



Satellite tags describe movement and diving behaviour of blue sharks *Prionace glauca* in the southwest Pacific

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ABSTRACT: The blue shark *Prionace glauca* is the most abundant, widely distributed and exploited pelagic shark species. Its population is declining in almost all major oceanic basins. Population management and conservation efforts have traditionally depended on fishery bycatch and observer data. Recent studies correlating animal distribution derived from satellite tags, with commercial fishery impacts, across multi-jurisdictional regions, have provided an improved data platform for population management. Here we present the first fishery-independent data of blue shark distribution in the southwest Pacific Ocean. Fifteen blue sharks were satellite tagged, adding to the global dataset of approximately 179 individuals successfully tracked using bolt-on satellite tags. Smart Position and Temperature (SPOT) tags transmitted between 66 and 505 d, and SPLASH tags between 200 and 343 d. Individual track lengths ranged from 3000 to 14 559 km, spanning 10 exclusive economic zones, from latitudes 0.1° to 43.1° S, and longitudes 160.1° E to 150.8° W. Horizontal movements revealed age/sex segregation and large-scale horizontal migration patterns. Dive data collected with SPLASH tags showed fine-scale vertical habitat use at depths between 0 and 1364 m and temperatures of 5 to >30°C. Behavioural events, such as foraging, searching and travelling, were inferred from commonly repeated patterns in the retrieved dive profiles. This study provides a characterisation of critical habitat use in a region never before sampled, adding to the global understanding of blue sharks, and the fishery-independent database necessary to inform blue shark population management.

KEY WORDS: Habitat use · Sex segregation · Diving · Satellite · Tag · Migration

1. INTRODUCTION

Recent publications have highlighted how studies of animal distribution based on animal tracking are enabling a step change in the management of highly migratory marine species (Harcourt et al. 2019, Hays et al. 2019, Queiroz et al. 2019, Sequeira et al. 2019). Satellite tagging has enabled the tracking of individuals through the complex, 3-dimensional oceanic environment (Andrzejczek et al. 2019, Queiroz et al. 2019). This allows inference of potential drivers for movement, but also specific behaviours, related to op-

timal foraging theory, predator avoidance, energy efficiency, reproduction and physiological constraints imposed by the environment. Ultimately, if this information is gathered throughout the home range of a species, it can provide insights on how its distribution and behaviour may expose populations to interactions with commercial industries or environmental change.

The blue shark *Prionace glauca* is the most abundant and widely distributed pelagic shark species (Nakano & Stevens 2008). It is also the most exploited in tuna longline fisheries, with increasing catch rates (Campana et al. 2006, Dulvy et al. 2014) related to

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high prevalence in the fin trade (Clarke et al. 2006a,b) resulting in observed population declines (Simpfendorfer et al. 2002, Baum et al. 2003, Ward & Myers 2005, Kleiber et al. 2009, Baum & Blanchard 2010, Pacoureau et al. 2021). Effective management of blue sharks requires a global approach (Aires-da-Silva et al. 2009), identifying stocks and defining spatio-temporal patterns in habitat use and behaviour for demographics of each population.

Studies on blue shark distribution outnumber those on many other large pelagic shark species. The consensus is that each major oceanic basin contains a single stock (Kohler & Turner 2008, da Silva et al. 2010) and within each stock, blue sharks segregate and aggregate spatio-temporally, by age and sex (Mejuto & García-Cortés 2005, Nakano & Stevens 2008, Coelho et al. 2018, Boldrocchi & Storai 2021, Fujinami et al. 2021). Important habitats, such as nursery and breeding grounds, have been correlated with subtropical convergence zones (STCZs: between 35° and 45° N or °S), coastal zones of upwelling and temperate waters with seasonally changing currents that control prey availability or act as migration stimuli (da Silva et al. 2010, Queiroz et al. 2010, 2012, 2017, Stevens et al. 2010, Campana et al. 2011, Van-

deperre et al. 2014, Coelho et al. 2018, Fujinami et al. 2021). Biological trade-offs, including the necessity of mating balanced against energy expenditure involved with copulation, as well as foraging competition or predation, also influence distribution. Collectively, these variables are suggested to cause adult males to utilise off-shelf, pelagic habitat, while adult females reside in nearshore waters until parturition and copulation near STCZs. In contrast, juveniles seemingly remain inshore, or in shallower waters, where coastal upwelling enables high juvenile density away from larger predators (Nakano 1994, Fujinami et al. 2021) (Fig. 1).

A large proportion of blue shark studies have used fisheries bycatch data, resulting in sample sizes 6 to 7 orders of magnitude larger than those from rarer, satellite tag studies, but which are recognised as biased due to misreporting, low observer coverage and spatio-temporal biases (Campana et al. 2006). Because satellite tags independently track individual animals, avoiding these data restrictions, satellite tagging data are beneficial for understanding the distribution and behaviour of such species (Block et al. 2011, Queiroz et al. 2019). However, the expense of satellite tags and implementation within a commercial

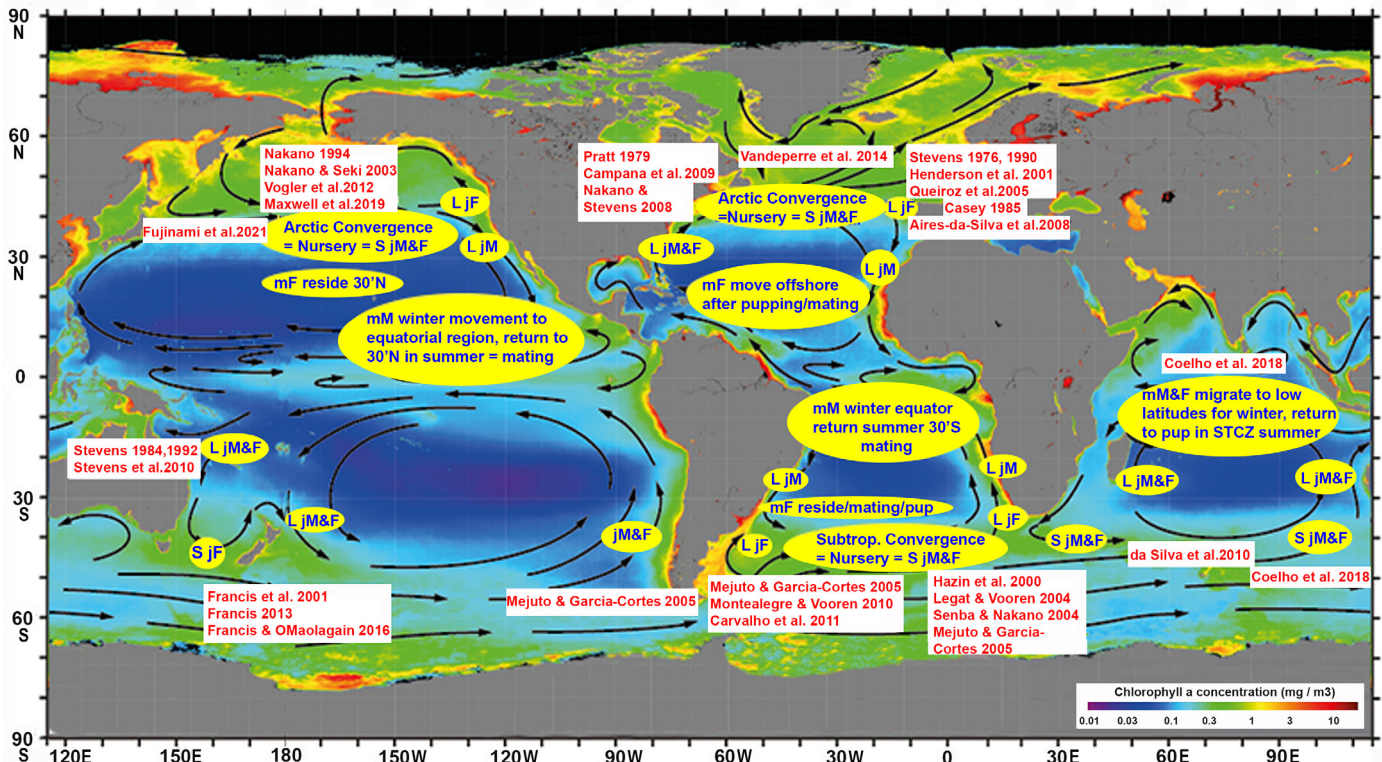


Fig. 1. Summary of literature revealing common patterns of blue shark age/sex segregation within each major oceanic basin, mapped over mean annual surface chlorophyll a levels as an indicator of primary production and potential prey distribution derived from NASA MODIS (https://modis.gsfc.nasa.gov/data/dataproduct/chlor_a.php). STCZ: subtropical convergence zone; S: small; L: large; J: juvenile; m: mature; F: female; M: male

industry have restricted the number of studies and/or tags deployed on blue sharks (approximately 19 studies globally; Table 1). Most of these studies have used pop-up satellite archival tags (PSATs) (Wildlife Computers; www.wildlifecomputers.com) (17/19, either entirely or in combination with other tag types), often providing short-term monitoring due to dart and tether fixing, aimed most often at addressing bycatch mortality rates, but also vertical movement and behaviour. Nine studies have deployed dorsal fin-mounted Smart Position Only and Temperature (SPOT) tags (Wildlife Computers), comprising approximately 179 individual blue sharks (Table 1), which provided long-term, fine-scale monitoring of movement, with 2-dimensional surface location data.

