

Sex-specific and individual preferences for hunting strategies in white sharks

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Summary

1. Fine-scale predator movements may be driven by many factors including sex, habitat and distribution of resources. There may also be individual preferences for certain movement strategies within a population which can be hard to quantify.

2. Within top predators, movements are also going to be directly related to the mode of hunting, for example sit-and-wait or actively searching for prey. Although there is mounting evidence that different hunting modes can cause opposing trophic cascades, there has been little focus on the modes used by top predators, especially those in the marine environment.

3. Adult white sharks (*Carcharodon carcharias*) are well known to forage on marine mammal prey, particularly pinnipeds. Sharks primarily ambush pinnipeds on the surface, but there has been less focus on the strategies they use to encounter prey.

4. We applied mixed hidden Markov models to acoustic tracking data of white sharks in a coastal aggregation area in order to quantify changing movement states (area-restricted searching (ARS) vs. patrolling) and the factors that influenced them. Individuals were re-tracked over multiple days throughout a month to see whether state-switching dynamics varied or if individuals preferred certain movement strategies.

5. Sharks were more likely to use ARS movements in the morning and during periods of chumming by ecotourism operators. Furthermore, the proportion of time individuals spent in the two different states and the state-switching frequency, differed between the sexes and between individuals.

6. Predation attempts/success on pinnipeds were observed for sharks in both ARS and patrolling movement states and within all random effects groupings. Therefore, white sharks can use both a 'sit-and-wait' (ARS) and 'active searching' (patrolling) movements to ambush pinniped prey on the surface.

7. White sharks demonstrate individual preferences for fine-scale movement patterns, which may be related to their use of different hunting modes. Marine top predators are generally assumed to use only one type of hunting mode, but we show that there may be a mix within populations. As such, individual variability should be considered when modelling behavioural effects of predators on prey species.

Key-words: acoustic telemetry, foraging mode, fine-scale movement, hidden Markov Model, predator–prey

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Introduction

Animals may use a variety of movement strategies to locate prey including systematic searching and a variety of types of random walk (e.g. Papastamatiou *et al.* 2011; Sims *et al.* 2012). The type of strategy used will also depend on the hunting mode of the predator with two general modes: 'active search/patrolling' and 'sit and wait' (Huey & Pianka 1981; O'Brien, Browman & Evans 1990). 'Patrolling' or 'roving' behaviour is defined by a predator moving through its environment looking for prey (although the movement strategy may vary, e.g. random walks vs. directed), whereas 'sit-and-wait' or area-restricted searching (ARS, especially if the predator must move continuously) behaviour sees the forager waiting for prey to cross the boundary of its strike space over long time periods (O'Brien, Browman & Evans 1990; Alpern *et al.* 2011). Experimental work in terrestrial systems has suggested that patrolling/roving or sit-and-wait hunting modes in predators may cause trophic cascades that act in opposing fashion and on different trophic levels (Schmitz 2008). Although predator hunting mode may cause variations in predator-induced trophic cascades, it is rarely considered in studies of top-level predators (Heithaus *et al.* 2009; Martin & Hammerschlag 2012; Higginson & Ruxton 2015).

Predator movements are not going to be solely concerned with finding prey but also include other factors such as finding mates or optimal environmental conditions. Movement path structure will vary in time and space in response to the environment and as the goals of movement change (e.g. Papastamatiou *et al.* 2011; Langrock *et al.* 2012). Predator movements are commonly found to differ between time of day, sex, season and in response to prey distribution. There may also be considerable variability in individual movements within a population potentially due to individual specialization. Individual specialization in animal behaviour is being increasingly recognized as prevalent in animal populations and may manifest itself in an animal's diet, patterns of movement or other specific behaviours (e.g. Bolnick *et al.* 2003; Estes *et al.* 2003; Matich, Heithaus & Layman 2011). The presence and degree of individual specialization can have large-scale implications from both an ecological and conservation standpoint, and may even affect a population's stability (Bolnick *et al.* 2003). Individual specialization may be driven by levels of intra and interspecific competition and/or be related to size, sex, habitat and available prey (Matich, Heithaus & Layman 2011; Nifong, Layman & Silliman 2015; Rossenblatt *et al.* 2015).

