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Active acoustic telemetry reveals ontogenetic habitat-related variations in the coastal movement ecology of the white shark

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Abstract

Background: Little is known about the fine-scale behavioural choices white sharks make. The assessment of movement at high spatio-temporal resolution can improve our understanding of behavioural patterns. Active acoustic telemetry was used along a coastal seascape of South Africa to investigate the movement-patterns of 19 white sharks tracked for 877 h within habitats known to host different prey types.

Results: A three-state hidden Markov model showed higher ontogenetic variability in the movements of white sharks around estuary-related coastal reef systems compared to around a pinniped colony. Our results further suggest white sharks (1) use the same searching strategy in areas where either pinnipeds or fishes are present; (2) occupy sub-tidal reef habitats possibly for either conserving energy or recovering energy spent hunting, and (3) travel directly between the other two states.

Conclusions: White sharks appear not to simply roam coastal habitats, but rather adopt specific temporally optimized behaviours associated with distinct habitat features. The related behaviours are likely the result of a balance among ontogenetic experience, trophic niche, and energetics, aimed at maximizing the use of temporally and spatially heterogeneous environments and resources. The possible implications for the future conservation of white sharks in coastal areas are discussed, with particular attention to South Africa's present conservation and management challenges.

Keywords: White shark, Acoustic telemetry, Conservation, Tracking, Movement ecology, Ontogeny, *Carcharodon carcharias*, Habitat use

Background

The drivers of animal movement range from individual daily survival (e.g., regular foraging, predator avoidance, resting) to long-term breeding success and multigenerational gene flow obtained through dispersal and migration of individuals [86]. As animal movements

are intrinsic to behavioural strategies, the assessment of movement states may provide a tool to better understand the underlying behavioural choices animals make, result of internal (e.g., metabolism, searching for a mate) and external (e.g., thermal optimum range, predator/prey presence) factors. For example, these factors may motivate a hungry individual to search for food over a small area or flee from a predator when threatened in a more directional path. Therefore, investigating how an animal moves can provide insights into both the internal motivations and the adaptive behaviours responsible for

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maximizing the utilization of temporally and spatially heterogeneous environments and resources [75].

Nevertheless, our ability to understand movement data is still exceeded by our ability to collect it [59]. Such limitations are due in part to the complexity of factors determining animal movement, including physiological, environmental, ecological, and genetic elements [40]. Behavioural studies on non-air breathing marine species are further complicated by the difficulty of keeping an animal in sight (either visually or through telemetry) continuously and for extended periods. To date, most fish research has focused on describing and characterizing movement patterns, paying limited attention to identifying the drivers behind the movement [66, 79]. Integrating statistical approaches with local knowledge of species ecology and the seascape in which it moves allows us to bridge the gap between describing where/when/how an animal moves and understanding why it moves [47].

Satellite telemetry provides important information on large-scale migrations [8, 14] and population connectivity [7, 29]. Behavioural decision-making processes often operate on a temporal and spatial scale much smaller than the resolution of satellite telemetry [34, 40]. This is where active acoustic telemetry provides an advantageous means of obtaining multi-day movement data in a coastal area with higher spatial and temporal resolution [3]. Few studies have focused on the movement-related behavioural characterization of white sharks, *Carcharodon carcharias*, in different areas of the world [10, 62, 94, 96, 99], however they were limited by the durations of the tracking bouts. Mossel Bay is one of the few sheltered embayments along the exposed South African coastline and provides a unique opportunity to collect extended, continuous, and repeated movement data on semi-resident white sharks. In Mossel Bay, white sharks use the inshore areas of the bay. This area encompasses a Cape fur seal (*Arctocephalus pusillus pusillus*) rookery, coastal reef systems, and three small estuaries [55, 58].

The hidden Markov model (HMM) allows for input of a time series with serially correlated observations of regular animal displacement data (step lengths and turning angles) and estimates the underlying, “hidden”, time series of movement-based states driving the “observed” time series [64]. Within an HMM framework [105], the Markov chain of states is a stochastic process for which the probability of a state is dependent only on the state of the previous step. These states influence the distributions of the observed step lengths and turning angles.

Recent research has shown that white sharks use different swim speeds (and thus step lengths) to optimize

energy expenditure across different behaviours [99]. The extension of HMMs to include covariates [71] thus shifted the aim of this study from describing movement per se, to identifying and modelling behaviour-related movements. These movements may be driven by inter and intra-specific ecological processes such as ontogenetic patterns, diel foraging cycles, and the use of fragmented habitats. Because the area where pinnipeds predictably occur in Mossel Bay is well separated from where coastal reef fishes abound, one of the objectives of this study was to understand how the movement patterns of white sharks may change with the presence of pinnipeds or in areas where other prey resources are available. A further objective was to quantify how ontogenetic plasticity, which is especially important in a predator–prey context [44, 65], influences the spatio-temporal habitat use patterns of this species in a coastal environment.

Several hypotheses were tested: (1) the movement pattern used by white sharks to hunt pinnipeds is spatially restricted only to the area where pinnipeds are predictably found (i.e., Seal Island); (2) if foraging for fish was sporadic, no spatial or temporal pattern should be discernable over reef structures; (3) each movement pattern should differ by size classes linearly if the result of a gradual learning of skills.

The importance of understanding how white sharks use the coastal seascape has become even more pressing following the recent disappearance of white sharks from Gansbaai and False Bay, the other two main coastal aggregation sites in South Africa [39], Towner et al. in review).

Results

During the study period, 19 white sharks ranging from 1.5 to 4.2 m estimated TL, were externally tagged and manually tracked within Mossel Bay for a combined duration of 877 h (mean = 46.1 h, SD = 43.6 h: Table 1). We ran both a three-state and a two-state (to confirm our choice quantitatively) HMM over 97 bivariate independent time series of step lengths and turning angles, with the same variables and similar constraints (AIC were 143,399 and 151,832, respectively).

