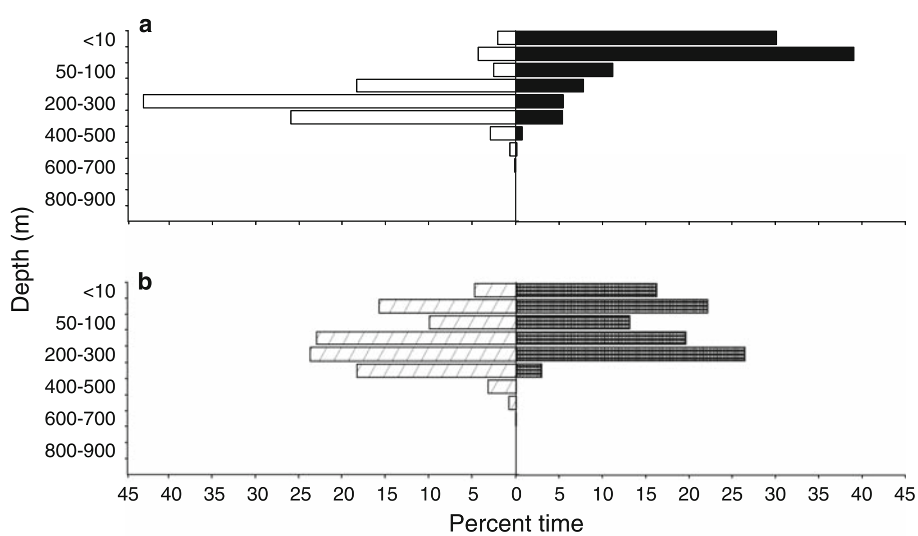


Fig. 7 *Alopias vulpinus.* Histograms of percentage time-at-depth from PAT **a** day (0600–1800 h) open histograms and night (2000–0400 h) solid histograms, **b** dawn (0400–0600 h) hatched histograms and dusk (1800–2000 h) stippled histograms



in a SST of 26°C (Fig. 8a, b). At its most southern latitude (35°S), this shark spent 89% of its time in temperatures of 15.1–20.0°C while at its most northern latitude (21°S) it spent 54% of its time in temperatures of 20.1–27.5°C and 41% at 12.6–20°C (Fig. 8a, b). Similarly, we used temperature data for shark B4 from 23 to 25 September at 28°S (19°C SST) and again from 10 November to 31 December at 17°S (27°C SST; Fig. 8c, d). At its most southern latitude

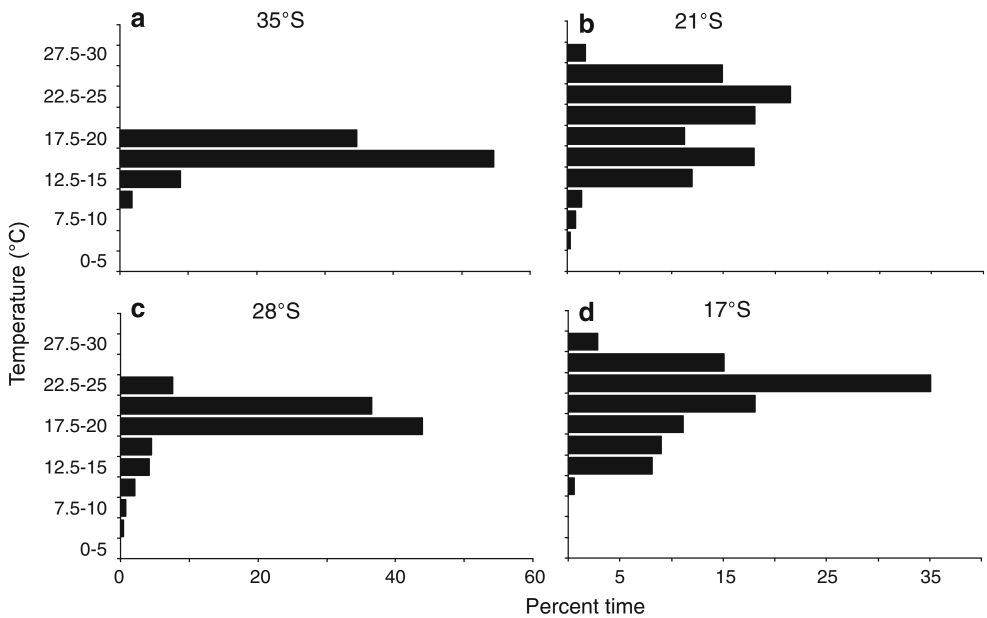


Fig. 8 *Prionace glauca.* Histograms of percentage time-at-temperature from SPOT tags **a** shark B5 from 6 to 8 November at 35°S (18°C SST), **b** shark B5 from 25 December to 5 February at 21°S (26°C SST), **c** shark B4 from 23 to 25 September at 28°S (19°C SST), **d** shark B4 from 10 November to 31 December at 17°S (27°C SST)

(28°S), the shark was in 17.6–22.5°C water for 80% of its time, while at its most northern latitude (17°S) it was in 20–27.5°C water for 69% of its time (Fig. 8c, d).

