



Broad-scale movements and pelagic habitat of the dusky shark *Carcharhinus obscurus* off Southern Australia determined using pop-up satellite archival tags

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ABSTRACT

We investigated the broad-scale movements and pelagic habitats of large juvenile dusky sharks (*Carcharhinus obscurus*) off Southern Australia. Pop-up satellite archival tags (PSATs) were deployed on three large juvenile dusky sharks (~2.2–2.6 m total length) for 6 months in Spencer Gulf during 2010. Tagged dusky sharks all migrated westward and across the Great Australian Bight (GAB) during autumn to offshore shelf waters off Western Australia. Estimated minimum distances travelled ranged from 1760 to 2736 km. Depths occupied by tagged dusky sharks ranged from the surface to 355 m. The most common thermal ranges occupied were 19–22°C. Broad-scale movements of large juvenile dusky sharks across the continental shelves combined with periods of residency in semi-protected gulf waters indicated that a multi-jurisdictional management approach may be appropriate for this species.

Key words: carcharhinid, Great Australian Bight, habitat use, Indian Ocean, migration, Southern Ocean, telemetry

INTRODUCTION

Identification of ecologically significant areas is central to the development of management measures for

marine predators (Block *et al.*, 2003). Satellite telemetry represents a key tool for describing the spatial dimensions of these discrete areas within vast ocean habitats (Block *et al.*, 2001; Hindell *et al.*, 2011). During the past decade, satellite telemetry has led to substantial steps forward in our knowledge of the spatial distribution and sharing of these habitats by a broad range of species (Block *et al.*, 2011; Hindell *et al.*, 2011). While there is considerable potential to integrate the space- and time-related information collected using telemetry into fishery management processes (Hooker and Gerber, 2004; Hooker *et al.*, 2011), there are few cases where this has been applied in Australian management jurisdictions, except for southern bluefin tuna (Hobday and Hartmann, 2006; Patterson *et al.*, 2008; Hobday *et al.*, 2010).

The dusky shark (*Carcharhinus obscurus*) is a large apex predator (3.65 m, total length, TL) with a cosmopolitan distribution (Compagno, 1984; Last and Stevens, 2009). Their life history is characterized by a long life-span (55 yr), slow growth ($k = 0.037$), late maturity (29.6 yr) and low fecundity (two female offspring per year), which renders populations particularly slow to recover from additional mortality, such as that induced by fisheries (McAuley *et al.*, 2007; Romine *et al.*, 2009). Age-structured demographic modeling suggested that the dusky shark population off Western Australia (Fig. 1) is sensitive to removal of older juveniles outside the nursery areas (Simpfendorfer, 1999; McAuley *et al.*, 2005, 2007; Kinney and Simpfendorfer, 2009), and this issue formed part of the impetus for the current study.

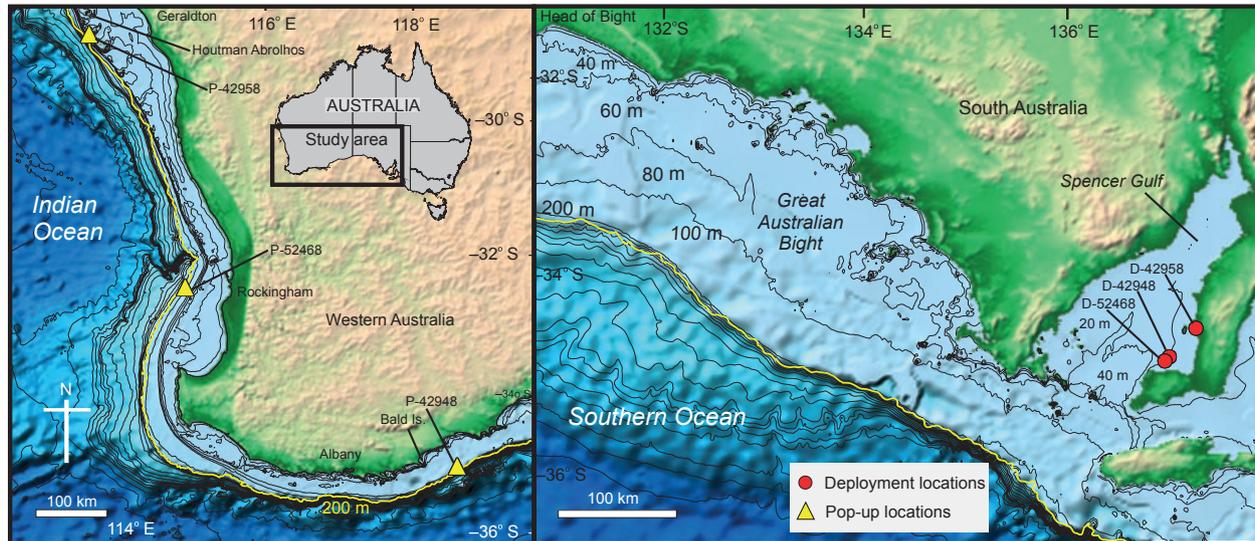
Prior to the current study, descriptions of habitat use by dusky sharks have been limited to a study conducted in the Gulf of Mexico, which showed large juvenile and adults were capable of broad-scale movements and displayed an affinity for continental shelf slope waters (Hoffmayer *et al.*, 2010). Small juveniles and neonates (<100 cm, pre-caudal length, PCL) tend to be less mobile, with most conventional tagging recaptures occurring within 100 km of the release sites during a study off South Africa (Hussey *et al.*, 2009). Similarly, a conventional tagging study of neonate and

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Received 14 November 2011

Revised version accepted 3 October 2012

Figure 1. Locations of pop-up satellite tag deployments on large juvenile dusky sharks (D-tag ID) and pop-up locations (P-tag ID) in Southern and Western Australian waters. Yellow line represents the 200-m contour at the continental shelf slope.



small juveniles captured by the commercial gillnet fishery off the southwest coast of Western Australia showed movements were mostly localized with limited connectivity with the neighboring South Australian whaler shark fishery (Simpfendorfer *et al.*, 1999; Simpfendorfer, 2000). This latter fishery targets the bronze whaler (*Carcharhinus brachyurus*) but juvenile dusky shark are also present in catches in semi-protected waters of Spencer Gulf, which is a seasonally subtropical (SST up to 26°C), inverse estuarine habitat adjacent to the eastern Great Australian Bight (GAB) (Fig. 1). This may be an important issue for management of the dusky shark population, and the need for this study stemmed from uncertainty regarding the degree of connectivity between these two regions.