There remains a need for long-term, large-scale, detailed behaviour studies to assist stock assessments, catch modelling and population management (Howey et al. 2017). This need is most apparent in the southwest Pacific region, where no stock assessments have been possible (Fisheries New Zealand 2018) and no satellite tagging has occurred, yet influential oceanic features associated with nursery and breeding grounds exist, and where historic blue shark mortality in New Zealand waters was 525–1415 t yr⁻¹ prior to a 2014 shark fin ban (Ministry for Primary Industries 2015). Therefore, the objective of this study was to provide, for the first time, fishery-independent satellite tagging data of blue sharks in

the southwest Pacific, to define spatio-temporal patterns in movement and behaviour. These data provide novel insight for the southwest Pacific region, but also add to the global understanding of blue shark movement necessary for population management.

2. MATERIALS AND METHODS

2.1. Shark capture and handling

Between December and April 2012/13, 2013/14, 2014/15 and on 26 June 2015, tagging trips took place in northeastern waters of New Zealand (3–25 nautical miles from shore, between 36° 50' and 37° S) under University of Auckland Animal Ethics Committee application 001075. Based on New Zealand blue shark maturity defined by Francis & Duffy (2005), immature (juvenile) blue shark males were <190 cm in fork length, immature (juvenile) females were <180 cm in fork length, and mature sharks were greater than these measurements. Because blue sharks have a relatively small dorsal fin, only sharks >150 cm fork length were tagged, as smaller individuals were deemed too risky for carrying a tag, due to unlikely signal transmission from a tag being low in the water and greater potential of hindering natural behaviour or affecting health. Sharks were attracted to the research vessel using tuna offcuts that were minced in a bucket and were either circle hooked or lured with bait into a stretcher or onto a duckboard, both of which were submerged to maintain ventilation yet allowing physical restraint by researchers.

Table 1. Summary of blue shark satellite tagging studies to date by region (based on first deployment of tags, not repeat use of these data in later publications). SPOT: Smart Position and Temperature; PSAT: pop-up satellite archival tag

Ocean region	Study	Tag(s) used (n)	
		SPOT	PSAT
North Atlantic	Teo et al. (2004)	4	4
	Campana et al. (2009, 2011, 2015)	–	40
	Queiroz et al. (2010, 2016)	11	43
	Vandeperre et al. (2014)	22	15
	Doyle et al. (2015)	3	2
	Howey et al. (2017)	–	10
	Braun et al. (2019)	15	15
South Atlantic	Carvalho et al. (2015)	–	16
Tasman/Indian	Rogers et al. (2009)	1	–
	Stevens et al. (2010)	10	5
North Pacific	Musyl et al. (2011)	–	32
	Moyes et al. (2006)	–	11
	Block et al. (2011)	59	–
	Musyl & Gilman (2018)	–	48
	Maxwell et al. (2019)	54	–
	Fujinami et al. (2021)	–	21
South Pacific	–	–	–

2.2. Tags, settings and data treatment

SPOT tags (model 196) and SPLASH tags (models 289 and 316) (Wildlife Computers) were attached to blue sharks using a neoprene-lined, 1 mm thick Perspex base plate with stainless-steel bolts (20 mm × 5 mm), nylock nuts and washers. Tags were anti-fouled using non-toxic, silicone based Prop-speed (www.propspeed.com) and set with an 'on/off cycle' every second day after 6 mo, and a 250 transmission d⁻¹ limit.

When a dorsal fin (and thus the tag) broke the surface of the water, tags relayed time-stamped locations and associated accuracy measures to Argos satellites that were over the study site, and thus capable of receiving

tag transmissions, between 03:00 and 12:00 h and between 15:00 and 00:00 h, i.e. 75 % of the time. The surface location data were downloaded as CSV files using STAT (www.seaturtle.org). Locations were filtered, removing illogical outliers of invalid (Z) locations, identical locations, locations closer than 20 min apart and location bouts with swim speeds over 10 m s^{-1} (derived from the combination of maximum underwater swim speed recorded for a blue shark, 2.95 m s^{-1} [Fontes et al. 2018], maximum ocean current of 3 m s^{-1} and additional allowance for Argos location error). It was deemed that retaining some locations with inaccuracy was more valuable for this long-term study, as 'good' positions (location classes 3, 2, 1) are 68th percentile accurate to <1.5 km, while O positions are <5 km, and A and B are <10 km (Hazel 2009, Costa et al. 2010, Boyd & Brightsmith 2013).

While providing surface location data of sharks, SPLASH tags also archived depth and temperature data internally at 10 s intervals. SPLASH tags are non-retrievable (unless the tagged shark is captured and the tag returned). The tags transmitted dive data, as opportunistic segments of depth and/or temperature data recorded, at 10 min resolution, with the amount of dive data received determined by the exposure time of tags at the ocean surface (www.argos-system.org). These data were stored and downloaded as DS files from STAT, processed via DAP and viewed in IGOR pro (www.wildlifecomputers.com).

2.3. Dive profile analysis

Dive data were split into day and night observations, based on local sunrise and sunset. Dive profiles were viewed manually by 1 person in IGOR pro at a consistent screen resolution/zoom. Manual classification was used in preference to computer analysis (Schreer & Testa 1996, Hochscheid et al. 1999, Hassrick et al. 2007, Schaefer et al. 2007, Wilson & Block 2009). To ensure objectivity, the person processing did not view dive profiles in conjunction with satellite tracks, any information of the environment or common dive patterns identified in the literature. Put simply, specific shapes in dive profiles consistently performed throughout the data set were identified and grouped. These were then compared with the literature on dive profile analysis specific to blue sharks (Sciarrotta & Nelson 1977, Carey & Scharold 1990, Stevens et al. 2010, Campana et al. 2011, Queiroz et al. 2017), but also other species (Hochscheid et al. 1999, Tremblay & Cherel 2000, Seminoff et al. 2006, Halsey et al. 2007, Horodysky et al. 2007,

Houghton et al. 2009, Braun et al. 2022) in order to justify inference of blue shark behaviour using the shapes and parameters of individual dives as indicators of behavioural state.

Dive data from SPLASH tags are time-stamped, indicating the actual occurrence time of a dive shape and thus the inferred behavioural event, even though such data are transmitted at a later surface time and location. To identify approximate locations of dive events, time of occurrence was tracked back along the surface location track (straight-line distance), based on average swim speed of that shark and available locations of the same or similar time, thus interpolating the location of inferred dive events as best possible. No behavioural/dive event greater than 24 h from a surface location was retained in this interpolation process.

2.4. Sea surface temperature data

Satellite maps of sea surface temperature (SST) were compiled into seasonal climatologies to provide context for the animal tracking data. Daily satellite images corresponding to the years of tracking data (2013–2016) were sourced from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor located on the 'Aqua' satellite as part of NASA's Earth Observing System (NASA 2014). Maps were then separated into austral summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November) and averaged.

3. RESULTS

3.1. Tagged shark demographics and performance

Fifteen blue sharks were tagged, 9 with SPOT tags and 6 with SPLASH tags (Table 2). The size and sex of sharks tagged were skewed towards mature males, with only 4 females tagged, and tagging was biased towards the summer months.