We were interested in whether there were any obvious differences in depth preferences or temperatures experienced by blue sharks that might be related to physical features when sharks were in different water masses. We used the PAT data to select time periods (usually only a few days), when the sharks were in a discrete water mass based on consistent depth/temperature values (Fig. 9). From 20 to 23 July, shark B1 appeared to be in a body of water with a temperature of about 19°C extending from the surface to a strong thermocline at about 240 m, after which the temperature declined to about 13°C at 500 m. During this period, the shark spent 68% of its time in the mixed layer above the thermocline. This was supported by the tags modal temperature bin of 17.5–20°C. About 25% of the shark's time was spent close to the thermocline in the 200–300 m depth bin (Fig. 9a). From 2 to 3 September, shark B1 was in a water mass with a thermocline at about 150 m and spent about 66% of its time in the mixed layer and about 34% of its time below the thermocline (Fig. 9b). From the 20 to 22 September, this same shark was in a water mass with no apparent thermocline, where the temperature declined from about 21°C at the surface to 8–9°C at 600 m. Shark B1 spent 27% of its time in the top 10 m and 32% of its time in 300–600 m (Fig. 9c). The full archival record from shark B1 showed less regular diel behaviour from 25 July to 8 August (Fig. 6a) than during most of its track. From 25 July to 1 August, there was a strong thermocline extending to 300 m probably associated with a cold tongue of water (visible on satellite imagery). However, from 2 to 8 August, this thermocline was not present, so this feature alone is unlikely to explain the shark's behaviour. From 27 to 29 September, shark B9 was in a water mass with a thermocline at about 200 m. This shark spent about equal times above (53%) and below (47%) the thermocline (Fig. 9d).

Horizontal movements

The tracks for four SPOT-tagged blue sharks (B4, B5, B1 and B7) that transmitted for between 52 and 159 days are shown in Fig. 10a. Shark B1 remained in the general area in which it was tagged, while B4 and B5 covered a latitudinal range of about 1,400 and 1,900 km off the east coast of Australia, respectively (Fig. 10b–d). Shark B7 that was tagged in Storm Bay, southeast Tasmania, moved about 550 km north to off shore from Point Hicks, Victoria, before returning down the Tasmanian east coast to a position about 270 km south of Tasmania (Fig. 10e). This shark's tag last transmitted about 325 km off the mid-west coast of Tasmania. The average movement rate of these four sharks over the duration of their tracks was 1.47 (B5), 1.95 (B7), 2.12 (B4) and 2.27 km/h (B1). Shark B7 remained in Storm Bay, Tasmania from 26 March until 12 April 2007. While resident in this semi-enclosed body of water its average movement rate was slower at 1.87 km/h than during the rest of its track (2.03 km/h).

The raw and SST corrected PAT tracks for three blue sharks are shown in Fig. 11. Sharks B8 and B9 that

