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Living on the continental shelf edge: habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia

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ABSTRACT

We used satellite telemetry data to investigate the movement patterns and habitat use of juvenile shortfin makos *Isurus oxyrinchus* (Lamnidae) tagged in the Great Australian Bight, southern Australia. Tracking durations ranged from 49–672 days and six deployments were > 1 year. During winter and spring, some shortfin makos migrated to the tropical NE Indian Ocean and Coral Sea, and the Subtropical Front region. One shortfin mako undertook an extended migration of 25 550 km across the Indian Ocean. Areas characterized by sea-mounts in the NE Indian Ocean, the oceanic Subtropical Front region, and the continental shelf edge (200-m depth) and slope canyons were visited by several sharks. Juvenile shortfin makos used the outer continental shelf, the shelf edge, the slope and oceanic waters during migrations and mostly exhibited fidelity in the mid-outer shelf, the shelf edge and slope habitats characterized by high bathymetric relief and oceanographic frontal gradients. Our findings highlighted that the continental shelf and slope and associated submarine canyons of the Great Australian Bight represent ecologically important habitats for juvenile shortfin makos. The findings of this study will be pertinent during future management processes for this highly migratory species in this Southern Hemisphere region.

Key words: critical habitat, fidelity, Lamnidae, migration, movement, telemetry

INTRODUCTION

Migration is an ecological process that shapes population dynamics and observed patterns of distribution and abundance of marine predators. Knowledge of the seasonal timing and drivers of these transitory movements is required to understand periods of fidelity in specific areas of interest. Together, this information has become an increasingly important tenet of spatially explicit management of overlaps between threatened, endangered and/or protected marine predators and anthropogenic processes. Much of the recent impetus for application of satellite telemetry to address key knowledge gaps for migratory species has been in response to their roles in shaping the health and functioning of ecosystems (Weng *et al.*, 2005; Block *et al.*, 2011; Vandeperre *et al.*, 2014). Return movements to particular areas may relate to the presence of conspecifics, natal linkages, resource distribution, predator avoidance and foraging success (Pardini *et al.*, 2001; Kokko and Lo′pez-Sepulcre, 2006; Jorgensen *et al.*, 2010).

The prevalence of the International Union for Conservation of Nature (IUCN) listed pelagic sharks in fisheries bycatch (Dulvy *et al.*, 2008), and the process of at-sea finning in High Seas jurisdictions, has been broadly acknowledged as a global threat to these apex predator populations and their ecosystems (Clarke *et al.*, 2006). However, for the most part, the linkages between migration, ecological and oceanographic features and the spatial distributions of Southern Ocean predators has mostly focused on marine mammals and seabirds (Hindell *et al.*, 2011; Bestley

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et al., 2013; Raymond *et al.*, 2014), with only limited emphasis being placed on understanding the migratory schedules of listed oceanic sharks that are expected to exert top-down pressure on other predators and their prey in ecosystems off southern Australia.

During this study, we set out to elucidate the movement patterns of the highly migratory pelagic shark, the shortfin mako *Isurus oxyrinchus* (Lamnidae) (Last and Stevens, 2009) in the Great Australian Bight and Bonney Upwelling Region, which form a large part of the northern temperate boundary of the Southern Ocean (South-east Indian Ocean) off the south coast of Australia. This ecosystem is driven by a combination of continental shelf and slope currents, up- and down-welling, coastal upwelling and extended intrusions of warm, tropical Leeuwin Current water masses from the NE Indian Ocean (Middleton and Bye, 2007). This region has recently been identified as a globally significant 'hotspot' for resident and migratory apex predators (Goldsworthy *et al.*, 2013). This complex environment supports a large proportion of Australia's total fishery production and is a centre for small pelagic and southern bluefin tuna (*Thunnus maccoyii*) fisheries and mariculture.

The shortfin mako is taken as bycatch in commercial long-line and gill-net fisheries, targeted by game and recreational fishers, and is currently listed as Vulnerable by the IUCN, and as Migratory under Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) Appendix II; Migratory). In 2010, the species was the focus of controversy in Australia owing to protection measures that were proposed in response to the CMS listing under the provisions of the Australian Federal Government's *Environmental Protection Biodiversity and Conservation Act* (EPBC Act 1999). The shortfin mako possesses a suite of physiological specializations similar to that of members of the family Scombridae, which include longitudinal red muscle that elevates body temperatures several degrees above ambient water temperatures (Bernal *et al.*, 2001a,b). This is thought to be an adaptation for continuous and rapid swimming (Carey and Teal, 1969; Bernal *et al.*, 2001a,b; Sepulveda *et al.*, 2007), and may be advantageous during prey capture, predator avoidance, and periods of sustained swimming during migrations.

Our knowledge of the feeding preferences of juvenile shortfin makos in the Boney Upwelling Region led us to hypothesize that individuals would focus their migration and fidelity stages around bathymetric features and meso-scale oceanic features where prey, such as squids, small scombrids and other pelagic fishes typically aggregate (Rogers *et al.*, 2012). Previous satellite telemetry studies have provided valuable information on the broad-scale movements and fidelity of shortfin makos in the NW Atlantic Ocean (Loefer *et al.*, 2005), the SE, central and NE Pacific Ocean (Vetter *et al.*, 2008; Abascal *et al.*, 2011; Block *et al.*, 2011; Musyl *et al.*, 2011), and the SW Pacific Ocean off eastern Australia (Stevens *et al.*, 2010). These studies have shown that shortfin makos regularly inhabit the surface layer and migrate over substantial distances, making the species amenable to the application of dorsally-mounted satellite tags (Vetter *et al.*, 2008), and spatial modelling of telemetry and correlated environmental data (Block *et al.*, 2011).

Bayesian state-space models have been used to aid the biological and ecological interpretation of segments of satellite tracks of several marine predator species, including leatherback turtles (*Dermochelys coriacea*) (Jonsen *et al.*, 2003, 2007), bluefin tuna (Royer *et al.*, 2005), blue whales (*Balaenoptera musculus*) (Bailey *et al.*, 2009), shortfin mako, salmon shark (*Lamna ditropis*) and white shark (*Carcharodon carcharias*) (Block *et al.*, 2011). During this study, we used the switching state-space model to differentiate between periods of residency and transit/migratory movement, with the assumption being that the latter phase represents directional movement between known areas of biological and ecological importance (Jonsen *et al.*, 2005; Patterson *et al.*, 2008; Bestley *et al.*, 2013). We used satellite telemetry to investigate the patterns of fidelity, transit/migration by juvenile shortfin makos, with the key assumption being that observed movements were predominantly related to factors including preferential habitat use, social structuring and predator–prey dynamics, rather than reproductive pressures, as would be predicted for mature-sized individuals. Owing to the combination of a lack of high resolution depth (dive and ascent) data collected and transmitted by the satellite tags, and low surface time intervals compared with marine mammals, we did not make second-level behavioural differentiations based on the two movement phases, e.g., we did not state that individual animals were actively foraging or searching for prey in an area-restricted-search behavioural mode.