SPOT tags transmitted data for periods between 66 and 505 d (mean \pm SD = 250 ± 144 d) and SPLASH tags between 200 and 343 d (255 ± 63 d), with a cumulative transmission for all tags of 3785 d. Most tracks were comprised of continuous transmission, although some of the longest had considerable time gaps between location data. We recorded 6867 filtered location points through satellite transmission, between latitudes of 0.1° and 43.1° S and between longitudes

Table 2. Summary data for 15 satellite tagged blue sharks within the southwest Pacific Ocean. Maximum distance is measured from the tagging site, total distance is the length of the entire track. FL: fork length; m: mature; j: juvenile; M: male; F: female; EEZ: exclusive economic zone; PA: All Pacific Islands; IN: International; NZ: New Zealand; AU: Australia; Ne: neritic (≤ 200 m); Sh: shelf (201–999 m); Oc: oceanic (≥ 1000 m)

Shark ID	Tag model	FL (cm)	Maturity/sex	Date tagged (dd/mm/yy)	Days at liberty	Distance (km)		Time in EEZ (%)				SST range (°C)	Time in zone (%)		
						Max.	Total	NZ	PA	IN	AU		Ne	Sh	Oc
16	SPLASH 289	229	mM	27/03/13	267	3000	11110	37	53	10	–	16–28	4	16	80
17	SPLASH 289	208	mF	05/03/13	206	830	5658	100	–	–	–	14–22	22	38	40
68	SPLASH 316	160	jF	09/01/14	200	200	3291	100	–	–	–	15–21	34	68	4
69	SPLASH 316	150	jM	16/12/13	200	630	5616	100	–	–	–	16–21	38	41	21
70	SPLASH 289	215	mF	15/12/13	315	830	11259	82	–	18	–	15–24	2	15	83
71	SPLASH 289	220	mM	15/12/13	343	2900	14559	45	19	36	–	14–29	0	8	92
18	SPOT 196	197	mM	09/02/13	66	1200	3573	11	14	75	–	20–25	–	2	98
19	SPOT 196	205	mM	11/02/13	256	1450	7625	72	12	–	16	15–21	14	38	48
20	SPOT 196	215	mM	13/02/13	181	1250	4826	47	–	50	3	15–21	23	56	21
21	SPOT 196	203	mM	04/03/13	505	2000	8808	8	73	9	–	16–27	4	23	73
23	SPOT 196	193	mM	23/03/13	444	1500	13342	48	–	52	–	14–23	14	10	76
72	SPOT 196	195	mM	23/11/14	218	5200	11740	12	48	40	–	17–30	1	1	98
75	SPOT 196	160	jM	07/01/14	102	600	3000	100	–	–	–	18–23	19	43	38
76	SPOT 196	192	mM	25/11/14	216	3800	7856	29	51	20	–	16–29	26	27	47
77	SPOT 196	183	mF	26/06/15	266	410	7689	89	–	11	–	6–18	44	12	44

of 160.1° E and 150.8° W, spanning 10 exclusive economic zones (EEZs), the high seas and individual track lengths of up to 14 559 km (7996 ± 3729 km) (Table 2, Fig. 2; see also Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m689p077_supp.pdf).

In addition to horizontal track locations, SPLASH tags also transmitted 3923 h of dive data (depth and/or temperature at 10 min resolution). Data retrieved were extensive through time and space, both horizontally and vertically, thus providing a good characterisation of the full range of behaviours (Fig. 3).

3.2. Horizontal data reveal seasonal segregation by sex and age

Blue shark demographics showed clear differences in their horizontal, spatio-temporal distribution (Fig. 2). Juveniles moved the least from their tagging site, remaining almost entirely within the coastline and shelf break of New Zealand. Mature females showed similar restricted movement, residing close to or entirely within New Zealand waters throughout seasons. Mature females and juveniles showed restricted movement north and south of tagging sites. In contrast, mature males showed large longitudinal and latitudinal movements, with greatest displacements north of the tagging site from late summer through winter, moving to warmer waters until the following late-winter/spring when they migrated south, towards the tagging site. Mature males dis-

played a much larger range in longitude than other demographics, but with no consistent patterns. The spatio-temporal variation illustrates that the geographical location of the tagging site contained all demographics during tagging (summer), with lesser likelihood of aggregation of all life stages during other seasons. Variation in the calendar onset of migration or segregation is likely related to individual tracks coming from different years (2013–2016), and thus with potential differences in actual seasonal variation of environmental variables versus day of the year classification of season plotted (Fig. 2).

Two mature blue sharks displayed interannual aggregation and segregation. A mature female (observed with fresh mating scars and placenta matter) and a mature male were both tagged on the same day, in the same area during summer, in the presence of newborn pups. They then segregated mid-summer, with the female residing in the region, while the male migrated north, to lower latitudes through autumn and winter. Almost a year later (315 d), the male migrated south during spring, with both individuals returning at the same time to the tagging location (Fig. 4).

No seasonal migration was evident for mature female sharks or juvenile sharks, which respectively resided predominantly and entirely within New Zealand waters. Two mature females did briefly leave New Zealand's EEZ but only to adjacent international waters. By contrast, mature males moved through multiple EEZs, spending almost equal time

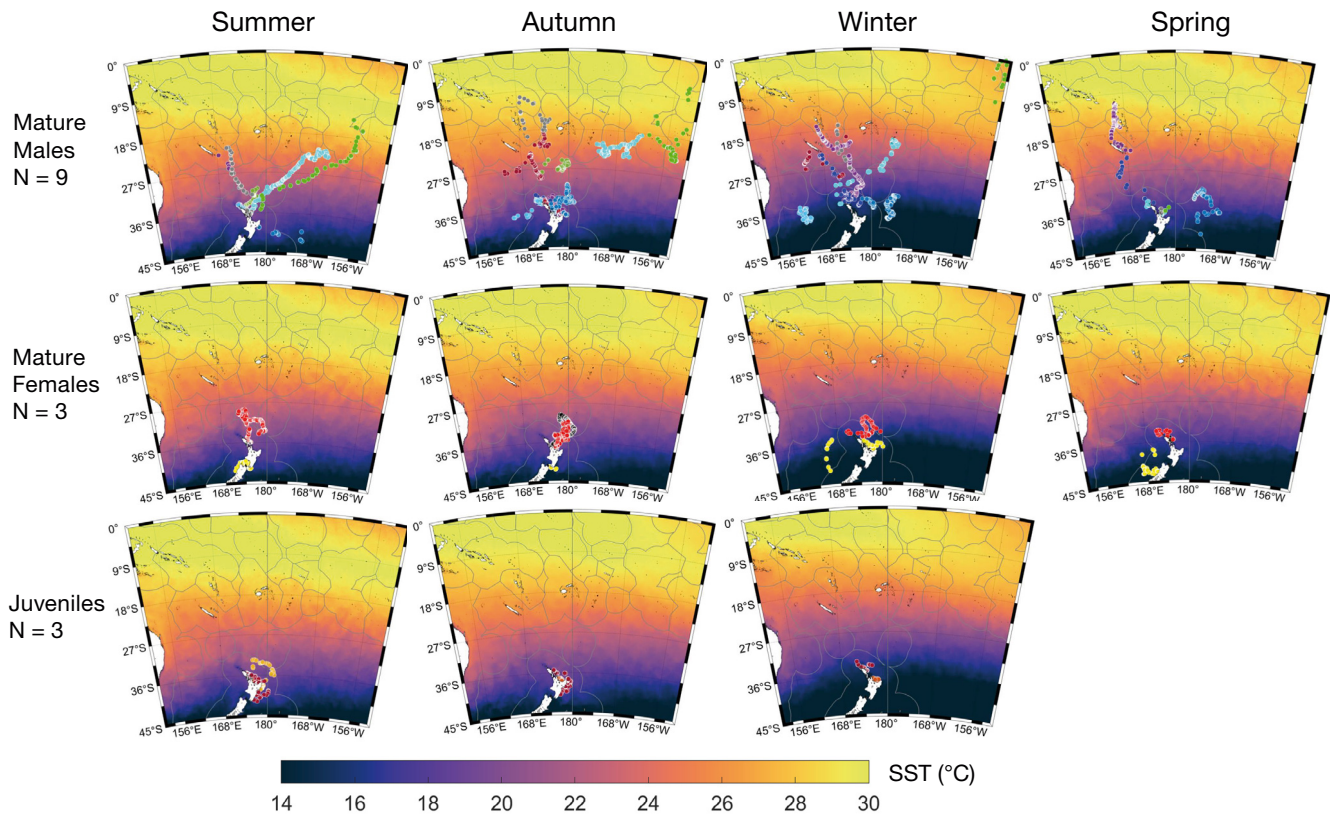


Fig. 2. Tracks of individual blue sharks (colour coded) constructed from filtered satellite tag surface locations (circles), separated by maturity, sex and austral season (Dec–Feb: summer; March–May: autumn; June–Aug: winter; Sep–Nov: spring). Background colour scale represents averaged seasonal maps of sea surface temperature (SST) for the years 2013–2016. Grey lines indicate national exclusive economic zones. Fig. S1 in the Supplement shows high-detail versions of each map

