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ORIGINAL PAPER

Oceanic nomad or coastal resident? Behavioural switching in the shortfin mako shark (*Isurus oxyrinchus*)

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Abstract

Pelagic sharks are vulnerable to overfishing because of their low reproductive rates, generally low growth rates, and high catch rates in tuna and billfish fisheries worldwide. Pelagic sharks often migrate long distances, but they may also occur close to shore, making it difficult to classify their behaviour on the continuum from oceanic nomad to coastal resident. This has important implications for fishery management, which must be targeted at an appropriate spatial scale. Conventional tagging indicates that shortfin mako sharks move widely around the southwest Pacific Ocean, but there is little information on their habitat use or mobility in the region. This study deployed electronic tags on 14 mostly juvenile New Zealand mako sharks to investigate their habitat use, and the spatial and temporal scale of their movements. Movement behaviour was classified as Resident or Travel, with the former focused in New Zealand coastal waters, and the latter in oceanic waters around New Zealand and along oceanic ridges running north towards the tropical islands of Fiji, Vanuatu and New Caledonia. Sharks regularly switched between Resident and Travel behavioural states, but their residency periods sometimes lasted for several months. Sharks spent most of their time in the New Zealand Exclusive Economic Zone (median 77%, five sharks > 90%), presumably because of the high coastal productivity and access to abundant prey. These results challenge the conventional view that mako sharks are nomadic wanderers, and suggest that fishing mortality should be managed at a local as well as a regional scale.

Introduction

Pelagic sharks are vulnerable to overfishing because of their low reproductive rates, generally low growth rates, and high catch rates in tuna and billfish fisheries worldwide. Most pelagic sharks fall near the middle of the shark productivity scale, but despite that, a disproportionately high number of them have been classed as Threatened on the IUCN Redlist (Dulvy et al. 2008; Smith et al. 2008), or have been assessed as 'high-risk' in ecological risk assessments (Cortés et al.

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2010, 2015). Pelagic sharks often migrate long distances and they are generally regarded as oceanic nomads that randomly wander the high seas. However, they may also occur close to shore, and without more specific details of their movement behaviour and degree of mobility, it is difficult to classify them on the continuum from oceanic nomad to coastal resident. This has important implications for fishery management, which must be targeted at an appropriate spatial scale.

Tuna longline fisheries catch large numbers of pelagic sharks. Although sharks are not usually the target of such fisheries, they are a desired bycatch because their fins are valuable as the main ingredient in shark fin soup (Dulvy et al. 2008) and their flesh is also frequently sold. Heavy fishing pressure in many parts of the open oceans has led to large reductions in shark abundance (Clarke et al. 2014).

Shortfin mako sharks (*Isurus oxyrinchus*, hereafter referred to as 'mako sharks') are frequently caught in tuna longline fisheries (Francis 1998, 2013; Griggs and Baird 2013; Clarke et al. 2014; Byrne et al. 2017). Mako sharks are globally distributed in all temperate and tropical oceans (Last and Stevens 2009; Ebert et al. 2013) and they occur from shallow coastal waters to the open oceans. Tagging studies have shown that some sharks make long-distance oceanic movements, but that they tend to remain within specific regions of ocean basins (Sippel et al. 2011; Rogers et al. 2015b; Byrne et al. 2017; Holdsworth and Saul 2017; Vaudo et al. 2017).

Management of mako shark fisheries throughout the western and central Pacific Ocean is the responsibility of the Western and Central Pacific Fisheries Commission (WCPFC). New Zealand fisheries fall within the WCPFC region, and New Zealand is responsible for ensuring that management measures applied within its waters are compatible with those of WCPFC (Ministry for Primary Industries 2017). Reported landings of mako sharks in New Zealand waters peaked at about 320 *t* in 2000–01, and then declined to 72 *t* in 2015–16 as a result of reduced effort in the tuna longline fishery, and the imposition of shipping restrictions on shark fins and regulatory restrictions on shark finning from 2013 to 2014 (Ministry for Primary Industries 2017). An annual Total Allowable Commercial Catch (TACC) of 406 *t* was introduced in October 2004, and reduced to 200 *t* in October 2012, but landings have never reached the TACCs (Ministry for Primary Industries 2017).

In the absence of a southwest Pacific stock assessment for mako sharks, a number of studies have attempted to identify trends in abundance 'indicators' (Clarke et al. 2012). Indicators derived from New Zealand tuna longline fisheries show that mako shark abundance may have declined during the late 1990s and early 2000s, but has increased since the mid-2000s (Francis et al. 2014; Francis and Large 2017). However, it is not known if this trend is common to the entire regional stock, or is a local phenomenon, because the geographical range of the mako shark stock fished in New Zealand is unknown.

Tagging of New Zealand mako sharks with 'conventional' plastic dart tags has shown that some sharks have been recaptured close to their tagging sites after 1–3 years at liberty, whereas others have moved extensively around the southwest Pacific Ocean, travelling to eastern Australia, New Caledonia and Fiji, with occasional movements as far north as Solomon Islands and New Britain, and as far east as French Polynesia (Holdsworth and Saul 2014, 2017). There have been no recorded movements out of the southwest Pacific or north of the Equator. However, conventional tags provide information only on the start and finish locations of a shark's track, and nothing on what happens in between, limiting their ability to characterise movement patterns.

Electronic tags offer opportunities for addressing some of the key questions in the movement ecology of marine megafauna, as detailed by Hays et al. (2016). In this study, we use tracking data to address their first key question: how can movement data be used to support conservation and management? Data collected by electronic tags enable an understanding of the habitat and environment in which the shark lives, and identification of behavioural patterns such as residency and mobility. This knowledge is crucial for interpreting mako shark abundance trends in terms of overall stock status. The aims of the present study were to use electronic tags to determine the spatial and temporal scales of New Zealand mako shark movements in the southwest Pacific Ocean, and to identify physical or environmental features that influence their behaviour and habitat selection. We use this information to test the hypothesis that mako sharks are oceanic nomads with little or no residency behaviour.

Materials and methods

Tagging

Mako sharks were caught by angling from small motorboats with the assistance of chumming. Sharks were brought to the vessel and restrained alongside in the water while the vessel motored forward at about 1 knot, maintaining a constant flow of seawater over the gills. Tags were fixed to the dorsal fin by drilling 3–4 small holes and attaching them with stainless steel bolts and washers. The total length (TL, in a straight line with the tail in a natural position) of each shark was measured in the water with a tape measure, and the shark was sexed and then released by removing the hook or cutting the leader or hook shank.

Thirteen sharks were tagged between 2012 and 2017 around northern North Island, New Zealand (Table 1, Fig. 1). A fourteenth shark tagged in south-eastern Australia in 2013 as part of another study is included here because it

Table 1 Tag statistics for 14 mako sharks. Sharks are numbered in increasing length order

Shark number	Tag number	Tag type	Total length (cm)	Sex	Date tagged	Last fix	Days tracked	Tagging latitude (°S)	Tagging longitude (°E)
Shark 1	113683	SPOT5	153	F	19 Feb 2013	04 Jan 2014	319	37.126	174.549
Shark 2	113681	SPOT5	154	F	15 Feb 2013	26 Sep 2014	588	35.857	174.726
Shark 3	113682	SPOT5	156	M	14 Feb 2013	21 Nov 2013	280	35.921	174.811
Shark 4	113678	SPOT5	171	M	13 Mar 2013	11 Oct 2013	212	36.013	175.111
Shark 5	113680	SPOT5	185	F	22 May 2012	10 May 2013	353	35.153	174.260
Shark 6	115159	Sirtrack PTT	187	F	11 Jul 2013	29 Nov 2014	506	38.360	148.570
Shark 7	73410	SPOT5	187	F	18 Feb 2017	09 Oct 2017	233	37.112	174.436
Shark 8	73411	SPOT5	198	F	18 Feb 2017	30 Jul 2017	162	37.119	174.423
Shark 9	168174	Splash10	203	F	05 Mar 2017	08 Apr 2017	34	36.883	175.903
Shark 10	168173	Splash10	205	F	06 Mar 2017	04 Jul 2017	120	36.905	175.903
Shark 11	148727	SPOT5	209	M	25 Feb 2017	02 Oct 2017	219	37.147	174.414
Shark 12	55618	SPOT5	230	F	01 Jun 2017	25 Oct 2017	146	34.908	173.868
Shark 13	148728	SPOT5	231	M	25 Feb 2017	01 Sep 2017	188	37.128	174.418
Shark 14	55613	SPOT5	240	M	01 Jun 2017	29 Oct 2017	150	34.910	173.930