Specifically, we examined three main questions: (i) What combinations of physical and oceanographic features characterize the migratory paths of shortfin makos? (ii) Which areas do shortfin makos exhibit periods of fidelity? and (iii) What combinations of explanatory variables explained the movement patterns observed within key habitats?

MATERIALS AND METHODS

A total of 10 dorsal-fin mounted satellite tags were deployed on juvenile shortfin makos in the Great Australian Bight in outer continental shelf, shelf edge (160–200 m) and slope (> 200–1000 m) waters, and in shelf waters (< 200 m) of the Bonney Upwelling Region off the south-east of South Australia (Fig. 1, Table 1). Satellite tags deployed included Sirtrack™ KiwiSat 202 (*n* = 3), Wildlife Computers™ (WC) smart position or temperature (SPOT) (*n* = 3) and data collecting Argos tags (SPLASH) (*n* = 4). Deployment details, including shark size, sex, and tagging locations are provided in Table 1 and Fig. 1. Deployments occurred from a commercial demersal long-line vessel and a chartered tuna fishery vessel (*n* = 8) in the Great Australian Bight, and game fishing vessels (*n* = 2) in the Bonney Upwelling Region (Fig. 1, Table 1). Shortfin makos were captured using a 12-mm-diameter capture rope and 70-mm-diameter rubber buoy, attached to a single ~1 m of stainless steel cable leader (2 mm diameter) and tuna circle or terashima semi-circle hook (size 12/0–14/0). Two individuals were captured on game fishing equipment. Once hooked, sharks were lifted from the water using either a solid aluminum or collapsible rubber sling. Once on-board, sharks were supported and restrained using a wet high-density foam mattress and the hook was removed. Sharks were aerated using a reinforced deck-hose and their eyes were covered. Sharks were sexed, and body lengths were measured by the total length (TL) or estimated based on marks on the sling. Based on published sizes at sexual maturity (Stevens, 1983; Francis and Duffy, 2005) and rapid physical assessments, all tagged sharks were juveniles. Satellite tags were attached to the first dorsal fin of each shark using two or three 3.5-mm-diameter stainless steel bolts, nylex locknuts and washers.

Given that shortfin makos are endothermic (Carey and Teal, 1969), four steps were taken to minimize on-deck handling time and stress. First, the stainless steel tag bolts were pre-glued into each tag using Araldite™ epoxy. Second, a modified Stanley™ bench-clamp attached to a tag shape template was used to enable the drilling of holes in the dorsal fin accurately to match the spacing of the tag bolts. Third, the stainless lock nuts were fastened using a cordless drill and deep socket. Finally, the total length of each animal was estimated (± 10 cm) from increments marked on the cradle. These steps minimized the on-deck handling time of each animal to between 3 and 6 min. Each Sirtrack tag contained two AA lithium batteries and the WC SPOT, and SPLASH tags contained a single AA lithium battery. Sirtrack tags and SPOTs were programmed to transmit signals every day. Transmission repetition rates were 45 s. SPLASHs were duty-cycled to transmit every second day to maximize the battery life. Time-depth and -temperature data from SPLASH tags were examined as part of a separate study.

Satellite tags transmitted signals to the low polar orbiting environmental satellite network to receiver stations, which were forwarded to Argos centres in France and the USA (Argos, 2008). Argos position estimates were accessed as .prv and .diag format files using Telnet and Tera Term Pro software. Position data were provided in seven location classes (cls) ranging from the highest to the lowest quality between 3, 2, 1, 0, A, B and Z (no positions) with predicted

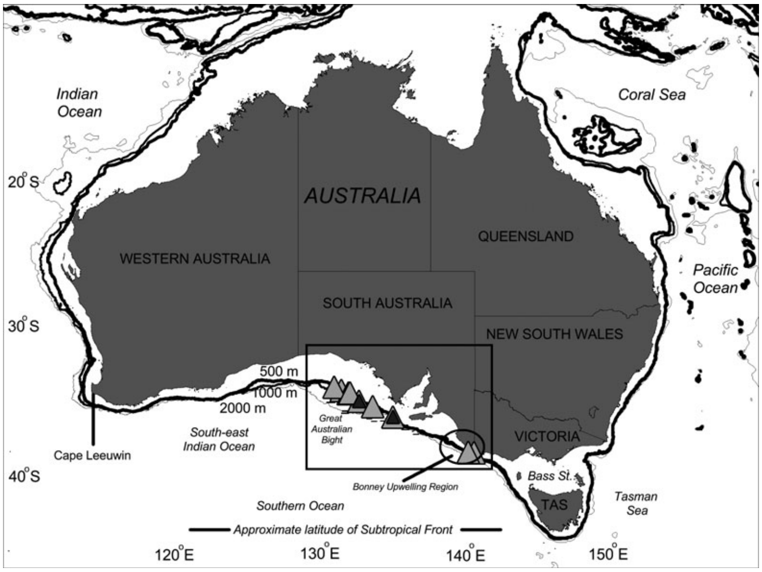


Figure 1. Locations where satellite tags were deployed on juvenile shortfin makos (light grey triangles) in the central and eastern Great Australian Bight and Bonney Upwelling Region off South Australia in 2008 and 2009. Dark small triangles show where two sharks were tagged. Rectangle shows the study area. Bathymetry lines represent the 500-, 1000- and 2000-m depth contours.

Table 1. Tagging statistics for satellite tracked shortfin makos between 2008 and 2010.