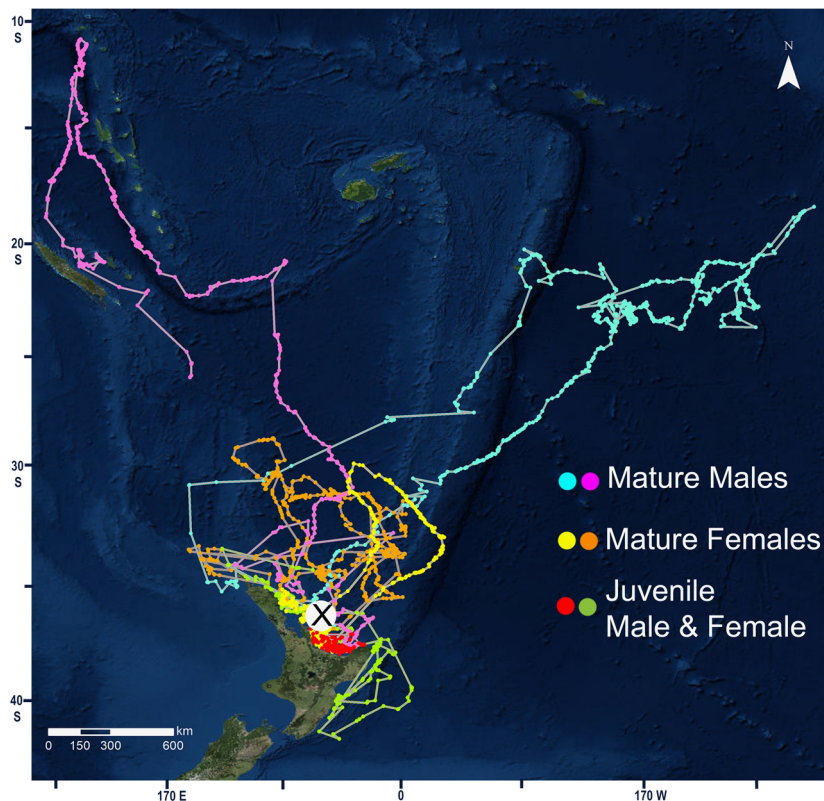


Fig. 3. Satellite-derived location tracks for 6 SPLASH-tagged blue sharks in the south-west Pacific, where opportunistic segments of dive data (depth and/or temperature) were transmitted during shark/tag surfacing events. Tagging location is indicated by the 'x'

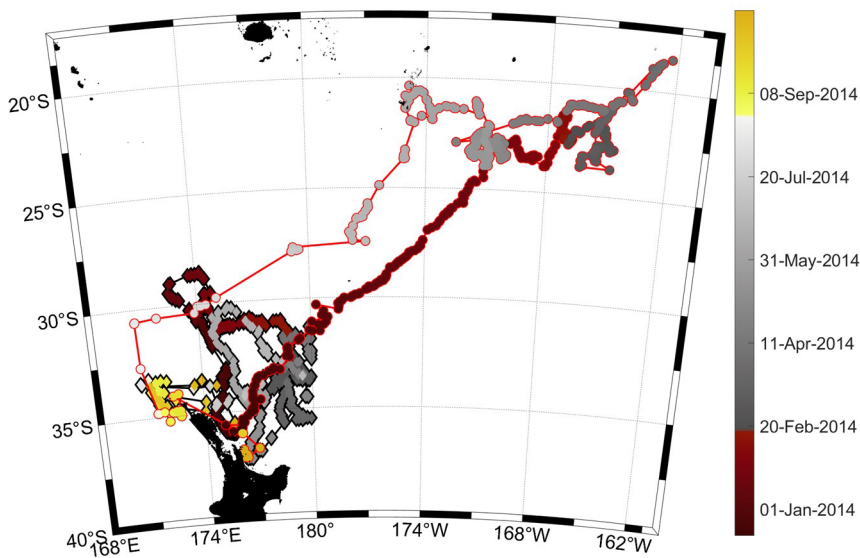


Fig. 4. Satellite tracks of 2 blue sharks (diamonds: mature female; circles: mature male), showing austral seasonal aggregation when tagged (early summer), followed by segregation (end of summer, autumn, winter), before aggregation again 315 d later (late spring), as indicated by the colour scale

in international waters and Pacific Island EEZs as in New Zealand's EEZ (Fig. 5a). Mature sharks predominantly achieved the longest track durations and distances (Fig. 5b). However, the greatest displacement from the tag site did not increase in relation to track duration (Fig. 5d). Juvenile blue sharks stayed

predominantly within, or in close proximity to, the continental shelf break (201–999 m depth), while mature blue sharks, male or female, spent the majority of their time outside continental shelf breaks, in water ≥ 1000 m in depth (Fig. 5c).

3.3. Age structures water column occupation

The 6 SPLASH tags provided opportunistic segments of dive data, showing that blue sharks in this study occupied depths between 0 and 1364 m, experiencing temperatures of 5 to $>30^{\circ}\text{C}$. The dive data received from these tags were robust not only in total compiled time (3923 h), but also in spatio-temporal coverage (mean track duration 255 d, mean track length 8582 km, maximum track length 14 559 km) (Fig. 3).

Juvenile blue sharks spent the majority of their time, day or night, in the upper 150 m of the water column (Fig. 6a), whereas mature blue sharks showed a bimodal distribution during the day, with preferences in the upper 150 m and at 400 m depth, whereas at night, they resided predominantly within

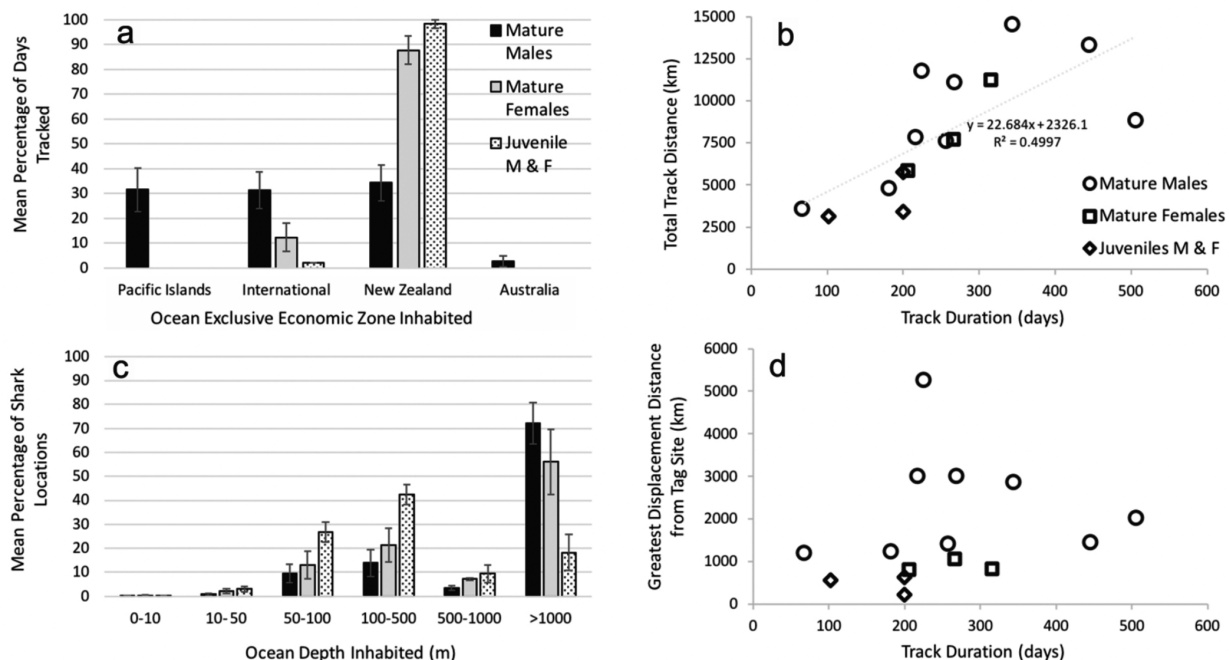


Fig. 5. Summary demographic data for satellite-tagged blue sharks, indicating (a) percentage of days in national exclusive economic zones, (b) total track distance in relation to track duration, (c) percentage of locations relative to ocean column depth and (d) greatest displacement distance from tagging site relative to track duration. Error bars indicate 1 SE