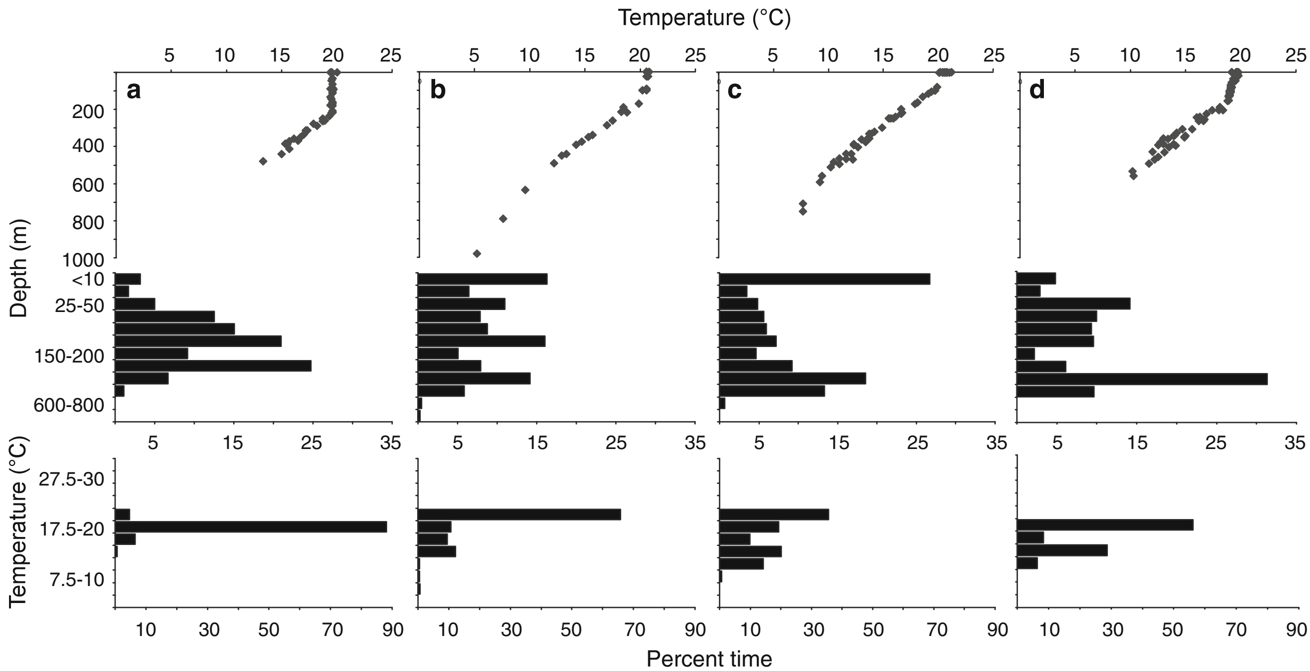


Fig. 9 *Prionace glauca.* Depth-temperature profiles and histograms of percentage time-at-depth and percentage time-at-temperature from PAT **a** shark B1 from 20 to 23 July, **b** shark B1 from 2 to 3 September, **c** shark B1 from 20 to 22 September, **d** shark B9 from 27 to 29 September

collected data over 32- and 35-day periods, respectively, showed localised movements off the New South Wales coast after being filtered on SST (Fig. 11b). Double-tagged shark B1 collected data over an 82-day period and showed movements off New South Wales and into southern Queensland to about 23°S (Fig. 11b).

The SST corrected PAT tracks for the shortfin mako and thresher shark are shown in Fig. 12. The shortfin mako, tagged off the central New South Wales coast, travelled north into southern Queensland waters before returning south to the waters offshore from Bass Strait (Fig. 12a). The thresher shark was tagged off southern Queensland and initially moved north, before travelling as far south as the central New South Wales coast (Fig. 12b). The bigeye thresher remained off the central New South Wales coast for the 14 days that the tag was collecting data.

We examined the tracks from the four SPOT-tagged blue sharks with respect to bathymetry, and to SST and Chl *a* (MODIS and SeaWiFS) from satellite imagery, to see if there were any obvious features that the sharks were orientating to. With the exception of shark B4 which tracked north appearing to follow an oceanic ridge at about 160E, none of the other three sharks showed any obvious orientation to submarine features (Fig. 10). When the frequency of each environmental variable (SST and chl *a*) for each day was examined, there was no overall preference shown by the four sharks. Mean SST values experienced by sharks B1, B4, B5, and B7 were 20.3 (SE 0.049), 24.0 (SE 0.140), 18.7 (SE 0.213) and 15.7°C (SE 0.102), respectively. Mean Chl *a* values experienced by these sharks were 0.206 (SE 0.004), 0.089 (SE 0.004), 0.248 (SE 0.012) and 0.176 mg/m^3 (SE 0.018), respectively. This lack of selection is illustrated by sharks B4 and B5 which were released on the 23rd and 24th of September at about 28°19′S, 160°28′E. Shark B4 headed north into 25–27°C water that had low Chl *a* concentrations (Fig. 13a, b). However, shark B5 headed south and remained mainly in association with the frontal zone between 18 and 20°C water that had relatively high chl *a* concentrations (Fig. 13c, d). We examined the satellite imagery for the period July 25 to 8 August when shark B1 showed different diel behaviour (Fig. 6a); we used the track positions from the SPOT tag during this period. The satellite imagery showed a tongue of cold water adjacent to the sharks position at this time, which may have been related to its behaviour.

Comparison of SPOT and PATs from double tagging

A 240-cm FL male blue shark was double-tagged with a PAT and SPOT; the SPOT transmitted over a 52-day period, while the PAT collected data over an 82-day period and was subsequently recovered (Table 1). The movements of this shark obtained from light-based geolocation estimates, and corrected using the SST model (Patterson et al. 2008), were restricted to the same time period as that from the SPOT tag. A comparison of the shark's track based on data from each tag is shown in Fig. 11c and are similar, although the PAT track extends further north with