Shark No.	Tag type	Duty cycle (days)	Capture date (GMT)	Sex	TL (cm)	Date last location (GMT)	N ARGOS estimated positions (cls 3–B)	N ARGOS estimated positions (cls 3–0)
M1	Sirtrack202	–	11-3-08	m	170	11-1-10	1591	389
M2	Sirtrack202	–	13-3-08	m	180	30-4-08	148	78
M3	Sirtrack202	–	5-4-08	f	150	20-7-08	197	78
M4	WC SPLASH	2 days	1-6-08	f	180	10-10-09	705	345
M5	WC SPLASH	2 days	4-6-08	f	200	16-9-09	595	312
M6	WC SPOT	–	30-3-09	f	180	1-7-10	1255	614
M7	WC SPLASH	2 days	31-3-09	f	240	26-7-10	528	349
M8	WC SPLASH	2 days	7-5-09	m	170	9-11-10	1223	682
M9	WC SPOT	–	9-5-09	m	215	26-1-10	800	390
M10	WC SPOT	–	22-11-09	m	174	12-10-10	1280	714

WC, wildlife computers; GMT, Greenwich mean time; TL, total length; Cls, Arogos location error classes.

accuracies of 3 = < 250 m, 2 = 250–500 m, 1 = 500–1500 m and 0–B = > 1500 m, Z = no position (http: //www.argos-system.org). The switching state-space model (SSSM) of Jonsen *et al.* (2005, 2007) was fitted to Argos positions of classes 3–B to classify segments of each track into fidelity (or residency), transit (migratory or directional movement) or uncertain, where the model was unable to classify positions. Detailed SSSM methods are provided in Jonsen *et al.* (2005, 2007) with Appendices containing the R code (adapted by M. Hindell, University of Tasmania) applied during this study. Bailey *et al.* (2009) showed duty cycling of tags did not significantly impact the certainty of SSSM classifications. The SSSM integrates a correlated random walk (CRW) model to replicate and predict movement stages (fidelity or transit) during each deployment (Jonsen *et al.*, 2005). Models for each Argos position dataset were fitted in R 2.12 (2010-10-15, The R Foundation for Statistical Computing), using the *R2WinBUGS*, *RODBC*, *bssm*, *mapdata*, *diveMove* and *trip* packages. SSSM were fitted using WinBUGS 14 Software (Lunn *et al.*, 2000) (http://www.mrc-bsu.cam.ac.uk/bugs), which uses Markov Chain Monte Carlo (MCMC) simulations to run the Bayesian model. Individual-based models were fitted using each Argos tracking dataset, with 40 000 MCMC samples. In each fit, 20 000 samples were used to 'burn in' or select a starting probability distribution position at the start of the MCMC run. Every 10th sample was retained to estimate the state, parameter and the two behavioural modes. The mean number of locations per day for each shark and the proportion over a 24-h period (0.2–0.33) was used as the initial time-step value for interpolations in each model. Model output means of the MCMC generated samples were used to classify segments of tracks into fidelity or transit (Jonsen *et al.*, 2007). Estimates with mean movement modes < 1.25 were classified as transit, and those > 1.75 were classified as fidelity. Means between 1.25 and 1.75 were classified as uncertain according to Jonsen *et al.* (2007). These reflect the probabilities of the animal being in one of two of the assumed stages. Positions classified as transit, fidelity, or uncertain were plotted on either the NOAA ETOPO1 Global relief bathymetry layer (Amante and Eakins, 2009), or the Australian bathymetry and topography grid at 250-m resolution provided by Geoscience Australia using MapInfo Ver. 8 (Mapinfo Corporation, New York) GIS software. SSSM-filtered Argos data were plotted by individual shark by Austral season (summer: Dec–Feb, autumn: Mar–May, winter: Jun–Aug, spring: Sept–Nov) and year to differentiate between seasonal movement patterns. The mean swim speed and cumulative distances travelled were estimated from positions in combined stages, as well as individual fidelity and transit stages where sharks maintained a given stage for > 48 h. This ensured that each shark was clearly established in either a transit or fidelity stage. We were interested in examining the question: Which spatial, temporal and environmental variables best explained transitory movements and fidelity in the key regions used by shortfin makos? The spatial, temporal and remote-sensed environmental variables assessed and plotted against transit and fidelity classified positions included:

- Distance to the continental shelf edge (200 m isobath);
- Distance from shore;
- Season (Austral summer, autumn, winter and spring);

- Depth (m) calculated from the ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins, 2009);
- Sea surface height (SSH) calculated from mean absolute dynamic topography; (source: http://www.aviso.oceanobs.com). SSH provides an indicator of proximity to eddies and sea-surface temperature (SST) fronts: warm core eddies force the sea-surface upward and vice-versa;
- SST data were obtained from Aqua and Terra MODIS data at 9-km and 8-day resolution from NASA OceanColor WEB (source: http://www.oceancolor.gsfc.nasa.gov);
- Chlorophyll-*a* concentration data were obtained from SeaWiFs, Aqua and Terra MODIS at a 9-km 8-day resolution from NASA OceanColour WEB (source:http://www. oceancolor.gsfc.nasa.gov);
- Ocean productivity in mg C m^{-2} day^{-1} (Source http://orca.science.oregonstate.edu).

RESULTS

Ten satellite tags were deployed on juvenile shortfin makos ranging in size from 150–240 cm, TL. Table 1 provides a summary of the deployment details for individual shortfin makos referred to hereafter as M1–M10. Deployment locations are shown in Fig. 1.

Deployment durations ranged from 49 to 672 days (mean = 387 ± 198 days, SD), and six tags provided long-term tracks ranging from 458 to 672 days (range: 1.3–1.8 years). Sharks M2 and M3 provided short-term tracks of 49 and 106 days and remained in the Great Australian Bight during movements of 1342 and 2772 km, respectively. The spatial range occupied by individual shortfin makos extended from tagging locations in the Great Australian Bight and Bonney Upwelling Region, to the Coral Sea and across the Indian Ocean (Fig. 3a,b). Estimates of minimal horizontal distances travelled ranged from 1342 km in 49 days to 25 550 km in 551 days (1.8 years). Three shortfin makos travelled minimum distances of 22 804 km in 469 days (M5), 21 229 km in 482 days (M7) and 25 550 km in 551 days (M8). Movement summary statistics are provided in Table 2.

During fidelity stages, the mean estimated daily distances travelled ranged from 4.6 and 43.7 km per day *c.f.* 18.5 and 93.8 km per day during transit stages. During periods of fidelity in the Great Australian Bight, mean distances travelled ranged between 24 and 35 km per day. Table 3 shows duration and range statistics for each individual shark in transit and fidelity stages.

Table 2. Switching state-space model fit statistics, times at liberty and distances travelled by satellite tracked shortfin makos.