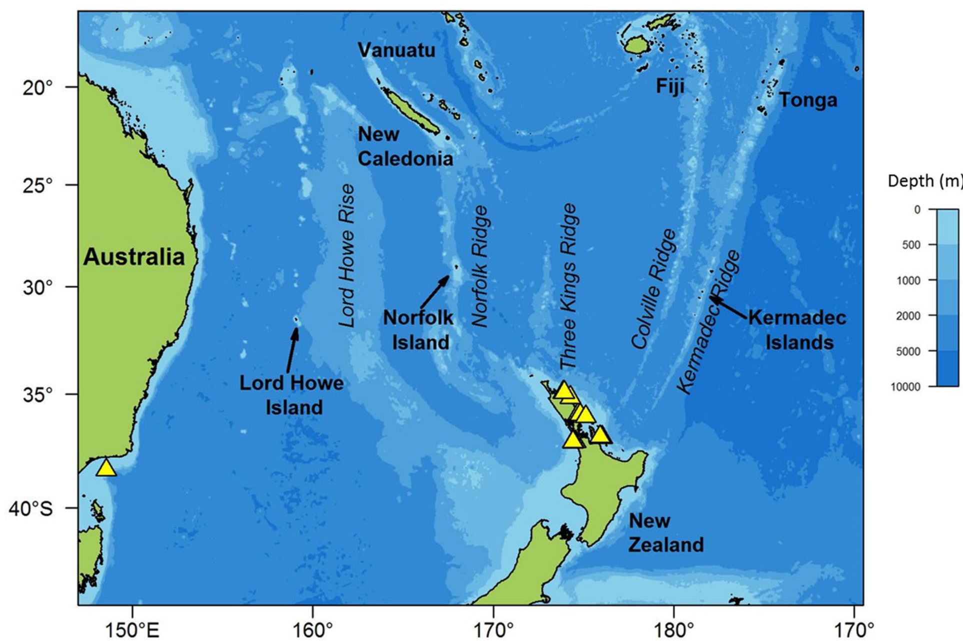

Fig. 1 Bathymetry of the south-west Pacific Ocean showing submarine ridges trending northwards from New Zealand. Mako shark tag locations are shown as yellow triangles (some points in northern New Zealand are obscured)

swam to New Zealand 5 months after tagging, and its subsequent track was similar to those of sharks tagged in New Zealand (Fig. 1, S1). Sharks ranged from 153 to 240 cm TL and comprised 5 males and 9 females (Table 1). To explore whether shark size influenced movement behaviour, we divided the sharks into 'small' (Sharks 1–7, 153–187 cm) and 'large' (Sharks 8–14, 198–240 cm) classes. However, all sharks were well below the maximum length of mako sharks (ca. 400 cm TL; (Ebert et al. 2013)). Based on lengths at maturity of 198–204 cm TL for males and 310–312 cm TL for females (converted from fork length after Francis and Duffy 2005; Francis 2006), our three largest males (Sharks 11, 13 and 14; Table 1) were probably mature, but no females were mature. Thus, our results apply to juvenile makos of both sexes, and mature males.

New Zealand sharks were tagged with Wildlife Computers (Redmond, Washington, USA) SPOT5 ($N=11$) or Splash ($N=2$) tags; Shark 6 from Australia was tagged with a Sirtrack (Havelock North, New Zealand) PTT tag (Table 1). All three tag types communicate with Argos satellites when the shark's dorsal fin breaks the surface, thus exposing the wet/dry contacts to air. None of the tags had GPS functionality.

The Splash and Sirtrack PTT tags were duty-cycled to transmit only every 2nd day to conserve battery power. Tags were limited to a maximum of 200 message transmissions per day. The tag's location was determined to varying degrees of accuracy, depending on the number of messages received by Argos satellites. Location accuracy is classified by Argos as class 3, 2, 1, 0, A, B and Z (http://www.argos-system.org/manual/3-location/34_location_classes.htm). Experimental studies indicate that location classes 3, 2, 1, and A are accurate to ~ 2 km, whereas locations 0 and B are accurate to ~ 5–10 km (Boyd and Brightsmith 2013). Class Z fixes are invalid and were discarded.

Depth and temperature

Ten of the 14 tags were programmed to transmit ambient temperature data. Eight SPOT5s recorded the time spent in a range of temperature bins during 12-h time periods. Temperature bins were not the same for all tags, so data were subsequently aggregated into 10 consistent bins: < 10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–24, 24–26, and > 26 °C. The two Splash10 tags recorded temperature every 5 min, and those higher resolution data were analysed separately, but were also aggregated into the same 10 temperature bins as the SPOT5s to allow direct comparison. The two Splash10 tags also recorded the depth of the tag at 5-min intervals. Not all temperature and depth data were successfully transmitted to satellites, so there were gaps in the data.

For sharks with Splash10 tags, times of dawn and dusk were used to allocate depth and temperature records to "Day" or "Night". Dawn was defined as the start of civil twilight, and dusk was defined as the end of civil twilight, where both reference points occur when the sun is 6° below the horizon. Times of dawn and dusk were calculated for the location having the highest quality Argos fix each day. Days without fixes were assigned the times of dawn and dusk for the previous day. For analysis of diel variation in depth distribution, tag-recorded UTC times were converted to New Zealand Standard Time (NZST = UTC + 12).

Track analysis

All tracks were analysed and figures generated using the open-source statistical programming language *R* version 3.3.3 (R Development Core Team 2017). Improbable Argos fixes were filtered out using the *argosfilter* package (Freitas et al. 2008) by removing positions that would require speeds between fixes of greater than 2 m s^{-1} (173 km day^{-1}), unless they were within 5 km of the previous position. This latter constraint prevents removal of locations that generate artificially high speed estimates as a result of two fixes being obtained within a short time (Freitas et al. 2008).

A hierarchical Switching State Space Model (SSSM) was fitted to filtered Argos locations to estimate daily locations and to classify movements into two behavioural states based on distance travelled and changes in course (Jonsen et al. 2007). One state, characterised by slow speeds and frequent changes of direction, was called *Resident*, and a second state, characterised by rapid movements over long distances with few or small direction changes, was called *Travel* (Jonsen et al. 2007; Block et al. 2011). This modelling approach was specifically developed for use with gappy and error-prone satellite tracking data (Jonsen et al. 2005; 2007). The hierarchical model was fitted to data from all 14 sharks simultaneously. Hierarchical models estimate a single set of movement parameters simultaneously for all sharks, rather than separately for each shark, and this provides improved behavioural state estimation through reduction of uncertainty (Jonsen 2016). Errors were modelled with *t*-distributions because Argos errors are non-normal, and different error distributions were allowed for each of the Argos location classes, thus, accounting for the variable location accuracy among classes (Jonsen et al. 2005; 2007). Two sets of 90,000 Monte Carlo Markov Chain samples were used, with the first 60,000 being discarded as the adaptation and burn-in phase. The remaining 30,000 samples were thinned to 1,000 (every 30th sample) to minimise within-chain sample autocorrelation (Jonsen et al. 2007). Models were fitted using the *bsam* package in *R* (https://cran.r-project.org/web/packages/bsam/bsam.pdf), which in turn used JAGS 4.2.0 software to perform the Bayesian analyses (https://sourceforge.net/projects/mcmc-jags/files/JAGS/4.x/Windows/).

Values of the behavioural mode parameter b were used to assign a behavioural state for each shark at each fitted track location. b values can range from 1 (Travel state with high certainty) to 2 (Resident state with high certainty). In this study, b values less than 1.3 were interpreted as Travel and b values greater than 1.7 as Resident. Intermediate values of b, which indicate an uncertain behavioural state, were classified as Undefined. These classification criteria are subjective, and the time step of the fitted model averages the movement signal across a 1-day period, so the inferred Resident and Travel locations may not reflect the true behaviour of mako sharks in those locations.