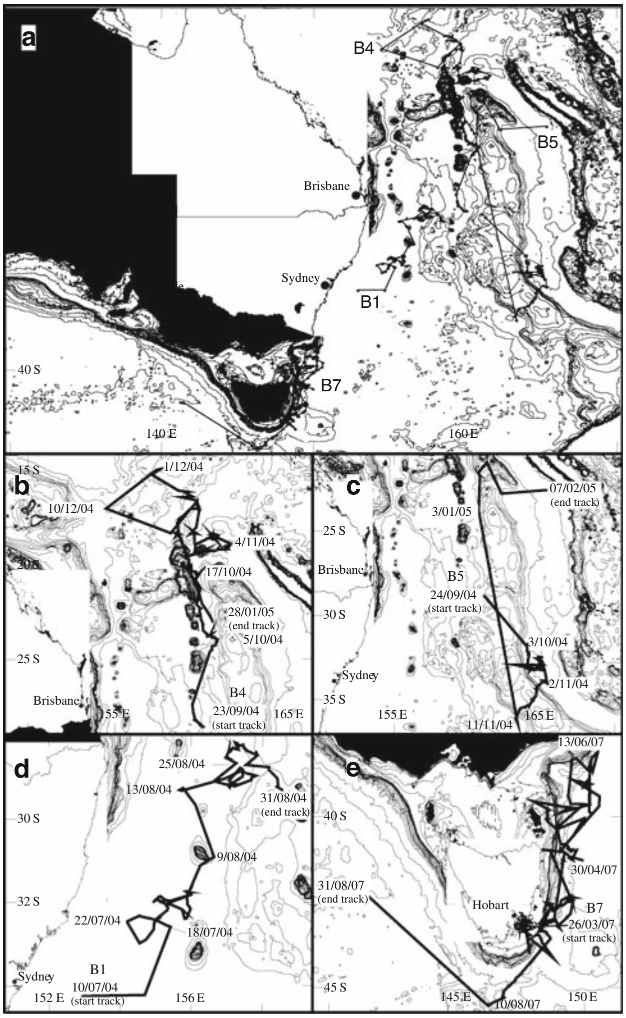


Fig. 10 *Prionace glauca.* Tracks from SPOT tags superimposed on bathymetry **a** composite of sharks B4, B5, B1 and B7, **b** detailed track of shark B4, **c** detailed track of shark B5, **d** detailed track of shark B1, **e** detailed track of shark B7

the end-points from the two tags about 5° of latitude apart. The SST field showed most contrast at the beginning of August when the two tracks were most closely matched; there was less SST contrast towards the end of the track period, but this is unlikely on its own to have resulted in the greater latitudinal error. While a number of other factors such as reduced opacity of the light sensor could be involved, we have no real explanation for the larger latitudinal error at the track end-points. The average light level longitude error estimate was 0.72 (SD 0.48; $n = 24$), and the average SST latitude error estimate was 1.85 (SD = 1.40; $n = 24$) from this shark (see "Methods" section for how these were derived).

A comparison of the temperature data from the two tags (restricted to the same time period) are shown in Fig. 2c, d and are very similar. Data from the SPOT tag showed that the shark spent 87% of its time in temperatures of 17.1–23°C, while the PAT showed 89% of the sharks time was spent in 17.5–22.5°C water.

Discussion

Tag performance

In this study, six SPOT tags and one Sirtrack tag were deployed on blue sharks; one shark died soon after tagging (B2) and the remaining six tags transmitted for 6–159 days. Of seven PATs deployed either on blue, shortfin mako, thresher or bigeye thresher sharks, one never reported, and of the others which did report, only one reached its pop-off date. The remaining PAT was on the double-tagged blue shark (B2) that died. The performance of PATs reported in the literature generally shows a high proportion that fail to reach their pop-off date. While 112 out of 160 (70%) PATs provided usable data, only 91 out of 693 (13%) reached their pop-off date (Wilson et al. 2006; Weng et al. 2007a, b; Chapman et al. 2007; Moyes et al. 2007; Domeier and Nasby-Lucas 2008). The transmission period for SPOT, SPLASH, Sirtrack or Telonics tags given in the literature is variable. Weng et al. 2005 reported a mean track length of 338 days for 38 salmon sharks using SPOT; the inclusion of an additional 30 tags in a subsequent study (Weng et al. 2008) resulted in a mean track length of 298 days. Other studies have achieved transmission periods ranging from 22 to 221 days (mean 92, $n = 14$) for white sharks (Bruce et al. 2006; Bruce and Bradford 2008), a mean track period of 114 days ($n = 27$) for blue sharks (Weng et al. 2005) and transmission times of 12–99 days ($n = 5$) for tiger sharks (*Galeocerdo cuvier*; Heithaus et al. 2007). Hays et al. (2007) investigated the reasons why Argos satellite tags on marine animals stop transmitting. They suggested that failure of the salt-water switch was the most common cause of transmission loss and that this was most likely due to biofouling. Wilson et al. (2006) also thought biofouling was a likely cause of transmission failure, along with malfunction due to repeated contraction and expansion of pressure housings due to deep-diving behavioural cycles.

In our study, although track periods were relatively short some SPOT had been stored (in the fridge or freezer) for up to about a year before deployment. However, battery voltage at the end of the tracks was 2.7–3.3 volts suggesting battery failure was not the cause of transmission loss. Biofouling is also less likely to be a cause of tag failure in the oceanic environment. Of our PAT-tagged sharks, one blue shark died soon after tagging, one did not report and the thresher shark reached its programmed pop-off date. The tag burn-pin was broken before pop-off date on one blue shark suggesting it had been forcibly seized and pulled-out by something while for the remaining blue,