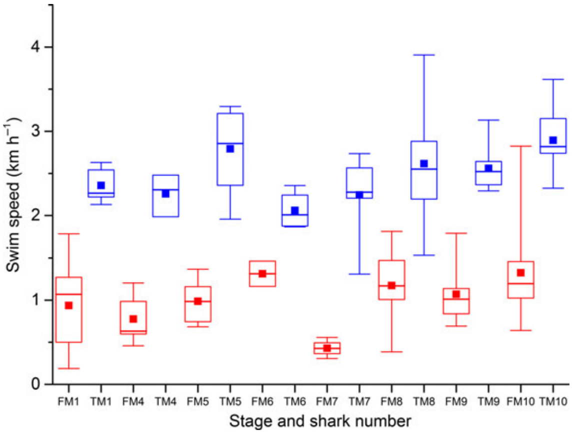
Shark No.	N SSSM estimated locations	N Fidelity positions (%)	N Transit positions (%)	N Unclassified positions (%)	Time at liberty (days) cls 3–B	Years at liberty	Minimum distance travelled (km)	Range distance per day (km)	Mean distance per day (km)
M1	3350	2135 (63.7)	543 (16.2)	672 (20.1)	672	1.8	17056	0.7–101.1	25.4 ± 21.6
M2	213	212 (99.5)	0	1 (0.5)	49	0.1	1342	9.5–67.4	31.0 ± 15.0
M3	321	316 (98.4)	0	5 (1.6)	106	0.3	2772	1.5–83.0	26.0 ± 17.5
M4	1984	1454 (73.3)	422 (21.3)	108 (5.4)	496	1.4	12158	1.6–97.7	24.5 ± 20.0
M5	1881	528 (28.1)	1105 (58.8)	248 (13.2)	469	1.3	22804	1.4–196.8	48.4 ± 30.0
M6	1783	470 (26.4)	1210 (67.9)	103 (5.8)	458	1.3	18284	1.2–105.0	41.0 ± 21.0
M7	1461	357 (24.4)	966 (66.1)	138 (9.5)	482	1.3	21229	1.2–146.2	44.0 ± 31.4
M8	2752	569 (20.7)	1608 (58.4)	575 (20.9)	551	1.5	25550	1.9–147.5	46.3 ± 23.5
M9	1051	515 (49.0)	252 (24.0)	284 (27.0)	262	0.7	9109	2.1–109.6	34.5 ± 20.2
M10	1610	677 (42.1)	775 (48.1)	158 (9.8)	324	0.9	15647	1.5–118.1	42.8 ± 24.7

Unclassified, model did not classify position as transit or fidelity. Error estimates, standard deviation.

Table 3. Switching state-space model fit statistics for satellite tracked shortfin makos showing average (± SD) and range of durations in transit and fidelity stages.

Shark No.	SSSM stage	N SSSM stages	Ave. duration (days ± SD)	Range duration of stage (days)
M1	Fidelity	10	43 ± 22	18–92
M2		1	42	
M3		1	105	
M4		5	72 ± 93	9–230
M5		6	22 ± 11	11–42
M6		2	59 ± 23	42–75
M7		4	29 ± 24	11–64
M8		15	8 ± 6	3–25
M9		13	10 ± 8	3–28
M10		10	18 ± 9	7–32
M1	Transit	6	21 ± 20	4–55
M2		0		
M3		0		
M4		3	35 ± 33	5–70
M5		7	39 ± 26	13–78
M6		4	76 ± 61	10–152
M7		8	45 ± 49	12–151
M8		25	13 ± 11	3–43
M9		8	8 ± 5	3–17
M10		9	21 ± 25	4–70

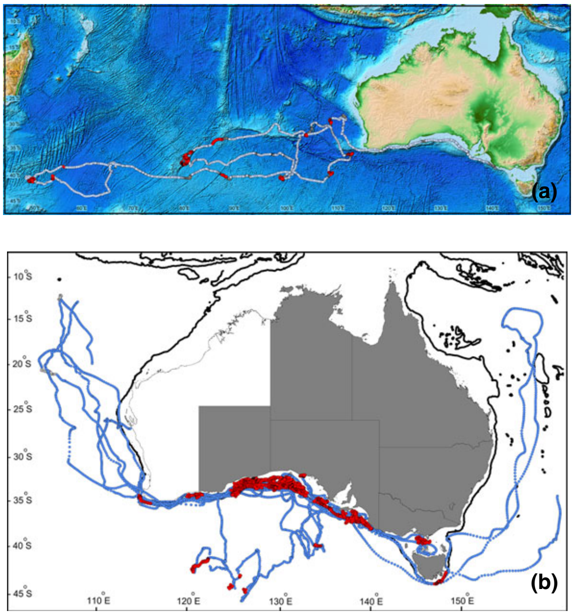
Figure 2. Box plots showing estimates of swim speed for shortfin makos during long-term tracks (M1, and M4–M10) in fidelity (red) (FShark# on *x*-axis) and transit (blue) (TShark# on the *x*-axis) stages. Boxes represent 25 and 75 percentiles, lines inside boxes show medians, squares in boxes are means, and the whiskers = 1% and 99% percentiles.



Estimated swim speeds ranged from 0.8 to 3.9 km h^{-1} (mean = 2.5 ± 0.6 km h^{-1}) during transit stages and were significantly faster than during fidelity stages (0.2 to 1.8 km h^{-1} (the mean = 1.0 ± 0.4 km h^{-1}) (Fig. 2) (*t*-test statistic = 16.8, d.f. = 121, $P < 0$). The mean proportion of days tracked classified as fidelity and transit was close to parity at 44 and 42%, respectively, with the remaining (14%) unclassified. Summary statistics are provided in Tables 2 and 3. The mean percentages of individual tracks classified as fidelity and transit were 52 ± 30% (range: 21–100%) and 36 ± 27% (0–68%), respectively. The mean percentage of unclassified positions was 11 ± 9% (0.5–27%). For the long-term tracks (n = 8, > 180 days), the means of 8 ± 5 fidelity and 9 ± 7 transit stages occurred. Positions classified as indicative of fidelity for shortfin makos were prevalent in the Great Australian Bight from longitudes of 125° to 135°E (Fig. 3a,b), and near the northern frontal extents of the Bonney Upwelling Region between spring and autumn.

The mean bottom depth that was correlated with fidelity classified positions between the 10–1000 m depth contours was 149 ± 145.1 m, which is located between a band of complex bathymetry known as the 'Sahul coastline' (An ancient submarine coastline located at ~130 m depth) and the continental shelf edge (200 m depth). The Great Australian Bight was the location of 65% of the positions classified by the SSSM as indicative of fidelity (Fig. 3b). Fidelity stages also occurred in the Bass Strait, in continental shelf waters off the south coast of Western Australia, near the Subtropical Front region, in the Indian and Southern Ocean, and to a lesser extent off SW Tasmania (Fig. 3a,b). Figure 1 shows the approximate location of the Subtropical Front that varies in latitude between ~40–44°S. The continental shelf, shelf edge and slope habitats (≤ 1000 m) from the SW of Cape Leeuwin to eastern Bass Strait encompassed 82% of positions classified as indicative of fidelity (Fig. 3b). Specific examples included M1, M4 (Fig. 4a) and M9 (Fig. 4d), which exhibited periods of fidelity in the central and western Great Australian Bight. Figure 4a–d shows seasonal movements for shortfin makos M1, M4 and M5–M10. Shark M4 was tracked for 496 days and spent 489 days (98.6%) in the Great Australian Bight (Fig. 4a). Similarly, shark M1 was tracked for 672 days and spent 552 days (82% of its time) in continental shelf and slope waters of the Great Australian Bight (Fig. 4a). Shark M9 was tracked for 262 days of which it spent 170 days (65% of its time) in the Great Australian Bight, interspersed by a return migration to the Subtropical Front region (Fig. 4d). This shark remained within a triangular region between the Great Australian Bight, Bonney Upwelling Region and Subtropical Front region for the entirety of its track and travelled 9109 km within this area.