The current study focused on large (~220–260 cm, TL) juvenile dusky sharks that are taken in the long-line fishery for bronze whalers in South Australia during mid- to late summer. These size classes are not typically found in nursery areas off southwestern Western Australia, yet large juveniles were highlighted as being important to the resilience of the population to additional mortality (Kinney and Simpfendorfer, 2009). We used satellite telemetry to investigate the broad-scale movements and habitat use of three large juvenile dusky sharks and predicted a westward migration in response to a combination of cooling of water temperatures in the southern gulfs and intrusion of the tropical Leeuwin Current (LC) water mass into the temperate shelf system in the GAB during the Austral autumn

period (Cresswell and Petersen, 1993; Ridgway and Condie, 2004). This study also provided information that is useful for assessing the vulnerability of this ontogenetic stage to fishery gear types.

MATERIALS AND METHODS

Three pop-up satellite archival tags (PSAT) were deployed on large juvenile dusky sharks that were caught on surface long lines targeting bronze whalers in the commercial Marine Scale Fish Fishery, in southern Spencer Gulf, South Australia (Fig. 1, Table 1). Long lines included 350 stainless steel hooks (14/0) attached to 1.7-mm diameter stainless steel leaders with stainless clips and floating 7–9-mm rope. Main-lines were floated using small floats attached with stainless clips. Hooks were baited with sea mullet (*Mugil cephalus*), set at dusk and hauled at dawn.

Sharks were tagged in the water while on the line using three PSATs manufactured by Microwave Telemetry (MT) (PTT-100; Columbia, MD, USA). Shark sizes were estimated by natural total length (TL) to the nearest 10 cm based on a known length on the vessel gunwale. Sex was determined for two sharks and one shark was not sexed. PSAT tethers consisted of 5 cm of 130-kg multi-flex monofilament crimped to a 10-cm length of 1.7-mm-diameter multi-strand stainless steel cable that was crimped to a Domeier plastic umbrella dart (<http://www.marine-csi.org/umbrella-darts>). Tethers and crimps were covered by black heat-shrink plastic tubing. Umbrella

Table 1. Summary of tagging statistics for PSAT deployments on juvenile dusky sharks in February 2010.

Shark PSAT ID	Sex	Size, m	Date deployed	Pop-up date	Pop-up location class	Minimum distance traveled (km)	Days at liberty	No. of temp-depth pairs	Percentage of data recovered
42948	f	2.6	9-02-10	9-08-10	2	1670	176	9507	76
52468	m	2.4	9-02-10	8-08-10	3	2270	177	9152	89
42958	ns	2.2	16-02-10	16-08-10	3	2736	182	10786	75
						*2225 ± 534	535	29445	*80 ± 8

*Mean and SD, ns, not sexed; DAL, days at liberty. Sums on bottom row are shown in bold.

darts were inserted into the dorsal musculature at the base of the first dorsal fin to a depth of ~ 4 cm using a 2-m aluminum tag pole with an applicator also constructed by M. Domeier (<http://www.marinecsi.org>). The applicator was then removed, leaving the dart, tether and trailing PSAT. Once a PSAT was deployed, each shark was released by removing the hook from the corner of the jaw using long-handled bolt cutters. The tag and release process took approximately 3 min for each shark.

PSATs were programmed to release following 6-month deployments (180 days) and then transmit location (lat-long) data to Argos satellites. PSATs were pre-programmed by the manufacturer to collect and transmit daily light, temperature and depth data (15-min intervals) to Argos satellites. The resolutions of the measurements of temperature and depth by the PSATs were $\pm 0.18^\circ\text{C}$, and ± 5.4 m, respectively. Estimates of latitude and longitude were provided by MT following the transmission of data from the drifting PSATs and were based on sunrise and sunset times (Microwave Telemetry Inc. personal communication). The seasonal timing of movements was estimated using MT's light-based calculations for longitude following Domeier and Nasby-Lucas (2008). Latitude estimates were not used (refer to Results and Discussion sections). Arrizabalaga *et al.* (2008) suggested that MT PSATs cannot resolve hourly depth variations ≤ 80.69 or >86.07 m. Dewar *et al.* (2011) also suggested this threshold was ~ 90 m, whereas Brunnschweiler and Sims (2012) suggested the limits of the tags capabilities were 166.8 m for descents and 172.2 m for ascents. Based on this, our depth data were filtered to ensure that deep accents and dives within hourly time-frames did not introduce error into our description of the vertical habitat.

TERATERM PRO software (ver. 2.3; T. Teranishi, RIKEN and University of Tokyo, 1998) was used to log the transmitted coded data via Telnet after the tags had surfaced. Argos data for the drifting PSATs were reported in seven location classes (cls) ranging from highest to lowest between 3, 2, 1, 0, A, B and Z (no positions) with predicted accuracies of 3 = <250 m, 2 = 250–500 m, 1 = 500–1500 m and 0–B = >1500 m, Z = no position (www.argos-system.org). Following the retrieval of the data from the drifting PSATs we estimated position error by comparing the Argos class 3 positions reported by the drifting PSATs with the averaged estimates of latitude and longitude estimated and provided by the manufacturer.

Percentage histograms of time spent in depth and temperature bins were plotted (preliminary analyses showed no differences were found between diel

periods). Temperature data reported by the drifting PSATs at the surface following the pop-up date were excluded from analyses of time spent at temperature. Deployment and initial pop-up locations for each tag were plotted using MAPINFO Professional (Ver.11.5: Pitney Bowes Software, North Sydney, NSW, Australia) geographical mapping software. Estimates of minimum distance travelled and average swim speed were determined using the deployment times (days at liberty, DAL) and by measuring vectors between the deployment and pop-up locations. Minimal distance travelled by each shark was determined as the difference between the deployment and pop-up locations with high quality ARGOS classes 3 and 2 that have predicted accuracies of <250 and 250–500 m respectively, (www.argos-system.org). Data-Interpolating Variational Analysis (DIVA) gridding tools (<http://modb.oce.ulg.ac.be/projects/1/diva>) in OCEAN DATA VIEW (ver. 4: Alfred Wegener Institute, Bremerhaven, Germany) oceanographic profiling software (Schlitzer, 2010) was used to construct depth and time (DAL) integrated thermal habitat profiles using the paired temperature and depth data. These were used to describe the vertical and thermal habitat of tagged juvenile dusky shark as they traversed spatial ranges identified using the longitude data.