The selected three-state model was evaluated for possible lack of fit via Quantile–Quantile plots and the autocorrelation of the pseudo-residuals (Additional file 1). The model appears to capture the values of step length well, while there is some mismatch around the median of turning angles. Overall, the calculated pseudo-residuals appear to fit well with the theoretical quantiles and can be considered normally distributed. The autocorrelation function (ACF) shows the model captured the

Table 1 Summary of the data obtained from 19 white sharks acoustically tagged and manually tracked in Mossel Bay between 2008 and 2012 (1.5–1.9 m 16%, 2–2.4 m 21%, 2.5–2.9 m 26%, 3–3.4 m 16%, 3.5–3.9 11% and 4–4.4 m TL 11%)

Shark #	Sex	Estimated TL (m)	Duration of combined sessions (h)
1	F	2.2	39.6
2	F	3.4	88.8
3	M	1.5	7.3
4	F	3.6	59.3
5	F	2.9	2.3
6	F	4.2	34.5
7	F	1.7	42.8
8	F	2.1	13.2
9	M	2.2	172.6
10	F	2.5	73.8
11	M	2	4.8
12	M	1.7	15.1
13	F	3.5	21.8
14	F	3	32.2
15	F	4	36.6
16	F	2.8	128.5
17	M	2.7	41.3
18	F	3.2	31.3
19	M	2.7	31.0
Total tracking time			876.6

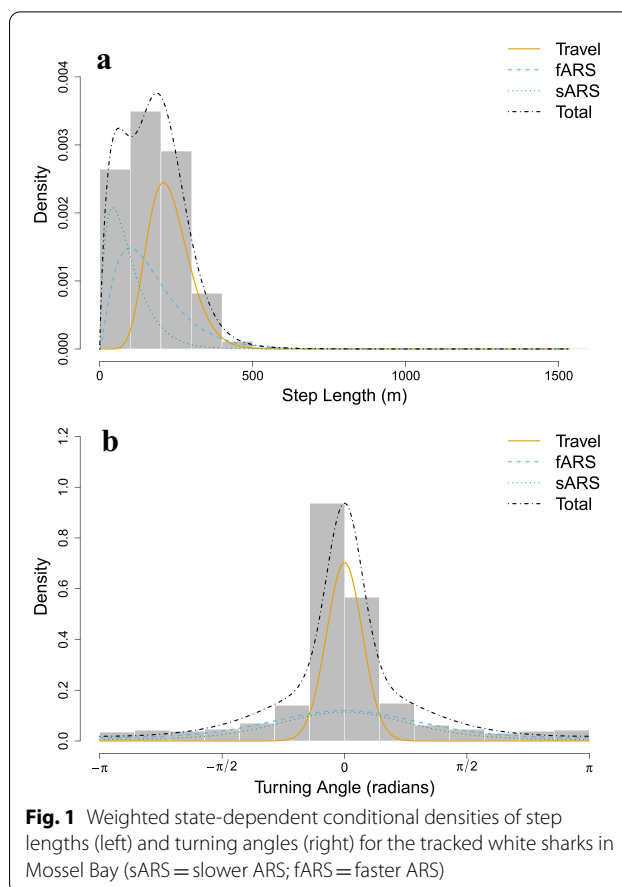


Fig. 1 Weighted state-dependent conditional densities of step lengths (left) and turning angles (right) for the tracked white sharks in Mossel Bay (sARS = slower ARS; fARS = faster ARS)

autocorrelation better when compared to the initial autocorrelation in the data, especially for the turning angles. However, there is significant remaining autocorrelation not captured by the model (Additional file 1).

The state with (1) the highest mean angular concentration; (2) the lowest standard deviation for step length and (3) the highest mean step length (229 m) (all indicative of directed movement) was inferred to represent traveling between focal sites (Fig. 1). The resulting mean rate of movement (ROM) for the traveling state was 0.8 m s⁻¹ (2.9 km h⁻¹). The remaining two states showed lower angle concentration than the more directed traveling state, with little difference in turning angle distributions between the two. These two states were inferred to represent a faster ARS (fARS) with a mean step length of 172 m (mean ROM of 0.6 m s⁻¹ or 2.2 km h⁻¹) and a slower ARS (sARS) with a mean step length of 92 m (mean ROM of 0.3 m s⁻¹ or 1.1 km h⁻¹).

The final model, incorporating a 12-h period for time of day (TOD as a circular variable with a 24-h period), a linear relationship with size, and a threshold distance of 500 m to either the closest estuary mouth or to Seal Island, was selected by AIC (Table 2 and Fig. 2). The stationary distributions obtained from the selected model

for the winter period (90 days either side of the winter solstice) were plotted by size classes to assess movement patterns for white sharks (1) within the bay (Fig. 3), (2) at 400 m from the nearest estuary mouths (Fig. 4), or (3) at 400 m from the pinniped colony (Fig. 5). Winter is the main hunting season for Cape fur seals and when white sharks use both primary habitat types [89].

The use of different movement states by different size classes is more variable within the bay or near an estuary mouth when compared to the movement choices adopted around Seal Island. Close to an estuary, the probability of being in the slower ARS state becomes higher with an increase in shark size. Near an estuary mouth larger size classes tend to be in this slower state with a higher probability before sunset and sunrise, with the smaller size classes occurring in the middle of day and night. In these areas the faster ARS state still occurs but it is used more by smaller white sharks and mainly around sunset and sunrise.

When not close to either an estuary mouth or Seal Island, the smaller white sharks have an almost equal probability of traveling or using the faster ARS state.

Table 2 Summary of model selection for data obtained for this study

	Name of model	TOD period	DOY period	Size relationship	ARS threshold distance	AIC
Model 1	fit.12 h.500	12 h	1 year	Linear (size)	500 m	143,493.0
Model 2	fit.12 h.250	12 h	1 year	Linear (size)	250 m	143,555.2
Model 3	fit.12 h.500.nojday	12 h	No Julian variation	Linear (size)	500 m	143,585.1
Model 4	fit.12 h	12 h	1 year	Linear (size)	1000 m	143,708.7
Model 5	fit.12 h.poly3	12 h	1 year	Polynomial (size + size ² + size ³)	1000 m	143,709.2
Model 6	fit.12 h.poly2	12 h	1 year	Polynomial (size + size ²)	1000 m	143,768.9
Model 7	fit.12 h.2 K	12 h	1 year	Linear (size)	2000 m	143,862.0
Model 8	fit.24 h	24 h	1 year	Linear (size)	1000 m	143,874.1
Model 9	fit.12.h.noSwitch	12 h	1 year	Linear (size)	No threshold	144,041.8
Model 10	fit.12 h.log	12 h	1 year	Logarithmic log(size)	1000 m	144,465.2

ARS = area restricted search, TOD = time of day, DOY = day of the year. The starting model (8) allowed for switching probabilities from Traveling to ARS ~ f (size × TOD + DOY) and from ARS to Traveling ~ f (size + DOY)