Figure 3. (a) Map showing the oceanic migration of shark M8 from the Bonney Upwelling Region to the western Indian Ocean. Blue symbols represent locations classified as transit (migration), red symbols represent fidelity stages and grey symbols represent positions classified as uncertain. (b) Map showing the fidelity and transit classified positions for shortfin makos in the Great Australian Bight, East Indian Ocean, Subtropical Front region, Coral Sea and SW Pacific Ocean. Heavy black contour = 500 (mid continental shelf slope).



Common migration or transit pathways were located: (i) in the mid-outer continental shelf, shelf-edge and slope waters of the Great Australian Bight; between SW Western Australia and Southern Tasmania, and in oceanic regions of the NE Indian Ocean and in the vicinity of the Subtropical Front region (Fig. 3a,b). Shortfin makos that migrated to the SE Indian Ocean (M5, M6, M8 and M10, Fig. 4b–d), the Tasman Sea and the Pacific Ocean (M7, Fig. 4c) moved off the continental shelf slope during the northern movements into oceanic regions.

Shark M8 migrated from the Bonney Upwelling Region to SW Western Australia and across the Indian Ocean to a location 1660 km from Madagascar, and 1800 km to the east of South Africa (Fig. 3a and Fig. 4c). This oceanic migration extended for 16 months and 22 709 linear km and covered a vast longitudinal range of 49° to 141°E. During this movement, highly directional transit stages ranging in length from 0.4 to 43 days (mean = 12 ± 10.2 days) were interspersed with shorter periods of fidelity of up to 25 days (mean = 7.0 ± 6.1 days). These bouts were between 390 and 1860 km apart. M8 visited the latitudinal range of the Subtropical Front (SFT) on several occasions.

Two females of 180 and 200 cm, TL (M5 and M10) (Fig. 4b,d) made three extensive northward migrations to an oceanic region in the NE Indian Ocean during winter and spring. This region spanned an area ranging from 540 to 1200 km south of Java, Indonesia, and 1100–1300 km NW of Shark Bay, WA. Sharks M5 and M10 were present in the Great Australian Bight during summer and autumn and migrated to the NE Indian Ocean in winter and spring. (Fig. 4b,d). Shark M5 migrated to this oceanic region twice from the Great Australian Bight over 469 days (Fig. 4b). The largest female (M7, 240 cm, TL) (Fig. 4c) moved SE from the Great Australian Bight along the continental shelf slope and around southern Tasmania through the SW Pacific Ocean to the Coral Sea during the winter–spring of 2009 (Fig. 4c). During the initial 21-day phase of this broad-scale movement, M7 travelled from the eastern boundary of the Great Australian Bight to the Tasman Sea, and maintained an average daily distance travelled of 88 km day^{-1} and an average swim speed of 3.7 km h^{-1}. The first northward migration passed several sea-mounts in offshore oceanic regions of the SW Pacific Ocean. During the following autumn, this shark followed a similar path along the continental shelf off western Tasmania (1 month earlier than in the previous year) to an offshore oceanic region in the SW Pacific Ocean by mid-winter. Figure 5 shows the overall monthly patterns of inhabitance with latitude for all shortfin makos tracked. The highest degree of variability in north-south movements, and the migrations to the highest latitudes occurred in the late winter and spring months between August and October. Movements to the lowest latitudes occurred in the late autumn and early winter months of May and June. No sharks migrated to the Subtropical Front region in 2008. However, this broad oceanic region was the focus of directed migrations by four individuals during the autumn, winter and spring in 2009–2010. These directional S and SW movements from the Great Australian Bight and the southern coastline of Western Australia were interspersed with periods of fidelity near or within the proximity of the Subtropical Front region by sharks M7–M10 (Fig. 4c,d).

The distributions of key environmental variables during movements indicated that during the fidelity stages, sharks experienced lower variation in sea-surface temperatures, sea-surface height and primary production values than during transit stages (Fig. 6). This pattern of lower variability during fidelity stages was

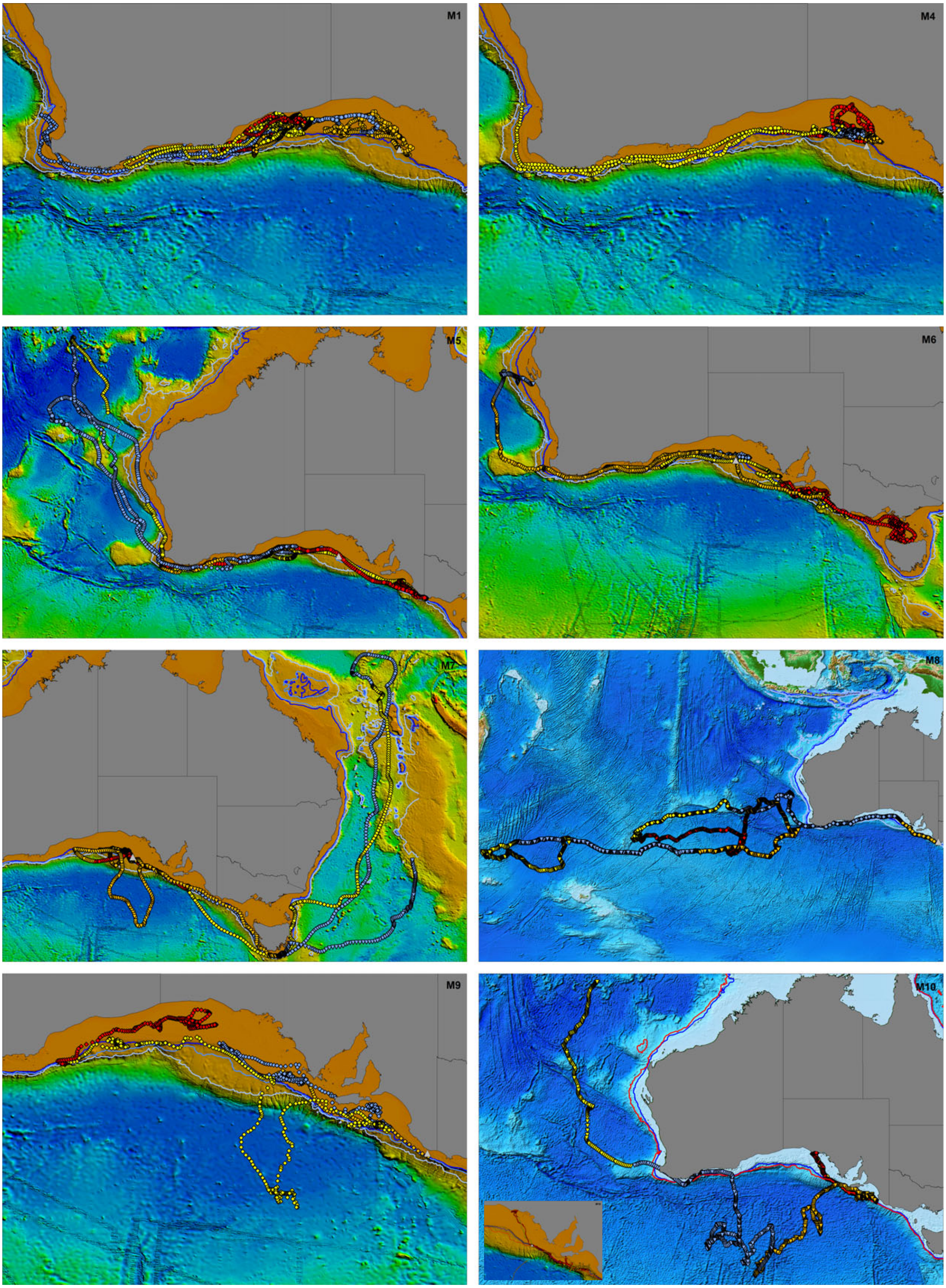
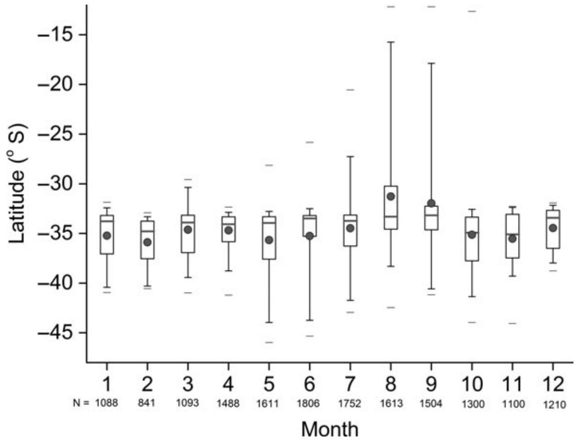