Generally, individual variability in movements is measured by comparing some aspect of the movement process to model predictions (e.g. correlated random walks), or the degree or even presence of cyclical behaviour (e.g. diel habitat shifts, Austin, Bowen & McMillan 2004; Papastamatiou *et al.* 2010, 2011; Matich & Heithaus 2015). Such an approach may miss movement processes at fine spatial

scales, which is ultimately the scale at which foraging occurs. Furthermore, these studies identified intraspecific variability, not specifically if individuals prefer a particular movement strategy or routinely reuse the same strategy.

An analytical framework is required to detect fine-scale differences in movements between individuals while accounting for other factors such as size and sex. Movement data from marine predators also suffers from large positional errors or being collected at irregular intervals, making it difficult to select suitable metrics. However, some movement data can still be collected somewhat regularly with relatively low spatial errors (e.g. active tracking) making movement analysis easier. In these cases, hidden Markov models (HMMs) offer a powerful and readily applicable set of analytical tools. In particular, HMMs can be applied to movement data in order to identify behavioural switches and how these are driven by environmental conditions (Patterson *et al.* 2009; Langrock *et al.* 2012). HMMs are time-series models where an observation model (e.g. step lengths and turning angles between movement steps) is driven by an underlying hidden process model (e.g. ARS or transient behaviour, Patterson *et al.* 2009; Langrock *et al.* 2012). HMMs directly account for the serial dependence prevalent in electronic tagging data and allow for the decoding of latent behavioural states, or at least proxies thereof (Patterson *et al.* 2009). Often, these states are assumed to be associated with foraging (ARS) and non-foraging (transient) behaviour, although designating foraging activity based purely on movement paths is problematic (e.g. Bestley *et al.* 2008). In the case where foraging can be verified, ARS movements prior to foraging would be considered a 'sit-and-wait' strategy, while patrolling movements and foraging would be a more active searching mechanism and considered 'patrolling or roving'.

White sharks, *Carcharodon carcharias*, are the world's largest carnivorous fish and are widely distributed in temperate and tropical waters. The species has received considerable telemetric focus, largely due to its charismatic profile, important ecological role and conservation status. White sharks often show seasonal residency to pinniped pupping areas, as juvenile seals or sea lions may present a suitable prey source (Klimley *et al.* 1992, 2001; Laroche *et al.* 2008). While associated with pinniped rookeries, sharks are thought to patrol parallel to the shoreline- or target-specific locations where prey may be vulnerable (e.g. entry or haul-out sites, Goldman & Anderson 1999; Klimley *et al.* 2001; Martin, Rossmo & Hammerschlag 2009; Jewell *et al.* 2014). Pinnipeds are primarily ambushed at the surface although previous studies have not quantified if the sharks were performing ARS or patrolling behaviour before the attack (e.g. Martin *et al.* 2005). There may be spatial segregation and differences in long-term movements or migration cycles between the sexes (Kock *et al.* 2013; Domeier & Nasby-Lucas 2013). Further complicating the study of white shark behaviour is that shark cage-diving ecotourism occurs at several aggregation sites, where bait and/or chum is used to attract individuals to boats for

tourist viewing. Available evidence suggests that cagediving operations will alter the short-term movements of white sharks but are unlikely to influence long-term migrations (Strong *et al.* 1992; Laroche *et al.* 2007; Huveneers *et al.* 2013; Gallagher *et al.* 2015). However, a statistical framework is required which can detect changes in behaviour while being able to account for the presence of eco-tourism activities, gender and shark size.