RESULTS

Deployments

Pop-up satellite archival tags were deployed on three dusky sharks in southern Spencer Gulf during February 2010 (Table 1). Tagged sharks ranged in size between ~2.2 and 2.6 m TL and comprised one male, one female, and one unsexed individual that remained dorsal side up during the tag and release process (Table 1). Other dusky sharks captured during the same period were 184–226 cm TL ($n = 18$) and were immature (P. Rogers unpublished data). [The smallest mature dusky shark examined by McAuley *et al.* (2005) off Western Australia was 250 cm fork length, less than the maximum of ~2.6 m TL in this study]. Deployment and pop-up locations are shown in Fig. 1. Dusky sharks tagged were hooked in the corner of the jaw and were released in excellent (swam away strongly, $n = 2$) and very good condition (swam away slowly, $n = 1$).

Performance and reporting by the PSATs

The three PSATs released on the programmed dates, surfaced and transmitted 176, 177 and 182 days (sum = 535) of archived hourly depth, temperature and light data, over 189, 182 and 182 days at liberty,

respectively. PSATs transmitted 76, 89 and 75% (mean = $80 \pm 8\%$, SD) of their potential data, comprising 9507, 9152, and 10 786 temperature and depth records respectively, (sum = 29 445) (Table 1).

Mean estimates of position error estimated by comparing the class 3 Argos positions and the geolocation-based positions at the surface were 1.23 ± 1.07 degrees for latitude (137 ± 118 km; range = 0.77–451 km) and 0.18 ± 0.15 degrees for longitude (15.03 ± 12.74 km; range = 0.32–49 km). Latitude estimates were not used for further analysis.

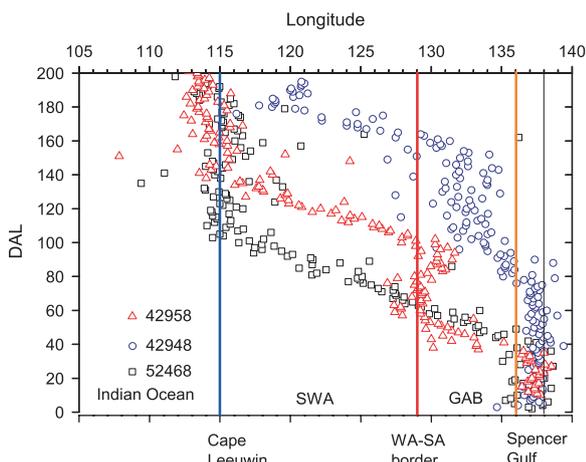
Shark 42958 remained at zero depth during the first 20.5 h following the deployment. Temperature and depth data for the first day of this deployment were excluded from the analysis. Following the pop-up dates, PSATs from sharks 42958 and 52468 were transported by currents off the continental shelf slope (200-m contour) into oceanic waters off the west coast of Western Australia. Tag 42948 was swept along the continental shelf and washed ashore on an island, to the SE of Esperance, off the southern coast of Western Australia. No PSATs were recovered due to the isolation of their final locations. Longitude estimates processed by MT, deployment and pop-up locations were used to describe broad-scale movements (following Domeier and Nasby-Lucas, 2008 and Dewar *et al.*, 2011).

Horizontal movement and mean swim speed

Pop-up locations (Fig. 1), and estimated changes in longitude with time (DAL; Fig. 2), showed that the three dusky sharks utilized Spencer Gulf for periods of 35–90 days during the late Austral summer and autumn period. Changes in longitude indicated that sharks 42958 and 52468 remained in Spencer Gulf until mid- to late March (~30 days), and then migrated across the Great Australian Bight (GAB) to shelf waters off Western Australia (Fig. 2). Estimates of longitude, temperature and depth data reported by the PSATs (Figures 2–4) indicated that the third dusky shark (42948) remained in Spencer Gulf until May (~90 days), before moving westward across the GAB between May and July.

All three tags popped up in waters off the Western Australian coastline within 8 km of the continental shelf slope (Fig. 1). Shark 52468 traversed a minimum straight-line distance of 2270 km in 177 days from southern Spencer Gulf to a location ~0.5 km inshore from the shelf slope, and 59 km off Rockingham, Western Australia (Fig. 1). Shark 42958 travelled a minimum straight-line distance of 2736 km in 182 days from southern Spencer Gulf, to Rat Island in the Houtman Abrolhos, 83 km west of Geraldton, Western Australia (Fig. 1). The pop-up location was 8 km

Figure 2. Longitude estimates for dusky sharks between February and August 2010. Symbols indicate the timing of movement. DAL = days at liberty. Vertical bars approximate the temporal extent of time spent in Spencer Gulf, the GAB, the southern coast of Western Australia (SWA) and the Indian Ocean. The orange vertical lines extending from the *x*-axis indicate the timing of when sharks moved through the entrance of Spencer Gulf into the GAB. The red line indicates the approximate timing of movement across the South Australian and Western Australian State border. The blue line indicates the approximate times when sharks moved past Cape Leeuwin and entered the SE Indian Ocean.



inshore from the continental shelf slope. Shark 42948 traversed a minimum distance of 1830 km in 176 days from southern Spencer Gulf to a location 8 km inshore from the continental shelf slope, off Bald Island, 53 km east of Albany, Western Australia (Fig. 1). Tagged dusky sharks travelled mean minimum distances of between 9 and 15 km per day (average = 12 ± 3 km per day) at average swim speeds of 0.4–0.6 km per hour.

Depth and thermal habitat

Comparisons of depth distribution data showed dusky sharks inhabited similar depth ranges. On this basis, the data were combined to describe the general patterns in depth habitats occupied by the three sharks. Preferred depth ranges occupied were 20–50 m in the southern gulf habitats and 50–100 m in shelf waters (Fig. 3). Mean depths inhabited by individuals were 47 ± 27 m (42948), 46 ± 32 m (52468) and 53 ± 32 m (42958), respectively. Maximum depths recorded for sharks 42948, 42958 and 52468 were 167, 258 and 355 m, respectively. One maximum depth record (527 m) was omitted as it exceeded the thresholds stated by Brunnenschweiler and Sims (2012) and Dewar *et al.* (2011) as being outside the range that MT PSATs were

capable of reporting within hour-long timeframes. Diel patterns of depth occupancy were investigated for the three sharks independently during the day, night, dawn and dusk periods. Sharks spent slightly more time in the surface layer (0–5, 5–10 m) during the dawn *cf.* dusk periods, and two sharks spent more time in the surface layer at night *cf.* during the day.