M1
M4
M5
M6
M7
M8
M9
M10

Figure 4. Maps show seasonal movements for shortfin makos M1 and M4–M10 between 2008 and 2010. Circles = 2008, diamonds = 2009, inverted triangles = 2010. Summer = red, Autumn = orange, winter = blue, spring = yellow. Grey triangle shows deployment locations. Indigo contour = 500-, blue = 1000- and sky blue = 2000-m depths.

Figure 5. Box plot showing the monthly pattern of latitude inhabited by shortfin makos in the Southern, Indian and Pacific Ocean. Grey symbols show the monthly means, boxes show the 25 and 75 percentiles, whiskers show the 5 and 95 percentiles, horizontal dashes above and below whiskers indicate the maximum and minimum values, and the grey lines inside the boxes indicate the medians.



also notable for the spatial variables, distance from shore and distance from the continental shelf edge (Fig. 6). In continental shelf waters, shortfin makos utilized a broad depth range of 5–200 m (median, $\tilde{X}$ = 81 m). In continental slope and oceanic waters, sharks used regions with depths from 200 to 6572 m ($\tilde{X}$ = 3430 m). In continental shelf waters, positions for shortfin makos coincided with SSTs of 12.4 to 24.4°C ($\tilde{X}$ = 18.4°C) and chlorophyll-*a* concentrations of 0–4.41 mg m^{-3} ($\tilde{X}$ = 0.15 mg m^{-3}). In slope and oceanic waters, positions ranged with SSTs of 8.0–27.2°C ($\tilde{X}$ = 17.4°C), and chlorophyll-*a* concentrations were less variable, ranging from 0 to 0.98 mg m^{-3} ($\tilde{X}$ = 0.0077 mg m^{-3}). In continental shelf waters, sea-surface height correlated with positions of shortfin makos from 0–96.6 cm ($\tilde{X}$ = 59.2 cm). In continental slope and oceanic habitats, positions correlated with a range of sea-surface heights from 49.6 to 132.2 cm ($\tilde{X}$ = 60.6 cm).

DISCUSSION

Our study provided evidence that juvenile shortfin makos in the Southern Hemisphere Indo-Pacific population(s) are highly migratory and individuals exhibited complicated movement strategies. In summary, these included extensive transit stages in oceanic, mid-outer continental shelf and slope habitats, and fidelity stages that were mostly restricted to mid-outer shelf, shelf edge and slope habitats. Some individuals undertook large-scale oceanic migrations to tropical waters during winter and spring, whereas others remained in the temperate southern continental shelf and slope waters throughout the year. Our findings for shortfin makos in the Great Australian Bight continental shelf and slope ecosystem were generally consistent with those of a previous study in the Southern Californian Bight in the North-east Pacific Ocean, where fidelity tended to decline in offshore oceanic areas (Block *et al.*, 2011). The outer continental shelf region off Cape Leeuwin (Fig. 1) is characterized by a convergence of tropical and sub-tropical oceanic water masses, with the area known as the Naturaliste Plateau representing a 'gate way' to the Indian Ocean where shortfin makos left the continental shelf slope and commenced oceanic migration stages during late autumn and winter. The roles of significant bathymetric features as navigation reference points warrant further investigation in this and other pelagic shark species, as there is potential to use seamounts, mid-ocean ridges and submarine canyons as pelagic management boundaries in High Seas areas.

One shark (M8) travelled ~ 25 550 km across the Indian Ocean from the Great Australian Bight to an area SE of Madagascar, Africa (Fig. 3a). To the best of our knowledge, this is the longest published migration reported for a shortfin mako. This long distance migration was interspersed by short periods of fidelity in several oceanic areas including along the Subtropical Front region, which is known to support a diverse predator assemblage (Bost *et al.*, 2009). Regions of the NE Indian Ocean south of Java, Indonesia formed the focus of three separate oceanic migrations during winter–spring by two individuals that were in the Great Australian Bight during the summer and autumn. The area south of Java is also known to be a spawning area for southern bluefin tuna (Farley and Davis, 1998), which target similar prey to those consumed by shortfin makos. This migratory linkage, along with the shared affinity for pelagic foraging areas in the Great Australian Bight during juvenile stages (Bestley *et al.*, 2008; Goldsworthy *et al.*, 2013), represents evidence of habitat-overlaps between Scombrids and Lamnids in this region, which is interesting given their co-evolution of physiological traits for maintenance of high