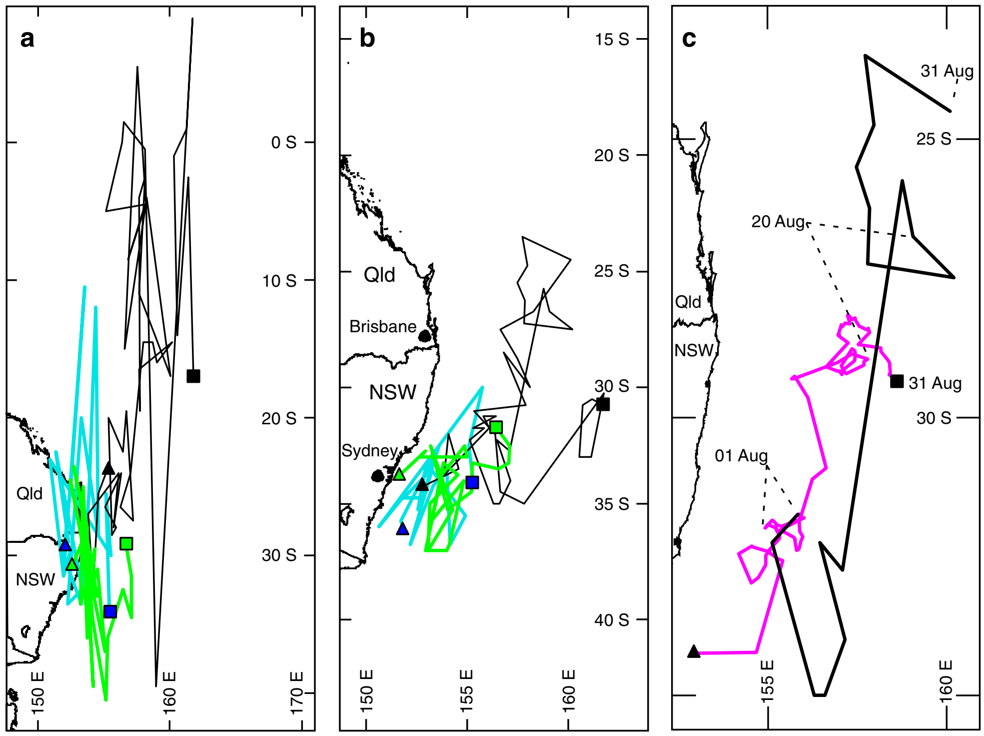


Fig. 11 *Prionace glauca.* Tracks from PAT **a** uncorrected light-based locations, **b** SST corrected locations, **c** comparison between SPOT and SST corrected PAT locations from the same shark and restricted to the same time period. *Green* = shark B8, *blue* = shark B9, *black* = PAT from shark B1, *red* = SPOT from shark B1. *Triangles* start of the track, *squares* finish of the track (see online version for colour figure)

shortfin mako and bigeye thresher sharks the tag burn-pin was not broken suggesting the tags had been shed due to failure of the Floy anchors.

With one exception, all sharks tagged in this study were captured from commercial longline vessels. They were either tagged in the water using a pole spear, or landed on deck using a cradle; only sharks considered to be in good condition were tagged. Despite this, one out of the 10 blue sharks tagged died. Moyes et al. (2006) attempted to predict the survival of large pelagic fish, mainly blue sharks, by combining blood chemistry analysis with a PAT tagging approach. The fish were caught from research vessels using commercial longline fishing techniques and gear. Their analyses suggest that sharks landed in an apparently healthy condition are likely to survive long-term if released. Campana et al. (2009) came to a similar conclusion for sharks released in good condition. However, they estimated (from PAT) a discard mortality of 19% for blue sharks released alive from normal commercial longlining operations in the North Atlantic off Canada.

Electronic tagging studies need to be considered in terms of the results they provide, the cost of the tags, the extra stress they may impose on tagged fish and the benefits over conventional tagging techniques. In our study, PAT provided 335 days of summarised data which was 23% of the programmed attachment time. However, one PAT tag was recovered providing the detailed archival record over 82 days. During the transmission period, SPOT or Sirtrack tags transmitted on 56% of days and provided locations on 46% of days. The amount of transmissions depend on the behaviour of the fish and blue sharks, at least in this area, spend considerable time at the surface making them good candidates for this technology. While the number of days of data obtained may be low with respect to programmed deployment times (PAT) or possible track lengths based on battery life (SPOT tags), we still obtained 562 days of behavioural and movement data for species for which this information is still poorly known. However, as more electronic studies are carried out and these basic data are obtained there will be a greater need to maximise on the performance of these tags.

Depth behaviour and temperature experience

All of the sharks tagged in this study showed regular diving behaviour from surface waters to depths of about 550–750 m, and for one blue shark to nearly 1,000 m. Blue sharks spent 35–58% of their time in <50 m depths and 10–16% of their time in >300 m, while the proportions of time spent at these depths for the shortfin mako were 63 and 4%, respectively. Of the four species for which we have data, the bigeye thresher spent less time in the surface layers and more time at >300 m depth. As track lengths were relatively short, temperatures experienced partly reflected the areas in