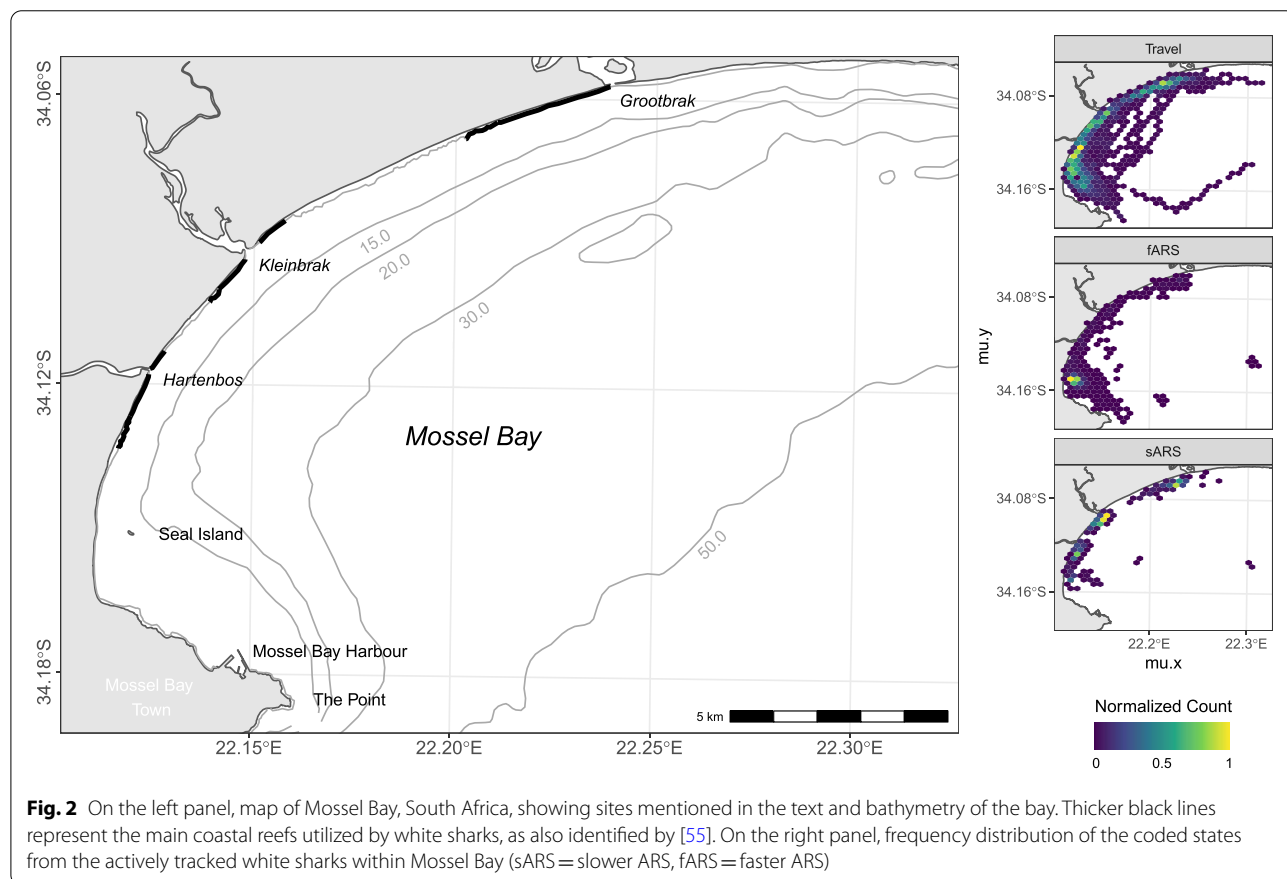


Fig. 2 On the left panel, map of Mossel Bay, South Africa, showing sites mentioned in the text and bathymetry of the bay. Thicker black lines represent the main coastal reefs utilized by white sharks, as also identified by [55]. On the right panel, frequency distribution of the coded states from the actively tracked white sharks within Mossel Bay (sARS = slower ARS, fARS = faster ARS)

Instead, larger white sharks are more likely to be in a traveling mode than using an active search pattern.

Lastly, even though all size classes are more likely to use the faster ARS movement pattern around the pin-niped colony, the time spent in that higher energy-consuming state decreased with size (Fig. 6), ANOVA [$F(2,168) = 6.9487, p = 0.0013$].

Discussion

Understanding the daily decisions that an individual makes throughout its ontogeny to maximize its survival, while modifying its Eltonian niche, requires the collection of high-resolution data, both spatially and temporally, as those are the scale at which fine-scale behavioural choices occur [80]. Movement data can be used as a behavioural

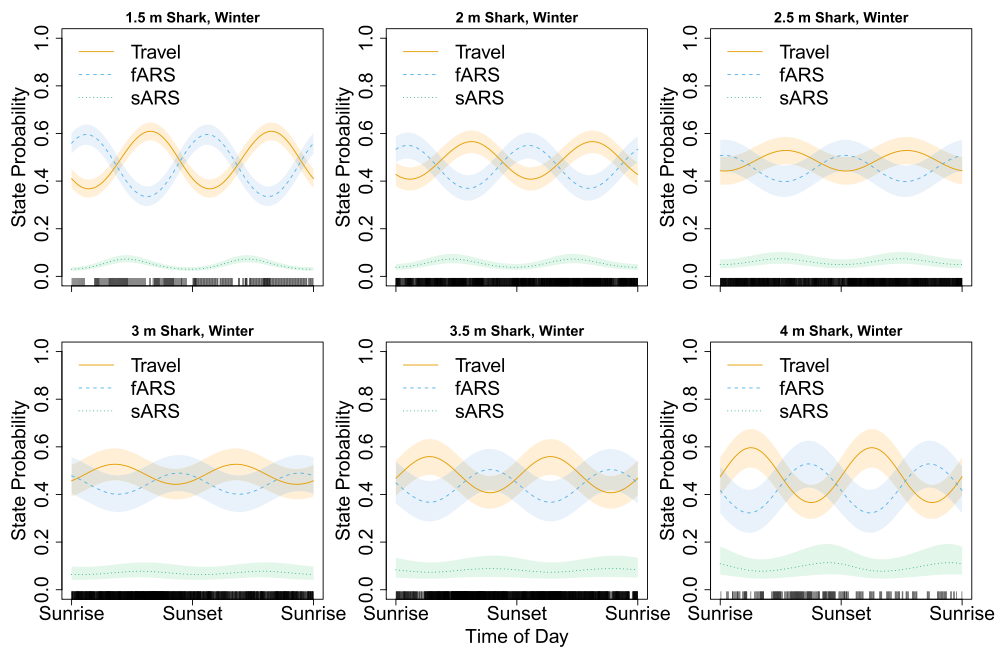


Fig. 3 Stationary distributions (and relative 95% confidence intervals) of hypothetical white sharks of different size classes (mean ± 0.25 m TL) in winter period (winter solstice ± 90 days) within the Mossel Bay area. Rug plots are added on the x-axis as index of effort. sARS = Slower ARS, fARS = Faster ARS