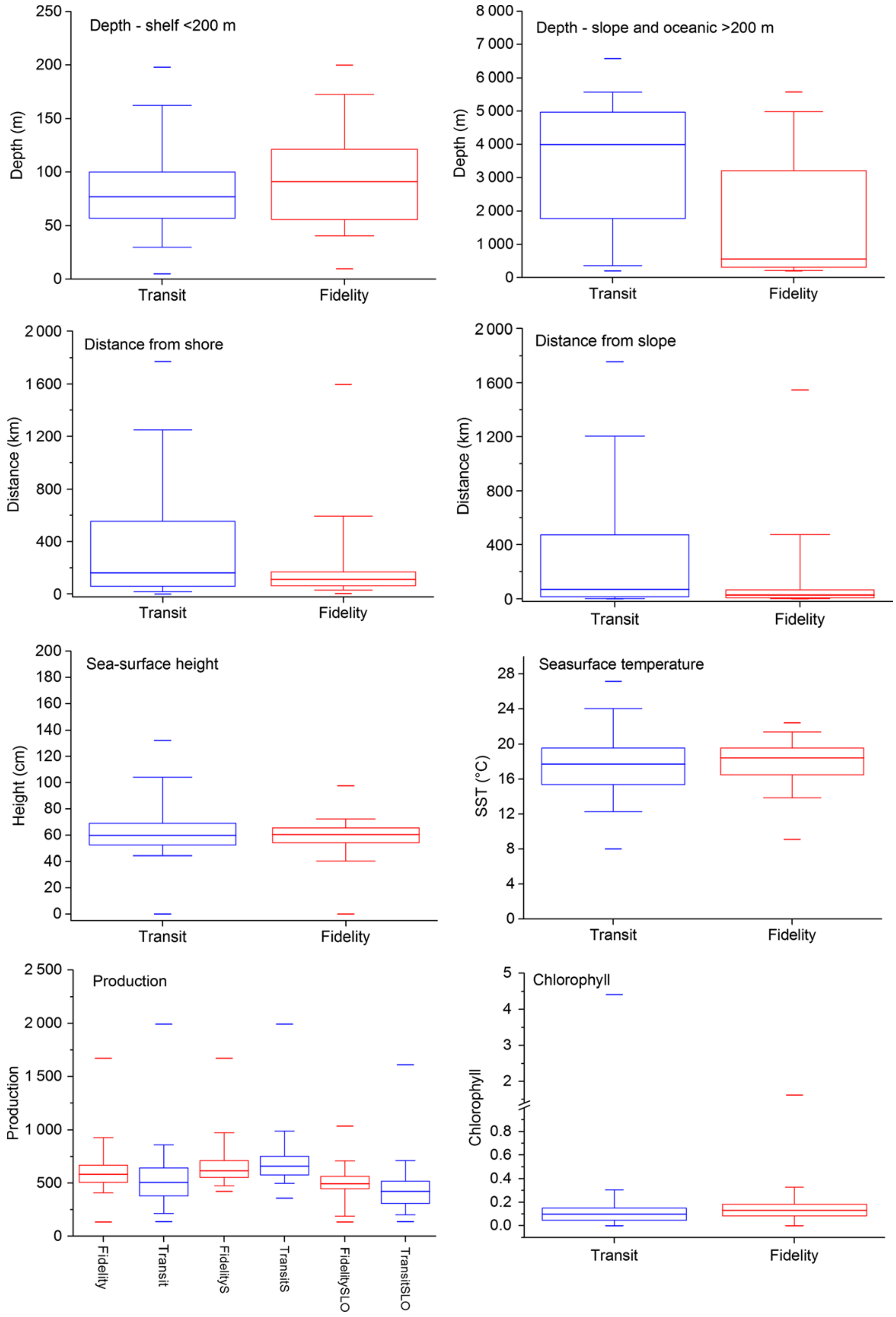

Depth - shelf <200 m
Depth (m)
250
200
150
100
50
0
Transit
Fidelity
Depth - slope and oceanic >200 m
Depth (m)
8 000
7 000
6 000
5 000
4 000
3 000
2 000
1 000
0
Transit
Fidelity
Distance from shore
Distance (km)
2 000
1 600
1 200
800
400
0
Transit
Fidelity
Distance from slope
Distance (km)
2 000
1 600
1 200
800
400
0
Transit
Fidelity
Sea-surface height
Height (cm)
200
180
160
140
120
100
80
60
40
20
0
Transit
Fidelity
Seasurface temperature
SST (°C)
28
24
20
16
12
8
4
0
Transit
Fidelity
Production
Production
2 500
2 000
1 500
1 000
500
0
Fidelity
Transit
FidelityS
TransitS
FidelitySLO
TransitSLO
Chlorophyll
Chlorophyll
5
4
3
2
0.8
0.6
0.4
0.2
0.0
Transit
Fidelity

Figure 6. Box plots of the distributions for environmental and spatial variables summarized for each movement stage, transit and fidelity. Continental shelf = S and slope-oceanic = SLO. Whiskers show the 5 and 95 percentiles, line inside box is the median, the upper and lower box margins are the 75% and 25% percentiles, and the horizontal dashes above and below the whiskers show the maximum and minimum values.

metabolic outputs (Bernal *et al.*, 2001a,b; Sepulveda *et al.*, 2007).

One benefit of adopting the state-space modelling approach was that it utilizes the lower quality class Argos data, which represented 53% of the satellite positions, and omitting these data using swim speed filtering processes may have represented a significant loss of information. However, one weakness of this approach was that it did not classify 14% of the telemetry data, and a previous study by Bailey *et al.* (2009) found that model outputs improved when there were more positions within the tracked time intervals, which is consistent with our findings. This has the potential to limit applications of this model for species where satellite tracks are of short to medium durations. Other potential weaknesses of this approach include the setting of time steps for the interpolation of positions as this may introduce a bias during stages when there are no positions for considerable periods. However, in the case of our study, we recorded an average of ~3–5 positions per day as shortfin makos regularly swam at the surface, and, therefore, this was unlikely to impact our interpretations of movement patterns.