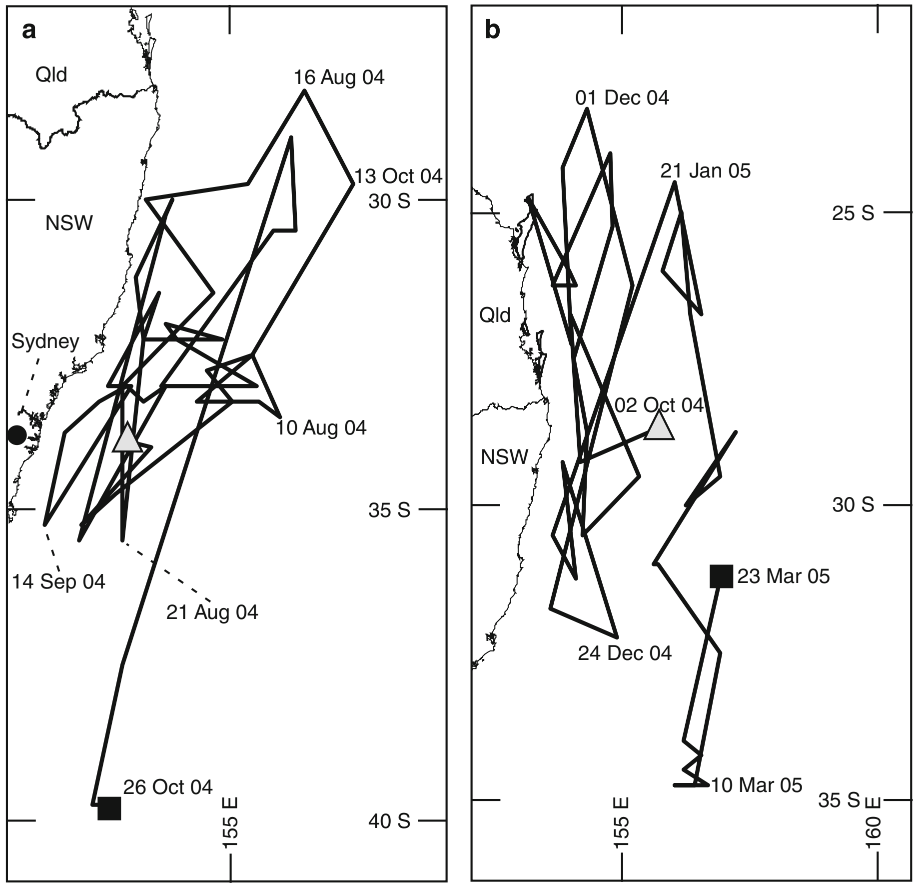


Fig. 12 PAT tracks based on SST corrected locations for **a** *Isurus oxyrinchus*, **b** *Alopias vulpinus*. *Triangles* start of track, *squares* finish of track

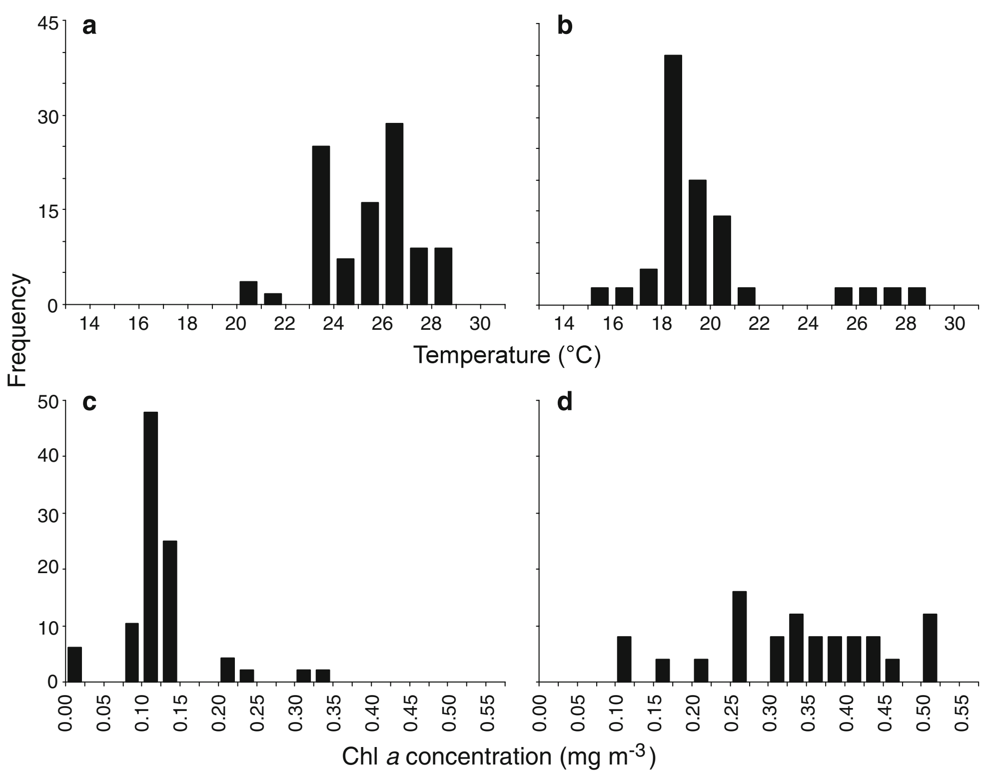


Fig. 13 Sea surface temperature and chlorophyll *a* concentrations experienced by sharks over the course of their tracks, **a**, **c** shark B4, **b**, **d** shark B5