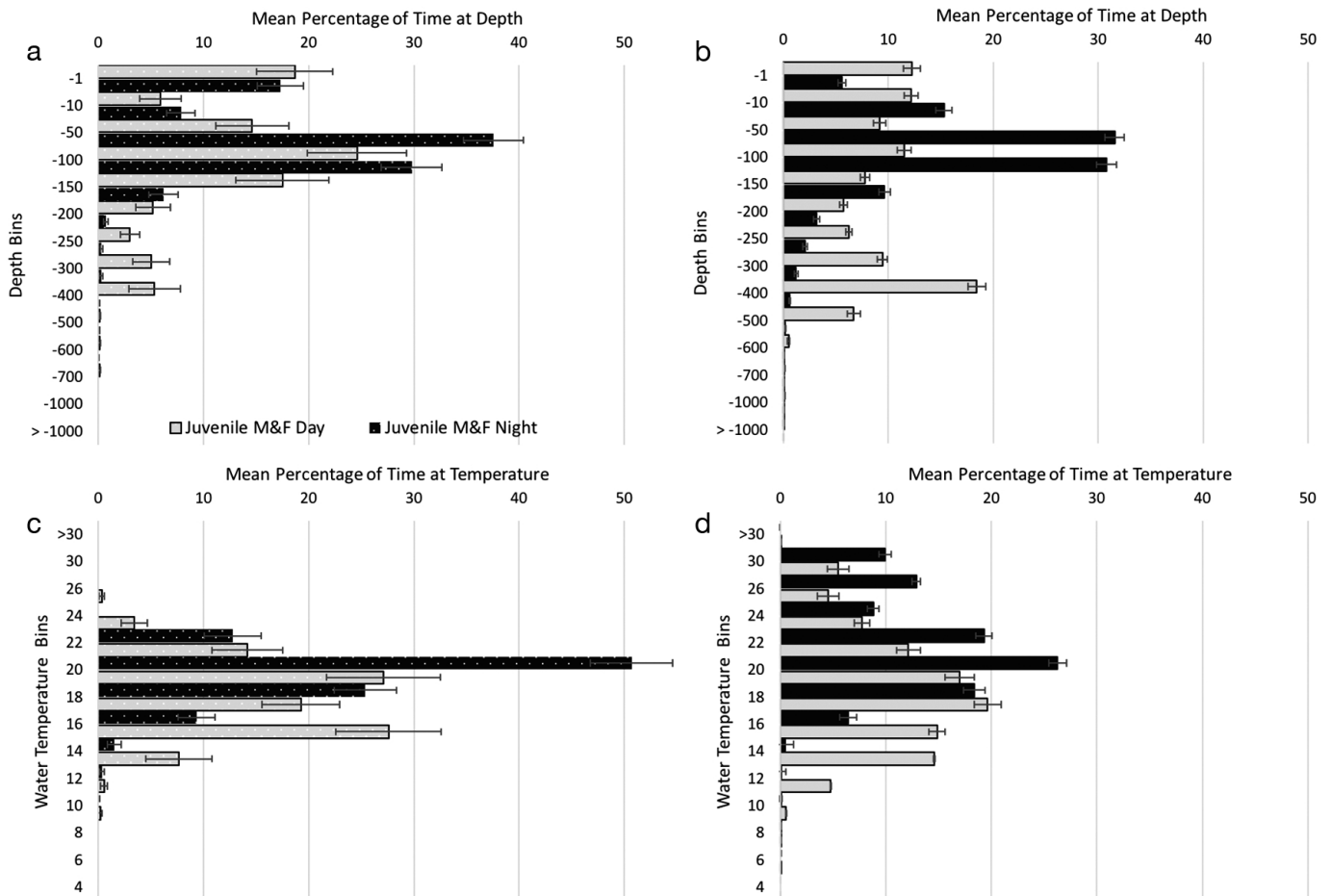


Fig. 6. Mean percentage of time spent at depth as a function of day and night, for (a) all juvenile blue shark dive data, and (b) all mature blue shark dive data. Mean percentage of time at temperature as a function of day and night, for (c) all juvenile blue shark dive data and (d) all mature blue shark dive data. Error bars indicate 1 SE

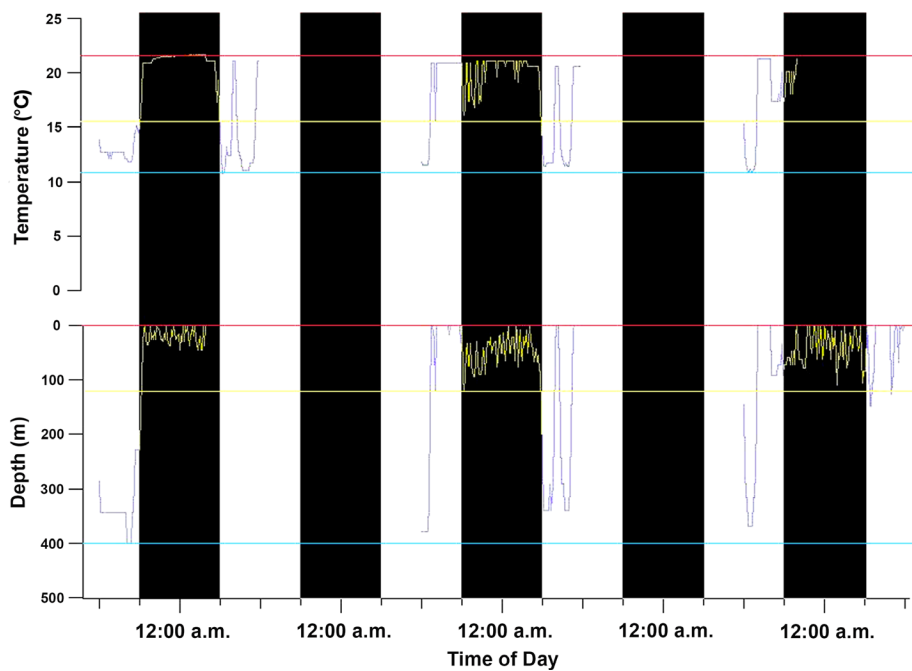


Fig. 7. Opportunistic segments of SPLASH tag dive data from mature female blue shark ID 17. Temperature and depth at 10 min resolution, with sea surface indicated by the red line. Mean nighttime (daytime) depth/temperature from all dive data indicated by yellow (blue) line. Black columns represent local night-time, white is local daytime

the upper 100 m (Fig. 6b). Juvenile blue shark time at temperature was more restricted than that of mature animals (Fig. 6c,d), largely related to limitations in vertical and latitudinal movements. For juvenile and mature sharks, coolest temperatures were experienced in the day, related to the deepest dives occurring in the daytime, while the upper end of temperatures experienced by mature blue sharks was related to latitudinal migration to tropical waters, primarily by mature males.

The distribution of maximum daily depth showed a wide range between sex and maturity demographics. Mature males performed significantly deeper dives during the day (mean \pm SD = 386 ± 186 m) and night (227 ± 185 m), than mature females (day: 308 ± 157 m, $t_{606} = 5.83$, $p < 0.01$; night: 170 ± 118 m, $t_{493} = 4.76$, $p < 0.01$) and juveniles (day: 158 ± 111 m, $t_{147} = 13.02$, $p < 0.01$; night: 129 ± 85 m, $t_{411} = 7.50$, $p < 0.01$). The deepest dive recorded in this study was by mature male (ID 16) to a depth of 1364 m.

3.4. Fine-scale variability of diving behaviour

Although SPLASH tags only transmit dive data at 10 min resolution for depth and/or temperature data, the vertical scale of movements for mature blue sharks, i.e. hundreds of metres and hours, was large enough to enable the identification of patterns in dive profile data. When individual dive depth was shallower than 150 m, no patterns in dive profiles could be identified. This resulted in the majority of juvenile blue shark data, and all night-time data, being excluded. In shelf and oceanic waters during the day, blue sharks repeatedly descended below the thermocline to ~ 400 m ($10\text{--}11^\circ\text{C}$), for a prolonged period (mean bottom time = 79 min), before ascending to surface waters for a prolonged period (mean post-dive surface time = 41 min), before repeating the profile. At dusk, they ceased this diving behaviour and remained in the upper 100–150 m through the night (see Fig. 7 as an example; note that breaks in the dive profile are relative to opportunistic surface transmissions to the satellite).

3.5. Dive profile patterns and inferred behavioural patterns

Blue shark dive data were transmitted on 1531 d, containing 1323 h of identified dive patterns totalling 321 'U', 22 'VU' and 30 'UV' dives, collectively grouped to represent foraging behaviour, while 42 'V'

and 52 'W' dives were grouped to represent searching behaviour, and 83 segments of non-diving data were defined as travelling behaviour. Mean dive profile parameters were defined for each pattern (Fig. 8). Of the identified dive patterns (excluding no dive), 91 % were observed when sharks were on or outside the continental shelf break (> 200 m).