The spatial probability distributions of mako sharks during their Resident and Travel behavioural modes were identified using Kernel Utilisation Distributions (KUDs) and the *R* package *adehabitatHR* (Worton 1989; Calenge 2006). That package was developed for small-scale, equal-area spatial grids, which is not appropriate for the large distances covered by mako sharks in the present study, nor the use of a latitude/longitude coordinate system. Consequently, we converted our SSSM locations from latitude/longitude to Universal Transverse Mercator (UTM) locations centred on zone 60 (174°E–180°) using package *PBSmapping* (Schnute et al.

2018), and then formatted them as a *SpatialPoints* object with package *sp* (Pebesma and Bivand 2005). KUDs were then estimated using the function *kernelUD* in *adehabitatHR* and a pre-defined spatial grid, and 50% and 80% probability contours were generated. Probability contours greater than 80% were not informative because they encompassed most of the grid. The results were then back-converted to latitude/longitude co-ordinates for plotting on maps.

Environmental variables

Depth data were extracted from the GEBCO_2014 GRID dataset for study areas east and west of the International Dateline (http://www.gebco.net/data_and_products/gridded_bathymetry_data), and then combined in *R* and the spatial resolution was reduced from 30 s to 1 min. The seabed depth at each SSSM track location was then determined using the package *marmap* (Pante and Simon-Bouhet 2013).

Sea surface temperature (SST) and chlorophyll A (chlA) data were extracted from the NOAA ERDDAP database (http://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html?page=1&itemsPerPage=1000). Specific datasets extracted were the 8-day composite Aqua MODIS products available for the Pacific Ocean since 2006 (*erdMBsstd8day* and *mbchla8day* for SST and chlA, respectively, both at 0.025° resolution). We aggregated the data into 0.1° cells during downloading and used the median cell values as estimates of SST and chlA. Seasons were defined as quarters of the year; e.g. summer was the first quarter (January–March) and winter was the third quarter (July–September).

Results

Data filtering

All 14 tags transmitted useful data, and mako sharks were tracked for periods of 34–588 days (mean = 251 days), giving a total of 3510 days (9.6 years) coverage (Table 1). Filtering out unreliable locations removed 7.0% of fixes, mostly from location classes 0, A and B (all class Z locations were deleted). Two tags had large gaps in transmissions, possibly because of biofouling of the wet/dry sensors or aerials. Long data gaps cause problems for fitting SSSMs (Bailey et al. 2008), so we omitted time periods as follows. Shark 2 produced few transmissions over a 22-week period (Figure S2), so we treated the data received before and after the large gap as separate tracks (by omitting weeks 48–69). Shark 4 produced no transmissions over a 7-week period (Figure S2), so we omitted all data before week 20, and also after week 38 when tag performance was apparently declining and few fixes were received.

The first 52 weeks of data from Shark 6 (about 39% of its track) were also omitted. That shark was tagged in south-eastern Australia (Figure S1) and we used data received after its arrival over the New Zealand continental shelf to simulate a shark that had been tagged in New Zealand. (Note that Shark 6 arrived in New Zealand on 18 December 2013 in week 50, but only 12 fixes were obtained in weeks 50–52, so they were omitted and track fitting began in week 53 (1 January 2014)).

Shark 9's Splash10 tag ceased transmission abruptly 34 days after tagging, soon after arrival in the Lau Island group in southern Fiji (Figure S3). The other Splash10 tag transmitted for 120 days, so the 34-day transmission period of Shark 9's tag was unexpectedly short and unlikely to be explained by battery failure. We suspect that Shark 9 was caught by a fishing vessel. Shark 3 is known to have been caught and killed on 15 July 2014, 7.8 months after the last satellite transmission was received. A Spanish tuna longliner caught the shark in international waters north of New Zealand (Figure S3), and sent us images of the tag. Shark 3 grew from 156 cm TL at release to about 202 cm TL at recapture (estimated from the fork length of 185 cm measured by the vessel), thus growing 46 cm in 17 months.

Shark movements and behavioural states

All mako sharks were tagged in shelf waters, and all except one (Shark 4) subsequently travelled into oceanic waters. Most sharks exhibited highly variable movement patterns. At times, they spent up to several months continuously within a strip of New Zealand continental shelf less than 200 km long; at other times they made long-distance ocean crossings > 1000 km (Fig. 2, S3). Oceanic movements often took sharks near the tropical and subtropical islands north of New Zealand, including Tonga, Fiji, Vanuatu, New Caledonia, Chesterfield, Norfolk, and Kermadec islands. Maximum straight-line distances from the tagging locations were 311–2904 km (median 1443 km) with 12 out of 14 sharks exceeding 1000 km (Table 2). These oceanic journeys often culminated with a return to the New Zealand shelf, sometimes ending up very close to the tagging location. The most extreme example of this was Shark 1, which travelled almost 14,000 km, but its last satellite fix was only 42 km from the tagging location (Table 2, Figure S3). Summed great circle distances travelled between individual fixes by each of the 14 sharks ranged from 2154 km to 20,140 km (mean 9970 km) (Table 2). Three sharks (Sharks 2, 5 and 6) travelled total distances of about 19,000–20,000 km, and for Shark 6, that distance was in addition to the distance she travelled between being tagged in Australia and arriving in New Zealand.

Fitted SSSM tracks closely resembled the tracks based on raw satellite fixes, but the 1-day SSSM time steps smoothed

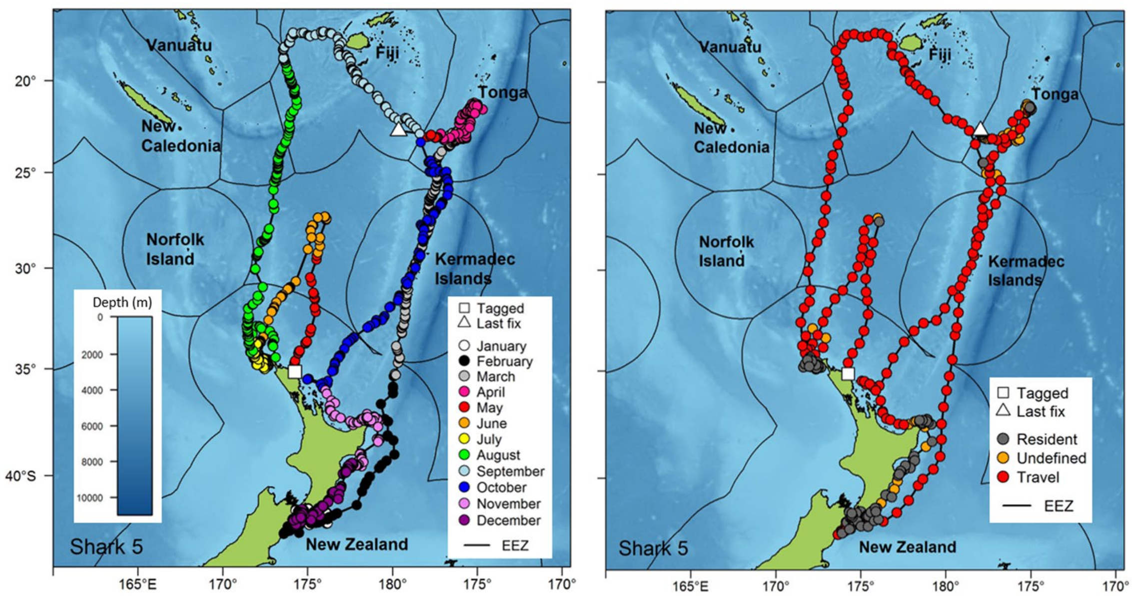

Fig. 2 Shark 5 tracks showing (left) filtered satellite fixes colour-coded by month of the year, and (right) fitted switching state space model track with daily locations colour-coded by behavioural state

Table 2 Track statistics for 14 tagged mako sharks, including maximum straight-line distance from the tagging location, total track distance (summed distances between all fixes), and total and median SSSM daily displacements