The relative quantity of time spent in transit and fidelity stages could be used to provide valuable insights into the pelagic productivity of continental shelf and oceanic regions shared by shortfin makos, white sharks (Bruce *et al.*, 2006), blue whales (Gill *et al.*, 2011) and southern bluefin tuna (Bestley *et al.*, 2008) off southern Australia, and there is a need to understand the patterns of shared habitat utilization by these and other top predators. Switching state-space model fits to telemetry data for juvenile shortfin makos showed that a large percentage of the positions classified as fidelity occurred in mid-outer continental shelf and slope waters off southern Australia, with ~65% occurring in the Great Australian Bight. The temporal and spatial extent of fidelity exhibited by shortfin makos, and the consistent use of the mid-outer continental shelf and slope suggested that these broad regions may form part of the critical habitats of this ontogenetic stage. In contrast, when juvenile shortfin makos entered offshore oceanic habitats, periods of fidelity became comparatively sparse which may be a response to differences in prey distribution and abundance between the continental slope and oceanic habitats. Oceanic migrations to the Subtropical Front region by shortfin makos were coupled with short periods of fidelity in discrete patches, which suggests that these individuals may have located favourable offshore oceanic foraging areas. The STF supports pelagic cephalopods (Kojadinovic *et al.*, 2011), which form important prey of shortfin makos in the SW Pacific Ocean (Stevens, 1984), and in the Bonney Upwelling Region of the Great Australian Bight (Rogers *et al.*, 2012). This association is consistent with previous studies in the Southern Californian Bight where the jumbo squid (*Dosidicus gigas*) was identified as an important prey item of shortfin makos through analysis of stomach contents (Preti *et al.*, 2012), via the presence of dermal sucker scarring (Vetter *et al.*, 2008), and as an explanatory factor of linkages between the deep scatter layer and vertical movement behaviour of white sharks (Nasby-Lucas *et al.*, 2009). Collectively, this information highlights the importance of pelagic cephalopods to lamnids during offshore oceanic movement stages.

Daily estimates of distance travelled during transit stages were high compared with during periods of fidelity, which is similar to findings for shortfin makos in the North eastern Pacific Ocean (Vetter *et al.*, 2008). Lamnids have a suite of physiological adaptations (Bernal *et al.*, 2001a,b) that allow them to sustain high swimming speeds and high routine metabolic rates (Sepulveda *et al.*, 2007), which partly explains the broad-scale cross-oceanic migrations we observed during this study. One shortfin mako that swam 25 550 km in < 2 years attained estimated maximal speeds as high as those reported for adult white sharks in the NE Pacific Ocean (Domeier and Nasby-Lucas, 2008). White sharks have also been shown to swim at high average speeds during oceanic migrations; juveniles travelled at up to 5.8 km h^{-1} (Bruce and Bradford, 2008), and sub-adults maintained 3.7–6.2 km h^{-1} in the SW Pacific Ocean (Duffy *et al.*, 2012), 4.7 km h^{-1}in the Indian Ocean (Bonfil *et al.*, 2005), 3.2 km h^{-1} in the NE Pacific Ocean (Domeier and Nasby-Lucas, 2008) and 1.1–3.8 km h^{-1} in Australian continental shelf and-slope waters (Bruce *et al.*, 2006). Previously, the longest reported distances travelled by a lamnid was for a salmon shark that moved 18,220 km over 640 days in the NE Pacific Ocean (Weng *et al.*, 2005), and a white shark that made a trans-oceanic migration of > 20 000 km in < 9 months in the Indian Ocean (Bonfil *et al.*, 2005).

However, this later specimen was not tracked for the entire reported period.

Previous studies have shown that SST frontal gradients and associated planktonic production provide important focal foraging habitats for a range of marine predators (Bradshaw *et al*., 2004; Page *et al*., 2006; Cotté *et al*., 2007; Bost *et al*., 2009), including loggerhead sea turtles (*Caretta caretta*) in the central North Pacific Ocean (Polovina *et al*., 2000), blue whales in the NE Pacific Ocean off Mexico (Etnoyer *et al*., 2006) and the green turtle (*Chelonia mydas*) in the eastern tropical Pacific Ocean off the Galapagos Islands (Seminoff *et al*., 2008). The temporal and spatial extent of fidelity we observed in the mid-outer continental shelf and slope waters suggested that shortfin makos may focus on this region to utilize prey aggregations, such as the unidentified taxa that comprise the rich 'deep scatter layer' fauna that is prominent in the slope waters of the Great Australian Bight (Hall, 1981). Dissection of large demersal teleosts sampled on commercial vessels at the time of tag deployments suggested some of these prey taxa in slope waters were Myctophidae (P. Rogers, unpublished data). By contrast, when shortfin makos entered the offshore oceanic habitats, periods of fidelity were sparse or largely non-existent (with the exception of when in the Subtropical Front region), which may be a response to greater patchiness in oceanic prey fields when compared with those in continental shelf, shelf edge and slope regions.

Our finding showed that shortfin makos use an extremely diverse range of habitats and individuals exhibited complex and highly variable movement patterns. Integration of the switching state-space model fits and available habitat data revealed that the outer continental shelf, edge and slope and their associated frontal zones each contributed to explaining the complex array of factors that define pelagic habitats where shortfin makos exhibit fidelity. While thermal conditions may play a role in influencing the seasonal movements of some individuals during winter and spring, telemetry data showed that this species can exploit a broad thermal range of up to 19°C. However, during periods of fidelity, shortfin makos often inhabited meso-scale patches and moved at slow to moderate mean swim speeds (0.2–1.8 km h^{-1}) while experiencing lower spatio-temporal variability in SST – proximity to the continental slope was also an important factor. Sharks spent similar amounts of time in transit stages, but generally swam faster (up to 3.9 km h^{-1}) and environmental variability (e.g., in SST and SSH) tended to be higher in habitats that were characterized by directional transit movements stages. Prior to this study, a lack of knowledge of the spatial and temporal scales that help to explain the functioning of the shortfin mako populations in the South-east Indian Ocean represented a major impediment to the development of suitable assessment and management processes.

Importantly, this study highlighted that the Great Australian Bight is a significant continental shelf, edge and slope area for juvenile shortfin makos that also utilize oceanic habitats of the Indian, SW Pacific and South-east Indian Oceans. Despite undertaking large oceanic migrations, most shortfin makos remained faithful to the continental shelf, edge and slope waters, and no sharks migrated northward beyond 12.2°S. Our telemetry data suggest that this population may utilize multiple strategies for dispersal, whereby some individuals form a migratory component as suggested by Secor *et al*., (1999), and others display extended periods of fidelity within basins and/or display affinities to bathymetric and seasonally predictable oceanic features, such as sea-mounts, submarine canyons, SST and frontal features. This suite of movement strategies may result in population structuring at spatial scales that integrate multiple ocean basins with degrees of philopatry exhibited in selected, productive nursery areas. To better resolve the connectivity we have partially uncovered, further telemetry studies will be required to resolve the movement patterns and habitat use of adult stages of shortfin makos in ecologically important bio-regions of the South-east Indian, Indian, and SW Pacific Oceans. Integration of telemetry-based distribution information, time integrated prey field and habitat data for shortfin makos and a range of other highly migratory marine predators represent a high priority in order to understand the potential impacts of a range of anthropogenic factors in these regions.

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