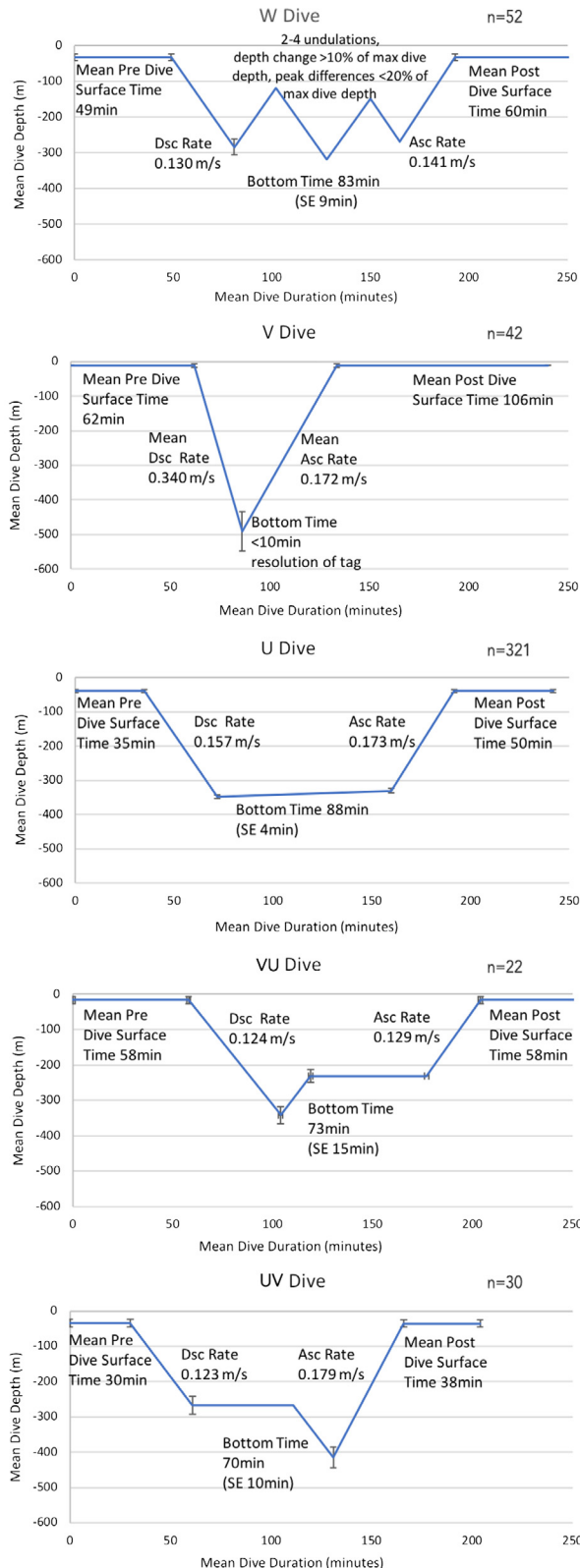
Time-stamped behavioural events inferred from SPLASH tag data were successfully interpolated along respective satellite tracks (Fig. 9). Foraging events were the predominant behaviour identified and occurred throughout the entire spatio-temporal range of distribution.

Dive parameters and post-dive behaviour varied with dive type. After a foraging dive, ascent rates were on average faster (0.19 ± 0.07 m s⁻¹), than after a searching dive (0.12 ± 0.06 m s⁻¹). Post dive surface time was on average shorter after a foraging dive (34.1 ± 4.6 min) than after a searching dive (85.9 ± 86.0 min). Sharks would descend faster after a foraging dive (0.18 ± 0.06 m s⁻¹) than after a searching dive (0.11 ± 0.08 m s⁻¹). Mean bottom time of a second dive, after a foraging dive (77.8 ± 48.8 min), was longer than that spent after a searching dive (55.4 ± 51.7 min). An initial foraging dive was followed by another foraging dive 95.5 % of the time, whereas a searching dive was followed by a foraging dive only 33.3 % of the time, but by a searching dive 66.6 % of the time. In addition, foraging dives returned to the same depth (within 5 m) 72 % of the time. Searching dives returned to the same depth only 39 % of the time. Mean bottom depth of 'revisited' foraging dives was 354 ± 97 m. Mean bottom depth of 'revisited' search dives was 359 ± 298 m, reflecting greater diversity in depth when searching.

Although night-time data were not investigated for dive patterns, mean depth of blue sharks at midnight during 66.7–100 % full moon phase (61 ± 61 m) was significantly deeper than during 0–33.3 % full moon phase (24 ± 29 m, $t_{67} = 2.53$, $p = 0.01$), reflecting an influence of increased light at night on their vertical distribution.

4. DISCUSSION

Conservation action for highly migratory oceanic species requires an extensive knowledge of their habitat use (Andrzejczek et al. 2019, Harcourt et al. 2019, Hays et al. 2019, Sequeira et al. 2019). This study is the first to showcase satellite tagging of blue sharks in the southwest Pacific, and only the tenth in the world using dorsal fin-mounted satellite tags.



Search Behaviour

Multiple undulations at various depths, surveying stratified ocean layers.

(peak:peak depth differences <100m apart; peak:trough depth differences >50m apart).

Search Behaviour

A bounce dive, fast survey of the environment, presumed for searching for prey patches, navigation or orientation.

Foraging Behaviour

Often repeat dives, to a similar depth, with fast ascent/descent rates, long bottom time at a relatively constant depth. Assumed to be indicative of prey resources present at bottom depth, given thermal cost of lower water temperatures at depth.

Foraging Behaviour

Searching for a prey resource (V aspect), locating prey and commence foraging (U aspect).

Fig. 8. Mean parameters for 5 common dive profile patterns of blue sharks, identified in this study from SPLASH tag dive data at 10 min resolution. Error bars indicate 1 SE, where specific parameters were measured: pre-dive depth, maximum dive depth, 'Stop' depth on 'VU' and 'UV' dives and post-dive surfacing depth. Bottom time is defined as the time from maximum dive depth to start of final ascent. Dive profiles are all to same depth and time scale, with descent (dsc) and ascent (asc) rates, depths and bottom times applied in order to reflect actual shapes of mean dive parameters for each common pattern; n = sample size of dives for each dive pattern

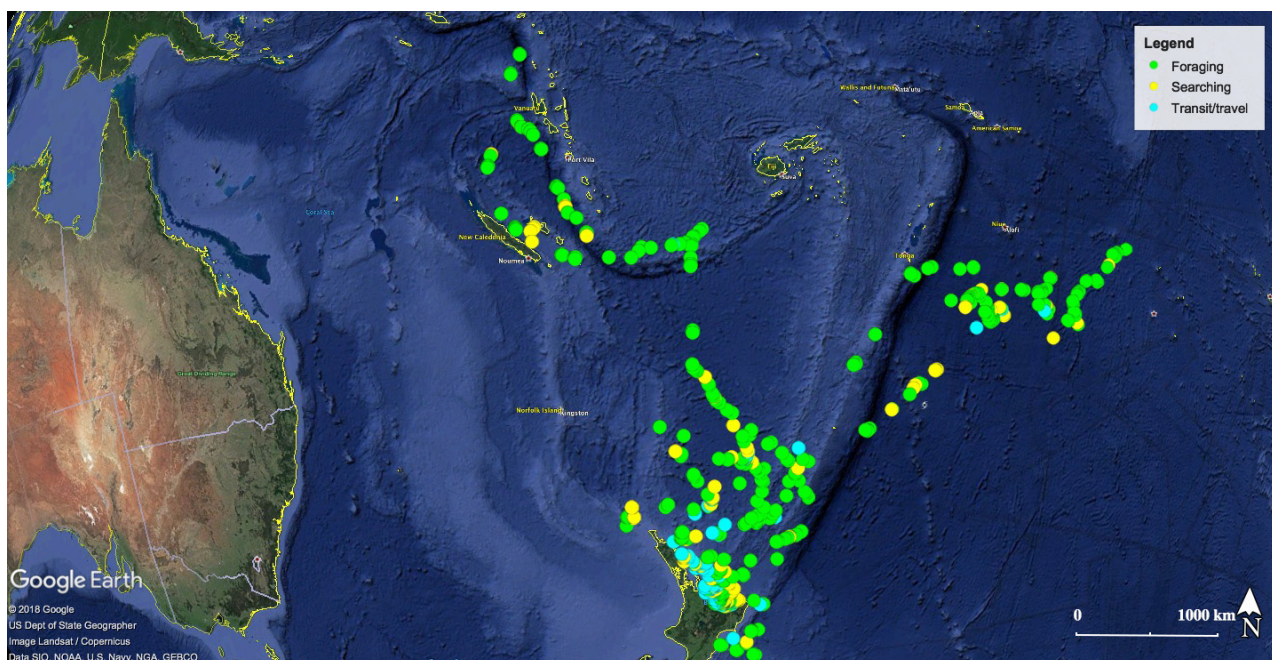


Fig. 9. Behavioural events inferred from common dive profile patterns, interpolated along satellite-derived location tracks for 6 blue sharks carrying SPLASH tags in the southwest Pacific

The use of SPLASH tags on blue sharks resulted in dive data that are more spatially accurate than commonly used PSATs. With 15 blue sharks tagged, this study adds to the previous data set for bolt-on satellite tags, which comprises approximately 179 individuals that have produced viable tracks.