Shark number	Total length (cm)	Max. distance (km)	Total days	Total distance (km)	SSSM days	Total SSSM displacement (km)	Median SSSM displacement	Percent of days in NZ EEZ
Shark 1	153	1150	319	13981	319	10167	24.0	94.1
Shark 2	154	1209	588	20140	440	12109	19.5	99.8
Shark 3	156	747	280	10873	280	6524	17.1	95.0
Shark 4	171	311	212	3880	130	2163	11.8	100.0
Shark 5	185	1995	353	18870	353	14827	38.5	63.8
Shark 6	187	2876	506	19606	303	10960	28.4	64.5
Shark 7	187	2904	233	10273	233	8320	31.0	64.5
Shark 8	198	1061	162	6686	162	5979	30.5	79.8
Shark 9	203	1886	34	2154	33	1905	61.8	64.7
Shark 10	205	1880	120	6390	119	5933	50.6	41.7
Shark 11	209	1222	219	8320	218	5585	16.5	83.1
Shark 12	230	1413	146	4981	146	4659	29.3	49.7
Shark 13	231	1518	188	8292	188	6349	25.9	90.5
Shark 14	240	1473	150	5135	150	4085	14.8	74.2

SSSM switching state space model, *NZ EEZ* New Zealand Exclusive Economic Zone

the raw tracks, and occasionally interpolated across gaps during which no fixes were received (Fig. 2). Summed daily displacements between SSSM locations ranged from 1905 to 14,827 km (mean 7112 km) (Table 2). Daily displacements were often (43.4%) less than 20 km day^{-1}, with two-thirds (66.9%) being less than 40 km day^{-1}; however, there was a long tail of greater displacements, and the maximum recorded was 141 km day^{-1} (Fig. 3). Individual sharks typically showed the same broad range of displacements as seen in the aggregated data (Figure S4), although there was considerable variability among sharks. For example, Sharks 9 and 10 had median daily displacements (61.8 and 50.6 km day^{-1}, respectively) well above the overall median for all sharks (24.4 km day^{-1}). Sharks 9 and 10 spent their entire tracks in the open ocean with negligible Resident periods (Figure S3). Conversely, Shark 4 remained over the

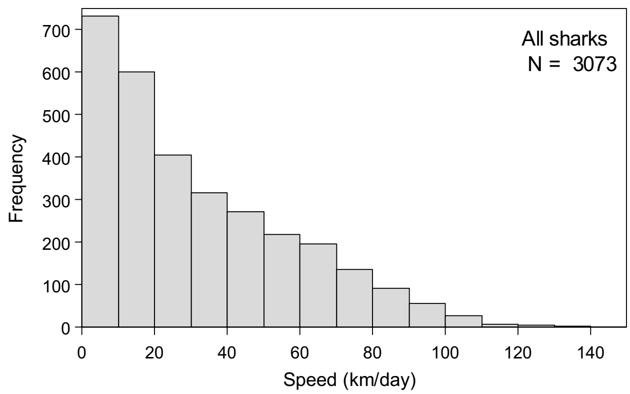

Fig. 3 Distribution of SSSM daily displacements for all 14 mako sharks

New Zealand continental shelf for its whole track, being the only shark not to move into oceanic waters; it had the lowest median displacement of 11.8 km day^{-1} (Figures S3, S4).

There was a weak tendency for sharks to be further north in autumn–spring than in summer (Fig. 4), but there was considerable variability and overlap among seasons. There was no clear distinction in seasonal behaviour between small and large sharks (Fig. 4).

The percentage of time spent by mako sharks in the New Zealand Exclusive Economic Zone (EEZ) (including the zone around the Kermadec Islands) ranged from 42% (for Shark 10) to 100% for Shark 4 (median 77%) (Table 2). Five of the 14 sharks spent more than 90% of their time in the

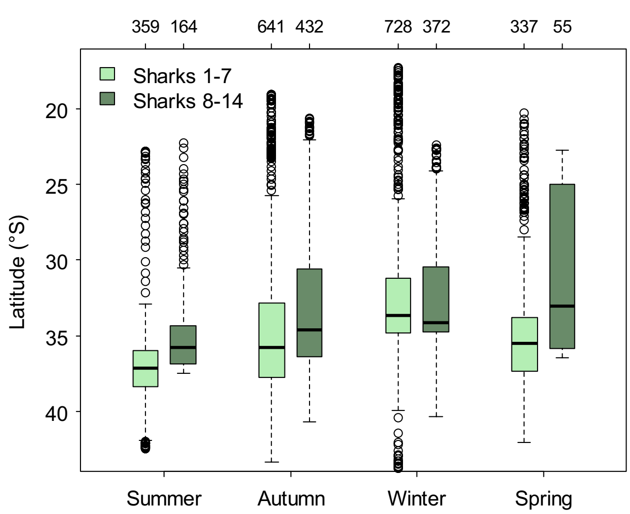

Fig. 4 Seasonal distribution of latitude for SSSM tracks for 14 mako sharks. Sharks 1–7 are small (153–187 cm TL) and sharks 8–14 are large (198–240 cm). The central black bar is the median, the box spans the first to third quartiles, and the whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. Circles represent outliers. Sample sizes (number of SSSM track locations) are given on the top axis

New Zealand EEZ. There was no significant correlation between the percentage of time spent in the EEZ and track duration ($r=0.39$, $p=0.17$; the two track segments for Shark 2 were combined for this test). When not within the New Zealand EEZ, sharks were often in the EEZs of the other island nations mentioned above (Figure S3).

Across all sharks, 47.3% of SSSM locations were classified as Resident, 35.4% as Travel; and 17.3% as Undefined. Resident behaviour was concentrated around the coast of New Zealand, while Travel behaviour was spread widely through the southwest Pacific as well as near the coast of New Zealand (Fig. 5). The 50% KUD for the Resident state was focused strongly around the northern half of North Island, New Zealand, and the 80% KUD mainly encompassed North Island and northern South Island (Fig. 6). The Travel state was more broadly distributed, with the 50% KUD forming a V-shape with arms extending north and northeast of New Zealand along the Norfolk Ridge and the Colville/Kermadec ridges (Fig. 6; see Fig. 1 for bathymetric features). The 80% Travel KUD was more diffuse and included a third indistinct arm extending northwest along the Lord Howe Rise.

There was a strong association between behavioural state and seabed depth. Resident behaviour occurred mainly in shallow shelf locations (median depth 105 m, inter-quartile range 72–316 m) whereas Travel behaviour occurred mainly over deep water (2239 m, 1259–3311 m) (Fig. 7, S5, S6). Undefined states were generally found at depths intermediate between Resident and Travel states.

Chlorophyll A values were lower at shark locations in the Travel state (medians 0.18 and 0.18 mg m^{-3} for small and large sharks, respectively) than in the Resident state

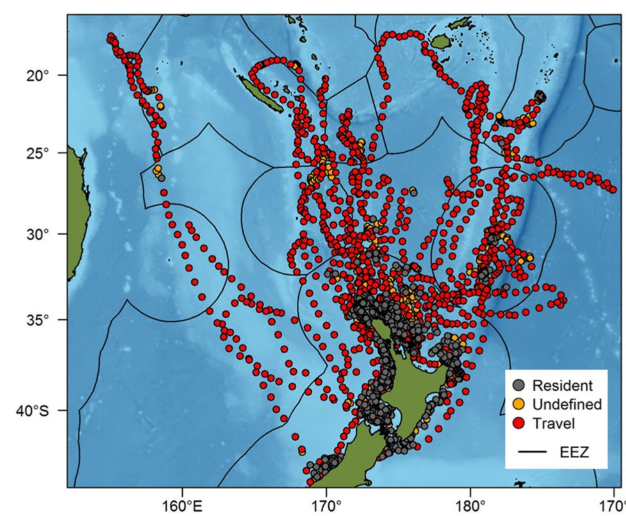

Fig. 5 Fitted switching state space model tracks for all 14 mako sharks. Some Travel locations near the New Zealand coast are obscured by Resident locations