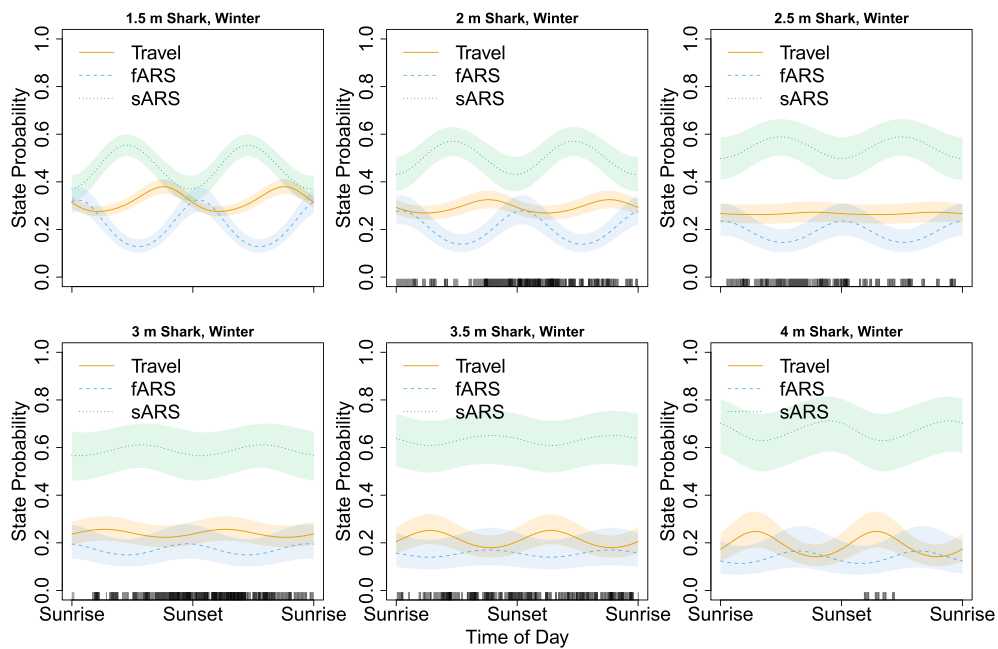
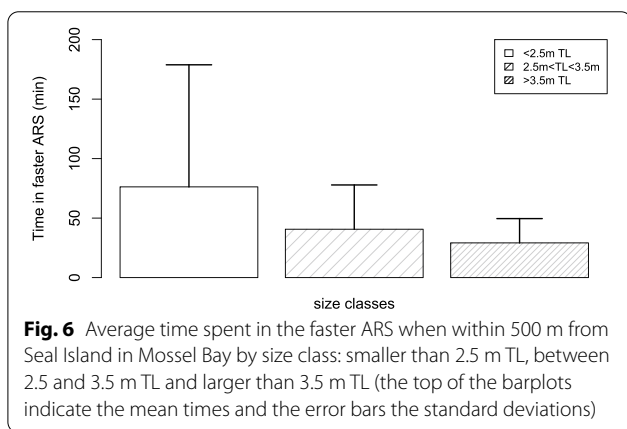
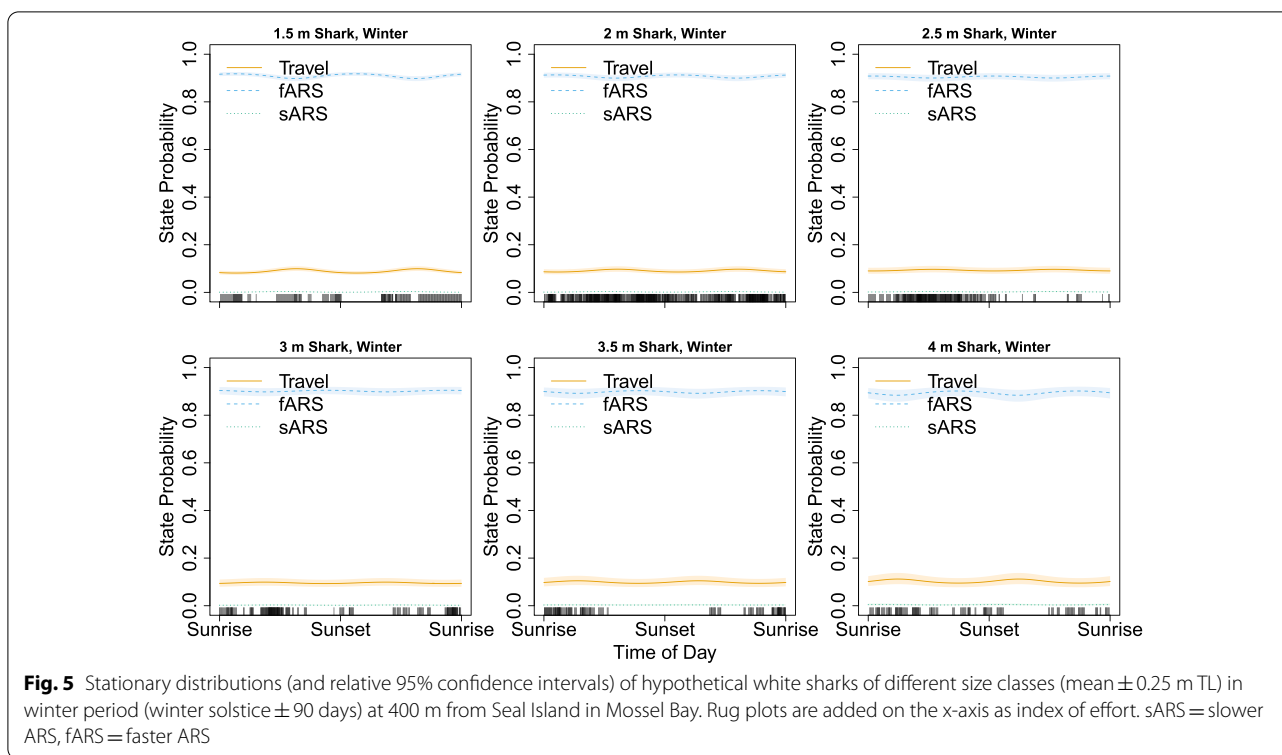


Fig. 4 Stationary distributions (and relative 95% confidence intervals) of hypothetical white sharks of different size classes (mean ± 0.25 m TL) in winter period (winter solstice ± 90 days) at 400 m from a river mouth in Mossel Bay. Rug plots are added on the x-axis as index of effort. sARS = slower ARS, fARS = faster ARS



proxy, especially when correlated to habitat features and a species' phenotypic characteristics [71, 72, 88]. In this study, 19 white sharks were acoustically tracked and their positions were modelled using a hidden Markov model. Movement-based behavioural states were a function of ontogenetic development, time of day, season, and habitat features.