which they were tagged. Blue sharks were mainly in 17.5–20.0°C water, while the thresher sharks showed more of a bimodal temperature distribution reflecting their greater time spent at depth, particularly the bigeye thresher which spent most time either in 12.5–15.0 or 20.0–22.5°C water. All four species showed clear diel behaviour generally occupying shallower depths at night than during the day. The full archival record from blue shark B1 showed normal diel behaviour for most of its track but from 25 July to 8 August showed a different pattern (Fig. 6a) with less frequent and shallower dives between the surface and depth during the day and less time spent at the surface at night. However, the summarised PAT data were not particularly useful in discriminating between these behaviours, and we could not explain them on water column structure or habitat features. Analysis of high resolution vertical movement data from archival tags has identified different behavioural components including reverse diel migrations in other pelagic sharks (Sims et al. 2005; Graham et al. 2006; Pade et al. 2009). These behavioural patterns have been related to movements of their prey.

In an eastern North Pacific study, blue sharks spent 67% of their time above 50 m in the upper mixed layer and 74% of their time in 14–27°C waters. They encountered <10°C temperatures only on short dives below the thermocline, which comprised 6% of their depth records (Weng et al. 2005). Acoustic tracking of blue sharks in the North Atlantic showed frequent vertical excursions between the surface and depths of 200–400 m (600 m in one shark). The amplitude of these dives was greatest during the day and confined to depths near the thermocline at night, however, this pattern was not seen in June and July. The authors suggested this diving behaviour was a hunting tactic and that returns to the surface might also be to warm the shark's muscles after deep-dives to cool temperatures (Carey and Scharold 1990). In another ultrasonic telemetry study of blue sharks off California, Sciarrotta and Nelson (1977) showed nocturnal behaviour with highest activity in the early evening and lowest activity early in the day. The sharks were found in temperatures of 8.5–17.5°C, but 73% of the time they were in 14–16°C water. Klimley et al. (2002) found that blue sharks spent 70% of their acoustic track-time swimming at <1.8 km/h, with a maximum of 9.0 km/h. Tropical submergence has been reported for blue sharks (Compagno 1984); and data from Laurs et al. (2008) support this. However, in tropical latitudes off eastern Australia, the sharks we tracked still spent the majority of their time in the surface layers in temperatures of 20–27.5°C.

Acoustic telemetry studies of juvenile shortfin makos off southern California suggest they spend about 80% of their time in surface waters <12 m deep and that excursions into deeper, cooler water are more frequent during the day. These studies show that while they frequent the upper mixed layer, they make frequent vertical oscillations and that larger sharks swim to greater depths than do smaller individuals (Holts and Bedford 1993; Klimley et al. 2002; Sepulveda et al. 2004). A large shortfin mako tracked in the northwest Atlantic spent most of the time well below the mixed layer and reached depths greater than 400 m (Carey and Scharold 1990). The juvenile sharks off southern California spent about 82% of their time in 20–21°C, and another 11% in 18–20°C (Holts and Bedford 1993). However, two sharks tracked by Klimley et al. (2002) showed modal temperatures experienced of 13–13.9 and 17–17.9°C, while a large individual in the northwest Atlantic was in 18–20°C most of the time (Carey and Scharold 1990).

The bigeye thresher in our study spent 42% of its time at less than 100 m during the night but remained at depth during the day, mainly at 400–600 m. In the eastern tropical Pacific, acoustic tracking of two individuals showed that they were at 80–130 m during the night and at 200–500 m during the day (Nakano et al. 2003). These authors recorded a pattern of slow ascents and relatively rapid descents during the night and suggested this aided hunting as the prey would be highlighted against the sea surface from below. The sharks remained in water temperatures of 6–11°C during the day and 15–26°C during the night, when they were in the mixed layer (Nakano et al. 2003). Similar results were obtained by Weng and Block (2004) who used PAT on two bigeye threshers, one in the Gulf of Mexico and the other off Hawaii; both showed strong diel behaviour. The Gulf of Mexico shark spent most of the day below the thermocline at 300–500 m (6–12°C) and most of the night in the mixed layer at 10–100 m (20–26°C). The Hawaii shark was above the thermocline at 10–50 m (20–26°C) at night and below the thermocline at 400–500 m (6–12°C) during the day (Weng and Block 2004).

Deep-diving and diel depth behaviour is a common feature of most large pelagic fish and has been reported in several other pelagic shark species including white, whale, basking, salmon, porbeagle (*Lamna nasus*) and Caribbean reef sharks (*Carcharhinus perezi*; Sims et al. 2003; Wilson et al. 2006; Weng et al. 2005, 2007a, b; Chapman et al. 2007; Pade et al. 2009). Patterns of vertical movements in large pelagic fish predators can be very complex reflecting behaviours such as foraging, thermoregulation, energetics and reproduction (Shepard et al. 2006). The shark species tagged in this study feed mainly on small pelagic fish and cephalopods (Last and Stevens 2009) and their vertical movements are probably primarily related to the location and movements of these prey.