4.1. Tag performance and data received

No mortalities were associated with the tagging process or following animal release, reflecting ethical and appropriate methodology. The total number of locations ($n = 6867$, mean per shark = 457), days tracked ($n = 3785$, mean per shark = 252), longitudinal and latitudinal spread of tracks (43 and 41° , respectively), number of EEZs crossed ($n = 10$), hours of dive data ($n = 3923$, mean per shark = 653), deepest dive (1364 m) and mean individual track length (7996 km), sit at the upper end of the scale of data gathered in existing studies using bolt-on tags for blue sharks (from $n = 9$ studies, 179 tags: range in mean days tracked: 41–306, Teo et al. 2004, Rogers et al. 2009, Stevens et al. 2010, Block et al. 2011, Vandeperre et al. 2014, Doyle et al. 2015, Queiroz et al. 2016, Braun et al. 2019, Maxwell et al. 2019; mean track length range: 5453–8346 km, Braun et al. 2019, Vandeperre et al. 2014) complementing the global data set for this species.

Although dive data retrieved in this study were at lower resolution than PSATs, and were comprised of segments of time, the number of days with transmission was greater than in most PSAT studies on blue sharks (from $n = 10$ studies, 161 tags: mean \pm SD days tracked = 85 ± 59 , Teo et al. 2004, Queiroz et al. 2010, 2016, Stevens et al. 2010, Campana et al. 2011, Musyl et al. 2011, Vandeperre et al. 2014, Carvalho et al. 2015, Doyle et al. 2015, Howey et al. 2017). This seems to be related to PSATs having high rates of transmission failure (50%) (Moyes et al. 2006) and premature pop-off (87%) (Stevens et al. 2010).

The SPOT 196 trapezoid model (Wildlife Computers), predominantly used in this study, seemed best suited to the shape of the blue shark dorsal fin, and the data received reflect its success. Interestingly, SPLASH tag models are often larger than most SPOT tag models, with model 289 in particular being double the size and weight and yet having an expected battery life often half that of a SPOT tag (due to extra data gathering). In our study, however, SPLASH tags provided some of the longest track durations (255 ± 63 d) when compared to SPOT tags (250 ± 144 d). They also exceeded their 100–180 d life expectancy (models 316 and 289, respectively). Life expectancies are calculated at the 250 transmissions d^{-1} limit used in this study; however, the ‘on/off cycle’ used after 6 mo in this study likely explains the extended lifespan of the SPLASH tags, highlighting the value of

that setting choice. Given that SPLASH tags also provided dive data, and their use on blue sharks had not previously been tested, it seems evident that their overall performance was more beneficial than that of the SPOT tags used in this study. SPLASH tags were seen to be beneficial for spatio-temporally accurate assessment of movement and behaviour, whereas PSATs, which dominate blue shark satellite tagging research (Teo et al. 2004, Moyes et al. 2006, Campana et al. 2009, 2011, 2016, Queiroz et al. 2010, 2016, Stevens et al. 2010, Musyl et al. 2011, Vanderperre et al. 2014, Carvalho et al. 2015, Doyle et al. 2015, Howey et al. 2017, Musyl & Gilman 2018, Braun et al. 2019) are more advantageous for capturing continuous dive data at high resolution and can address specific incidence of mortality events. It is therefore clear that research objectives should dictate which tag model is used.

4.2. Age-based regional segregation

Juvenile blue sharks in this study showed very little displacement from tagging sites. Their habitat use was consistent with Litvinov (2006), i.e. predominantly inshore of the continental break and separated from that of mature animals. Nursery habitat theory supports residency within sheltered waters, with smaller prey, localised productivity and protection from predation (Heupel et al. 2007). Intraspecific predation of newborn pups in the presence of mature blue sharks (R. Elliott pers. obs.) supports the predation aspect of this theory. Juvenile preference for STCZs (between 35° and 45° N or °S) has been observed (Queiroz et al. 2010, 2012) but was not tested in the present study; however a tagged juvenile (ID 69) did travel down the east coast of New Zealand towards where the STCZ predominates, perhaps reflecting a preference for such habitat. Interestingly, a tagged mature female (ID 77) showed the same movement, perhaps reflecting parturition, as the timing aligned with potential gestation.

4.3. Spatio-temporal segregation by sex

Spatio-temporal segregation by sex was observed within the mature blue shark demographic in this study, along with periods of seasonal aggregation. These findings are consistent with those from other studies (Springer 1967, Bass 1978, Klimley 1987, Litvinov 2007, Queiroz et al. 2010, 2012, 2016, Vanderperre et al. 2014, Coelho et al. 2018, Boldrocchi &

Storai 2021, Fujinami et al. 2021), which largely relate segregation to mating pressure (Wearmouth & Sims 2008). This theory predominates across shark species, even considering evolutionary adaptations to reduce physical trauma from shark copulation, including changes in the dental structure of mature males and increasing skin thickness in mature females (Litvinov 2006). Reproduction requirements likely explain seasonal aggregation among mature individuals, evidence of which was observed in this study; however, seasonal productivity and foraging opportunities may also catalyse aggregation.

Fishery bycatch data suggest that mature males most commonly utilise pelagic waters, where they associate with large-scale bathymetric features such as seamounts, islands and zones with productive water dynamics (Litvinov 2007). Interestingly, fishery-independent satellite tagging data have recently linked mature male blue shark distribution with anti-cyclonic eddies, characterised by low surface primary productivity, lack of bathymetric features, but warmer temperatures at depth, allowing optimal foraging in the mesopelagic (Braun et al. 2019). Mature males in our study used seemingly preferential, seasonal foraging habitat, alongside mature females, post pupping and fertilisation. They then segregated via migration to lower latitudes, while mature females remained in higher-latitude shelf waters during possible gestation of 9–12 mo. This annual cycle of segregation and aggregation was reflected by 2 tracked blue sharks which returned to the same location, after 315 d, in the presence of newborn pups and mating wounds on the female.

Newborn blue sharks (35–50 cm) are suggested to move from shelf water to coastal waters, away from oceanic zones, likely due to intra-species predation (as observed in this study). Intra-species predation may also explain the high fecundity of blue sharks (up to 135 pups have been recorded in a single litter; Fisheries New Zealand 2018). Capture-induced parturition (premature birth or abortion, Adams et al. 2018) suggests the possibility that the presence of neonate blue sharks is misrepresentative of birthing grounds. However, the size of neonates (45–55 cm) observed in our study suggests full-term pups. Da Silva et al. (2010) observed similar evidence of pupping grounds off South Africa, including small juveniles with open umbilical scars, a large female with uterine post-parturition scars, and high frequencies of small juveniles caught on longline gear. This area is comparable with the field site in the present study, i.e. of similar latitude and oceanic features, where shelf break upwelling regions are in relative proximity to subtropical

convergences. Parturition and nursery areas have been reported in other studies, from the northeast Atlantic (Pratt 1979), the north Pacific (Nakano 1994), the southwest Atlantic (Montealegre-Quijano & Vooren 2010) and the Mediterranean (Megalofonou et al. 2009, Boldrocchi & Storai 2021), all of which are associated with oceanic fronts where temperature gradients and upwelling result in high productivity convergence zones. These findings support the theory of the study site being utilised as a pupping and breeding habitat.

When newborn blue sharks reach 70 cm, they begin to segregate by sex, until females near maturity and migrate back to the oceanic mating zone, where they can copulate and store sperm before fertilisation takes place (Springer 1967, Bass 1978, Pratt 1979, Klimley 1987, Hazin et al. 1994, Nakano 1994, Litvinov 2006, da Silva et al. 2010, Montealegre-Quijano & Vooren 2010, Queiroz et al. 2010, Vandeperre et al. 2014).

4.4. Migratory behaviour of mature males

Mature male blue sharks coincided their movement to lower-latitude, tropical waters with the seasonal retreat of warmer SST, which at the tagging site was associated with the East Australian Current (EAC). In spring, the return of mature males to the tagging site also coincided with the return of warmer waters driven by the EAC moving south. Seasonal movement of other large pelagic species has been associated with the EAC (Holdsworth et al. 2016), which seemingly acts as a pelagic highway, shown to generate frontal systems that provide prey availability in larger mass than open ocean habitat (Young et al. 2010). For reasons unknown, mature male blue sharks moved beyond the scope of the EAC, into Polynesian EEZs, associated with warmer SSTs than those experienced by mature females or juveniles.