The ACF for step length suggests the possibility that some other variables, which were not accounted for, could explain the remaining autocorrelation. This could be the focus of future projects, for example collecting

in situ data on environmental variables while manually tracking white sharks in coastal areas.

The extended use of Mossel Bay's main coastal habitats (coastal reef systems and the pinniped colony) by all the tracked white sharks during this study was similar to previous studies which investigated white shark activity in the area since 2005 [55, 58, 89]. This suggests a consistent use of this bay by white sharks.

A potential caveat of our modelling approach lays in the difficult ecological interpretation of the states [105]. One of the original objectives was to investigate whether different size classes show certain movement types in different areas and at different times of the day and/or the year. Consequently, the states were initially loosely named "At Seal Island", "At estuary mouths" and "Travelling". The choice of three states was an a priori decision but was also tested, as suggested by [83] and similarly to what Towner et al. [96] did. However, the states turned out to have different movement characteristics than expected: for instance, the occurrence of both ARS states close to estuary mouths. Therefore, the behavioural interpretation of the three states and their names had to change. Hence, the constraint of non-transition between the two ARS states and/or the subjective interpretation of the results could not hold any longer. Future research using different technologies, such as multi-sensor data loggers equipped with a combination of a video camera

and a high-resolution accelerometer [99], could show whether our interpretations of the states are still valid as well as, for instance, whether transitions between the two ARS states do indeed occur. Another potential limitation of our movement-based behavioural interpretation was related to the fact that, although marine animals move within a three-dimensional environment, we defined behaviours based on two-dimensional movements (as also done by others: e.g., [96]). Because the parts of the bay where white sharks moved seldom exceeded 20 m depth and lacked a thermocline for most of the year, we are confident that the horizontal dimensions of the movement patterns we assessed over 5-min intervals in Mossel Bay, can adequately approximate the three-dimensional movement of white sharks within this bay, and possibly other shallow coastal environments, as suggested when comparing our results to the mode cruising speeds for white sharks assessed using speed sensors in Harding et al. [41] (Additional file 1).

Model selection highlighted a few temporal aspects of the behaviour of white sharks in Mossel Bay. Firstly, seasonality is important, not only in terms of the general distribution of white sharks within the bay [89], but also because the use of different modelled states appear to vary at different times of the year. Secondly, white sharks behave with a 12-h cyclical periodicity in Mossel Bay, and not circadian as shown in other nearby white shark aggregations such as Gansbaai [56, 96] and False Bay [51]. In False Bay white sharks have shown a preference for smaller groups or solitary Cape fur seals traveling back to the colony, mainly around sunrise [69]. In Mossel Bay, the temporal variations in the traversing behaviour of Cape fur seals around the colony, especially in winter [73], peak the probability of encounter for white sharks around both dusk and dawn.

Examination of the state-dependent distributions of the movement parameters showed that, although the two ARS states were almost identical in the distribution of turning angles, their step length distributions were statistically different, with one mean being around double than the other. As one of the main assumptions of HMMs requires equally spaced measurements of the observed variables, a longer step length (over the same time interval) relates to a faster movement segment. Therefore, the difference between these two states has more to do with the speed of movement than the tortuosity of the search pattern. Hence, these two states were named “faster” and “slower” ARS.

In proximity to the pinniped colony in winter, the faster ARS state, interpreted here as “patrolling”, was the most likely state to be used by all white shark size classes identified in this study. This may be because higher speeds are required to increase the frequency of

encounters with traversing Cape fur seals. This pattern can then be followed by momentary burst speeds by the shark, quantified at up to 6.5 m s^{-1} [91]. The faster ARS is still slower than the traveling bouts used to arrive in or leave an area of interest (as confirmed by [99]). A “random walker” must indeed exercise a trade-off between moving too fast (with the risk of leaving a spatially limited, resource-rich, patch) against maximizing the probability of encountering traversing prey [97]. A shark will also increase its attention to its surroundings when reducing its speed and increasing its frequency of turning [60, 99].

The larger tracked white sharks spent less time in the patrolling state near the pinniped colony compared to the smaller conspecifics. These larger size classes were also more likely to be found in this faster ARS state before sunrise and sunset. During these two optimal scotopic periods, the ambient light levels are too low for the prey to distinguish an ambushing predator below but sufficient for a white shark to identify the silhouette of its prey at the surface [69]. Intraspecific competition and/or less accrued hunting experience [70] are likely to force the smaller white sharks to forage for longer and outside these crepuscular, optimal, hunting periods. While the hunting behaviour of smaller white sharks changes spatially to suboptimal conditions in False Bay [70] and at the Farallon Islands [36] the shift towards suboptimal conditions appears to be temporal in Mossel Bay. This is possibly because of the small size of its pinniped colony: different behavioural patterns related to different size in the islands with pinniped colonies was also observed in two other white shark aggregations, such as Guadalupe and South Farallon Islands [48].

Originally, we expected the faster ARS to be related only to Seal Island, the area where Cape fur seals predictably occur. However, this patrolling state also occurred over coastal reefs nearby the estuary mouths, changing our initial interpretation of both ARS states. Due to the absence of pinnipeds confirmed by the tracking teams the faster ARS state in these areas may be interpreted as an intensive, meticulous, search pattern for other prey: most likely smaller demersal elasmobranchs and bony fishes, as also predicted by [48]. These groups are common in the diet of white sharks, especially when smaller than 3 m TL [19, 31, 33]. It is important to note that while movement data can be used as a proxy for behaviour, it provides no insight into prey availability. Other studies support the high frequency of occurrence for both teleost and elasmobranch species over reef systems in Mossel Bay (Ralph Watson, PhD thesis submitted) and neighbouring coastal areas [26, 77]. The patrolling pattern over reefs associated with estuary mouths may potentially define these sites as important foraging grounds, not only for many bony and cartilaginous fish species [2, 101],

but also for white sharks. White sharks are known to prey on such reef-associated demersal species [23, 38] specifically in inshore areas and at other white shark aggregations in South Africa [33, 50, 51]. Future research using baited remote underwater video systems (BRUVs) concurrent with active acoustic tracking, or multi-sensor data loggers fitted with video cameras deployed on white sharks (as done by [22] around a pinniped colony), could shed light on the composition and abundance of possible prey species, as well as the behavioural choices white shark make at these coastal reef sites.