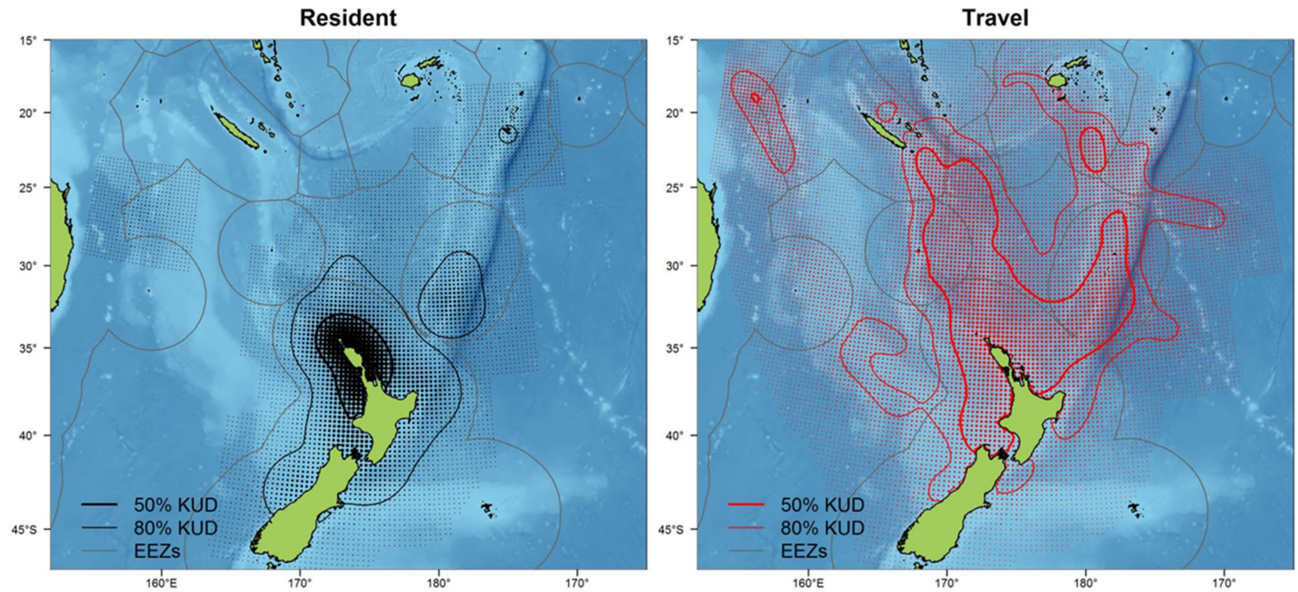

Fig. 6 Kernel utilisation distributions (KUD) for Resident (left) and Travel (right) behavioural states for 14 mako sharks

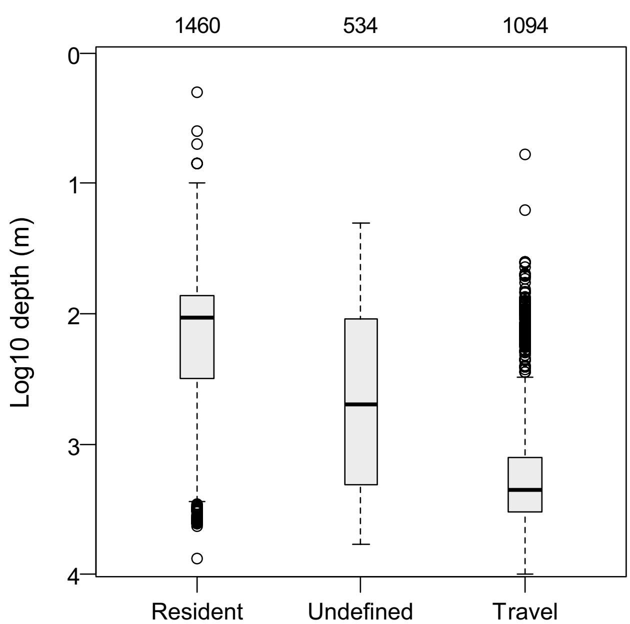

Fig. 7 Relationship between behavioural state and seabed depth at each SSSM track location for 14 mako sharks. For boxplot details, see Fig. 4 caption

(medians 0.31 and 0.41 mg m^{-3}, respectively), though variability was high (Fig. 8). SST tended to be higher for the Travel state than the Resident state (median SSTs 18.6 and 21.0 °C for Travel and 17.7 and 17.5 °C for Resident, respectively) and latitude was more northerly (median latitudes 32.6 and 30.4°S for Travel and 36.0 and 34.8°S for Resident, respectively), reflecting the fact that most Travel locations occurred in warmer waters to the north of New Zealand.

Depth and temperature

High-resolution depth and ambient temperature data were received (with gaps) from Sharks 9 and 10 (Fig. 9). The data covered only 1 month for Shark 9 but almost 4 months for Shark 10. Both sharks made frequent vertical movements between the surface and 300–400 m depth throughout their tracks. Shark 9 reached a maximum depth of 605 m and Shark 10 reached 515 m. However, both sharks spent most of their time (83.9% and 78.3% for Sharks 9 and 10, respectively) shallower than 100 m (Fig. 10). The amount of time spent deeper than 300 m was only 3.0% and 3.4% for the two sharks, respectively.

There were clear day/night differences in the depth distribution of both sharks. Both spent a high proportion of their time during the day in depths shallower than 25 m (Fig. 10, S7). At night, both sharks had a broader depth distribution between the surface and 100 m. However, the two sharks showed different night-time depth distributions: Shark 9 spent a high percentage of time at 25–75 m whereas Shark 10 preferred surface waters of 0–25 m. Nearly all deep diving (to depths greater than 150 m) occurred during the day (91.2% for Shark 9 and 92.5% for Shark 10).

Sharks 9 and 10 both experienced a wide range of ambient water temperatures (9.1–27.5 °C and 9.6–28.3 °C, respectively), although most of their time was spent at 14–27 °C (Figs. 9, 10). Temperatures below 17 °C occurred mainly during daytime deep dives. Both sharks were tagged

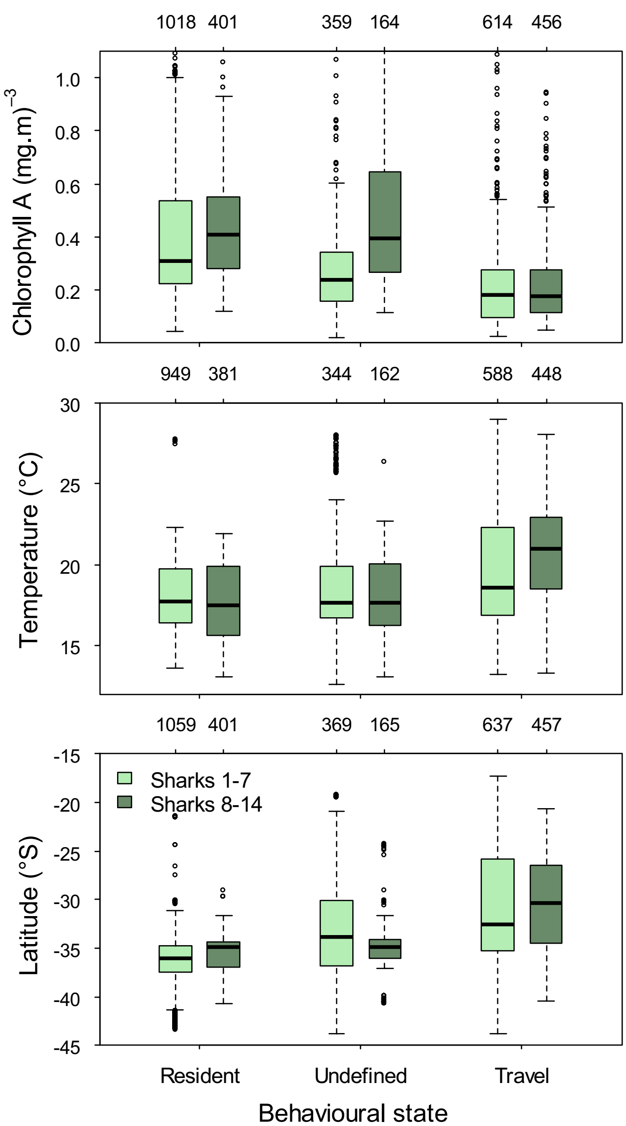

Fig. 8 Relationship between behavioural state and chlorophyll A, sea surface temperature, and latitude at each SSSM track location for 14 mako sharks. Sharks 1–7 are small (153–187 cm TL) and sharks 8–14 are large (198–240 cm). For boxplot details, see Fig. 4 caption

in temperate New Zealand during late summer (March) and swam soon afterwards to tropical southern Fiji (Figure S3); Shark 10 subsequently returned to New Zealand in early winter (June). Shark 10 thus experienced a large seasonal temperature range, and both sharks experienced large latitudinal and depth-related temperature ranges.