Time spent at temperature data indicated that two of the dusky sharks (52468 and 42958) occupied similar water masses, with mean temperatures of $20.8 \pm 1.5^\circ\text{C}$ and $20.1 \pm 1.6^\circ\text{C}$ respectively, (ranging from 12.9 to 24.3°C , and 13.1 to 24.1°C respectively), (Fig. 3). Shark 42948, remained in gulf habitats for longer, and occupied bi-modal thermal habitats ranging from 15.3 to 23.6°C , mean $19.7 \pm 2.0^\circ\text{C}$. Temperature minima (12.9 and 13.1°C) experienced by sharks 52468 and 42958, and their temperature-depth profiles (Fig. 4) showed these individuals traversed a cool water mass at longitudes that correlated with the entrance to Spencer Gulf and the area to the west of Kangaroo Island. The most common thermal ranges occupied by all sharks were 19– 22°C , 71% of time spent at temperature during the 6-month deployments.

Water mass features inhabited during residency and migration

Comparison of temperature at depth plots (Fig. 4a) and longitude estimates showed that dusky shark 42948 inhabited a warm (22 – 24°C), well mixed, Spencer Gulf water mass for 80–90 days, and then migrated through the ‘GAB Warm Pool’ water mass (17 – 20°C) (McClatchie *et al.*, 2006) to southern Western Australia. This shark also travelled through a cold water mass in the GAB (12 – 15°C) at depths of 120–150 m after 100–115 DAL. Figure 4b indicates that shark 42958 remained in the warm waters of Spencer Gulf for 25–30 days, and then traversed a cold water mass (12 – 15°C) in mid-March at the approach to Spencer Gulf, West of Kangaroo Island, at depths of 50–100 m. This shark then swam through warm surface water in the eastern GAB (17 – 20°C), and remained in the ‘GAB Warm Pool’ in the central GAB for 70–80 days, where water temperatures were 20 – 23°C . Following this, shark 42958 migrated westward against a homogeneous, well mixed, eastward (0.4 m s^{-1}) Leeuwin Current (LC) flow (17 – 20°C) that was dominant in shelf waters off S Western Australia and in the GAB during July. After 130 DAL, shark 42958 reached a thermal convergence between shelf waters off S Western Australia and warm subtropical waters of the Indian Ocean. Temperature and depth profiles for shark 52468 (Fig. 4c) show this individual traversed the same Spencer Gulf frontal systems and similar

Figure 3. Percentage of time spent at depth (bins span ranges from 5 to 50, accuracy $\approx \pm 5.4$ m) and temperature (bins are $1^\circ\text{C} \pm \approx 0.18^\circ\text{C}$).

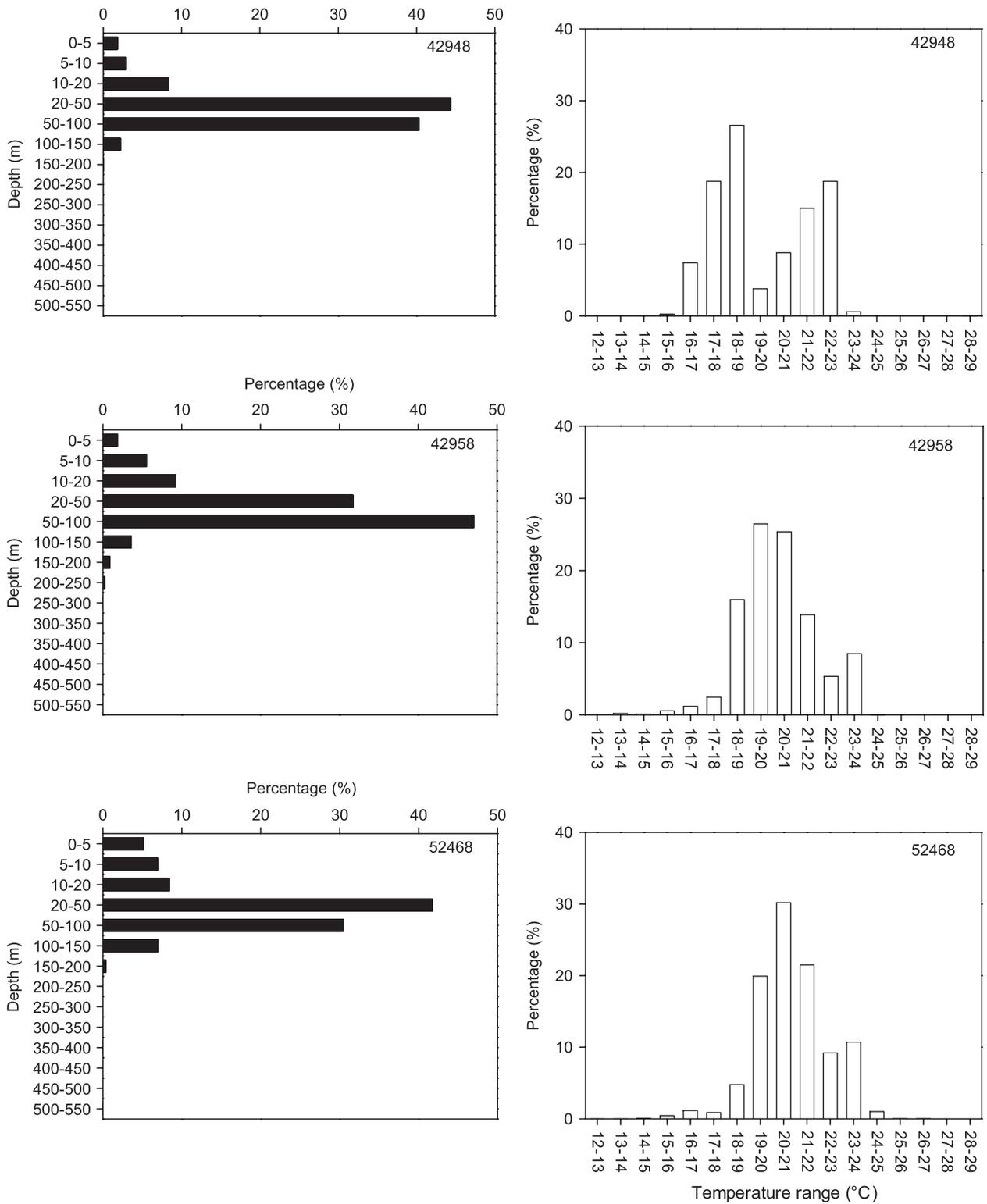
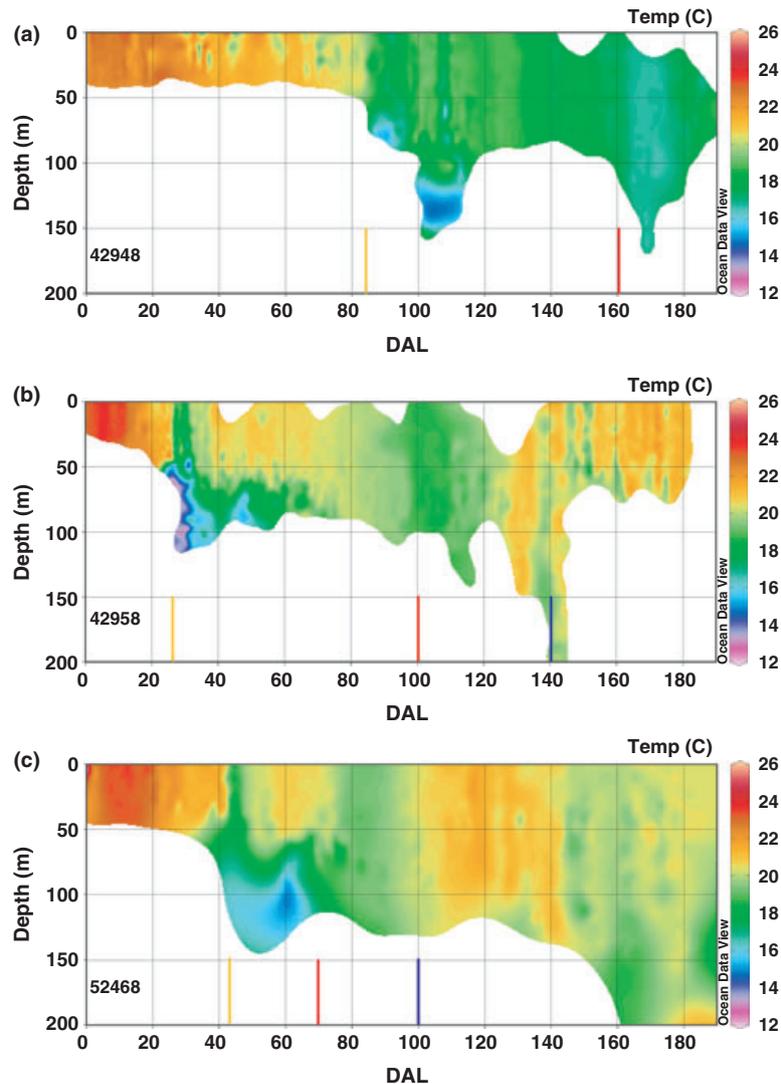