The patrolling state of white sharks over reefs mainly occurred around twilight conditions. This conforms to the activity patterns of other predators which are also able to predict and respond to periodical prey availability [37]. Around sunset, diurnal fish species seek cover, and after a “quiet period” the nocturnal species emerge (twilight hypothesis: [74]. An ambushing predator seeks those species exiting their refuges, giving it a predictable advantage [43, 82]. White sharks could exploit moments of higher competition for refuges, between diurnal or nocturnal species: a competition that may causes reef fish to become less vigilant toward predators [87].

Being an obligate ram ventilator [67] a white shark is expected to either actively search for mates and or food (patrolling) or travel between important resource-rich areas [70]. A possible explanation for the main movement pattern found over estuary-related reef structures may be related to its slower nature, possibly to the need to reduce swimming-related energy costs at times, while maintaining the higher metabolic requirements of a regional endothermic species [32, 98]. This type of behaviour was regularly recorded when the tracked sharks slowed down for hours along those reefs, and often they were even visually observed drifting in the slow current at the surface. This behaviour could be furthermore facilitated by environmental variability in specific areas, within the context of the energy landscape [92]: for example, a possible increase in oxygen content, caused by coastal wave breaking around the estuary-related reefs of Mossel Bay (as firstly suggested by [58], and confirmed by in situ measurements of dissolved oxygen by Logston [52]), could allow white sharks to slow down their swimming requirements while turning to remain in the same advantageous area. This slowest movement pattern was parameterized as an ARS (sARS) although not functionally a search for food (not an ARS *sensu stricto*). White sharks use this behavioural pattern over coastal reefs mainly around sunrise and sunset. This is likely in anticipation of, or following, higher energy expenditure at the pinniped colony, as witnessed a few times while tracking, when directed movement

from Seal Island to one of the estuaries followed a natural predation, or vice versa. The slower ARS state over coastal reef habitats, described as “resting”, was particularly prevalent in the larger white shark size classes. As previously discussed, the larger and more experienced sharks are found at Seal Island during the optimal temporal windows for hunting pinnipeds. Thus, they are more likely to be successful during those hunting forays aimed at pinnipeds. A greater hunting success would be more often linked to higher metabolic heat [90] related to the digestion of pinniped blubber which is high in energy and lipid content [17]. When moving away from the pinniped colony (as described by [58] they would need to recover from the Specific Dynamic Action, more often than their smaller counterparts. Few of the tracked white sharks were also fed with an acoustic transmitter fitted with a temperature sensor which confirmed, together with visual observations, few predation events on Cape fur seals: in those cases a straight move toward those coastal reefs was followed by an increase in stomach temperature and a concomitant reduction in rate of movement (Gennari et al. in preparation). If this behavioural choice was confirmed also in terms of energy expenditure, it could represent an energetically adaptive advantage [12, 78] for these regional endothermic, obligated ram ventilators, with a high metabolic scope [11, 63]. Ontogenetically, while the ratio between body volume and body surface area increases so does the importance of recovering spent energy [5, 18]. ARS state close to an estuary mouth could reveal the possible importance of estuary-related reef systems for white sharks.

The high probability of this slower and tortuous movement pattern could emphasize the importance of those coastal reefs for white sharks, especially around estuary mouths, not only for foraging but also for energy conservation, as suggested by Johnson et al. [58]. Testing this area-specific and energy-related hypothesis, linking environmental and movement variables, looking at explaining the higher presence of white sharks around estuaries, in Mossel Bay and elsewhere [15, 51, 76, 93] could be of interest to future studies using animal-borne accelerometers and speed sensors.

Larger, presumably more experienced, white sharks were more likely to be in the traveling state, particularly after sunrise and after sunset, when moving away from estuary-related reefs and the pinniped colony. This would allow them to move quicker among important areas of the bay. In most animal species, the cost of transport decreases with increasing mass, which is also valid for ram-ventilating sharks [20], and so larger white sharks can maintain a higher traveling speed for longer. Smaller

conspecifics are equally likely to be in search of food or travelling, possibly related to their higher reliance on a fish-based diet [31, 33]. This reiterates the higher focus, and experience, the larger white sharks showed in this study by patrolling mainly over very restricted areas of coastal reefs, possibly over areas with higher fish abundance [103].

Another study modelled the movement of white sharks in a nearby bay [96] and identified two separate hunting strategies to prey upon pinnipeds at the surface: a slower sit-and-wait state (ARS) and a faster active searching (patrolling) state [98]. While we believe their patrolling state is similar to our faster ARS state, their slower ARS state (with similar distributions of the movement parameters to the sARS state in this study) was assigned to an ambushing, foraging-related state, because they observed five predation attempts on Cape fur seals. One could argue that a white shark constantly in a pinniped-hunting mode (patrolling or ambushing) would be extremely inefficient [98] particularly in inshore areas where pinnipeds are not predictable. Observation of a predation by an opportunistic forager might not necessarily define the movement state it was in just before the predation attempt. A white shark could be moving slowly and resting, but if a prey happened to be nearby, the shark could still take its chance. Our alternative hypothesis to Towner et al. [96] suggests that similarly to other marine predators [42] white sharks might use a single, general, search strategy (patrolling) to target different prey types over different habitats: around the pinniped colony or over coastal reef systems, especially nearby an estuary mouth. When a prey is identified a white shark will increase its activity and the final metabolic cost of its search. However, that final bout is not discernible with a method based on 5-min sampling intervals. This will require further investigation, possibly using continuous technology like accelerometers and gyroscopes.

Even though the large sample size, we did not manage to obtain sufficient data from all size classes, across all habitats and throughout the entire diel period. While this could be seen also as a result in terms of behavioural preferences, we decided not to focus our interpretation of the results on specific size classes but rather describe ontogenetic trends in movement-based behavioural choices. Through model selection, the data on the white shark movement strategy presented here suggests a linear ontogenetic trend. This is in line with the suggestion [36, 49, 55] that habitat knowledge and behavioural experience, not only concerning foraging on pinnipeds, may be gradually gained and accumulated as a white shark grows. Owing to the absence of parental care in all elasmobranchs, white sharks may take years to learn and

refine their behaviours through trial and error. This would explain different size-related patterns, both spatially and temporally [13, 36, 55, 70]. The increased efficiency in the use of resources is not related to an ontogenetic variation in speed used when foraging [14]. These speeds are likely to be adaptive and related to body shape and energetics. Rather, the improvement can be linked to a decrease in the area used [55] and/or in the time used during these phases by larger individuals. In this study older white sharks covered smaller areas and appeared to spend less time on faster, and thus more energy-costly, movement patterns. Differences in spatial and temporal patterns could also relate to intra-specific competition, forcing smaller white sharks to use specific behaviours within suboptimal, wider, spatio-temporal boundaries.