Direct comparison of temperature data among 10 sharks was achieved by aggregating the temperature data for Sharks 9 and 10 into 12-h time bins and the same 2° temperature bins used for eight other sharks whose SPOT tags were programmed to transmit temperature data (Figure S8). Most sharks had long periods during which a high percentage of their time was spent in relatively narrow temperature bands (one or two 2° bands; see dark blue cells in Figure S8). In contrast, Sharks 9 and 10 showed a greater spread of their time across multiple 2° bands, indicative of regular deep diving. This difference from the other eight sharks is probably explained by the fact that nearly the whole tracks of Sharks 9 and 10 were in oceanic rather than shelf waters, enabling them to make more vertical movements. Most of the other eight sharks also had short periods with wide temperature ranges, suggesting they too were diving deep while in oceanic waters. All sharks showed clear temporal changes in temperature patterns (Figure S8), reflecting a complex pattern of interacting seasonal and latitudinal variation.

Discussion

Data representativeness

Capture and tagging of sharks can affect their subsequent behaviour and survival, but limited data indicate that mako sharks are relatively hardy. Sharks caught and tagged by recreational anglers have shown low (0–10%) mortality rates (Hoolihan et al. 2011; French et al. 2015), whereas sharks caught on tuna longlines exhibit low-to-moderate mortality rates (3–31%) (Campana et al. 2016; WCPFC unpubl data). Most mortality of pelagic sharks (including mako sharks) released from tuna longlines occurs within 2 days of release (Campana et al. 2016). Short-term (2–5 days post-release) non-lethal effects have also been observed in tagged makos (Hoolihan et al. 2011). In the present study, all sharks appear to have survived the capture and fitting of tags on their dorsal fins, although we cannot rule out the possibility that Shark 9 died from delayed tagging effects after 34 days. The remaining 13 sharks survived for at least 120 days. These results suggest that tagging had a negligible effect on shark behaviour beyond the first few days of the tracks.

We tagged juvenile makos of both sexes, and mature males. No mature females were tagged. Although our results do not cover all demographic classes of mako sharks, they do represent the composition of mako sharks in New Zealand waters. Observer data show that the New Zealand tuna longline fishery, which operates mainly in oceanic waters beyond the shelf edge, catches mainly juveniles: most mako sharks are shorter than 220 cm TL (200 cm FL), and an estimated 89% of males and 99.5% of females are immature (Francis 2016). The habitat and behaviour of mature females are virtually unknown in the region, with only one pregnant female being reported from New Zealand waters (Duffy and Francis 2001). Juvenile makos dominate mako shark catches in temperate waters throughout the world (Stevens 1992; Maia et al. 2007; Bustamante and Bennett 2013; Doherty et al. 2014; Groeneveld et al. 2014; Rogers et al. 2015b; Ohshimo et al. 2016; Runcie et al. 2016). Few areas have

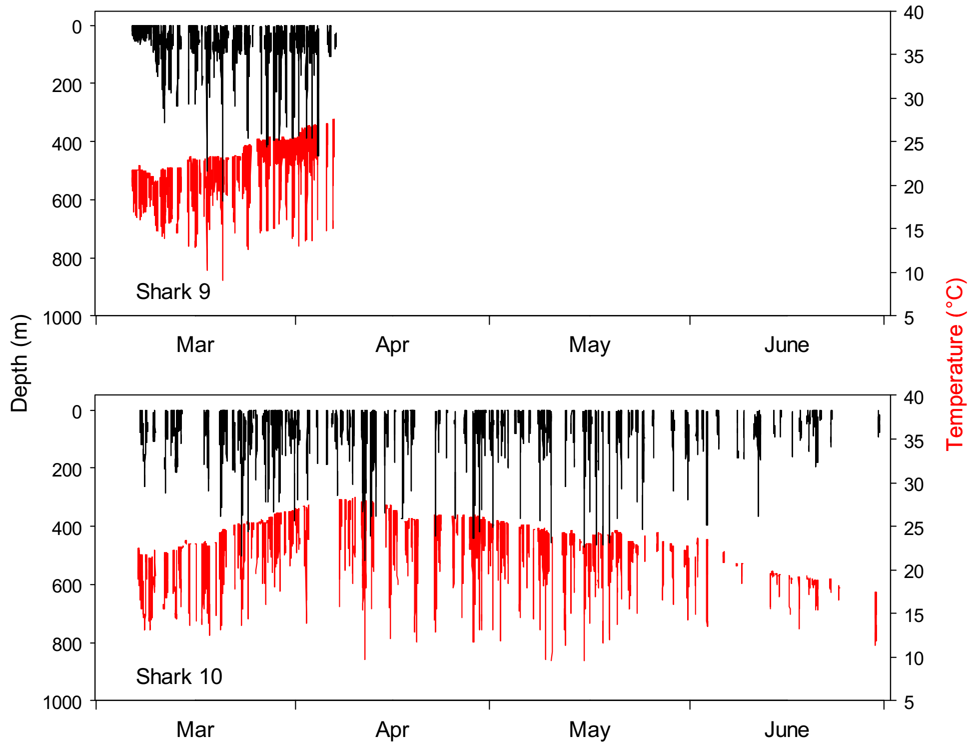

Fig. 9 Depth and temperature profiles for two Splash-tagged sharks from which high-resolution time series of data were transmitted. Gaps in the time series indicate missing data

significant proportions of adult mako sharks, but subtropical, coastal waters of eastern South Africa (centred on 30°S), and the subtropical and tropical central North Pacific (south of 30°N) are exceptions (Groeneveld et al. 2014; Sippel et al. 2015), pointing to a greater abundance of adults in warmer waters.

Stock distribution

Genetic studies indicate there are at least three genetic stocks of mako sharks in the Pacific Ocean, with significant differences between the North and South Pacific, as well as between the southwest and southeast Pacific (Michaud et al. 2011; Taguchi et al. 2015; Corrigan et al. 2018). Tagging data support the existence of a southwest Pacific stock, with few tagged animals leaving this region, and only one known to have crossed the Equator into the North Pacific (Sippel et al. 2011; Rogers et al. 2015a; Holdsworth and Saul 2017). Although mako sharks range into tropical waters, they are most abundant in subtropical and temperate waters of 20–45°S (Clarke et al. 2011; Campbell 2014; Rice et al. 2015). Mako sharks tagged in the present study remained within the southwest Pacific, consistent with the genetic stock hypothesis.

Tagging movements

Our study found a mixture of short- and long-distance movements, and recaptures at, or returns to near, the tagging locations after many months or years, consistent with the results of other studies that used both conventional and electronic tags (Rogers et al. 2015a; Queiroz et al. 2016). Conventional tagging of New Zealand mako sharks found that many recaptures were within 100 km of the tagging site more than 2 years after tagging, whereas others were 800–1300 km away after the same period (Holdsworth and Saul 2014). Our tagged sharks did not travel as far (maximum distance from release location 2900 km) as the greatest movements obtained from conventional tagging, which included movements to eastern Australia, Solomon Islands and Marquesas Islands, the last producing a displacement of 5489 km (J. Holdsworth, Blue Water Marine Research, pers comm). Most mako sharks tagged with conventional tags in south-eastern Australia were recaptured in eastern Australia, but one travelled to New Zealand, and others to Western Australia, Solomon Islands, Papua New Guinea and Philippines (the last travelling 5940 km and crossing the Equator) (Rogers et al. 2015a). A long-distance movement of 4541 km was reported in the North Atlantic (Casey and Kohler 1992).