Figure 4. Depth and temperature (degrees Celsius) profiles for dusky sharks: (a) 42948, (b) 42958 and (c) 52468. DAL = Days at liberty following tag deployment. Orange vertical lines extending from the x-axis indicate timing of movement through the entrance to Spencer Gulf into shelf waters of the GAB. Red lines indicate approximate timing of movement across South Australian–Western Australian State border, and blue lines indicate the approximate timing of the movement around Cape Leeuwin into the SE Indian Ocean.



water masses as 42958 during its large-scale westward movement, and then inhabited LC influenced shelf waters off SW Western Australia to depths of 180 m. Figures 4a–c indicate that sharks spent more time in the surface layer in 20–24°C water masses than when they were in cooler waters of 16–18°C.

DISCUSSION

Satellite telemetry provided valuable new information on the movements of large juvenile dusky sharks

between the semi-protected temperate waters of Spencer Gulf, and the sub tropical, shelf waters of the Indian Ocean off Western Australia. Although our sample size was small ($n = 3$), this was the first study to use satellite tags to provide high resolution information on the broad-scale movements, depth and thermal habitats of dusky sharks in Australian waters. Findings during this study enhanced the understanding of an important life history stage of this species, which is considered to be one of the coastal shark species most vulnerable to fishing (Smith *et al.*, 1998).

Bradshaw *et al.* (2007) emphasized the importance of considering the intrinsic error associated with geo-location data. We used the highest quality Argos position estimates transmitted while the PSATs were drifting at the surface to estimate mean position errors of 1.23 ± 1.07 degrees for latitude (137 ± 118 km; range = 0.77–451 km), and 0.18 ± 0.15 degrees for longitude (15.03 ± 12.74 km; range = 0.32–49 km). By comparison, error in light-based estimates of latitude have been calculated during several previous studies, including Weng *et al.* (2007), who described ranges of 17–434 km; Arnold and Dewar (2001), who described a broad range of ± 1 –10; and Wilson *et al.* (2007) who estimated root mean square errors (RMSE) of 5.16. By contrast, in terms of error associated with estimates of longitude, Musyl *et al.* (2001) predicted accuracies of 0.15–0.25; Weng *et al.* (2007) estimated RMSE of within 0.89; Arnold and Dewar (2001) predicted accuracies of ± 0.5 ; and Wilson *et al.* (2007) estimated RMSE of 2.00. Considering our estimates of position error, and the north–south-facing shelf in our study area, we decided that the estimates of longitude were appropriate for describing the movements of the dusky sharks (Bruce *et al.*, 2006; Domeier and Nasby-Lucas, 2008).

Data from tag 42958 suggested this dusky shark remained at the surface during the first 20.5 h following the capture and tagging process, which may have been indicative of a temporary post-release stress response to capture on the commercial long-line, and the subsequent tag-release (Hoolihan *et al.*, 2011). Other studies have provided evidence of temporary changes in vertical movements for short periods immediately following capture and tagging (Gunn *et al.*, 2003; Cartamil *et al.*, 2010; Dewar *et al.*, 2010). For example, shortfin makos and common threshers have been shown to dive immediately following tagging, before returning to what are assumed to be normal vertical oscillation behavioral patterns (Holts and Bedford, 1993; Klimley *et al.*, 2002; Cartamil *et al.*, 2010). Bigeye threshers (*Alopias superciliosus*) were also shown to take approximately 1 day to return to normal diving behavior following tagging (Nakano *et al.*, 2003).