Horizontal movements

While the blue sharks tracked in this study showed latitudinal movements of up to 1,900 km off the east coast of

Australia, none showed movements away from this general region. This may have been a function of the relatively short tracking periods which did not exceed 159 days. Conventional tagging of blue sharks in the same area of southeastern Tasmania where B7 was tagged, have yielded recaptures from as far away as the south east Atlantic (42°S, 014°E) after 29 months, off the African coast (32°S, 040°E) within 10 months and south of Java (10°30′S, 113°35′S) after 24 months (West et al. 2004). A blue shark tagged in New Zealand was recaptured in the eastern Pacific off Chile after 21 months, and central Pacific recaptures have been made from sharks tagged off California (Cox and Francis 1997; and summary in West et al. 2004). More extensive tagging of blue sharks in the North Atlantic has demonstrated numerous trans-Atlantic migrations (Stevens 1976, 1990; Kohler et al. 1998; Kohler and Turner 2008).

The shortfin mako and thresher sharks tracked in this study also remained in their general tagging area off eastern Australia for the duration of their tracks which did not exceed 177 days. Conventional tagging of shortfin makos off Australasia has shown movements in the southwest Pacific constrained to about 180°E (Cox and Francis 1997; Stevens unpublished data). Extensive tagging in the northwest Atlantic has shown movements mainly constrained to the west of the mid-Atlantic ridge (Kohler et al. 1998). There is little published information on the movements of thresher sharks from tagging programs; a few returns from the bigeye thresher have shown movements of up to 2,767 km from the New England or central Atlantic coast to Cuba, the Gulf of Mexico and out into the central Atlantic (Kohler et al. 1998).

The average movement rate of four SPOT-tagged blue sharks over the duration of their tracks varied from 1.47 to 2.27 km/h in this study. Sciarrotta and Nelson (1977) recorded mean daytime and nighttime speeds of 1.3 and 2.8 km/h, respectively for telemetered blue sharks off California; their data suggested speeds greater than 5 km/h rarely occurred. In another study off California, Klimley et al. (2002) recorded mean movement rates of 2.2 and 1.1 km/h and maximum rates of 9.0 and 2.2 km/h for two acoustically tracked blue sharks, but 70% of their tracktime was spent swimming at <1.8 km/h. In the northwest Atlantic, acoustically tracked blue sharks that were not known to be in currents swam at a mean speed of 1.5 ± 0.6 km/h, while those known to be in currents averaged 3.7 ± 1.2 km/h (Carey and Scharold 1990). For shortfin makos, Holts and Bedford (1993) recorded mean movement rates of juveniles of 1.33–3.70 km/h, with a maximum of 5.55 km/h with the average rate of movement lowest during the early to mid-morning. Klimley et al. (2002) recorded mean movement rates of 2.5–4.3 km/h, with a maximum burst of activity of 32.9 km/h for the juveniles that they tracked. Bigeye threshers tracked in the eastern tropical Pacific swam at 1.14–2.02 km/h (Nakano et al. 2003).

Comparison of SPOT and PATs from double tagging

The average errors of 0.72° and 1.85° that we obtained for geolocation longitude and SST latitude estimates, respectively ($n = 24$), were slightly higher than those of Teo et al. (2004) for four blue sharks (longitude 0.55°, SST latitude 1.06°, $n = 46$). These authors carried out double-tagging experiments on salmon and blue sharks to compare geolocation estimates based on light level and SST from PATs with Argos locations from SPOTs. They tagged two salmon sharks and four blue sharks with PAT 2.0 tags and compared geolocation estimates on a given day with location class 1–3 transmissions from SPOT2 tags. The average distance between the Argos locations and the geolocation estimates using light level longitude and SST refined latitude was 138.6 ± 79.6 km. Of the light level longitude estimates for salmon and blue sharks, 84.9% were within one degree of the Argos longitude estimates and 53.9% of the SST latitude estimates had errors of <1°.

Conservation and management implications

This study has provided new information on the vertical movements of several species of pelagic sharks in the southwestern Pacific. It has shown that blue, shortfin mako, and to a lesser extent thresher sharks, are ideal species for fin-mounted satellite tags in this area as they show high surface time. These data will assist in assessing the vulnerability of pelagic sharks to gear fished at different depths over the diel period. Many of the current difficulties in evaluating sustainable catch levels for pelagic sharks relate to poor estimates of catchability. By combining information from instrumented fishing gear with electronic tag data from species caught by that gear in the same area, improved habitat models can be developed to estimate catchability. While conventional tagging has demonstrated the wide-ranging nature of most pelagic sharks, of more interest to management are residency times and vulnerability within particular fisheries. Long-term shark tracks achieved through improved tag-attachment methods and tag technology will help justify the costs of large deployments required to clarify residency times and critical habitats for these species.

Acknowledgments We thank John Gunn for obtaining funds to purchase satellite tags to help in our understanding of the ecosystem supporting the East Coast Tuna and Billfish Fishery, Thor Carter for his help in deploying tags from commercial longline vessels, Alistair Hobday for some suggestions on data presentation and Barry Bruce and Colin Simpfendorfer, together with two anonymous referees, for helpful and constructive comments on the manuscript. This work was supported by CSIRO Marine and Atmospheric Research and the Wealth from Oceans Flagship Programme.

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