The maximum trip distances observed in this study (19,000–20,000 km) underestimate the true distances travelled because they assume straight-line movements between fixes. Nevertheless, they are comparable with distances travelled by mako sharks tagged electronically in Australia, where three sharks travelled more than 20,000 km with a maximum of 25,550 km (Rogers et al. 2015b).

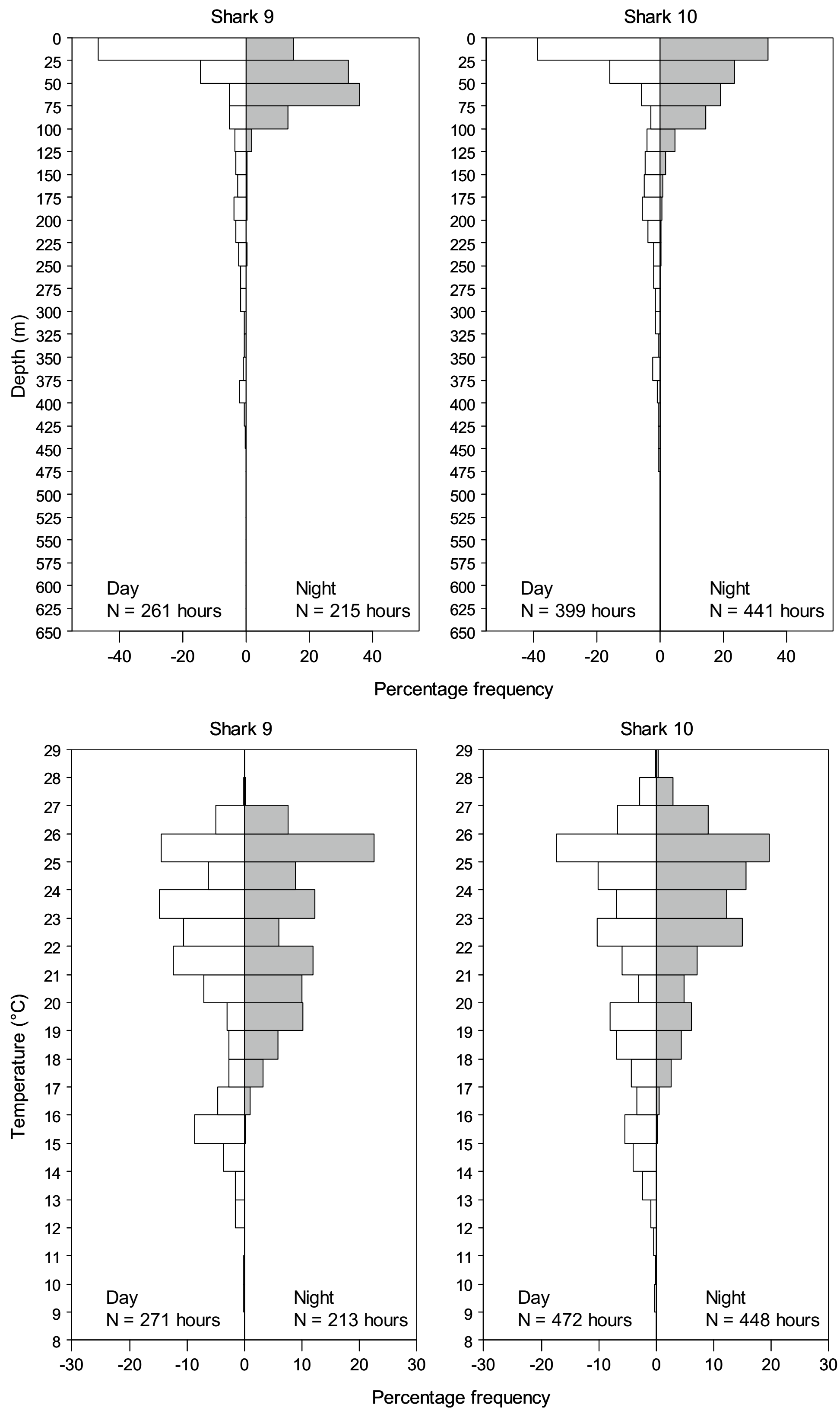

Fig. 10 Depth (top) and temperature (bottom) distributions by day (white) and night (grey) for Splash-tagged Sharks 9 and 10

Modelled tracks

Model-estimated daily displacements underestimate the swimming speed of a shark because of the smoothing involved. However, our displacement estimates (median 24.4 km day^{-1}, maximum 141 km day^{-1}) are similar to those found for juvenile mako sharks tagged with popup archival tags off Chile, which averaged 27 km day^{-1} (Abascal et al. 2011). Higher speeds were recorded for SSSM tracks of 10 juvenile mako sharks tagged off southern Australia, which had mean displacements of 25–48 km day^{-1} and a maximum of 197 km day^{-1} (Rogers et al. 2015b).

Mako sharks tended to move north in autumn–spring and south in summer but there was a lot of variability, and sharks could be found anywhere between 20°S and 40°S in any season. Similar, usually weak, seasonal movement patterns have been reported elsewhere. Drift net fisheries in the South Pacific found mako sharks to be most abundant at 25–45°S, with abundance at the southern end of that range being greater in summer–autumn than in spring (Yatsu 1995). Stevens (1984) reported mako sharks to be most abundant off Sydney, Australia (33–34°S) in winter–spring. Similarly, some sharks tagged in southern Australia migrated north in winter–spring, but others remained in temperate, southern, continental shelf and slope waters throughout the year (Rogers et al. 2015b). A large sample of mako sharks tagged in the northeast Pacific showed a clear seasonal cycle with locations averaging about 35°N in summer and 15–25°N in winter (Block et al. 2011), and the same north–south seasonal movements have been reported for mako sharks in the North Atlantic (Queiroz et al. 2016; Vaudo et al. 2017). However, no seasonality was observed in the Gulf of Mexico or off Chile (Abascal et al. 2011; Vaudo et al. 2017). In combination, these results indicate that mako sharks generally move towards lower (warmer) latitudes in winter, and higher (cooler) latitudes in summer, but that there is considerable local and individual variation that may reflect the spatial availability of food resources.

Behavioural states

Oceanic species, including mako sharks, are generally regarded as highly migratory, yet many of them show extended resident behaviour (Block et al. 2011; Rogers et al. 2015b). Rogers et al. (2015b) reported that 'fidelity' and 'transit' states comprised 44% and 42%, respectively, of the tracks of makos tagged in south-eastern Australia, which agree well with our results of 47% and 35% for Resident and Travel states, respectively.

The Resident state of mako sharks was focused on shallow, coastal regions of New Zealand, while the Travel state occurred mainly in oceanic water throughout the southwest Pacific as well as near the New Zealand coast. Median chlorophyll A values were higher at locations where sharks were classified as Resident than where they were in the Travel state, although variability was high. We have no independent information on what the sharks are doing during these behavioural states, but the Resident and Travel states each lasted for up to several months, so the sharks are undoubtedly feeding during both. Since all the females and most of the males tagged were immature, the behavioural patterns we observed do not reflect reproductive activity.

The spatial distribution of mako shark behavioural states may be biased by the fact that all tagging occurred near the New Zealand coast (the SSSM track of one shark tagged in Australia began in New Zealand to simulate a shark that was tagged there). It is therefore inevitable that the initial distributions of sharks would be focused on the New Zealand coast, and this could lead to bias in the estimation of Resident KUDs (Queiroz et al. 2016). However, such bias is mitigated by the long track durations (4 months or longer for 13 out of 14 sharks), and the fact that several sharks entered a Travel state and moved offshore soon after tagging (i.e. a coastal Resident state post-tagging was 'optional'). Nevertheless, it would be worthwhile tagging mako sharks in tropical waters north of New Zealand (e.g. in Fiji) to determine whether they move towards New Zealand, or have distributions that are focused in tropical regions. Catch rates of mako sharks on tuna longlines near Fiji and New Caledonia peak in the third quarter of the year (i.e. winter) (T. Peatman, Pacific Community, pers comm), which is consistent with our observation of a northward movement from New Zealand in autumn–spring. This supports the hypothesis that a single population moves seasonally between New Zealand and tropical regions.