Our conservative estimates of minimal distances traveled indicated that large juvenile dusky sharks are capable of migrating considerable distances, which supports the findings of previous conventional tagging studies off South Africa (Dudley *et al.*, 2005; Hussey *et al.*, 2009) and in the Atlantic Ocean (Kohler *et al.*, 1998). Our estimates of minimum distance traveled were similar to those reported for a mature dusky shark (265 cm, TL) that was tracked using a PSAT in the Gulf of Mexico (Hoffmayer *et al.*, 2010). All three

large juvenile dusky sharks we tagged remained in semi-protected Spencer Gulf waters for 1–3 months during the Austral summer and autumn, and then migrated across the GAB to offshore waters of Western Australia during autumn and winter. We assume this pattern was partly in response to declines in water temperatures in Spencer Gulf and seasonal changes in prey availability that may be associated with the breakdown of vertical thermal gradients and intrusion of the Leeuwin Current into the GAB (Fujioka *et al.*, 2012). In contrast to our study, a conventional tagging study that marked 2155 neonate and small juvenile dusky sharks (<110 cm, FL) off southern Western Australia suggested movements were mostly limited to <100 km from the tagging sites, with only 1.8% of 442 recaptures occurring east of the Western Australian border (Simpfendorfer *et al.*, 1999). Despite our small sample size, the consistency of the eastward movements of the large juveniles we studied may reflect ontogenetic differences in migration schedules of sharks that possibly originated from a broad nursery area off Western Australian.

Cooling of Spencer Gulf waters from 24°C in February to 19°C in May, combined with the eastward flow (0.2 – 0.4 m s⁻¹) (<http://oceancurrent.imos.org.au>) of warm tropical LC water into the GAB (Middleton and Bye, 2007) may act as a thermal cue for this species to move westward. The eastward intrusion of the LC was particularly strong during the study period, and this warm tropical water mass could be observed at the surface in the Southern Ocean off Victoria and to the west of Tasmania. Interannual variability in the strength of the LC flow may play an important role in the connectivity of dusky shark populations in the Southern and Indian Oceans, and this may influence the representation of this species in commercial shark catches in South Australia. This factor warrants consideration during future studies of the factors that drive connectivity of predator populations in this bioregion.

The PSATs we deployed on dusky sharks all surfaced within 8 km of the continental shelf slope (200 m contour) off Western Australia, suggesting that these high gradient benthic habitats may constitute an area of ecological importance for some large juveniles. This was consistent with an electronic tagging study in the Gulf of Mexico that showed juvenile and adult dusky sharks showed a preference for continental shelf slope waters near the edge of submarine canyons (Hoffmayer *et al.*, 2010). The coarse sediments and rocky banks along the shelf slope off Western Australia support a diverse elasmobranch and teleost fauna (Williams *et al.*, 2001, 2010), which may

provide a prey source for large juvenile dusky sharks. Diet studies have shown small juvenile dusky sharks (mostly <100 cm, FL) feed on sardine (*Sardinops sagax*), teleosts and cephalopods in inshore nursery habitats off the southern and western coasts of Western Australia (Simpfendorfer *et al.*, 2001). Large dusky sharks also consumed elasmobranchs (52% by mass) and teleosts (41%) off southern Africa (Dudley *et al.*, 2005), where their range also extends out to depths of 400 m. A recent diet study in the GAB and Spencer Gulf indicated that cephalopods, small and large pelagic teleosts, and elasmobranchs were among the most important prey consumed by dusky sharks (96–256 cm, TL). The residency and movement patterns we observed may be partially explained by seasonal and/or ontogenetic shifts in diet associated with changing energy requirements during sexual development (Lucifora *et al.*, 2009) and this warrants further investigation.

Patterns of depth and thermal habitat use by large juvenile dusky sharks suggested they spent considerable time within the typical thermocline and mixed layer depth ranges while in shelf waters (van Ruth *et al.*, 2010a,b). Temperature and depth data indicated that two of the dusky sharks occupied similar water masses, yet the third shark remained in gulf waters over autumn, did not traverse cooler water masses <15°C, and occupied a more stable thermal range. This third shark moved out of the gulf in autumn when the SST-salinity front at the mouth of Spencer Gulf was less prominent (Bruce and Short, 1990) and the LC water mass was dominant across the GAB. The thermal minima recorded by two PSATs during mid-to late March and April suggest that when sharks 52468 and 42958 left Spencer Gulf, they swam below the thermocline at depths of 95–130 m in cool (13–14°C) bottom water that may have been of upwelling origin. The temperature range and estimated longitudes suggest the sharks were within the ‘Kangaroo Island Pool’ water mass that forms off the west coast of Kangaroo Island (van Ruth *et al.*, 2010a). The inner-mid-shelf region is characterized by sporadic upwelling in late summer and autumn (van Ruth *et al.*, 2010a,b) that supports spatially and temporally dynamic pelagic production. It appears that two of the dusky shark exploited sub-thermocline patches in these shelf waters as they migrated west, through the ‘GAB Warm Pool’ water mass (McClatchie *et al.*, 2006) to an offshore thermal refuge provided by the homogeneous tropical LC water mass between Esperance and Geraldton off Western Australia.

Stevens *et al.* (2010) highlighted that spatial information collected during satellite tagging studies that

identified the relative vulnerabilities of pelagic sharks within particular fisheries was of key interest to management. In addition to this, Hooker *et al.* (2011) identified space- and time-sensitive factors to consider when developing protection measures for highly mobile marine predators. In summary these included, a need to tailor options to suit the life histories of the species of concern, the space–time dynamics of their habitat, and the extent and nature of the potential threats. The mobility of the three dusky sharks we tagged suggests that part of the juvenile component of the population in South Australia is connected to the Western Australian population. During the east–west migrations these individuals may be afforded temporary protection within several spatially managed, existing fishery and MPA zones that have cross-shelf boundaries in Spencer Gulf, the GAB and off S and SW Western Australia. Broad-scale movements of large juvenile dusky sharks indicated that a dual-State management approach that includes consideration of time spent in Commonwealth-managed waters may be appropriate for this species. However, given our low sample size, there remains a need for further information on the movement and residency patterns of dusky sharks in this bioregion to determine whether a series of spatially and temporally managed areas may be a suitable approach to provide adequate protection to all life history stages (Alpine and Hobday, 2007). Furthermore, the dusky shark was recently nominated for protection under the provisions of the Australian Commonwealth government’s Environmental Protection and Biodiversity Conservation Act (1999). If this nomination results in the listing of this species as Threatened, there will be a need to identify the critical habitats of all ontogenetic stages in Australian waters.