Mature males in our study travelled greater distances in relation to time at liberty than females or juveniles, whereas Vandeperre et al. (2014) found no significant difference between individuals or life stages with respect to distance in relation to time at liberty. Perhaps this discrepancy indicates a unique relationship between the southwest Pacific blue shark stock, local oceanographic features and potential prey opportunities.

4.5. Local habitat use by mature females

Mature females tagged in this study segregated from mature males after summer, when copulation

and pupping were observed on or outside the shelf break. They then remained largely within the New Zealand EEZ, where they used different habitats and thus likely different food resources, given seasonality in the environment, as reflected by their presence within cooler SSTs and in a greater diversity in ocean zones, ranging from neritic to oceanic. Preference for cooler waters is consistent with Howey et al. (2017) but partly contrary to the findings of Hazin & Lessa (2005), where females inhabited warmer waters, thought to potentially aid in fertilisation and embryonic development. However, mature females in our study did inhabit shallower waters than mature males, which is consistent with Hazin & Lessa (2005).

4.6. Potential overlap with fisheries

Tag data from this study reflect high residence in the New Zealand EEZ for mature female blue sharks, whereas commercial tuna surface long line catch data suggest that mature female blue sharks are rare or absent (Fisheries New Zealand 2018). Direct field observations during this study and reports from fishers on surface long line boats (Fisheries New Zealand 2018) suggest that misreporting causes this underrepresentation, as observed by Mejuto & García-Cortés (2005). There is also the potential of spatio-temporal bias in fishing effort, which may avoid overlap with mature females occupying habitat less beneficial for species targeted by fisheries. The majority of observer coverage for the tuna fleet in New Zealand occurs on the foreign fishing fleet, operating primarily in the southwest waters, related to fishery overlap with endangered sea birds and vessel size. Very little observer coverage occurs in the domestic fleet that targets tuna in the northeastern region (Highly Migratory Species Team 2017) where this study took place, where tagged females resided and where our observations and those of fishers were made, suggesting misreporting to be the likely driver of mature females deemed absent in fishery management policy for this area. This highlights how fishery-dependent data alone may lead to the mismanagement of a critical population demographic in this case.

4.7. Population fidelity to oceanic basins

Tagging results support the theory that blue sharks reside within major oceanic basins, as seen by all tracks remaining within the southwest Pacific, even

those that were tracked for >12 consecutive months. Further evidence may be interpreted from the mature male that migrated to within 1 km of the equator, before rapidly turning south in the opposite direction, with increased travel speed thereafter. Although 1 mark–recapture tag suggests population links across the South Pacific oceanic basin, from west to east (Holdsworth et al. 2016), no individuals in our study showed west to east movements of that magnitude. Stevens et al. (2010) also observed restricted movement in this context, where satellite-tagged blue sharks remained in the Tasman Sea, east of Australia. However, as Stevens et al. (2010) acknowledged, and as was the case in our study, such observations may be a function of short tracking periods, in comparison to mark–recapture tag records of oceanic crossing in the South Pacific, which primarily occurred after more than 24 mo (West et al. 2004, Holdsworth et al. 2016). It may be that multiyear tracks only reveal trans-oceanic migrations, perhaps related to age-induced movements, which a single year of monitoring may not capture. Sample size limitations of satellite tagging further reduce the likelihood of tracking a particular animal undertaking such a migration. However, it must still be acknowledged that observation of these transoceanic migrations are rare, given the robust number of sharks tagged in mark–recapture studies, or those satellite tagged.

4.8. Water column use and vertical distribution of temperature

Even with depth/temperature resolution of 10 min, SPLASH tags yielded dive data which provided insight into vertical distribution and behaviour of blue sharks. Although the tags were non-retrievable (unless the sharks were captured and the tags returned), and thus relied on dive data to be transmitted at lower resolution than what they are capable of recording (10 s), or what PSATs are able to archive and later transmit, their attachment durability provided superior time at liberty than most PSAT deployments.

It was clear from these data and from other studies that blue sharks are capable of diving to great depths (1364 m in the present study, 1517 m in Fujinami et al. 2021, and the deepest recorded 1706 m in Queiroz et al. 2017). Depths exposed blue sharks in this study to an extreme range in water temperature (5 to >30°C), similar to those reported by Howey et al. (2017) (3.9–31.3°C) and Fujinami et al. (2021) (3.1–32.6°C).

4.9. Diel patterns in the distribution of tagged sharks

Although night-time behaviour was not investigated, due to the repetitive pattern of zig-zagging within the upper 100 m, it still reflected the dominant habitat use by blue sharks at night, which is consistent with findings from other studies (Sciarrotta & Nelson 1977, Carey & Scharold 1990, Stevens et al. 2010, Campana et al. 2011, Queiroz et al. 2017, Fujinami et al. 2021). The only additional analysis of night-time dive data in the present study investigated the influence of moon phase on mean depth at midnight. Findings were similar to those addressed by Campana et al. (2011), where blue sharks resided deeper during full moons compared to new moons. These results suggest that blue shark diel vertical movement is likely influenced by the vertical migration of prey in the deep scattering layer because it not only mirrors such movements, but prey also resides deeper during a full moon to avoid light-associated visual predation (Prihartato et al. 2016).

Previous studies (Carey & Scharold 1990, Stevens et al. 2010, Campana et al. 2011, Queiroz et al. 2017) and the present study have demonstrated that blue sharks display regular, vertical oscillations during the day, every few hours, to depths between 200 and 400 m. Between these dives, they remain at or near surface water. In order to infer behavioural states from commonly repeated patterns in the dive profiles, the drivers/controlling factors for blue shark vertical movement need to be identified.

Braun et al. (2022) summarised likely drivers for patterns in dive profiles of large marine predators. With regard to blue sharks and supported by specific blue shark studies (Sciarrotta & Nelson 1977, Carey & Scharold 1990, Stevens et al. 2010, Campana et al. 2011, Queiroz et al. 2017), 2 key factors likely influence diel vertical migration patterns, and thus the inference of behavioural states from particular dive patterns: (1) predation of vertically migrating mesopelagic prey and (2) muscle temperature regulation in relation to water temperature variation with depth.

In light of these conclusions, 'U'-, 'VU'- and 'UV'-shaped dive patterns were aligned with foraging, and 'V'- or 'W'-shaped patterns with searching. The 'learning' behaviour observed in the present study, also noted by Queiroz et al. (2017), supports this foraging theory because dive parameters of blue sharks were positively geared towards optimal foraging.

The data type used to infer behaviour in the present study (SPLASH tag derived), enabled time-stamped locations of behaviour events to be mapped in a novel

and accurate way, providing useful insight on critical blue shark habitat. The scale at which these data were obtained was also novel, in that it spanned on average 255 d, 8582 km, 30° of latitude, 32° of longitude, 10 EEZs and 5 biogeographic realms (sensu Costello et al. 2017). Correlating location-specific behaviour events with environmental variables to identify critical habitat for blue sharks is likely more beneficial than using conventional bycatch data (e.g. McGregor & Horn 2015). This is because presence/absence relative to capture in a fishery may have little representation of what constitutes desirable habitat to a blue shark given that it is optimally targeting prey at depth. In addition, models based on catch data are inherently biased by fishing effort and location in comparison to data derived from free-swimming sharks.

5. CONCLUSIONS

This study aimed to expand the global understanding of blue shark movement and behaviour by satellite-tagging individuals in the southwest Pacific Ocean. 'Big data' studies have been acknowledged as a step change in the management of highly mobile pelagic species, but they require long-term, large-scale horizontal and vertical movement data which are restricted in sample size due to the expense of satellite tags required. Prior to our study, only 179 individual blue sharks had ever been tracked with dorsal fin-mounted satellite tags, so our contribution of 15 long-term, highly accurate satellite tracks, with a subset of attributed dive data, has added to the global dataset on blue shark movement and behaviour. Our data show a strong seasonal sex/age segregation and far-ranging migrations of mature male blue sharks across the South Pacific, as well as differences in diving behaviour at different life stages. The SPLASH tags allowed for the definition of fine-scale vertical diving behaviours, suggesting that these tags, which do not need to be recovered, could be used in the future. While these methods avoid the flaws and biases inherent with fishery-derived bycatch data, they are greatly limited in sample size. Encouraging more satellite tagging and extended utilisation of such data, through behavioural modelling of location-only data, for example, would complement fishery data and overall better inform management policy. This is imperative not only for pelagic shark populations, which have declined by 71 % over the past 50 yr (Pacoureau et al. 2021), but also to ensure we do not lose important ecosystem services these top predators likely provide to marine ecosystems and fisheries.

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