The relationship between New Zealand and Australian mako sharks also warrants further investigation. Some of the sharks that were tagged in New Zealand may have arrived there from Australia (as did Shark 6), and conventional tagging shows there is a two-way movement between the two countries. The magnitude of the connectivity across the Tasman Sea could be assessed by integrating the results from this study with those from Australian tagging studies (Rogers et al. 2015b; Corrigan et al. 2018).

SST tended to be higher and latitude was more northerly for the Travel state than for the Resident state, reflecting the fact that most Travel locations occurred in warmer waters to the north of New Zealand. Movement of mako sharks from New Zealand to the tropical islands does not appear to be to exploit concentrated food resources. There were few Resident locations in tropical areas, and sharks often made abrupt U-turns of around 180 degrees to retrace their tracks and return to cooler waters (Figure S3). The same behaviour was reported by Vaudo et al. (2017) for juvenile makos travelling southwards towards the Equator in the North Atlantic. Nevertheless, mako sharks probably do feed during such excursions even if they do not stop in one area to do so (discussed further below).

Other studies of mako shark movements have also found that resident states tend to be concentrated on or near continental shelves and areas of high productivity, with little resident behaviour observed in the open ocean (Block et al. 2011; Kai et al. 2015; Rogers et al. 2015b; Adams et al. 2016; Vaudo et al. 2017). In southern Australia, juvenile shortfin makos mostly exhibited resident behaviour in the mid–outer shelf, the shelf edge and slope habitats with high bathymetric relief and oceanographic frontal gradients (Rogers et al. 2015b).

Optimal search theory predicts that, in regions of sparse and unpredictable prey, predators will adopt a Lévy flight strategy, in which many, small movements are interspersed with longer relocations, whereas in areas of higher prey density, predators will show more random (Brownian) motion (Humphries et al. 2010). Using tracking data for 14 oceanic predators, Humphries et al. (2010) found that Lévy flight behaviour was associated with less productive waters and Brownian movements were associated with productive shelf or convergence-front habitats. Their dataset included only one mako shark, but the observations for the other species are consistent with the spatial delineation of Resident and Travel behavioural states in our study. To optimise their foraging success, predators have to trade off time spent searching within prey patches against time spent moving to locate new prey patches (Reynolds 2012); such decisions would drive the transitioning between Resident and Travel states. The prevalence of Resident behaviour around the New Zealand coast is probably indicative of high resource availability there relative to oceanic regions.

The spatial distribution of the Travel state suggests that mako sharks move along the submarine ridges that run northwards from New Zealand. This raises the possibility that they use seabed topography as a navigational clue, as has been suggested previously for white sharks (*Carcharodon carcharias*) and mako sharks in the south-western Pacific (Francis et al. 2012; Rogers et al. 2015b). However, alternative explanations exist, including that mako sharks are attracted to ridges by the distribution of their prey.

Depth, temperature and food

Two sharks that provided depth data made frequent vertical movements between the surface and 300–400 m depth throughout their tracks, and reached maximum depths of 515–605 m. Temperature ranges for most of the other eight sharks that provided temperature data suggested that they too were diving deep while in oceanic waters. Deep diving has often been reported for mako sharks elsewhere, with most of it occurring during daylight hours (Stevens et al. 2010; Abascal et al. 2011; Musyl et al. 2011; Vaudo et al. 2016). Mako sharks frequently dive beyond 500 m (Loefer et al. 2005; Stevens et al. 2010; Abascal et al. 2011; Vaudo et al. 2016), with 888 m apparently being the greatest recorded depth (Abascal et al. 2011). However, recent tagging of southwest Pacific Ocean mako sharks with ‘survival’ popup tags has produced a maximum depth of 1400 m (and an ambient temperature of 3.4 °C) (WCPFC, unpubl data).

Many studies report a SST preference for mako sharks of about 17–22 °C (Casey and Kohler 1992; Stevens et al. 2010; Runcie et al. 2016). In this study, accurately recorded ambient temperatures for two sharks covered a wide range of about 9–28 °C, with most of their time being spent at 14–27 °C. Sharks with tags that recorded temperatures in two-degree bins showed similar but highly variable patterns. Medium- and long-term cyclical patterns of experienced temperatures indicate the presence of both seasonal and latitudinal driven variation, while short-term temperature extremes show depth-related variation. Use of electronic tags has revealed that mako sharks frequently inhabit waters down to 10 °C and up to 28 °C, with extreme temperatures as low as 3–5 °C when diving and greater than 30 °C when in tropical waters (Abascal et al. 2011; Musyl et al. 2011; Rogers 2011; Kai et al. 2015; Vaudo et al. 2016). Mako sharks are endothermic and can maintain their core body temperatures 6–8 °C above ambient temperature (Carey et al. 1981), a characteristic that enables them to penetrate deep, cold, oceanic water.

Mako sharks eat a wide variety of prey including fish, sharks, squid and marine mammals (Stevens 1984; Preti et al. 2012; Groeneveld et al. 2014; Porsmoguer et al. 2015). In the southwest Pacific they mainly eat fish, particularly pelagic and mesopelagic fishes (such as carangids, bramids, berycids, scombrids and gempylids) and squid (Stevens 1984; Griggs et al. 2007; Rogers et al. 2012; Horn et al. 2013). Recent acoustic research has revealed that there is a much greater biomass of mesopelagic organisms in the deep sea than previously thought, with densities up to 7 animals m^{-3}, orders of magnitude higher than estimated from trawls (Sutton 2013; Giorli et al. 2018). Many large oceanic species, including tunas, swordfish and pilot whales, exploit this biomass (Josse et al. 1998; Howey et al. 2016). In the south-western Pacific, porbeagle sharks (*Lamna nasus*) spend most daylight hours at depths of 200–600 m and migrating white sharks frequently (but irregularly) dive to 200–800 m (Francis et al. 2012; 2015). Analyses of oceanic whitetip shark (*Carcharhinus longimanus*) dive profiles suggest that they actively forage in mesopelagic environments while optimising energy use (Howey et al. 2016; Papastamatiou et al. 2018). The deep dives made by mako sharks in the southwestern Pacific probably enable them to feed on mesopelagic fishes and squid, but they may also have other functions such as navigation.

Management implications

The sharks tagged in the present study spent most of their time in the New Zealand EEZ (median 77%, five sharks > 90%), which challenges the conventional view of mako sharks being oceanic nomads. However, large adult males and adult females may be more mobile than the mainly juvenile sharks we tagged, and further research on them is required. The propensity for small-to-medium mako sharks to remain within a restricted coastal area for several months, and to travel beyond the 200-mile EEZ limit only occasionally, indicates a relatively high degree of residency that must be considered when managing fishery removals. The current status of the south-western Pacific mako shark stock is uncertain, with conflicting trends found in different regions. In New Zealand, mako shark abundance may have declined during the late 1990s and early 2000s, but since then it has steadily increased (Francis et al. 2014; Francis and Large 2017). Clarke et al. (2012) found no significant trend in the abundance of mako sharks in the South Pacific (with most data coming from the south-western Pacific), although they noted that the performance of the standardisation model was poor, and the estimated trends were potentially unreliable. In an updated study from the same region, Rice et al. (2015) reported that some abundance indicators (distribution of high catch per unit effort (CPUE), percentage of positive sets) were declining, but that standardised CPUE was stable (excluding 2014, the last year in the time series, because of incomplete data). These differing results may indicate that mixing among the different parts of the stock is not homogeneous, and/or that data quality issues may be confounding the interpretation of trends. A formal stock assessment of the entire south-western Pacific mako shark stock is required to elucidate its current status. Nevertheless, our tagging results and the heterogeneity of reported abundance trends suggest that mako shark fishing mortality needs to be managed at a local as well as a regional scale.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards and fish tagging protocols of the New Zealand National Institute of Water and Atmospheric Research.

Data availability The datasets produced by this study are not publicly available because of multiple ownership, but may be requested from the senior author.

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