ACKNOWLEDGEMENTS

This project was supported by funding from Marine Innovations South Australia, Flinders University, SARDI Aquatic Sciences and L. Seuront is the recipient of an Australian Professorial Fellowship (project number DP0988554). We especially thank fishers in the South Australian Marine Scalefish Fishery for assisting with the satellite tag deployments. We thank Dr Rory McAuley (WA Fisheries) for useful discussions regarding factors that may influence movement of dusky sharks. Dr. Scoresby Shepherd provided comments that improved later versions of the manuscript. Procedures were performed under the guidelines of the Flinders University Animal Welfare Committee (E309) and within PIRSA-SARDI Animal Ethics Guidelines. This is contribution #8 of the Southern

Shark Ecology Group. We also thank the anonymous reviewers for providing constructive comments that helped to improve the manuscript.

REFERENCES

- Argos website (2010) www.argos-system.org [accessed 1 August 2010].
- Alpine, J.E., Hobday, A.J. (2007) Area requirements and pelagic protected areas: is size an impediment to implementation? *Mar. Freshw. Res.* **58**:558–569.
- Arnold, G., Dewar, H. (2001) Electronic tags in marine fisheries research: a 30-year perspective. In *Electronic Tagging and Tracking in Marine Fisheries*. J Seibert, J Nielsen (eds) Dordrecht: Kluwer Academic Publishers, pp 7–64.
- Arrizabalaga, H., Pereira, J.G., Royer, F. *et al.* (2008) Bigeye tuna (*Thunnus obesus*) vertical movements in the Azores Islands determined with pop-up satellite archival tags. *Fish. Oceanogr.* **17**:74–83.
- Block, B.A., Dewar, H., Blackwell, S.B. *et al.* (2001) Migratory movements, depth preferences and thermal biology of Atlantic bluefin tuna. *Science* **293**:1310–1314.
- Block, B.A., Costa, D., Boehlert, G.W., Kochevar, R.E. (2003) Revealing pelagic habitat use: the Tagging of Pacific Pelagics program. *Oceanol. Acta* **25**:255–266.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J. *et al.* (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* **415**:86–90.
- Bradshaw, C.J.A., Sims, D.W., Hays, G.C. (2007) Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. *Ecol. Appl.* **17**:628–638.
- Bruce, B.D., Short, D. (1990) Observations on the distribution of larval fish in relation to a frontal system at the mouth of the Spencer Gulf, South Australia. *Bur. Rur. R. P.* **15**:124–137.
- Bruce, B.D., Stevens, J.D., Malcolm, H. (2006) Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Mar. Biol.* **150**:161–172.
- Brunnschweiler, J.M., Sims, D.W. (2012) Diel oscillations in whale shark vertical movements associated with meso- and bathypelagic diving. *Am. Fish. Soc. Symp.* **76**:457–469.
- Cartamil, D., Wegner, N.C., Aalbers, S., Sepulveda, C.A., Baquero, C.A., Graham, J.B. (2010) Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. *Mar. Freshw. Res.* **61**:596–604.
- Compagno, L.J.V. (1984) FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO. Synopsis, (125). **4**:pt 2. 251–655.
- Cresswell, G., Petersen, J. (1993) The Leeuwin Current south of Western Australia. *Aust. J. Mar. Freshw. Res.* **44**:285–303.
- Dewar, H., Thys, T., Teo, S.L.H. *et al.* (2010) Satellite tracking the world's largest jelly predator, the ocean sunfish, *Mola mola*, in the Western Pacific. *J. Exp. Mar. Biol. Ecol.* **393**:32–42.
- Dewar, H., Prince, E.D., Musyl, M.K. *et al.* (2011) Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish. Oceanogr.* **20**:219–241.
- Domeier, M.L. (2010) umbrella darts <http://www.marinecsi.org/umbrella-darts> accessed [15 September 2010].
- Domeier, M.L., Nasby-Lucas, N. (2008) Migration patterns of white sharks (*Carcharodon carcharias*) tagged at Guadalupe Island, Mexico, and identification of an Eastern Pacific shared offshore foraging area. *Mar. Ecol. Prog. Ser.* **370**:221–237.
- Dudley, S.F.J., Cliff, G., Zungu, M.P., Smale, M.J. (2005) Sharks caught in the protective gill nets of KwaZulu-Natal, South Africa. 10. The dusky shark *Carcharhinus obscurus* (Lesueur 1818). *S. Afr. J. Mar. Sci.* **27**:107–127.
- Environmental Protection and Biodiversity Conservation Act (1999). <http://www.environment.gov.au/epbc> [accessed 1 February 2010].
- Fujioka, K., Hobday, A.J., Kawabe, R. *et al.* (2012) Departure behaviour of juvenile southern bluefin tuna (*Thunnus maccoyii*) from southern Western Australia temperate waters in relation to the Leeuwin Current. *Fish. Oceanogr.* **21**:269–280.
- Gunn, J., Patterson, T.A., Pepperell, J.G. (2003) Short-term movement of black marlin *Makaira indica* in the Coral Sea as determined through a pop-up satellite archival tagging experiment. *Mar. Freshw. Res.* **54**:515–525.
- Hindell, M.A., Lea, M., Bost, C. *et al.* (2011) Foraging habitats of top predators, and Areas of Ecological Significance, on the Kerguelen Plateau. *Kerg. Plat. Mar. Ecosyst. Fish. Société d'Ichtyologie* **2011**:203–215.
- Hobday, A.J., Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fish. Manage. Ecol.* **13**:365–380.
- Hobday, A.J., Hartog, J.R., Timmis, T., Fielding, J. (2010) Dynamic spatial zoning to manage southern bluefin tuna capture in a multi-species longline fishery. *Fish. Oceanogr.* **19**:243–253.
- Hoffmayer, E., Franks, J., Driggers, W., Grace, M. (2010) Movements and environmental preferences of dusky sharks, *Carcharhinus obscurus*, in the Northern Gulf of Mexico. SEDAR Report 21-DW-37. 13 pp.
- Holts, D.B., Bedford, D.W. (1993) Horizontal and vertical movements of the shortfin mako shark *Isurus oxyrinchus*, in the southern California Bight. *Aust. J. Mar. Freshw. Res.* **44**:901–909.
- Hooker, S.K., Gerber, L.R. (2004) Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. *Bioscience* **54**:27–39.
- Hooker, S.K., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J., Reeves, R.R. (2011) Making protected area networks effective for marine top predators. *Endang. Species Res.* **13**:203–218.
- Hoolihan, J.P., Luo, J., Abascal, F.J. *et al.* (2011) Evaluating post-release behavior modification in large pelagic fish deployed with pop-up satellite archival tags. *ICES J. Mar. Sci.* **68**:880–889.
- Hussey, N.E., McCarthy, I.D., Dudley, S.F.J., Mann, B.Q. (2009) Nursery grounds, movement patterns and growth rates of dusky sharks, *Carcharhinus obscurus*: a long-term tag and release study in South African waters. *Mar. Freshw. Res.* **60**:571–583.
- IMOS Integrated Marine Observer System website. Sea-surface temperature data <http://oceancurrent.imos.org.au> [accessed 15 September 2011].
- Kinney, M.J., Simpfendorfer, C.A. (2009) Reassessing the value of nursery areas to shark conservation and management. *Conserv. Lett.* **2**:53–60.
- Klimley, A.P., Beavers, S.C., Curtis, T.H., Jorgensen, S.J. (2002) Movements and swimming behaviour of three species