Conclusions

While most of the literature on the foraging ecology of white sharks focuses on their relationship with pinnipeds, we show here how all the movement-based behavioural patterns described for white sharks in a coastal environment were possibly focused on specific aims, namely foraging, resting, or directional movement. We recommend that some of these hypothesized behaviours should be the subject of further investigations using alternative technologies, such as multi-sensor data loggers and baited remote underwater video systems.

The findings of this study have implications for the conservation of white sharks in South Africa. The movement-based behavioural insights gained from this study highlight the use of ARS patterns in specific areas with higher abundances of reef-associated fish species occur, possibly foraging related. This supports the dependence of white sharks on available fish prey species (*inter alia* [49] and [33]) across the plasticity of its ontogeny, even in coastal areas where pinnipeds are abundant. The conservation status of the only pinniped species endemic to the African continent has improved and is now considered stable [61]. We propose that a major threat to the conservation of white sharks in South Africa may reside in the inefficient management of coastal fish species [25, 46, 81] particularly those associated with estuaries [101, 102]. This is of paramount importance to the white sharks population of southern Africa which comprises mainly juveniles and subadults along its coast [1, 28, 45, 89].

Prey availability is a major threat to several terrestrial predators [9, 104] and is likely to be even more important in marine food webs (Link 2002). In the United States a series of federal, state, and other regulations designed to restore marine populations using an ecosystem-based approach has proven successful [46]. Populations of meso-predator teleosts and elasmobranchs have been

increasing in Californian waters since the mid-1990s, following better regulations imposed on commercial fisheries [84]. This management approach together with the protection of marine mammals in federal waters since 1973 has led to an increasing population of white sharks along the North Eastern Pacific [16, 27, 53, 54, 68] and North Atlantic coastal areas [24].

We, therefore, recommend that conservation efforts in South Africa should avoid a predator-centric approach (single species conservation strategy) and rather adopt a holistic ecosystem-based approach that acknowledges the management needs of important prey species to sustain the carrying capacity of a top predator population [30], particularly when the population is of conservation concern, and has a high tourism value.

Methods

Study site

Mossel Bay is a large semilunar coastal embayment situated on the southern tip of Africa (34°10' S, 022°10' E; Fig. 2). The town of Mossel Bay is situated on the rocky headland (Cape St. Blaize) of the southern end of the bay. The bay hosts a small island (Seal Island) with a colony of approximately 5,000 Cape fur seals [61]. The coastline is characterized by long sandy beaches interspersed by a series of coastal reefs, which extend into the bay to a maximum depth of approximately 40 m, in association with the Groot Brak paleo river [21]. The mouths of three small estuaries (Hartenbos, Klein Brak and Groot Brak) are situated in the bay. Seal Island and the coastal reef systems, particularly those adjacent to the mouths of the three estuaries, make up the primary marine habitats used by white sharks in Mossel Bay [55, 58, 89]. Estuaries are considered nursery areas for many marine species and represent biomass hotspots along the coastline [100, 103]. The elevated abundance of demersal elasmobranch and teleost species over reef structures has been confirmed in Mossel Bay (Ralph Watson, PhD candidate, unpublished data) and other neighbouring areas [26, 77].

Tagging and tracking

White sharks were attracted to a research vessel using bait and chum, consisting of a mixture of sardines and water. The total length of the tagged shark was visually estimated using the width of the research vessel as a reference. Lengths were recorded to the nearest 0.1 m, after an agreement between two or more experienced researchers on board, following Johnson et al. [58], Kock et al. [50], and Towner et al. [95]. Sharks were externally tagged below the first dorsal fin with VEMCO V16TP continuous acoustic transmitters (VEMCO, InnovaSea Systems). Tags were placed using either a tagging pole or a modified speargun, according to the methods described by Gennari et al. [35].

Working in rotation (with crew changes every 6 or 12 h), tracking teams used a VEMCO VR100 acoustic receiver on board the research vessel to locate and follow a tagged white shark according to the method set out in Johnson et al. [58]. Positions were recorded when three consecutive signals were received at strengths of at least 70 dB (equivalent to circa 200 m under calm tracking conditions: [35]). Vessel speed was managed to obtain a desired GPS sampling interval of 10 min. Tracking around Seal Island had a sampling interval of 5 min, so as not to lose the tagged shark among the complex rock structures.

When a tracked shark was too close to the surf zone, a GPS position was taken directly offshore of the animal's location. In order to get the 'true' position of the tracked shark, a correction function was applied to the recorded position of the tracking vessel, using detection range testing data (after [35]) and the receiver's signal strength of the recorded tag detection. The distance to the tagged shark was calculated using the following equation:

$$\begin{aligned} \text{Distance to the tagged shark} \\ = (-0.4145 \times \text{signal strength} + 39.4181)^2. \end{aligned}$$

The duration of all continuous tracking sessions was terminated due to either adverse sea conditions or loss of the tracked shark. To reduce uncertainty in the location of individuals when they were momentarily lost by the tracking team, the tracking segments were split into continuous sessions using a minimum threshold of 2 h between consecutive relocations. Two hours was the maximum timeframe in the field to relocate a shark before terminating the tracking session. Continuous tracking sessions were further split into 12-h segments to improve convergence during model fitting.

Modelling approach

In order to test the influence of covariates on the state transition probabilities, a Continuous-Time Correlated Random Walk (CTCRW) model with a bivariate normal error radius of nine meters (listed GPS accuracy of the VEMCO VR100 receiver) was fitted to the filtered data using the packages *momentuHMM* [71] and *crawl* [57] in R version 4.0.0 [85]. The CTCRW model was then used to predict locations at regular 5-min intervals, meeting the requirement of regular time intervals for fitting an HMM. Tracking segments that produced no estimate of variance for the CTCRW parameters, or variance estimates that were unreasonably large, were removed. Model predictions were assessed visually and removed if the predicted locations were judged unrealistically distant from the observed locations.

A three-state HMM was then fitted to the regularized step lengths and turning angles calculated from the locations predicted by the CTCRW model [71]. Preliminary model fitting and selection by Akaike Information Criterion (AIC) suggested that a Gamma and a von Mises were the most appropriate distributions for step lengths and turning angles, respectively [71].