- of sharks in La Jolla Canyon. *California. Environ. Biol. Fish.* **63**:117–135.
- Kohler, N.E., Casey, J.G., Turner, P.A. (1998) NMFS Cooperative Shark Tagging Program, 1962–93: an atlas of shark tag and recapture data. *Mar. Fish. Rev.* **60**:1–87.
- Last, P.R., Stevens, J.D. (2009) Sharks and Rays of Australia, 2nd edn. Collingwood: CSIRO Publishing, p 644.
- Lucifora, L.O., Garcia, V.B., Menni, R.C., Escalante, A.H., Hozbor, N.M. (2009) Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecol. Res.* **24**:109–118.
- McAuley, R., Lenanton, R., Chidlow, J., Allison, R., Heist, E. (2005) Biology and stock assessment of the thick skin (sandbar) shark, *Carcharhinus plumbeus*, in Western Australia and further refinement of the dusky shark, *Carcharhinus obscurus*, stock assessment, Final FRDC Report – Project 2000/134, Fisheries Research Report No. 151, Department of Fisheries, Western Australia, 132 p.
- McAuley, R.B., Simpfendorfer, C.A., Hall, N.G. (2007) A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two long-lived shark stocks. *ICES J. Mar. Sci.* **64**:1710–1722.
- McClatchie, S., Middleton, J.F., Ward, T.M. (2006) Water mass analysis and alongshore variation in upwelling intensity in the eastern Great Australian Bight. *J. Geophys. Res.* **111**: doi:10.1029/2004JC002699.
- Middleton, J.F., Bye, J.A.T. (2007) A review of the shelf-slope circulation along Australia's southern shelves: cape Leeuwin to Portland. *Prog. Oceanogr.* **75**:1–41.
- Musyl, M.K., Brill, R.W., Curran, D.S. et al. (2001) Ability of electronic archival tags to provide estimates of geographical position based on light intensity. In: Seibert, J., Nielsen, J. (eds) *Electronic Tagging and Tracking in Marine Fisheries*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 343–367.
- Nakano, H., Matsunaga, H., Okamoto, H., Okazaki, M. (2003) Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* **265**:255–261.
- Patterson, T.A., Evans, K., Carter, T.I., Gunn, J.S. (2008) Movement and behaviour of large southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop-up satellite archival tags. *Fish. Oceanogr.* **17**:352–367.
- Ridgway, K.R., Condie, S.A. (2004) The 5500-km-long boundary flow off western and southern Australia. *J. Geophys. Res.* **109**:C04017. doi:10.1029/2003JC001921.
- Romine, J.G., Musick, J.A., Burgess, G.H. (2009) Demographic analyses of the dusky shark, *Carcharhinus obscurus*, in the Northwest Atlantic incorporating hooking mortality estimates and revised reproductive parameters. *Environ. Biol. Fishes* **84**:277–289.
- van Ruth, P.D., Ganf, G.G., Ward, T.M. (2010a) Hot-spots of primary productivity: an alternative interpretation to conventional upwelling models. *Estuar. Coast. Shelf Sci.* **90**:142–158.
- van Ruth, P.D., Ganf, G.G., Ward, T.M. (2010b) The influence of mixing on primary productivity: a unique application of classical critical depth theory. *Prog. Oceanogr.* **85**:224–235.
- Schlitzer, R. (2010). Ocean Data View 4, <http://odv.awi.de> [accessed 15 August 2010].
- Simpfendorfer, C.A. (1999) Demographic analysis of the Dusky Shark Fishery in south-western Australia. In: Musick, J.A. (ed.) *Life in the Slow Lane: ecology and Conservation of Long-Lived Marine Animals*. *Am. Fish. Soc. Symp.* **23**:149–160.
- Simpfendorfer, C.A. (2000) Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from south-western Australia estimated from tag-recapture data. *U S Fish. Bull.* **98**:811–822.
- Simpfendorfer, C.A., McAuley, R., Chidlow, J., Lenanton, R., Hall, N. and Bastow, T. (1999) Biology and Stock Assessment of Western Australia's Commercially Important Shark Species. FRDC Final Report. Project 96/130. 106 pp.
- Simpfendorfer, C.A., Goodreid, A., McAuley, R.B. (2001) Diet of three commercially important shark species from Western Australian waters. *Mar. Freshw. Res.* **52**:975–985.
- Smith, S.E., Au, W., Show, C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Mar. Freshw. Res.* **49**:663–678.
- Stevens, J.D., Bradford, R.W., West, G.J. (2010) Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: depth behaviour, temperature experience and movements. *Mar. Biol.* **157**:575–591.
- Weng, K.C., O'Sullivan, J.B., Lowe, C.G., Winkler, C.E., Dewar, H., Block, B.A. (2007) Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Mar. Biol.* **338**:211–224.
- Williams, A., Koslow, J.A., Last, P.R. (2001) Diversity, density and community structure of the demersal fish fauna of the continental slope off western Australia (20 to 35° S). *Mar. Ecol. Prog. Ser.* **212**:247–263.
- Williams, A., Althaus, F., Dunstan, P.K. et al. (2010) Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100–1100 m depths). *Mar. Ecol.* **31**:222–236.
- Wilson, S.G., Stewart, B.S., Polovina, J.J., Meekan, M.G., Stevens, J.D., Galuardi, B. (2007) Accuracy and precision of archival tag data: a multiple-tagging study conducted on a whale shark (*Rhincodon typus*) in the Indian Ocean. *Fish. Oceanogr.* **16**:547–554.