The choice of number of movement states by model selection was supported by our observations while tracking and by previous work [55, 58] on acoustically tracked white sharks in Mossel Bay. The first two patterns were area-specific with slower, focused, tortuous movements, over coastal reefs and around the pinniped colony. The third pattern related to faster more directed movement pattern in between the two habitats. The first two movement patterns bear similarity to the Area Restricted Search (ARS) described by Benhamou [4]. ARS patterns are known to increase encounter success with prey (yet not in all species: e.g., [6]) and to occur more often at focal sites which, in this case, are two habitat types with different prey presence: Seal Island (the pinniped colony) or the coastal reef complexes adjacent to estuary mouths, where pinnipeds are absent. As the behavioural patterns of pinnipeds and coastal reef fishes are different, different movement-related hunting patterns of white sharks may be expected. In contrast, a more direct movement was often observed when sharks moved between these focal sites.

The intervals between relocations were too long to identify bursts or short changes in activity (likely indicative of feeding events) and visual observations from a vessel of those feeding events are either too sparse (in the case of pinnipeds) or extremely unlikely (in the case of fish). Therefore, we focused on identifying ontogenetic differences in movement patterns in relation to the different habitat types within the main activity areas of white sharks [55, 58]. One of the objectives

movement state [71]: (1) the mean parameter for the Gamma distributions on step length was higher for state one (directed movement state) than for states two or three (area related states), (2) the variance parameter for the Gamma distributions was higher for states two and three than state one; (3) the concentration parameter of the von Mises distribution was higher for state one than for states two or three.

To account for any influence of distinct habitats, such as Seal Island or the main coastal reef complexes close to river mouths (Fig. 2), on the behavioural choices of the sharks, we calculated two variables for each positional fix. These variables represented the minimum distances to Seal Island and the closest estuary mouth. We incorporated them into the model to allow behavioural changes to be influenced by habitat features: the closer a white shark was to the pinniped colony or to an estuary, the likelier the switch to one of the ARS behaviours, as observed while tracking.

Lastly, the transition probabilities were constrained, such that the two ARS states could not switch between each other without first passing through a directed state (travel). The coastal reef areas do not overlap with the one around Seal Island and so a different movement pattern must occur over those in-between areas that white sharks do not focus on [58].

As a result, for each individual, k , the time-dependent transition probability matrix Γ is given by:

$$\Gamma^k(t) = \begin{bmatrix} \gamma_{11}^k(t) & \gamma_{12}^k(t) & \gamma_{13}^k(t) \\ \gamma_{21}^k(t) & \gamma_{22}^k(t) & 0 \\ \gamma_{31}^k(t) & 0 & \gamma_{33}^k(t) \end{bmatrix},$$

where $\gamma_{ij}^k(t)$ is the conditional probability of the individual k being in state j in the time interval $(t, t + 1)$, given it is in state i during the interval $(t - 1, t)$.

Covariates on the state transition probabilities were included by the following function:

$$\text{logit}(\gamma_{ij}^k(t)) = \begin{cases} \beta_{0ij} + \beta_{1Aij}x_{1Akt} + \beta_{2ij}x_{2kt} + \dots + \beta_{6ij}x_{6kt} + \beta_{7ij}x_{2kt}x_{3kt} + \beta_{8ij}x_{2kt}x_{4kt} + \beta_{9ij}x_{2kt}x_{5kt} + \beta_{10ij}x_{2kt}x_{6kt} + \epsilon, \text{for } i = 1, j = 2 \\ \beta_{0ij} + \beta_{1Bij}x_{1Bkt} + \beta_{2ij}x_{2kt} + \dots + \beta_{6ij}x_{6kt} + \beta_{7ij}x_{2kt}x_{3kt} + \beta_{8ij}x_{2kt}x_{4kt} + \beta_{9ij}x_{2kt}x_{5kt} + \beta_{10ij}x_{2kt}x_{6kt} + \epsilon, \text{for } i = 1, j = 3 \\ \beta_{0ij} + \beta_{2ij}x_{2kt} + \beta_{5ij}x_{5kt} + \beta_{6ij}x_{6kt} + \beta_{9ij}x_{2kt}x_{5kt} + \beta_{10ij}x_{2kt}x_{6kt} + \epsilon, \text{otherwise} \end{cases}$$

was to investigate whether the ARS patterns used by white sharks in a coastal embayment are specific to sites where different prey species are known to occur: i.e., whether the movement pattern related to foraging for pinnipeds is used only around Seal Island. We hypothesized that the ARS patterns would differ over coastal reefs and around a pinniped colony, indicating that a relationship exists between movement patterns and potential prey types.

The following parameters were constrained in the model to effectively capture the two more focused (tortuous) movement patterns, versus the more direct

where x_{1A} and x_{1B} are binary variables representing the distance of an individual from Seal Island or the closest estuary mouth, respectively. x_2 represents the size (TL) of the individual, x_3 and x_4 are the trigonometric functions $\sin \frac{2\pi t}{0.5}$ and $\cos \frac{2\pi t}{0.5}$ with a possible 12- or 24-h period, where t_c represents the fraction of the 24-h daily cycle. x_5 and x_6 are similarly the trigonometric functions $\sin \frac{2\pi t}{365.25}$ and $\cos \frac{2\pi t}{365.25}$ with a period of 1 year when t represents the Julian day of the year.

Different variations of the complete model were fitted and compared using AIC values (Table 2 ordered according

to AIC values). The starting model (final Model 8) allowed no transition between ARS states. Transition probabilities from traveling to one of the ARS states were allowed (i) to increase when the distance to Seal Island or an estuary mouth was less than 1 km, and (ii) to vary based on a) the Day of The Year (DOY as a circular variable with a 364-day period) and b) the interaction between a linear variability in body size (TL) and TOD. This was because the onset of the ARS states in specific core areas was expected to vary seasonally [89] and according to the different diel use of specific areas by different size classes [55, 58]. In the starting model, the transition probabilities from one of the ARS states to traveling were allowed to vary based on the DOY and only a linear variability in body size (TL). The end of the ARS was not expected to depend on a specific TOD, but rather on how long it took to achieve the goal of either ARS state.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-022-00295-x>.

Additional file 1. Visual assessment of pseudo-residuals obtained using the three-state HMM on the step lengths (top row) and turning angles (bottom row) data, obtained by manually tracking 19 white sharks in Mossel Bay.

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Author contributions

EG and PDC designed the study. DTI and EG analysed and interpreted the data. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

All tagging and tracking work was conducted under research permits issued by the South African Department of Environmental Affairs (including RES2009-11, RES2010-04, RES2011-27, RES2012-18).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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