We developed and fitted mixed HMMs to fine-scale acoustic tracking data to identify the drivers of switching movement states (ARS or patrolling) in individual white sharks within a heterogeneous seascape environment in South Africa. By definition, all white shark strikes of seals at the surface are ambush strikes, but individuals are faced with a choice regarding how to hunt; remain residential in a chosen location by performing ARS to wait for prey; or actively patrol to locate seals swimming on the surface (Klimley *et al.* 2001; Martin, Rossmo & Hammerschlag 2009). While these terms are associated with foraging, they are broader in scope and do not define the resource (e.g. shark movements may be non-foraging and associated with other functions such as digestion). By simultaneously recording predation attempts on seals at the surface by tracked sharks, we could specifically link the movement process to a hunting mode. Our goals were to (i) determine the role of shark size, sex and individual preference on movement state dynamics, and (ii) evaluate whether sharks use both ARS and patrolling to catch prey, and if individuals switch between them.

Materials and methods

STUDY SITE

Gansbaai is a semi-closed embayment situated on the south coast of the Western Cape in South Africa. Dyer Island lies 4 km from the nearest shore within Gansbaai. Geyser Rock lies directly southwest of Dyer Island, and contains a breeding colony of Cape fur seals *Arctocephalus pusillus pusillus*, with an estimated total population of c. 55 000 seals (Cape Nature unpublished data). The two islands – Dyer Island and Geyser Rock – are separated by a shallow channel known as Shark Alley, which measures approximately 160 m at its widest point with a maximum depth of 7 m. The Dyer Island system is surrounded by dense forests of kelp (predominantly *Ecklonia maxima*) as well as rocky reefs, outcrops and shallow reef pinnacles. Directly inshore of Dyer Island, a large reef system, Joubertsdam, runs parallel to a 4-km stretch of sandy beach. The reef is characterized by rocky patch reefs interspersed with gullies and patches of sandy bottom. Eight cagediving operators are permitted to anchor around the reefs at Dyer Island and Joubertsdam (Towner *et al.* 2013). Several other rocky reef and kelp forest structures exist within the bay.

ACTIVE TRACKING

We attracted 14 white sharks to a research vessel using a bait line and mixture of teleost-based chum and water (Jewell *et al.* 2014). Vemco (Halifax, Canada) V16 continuous acoustic transmitters (size 16 × 54 mm, frequency 50–85 kHz) with umbrella dart heads were inserted externally at the base of the shark's dorsal fin using a modified tagging pole. Animal ethics clearance was obtained from the Department of Environmental Affairs (permit number

RES2011/54). Shark size was estimated (total length, TL cm) as the shark swam past measured sections of the vessel. Active tracking commenced immediately after tagging using a Vemco VR100 receiver and hydrophone mounted to the side of the tracking vessel. To avoid impeding shark movements, a distance of 20 m minimum was maintained from the animal, determined by tag detections of approximately 80 dB (Johnson *et al.* 2009; Jewell *et al.* 2014). Geographic locations were recorded every 5 min, and surface predation events or attempts were noted during the track. Externally applied transmitters were bright red making it easy to visually recognize the tracked individual when it was attacking a pinniped. Due to frequent changes in weather, tracking was broken up into multiple smaller segments. Tracking at night was particularly difficult so most data were from daylight hours. For further information on tagging and tracking protocol, see Jewell *et al.* (2014).

MIXED EFFECTS HIDDEN MARKOV MODELS

We considered two measures of movement from white shark tracks: step length (distance moved between 5 min sampling intervals) and turning angles between movement steps in successive sampling intervals. We developed a 2-state HMM to analyse the 76 observed bivariate time series of step lengths and turning angles. These did not represent 76 individuals but rather multiple tracking segments of the 14 individuals tagged. Each time series is assumed to behave according to a (multi-state) correlated random walk with turning angles and step lengths generated by (state-dependent) von Mises and gamma distributions, respectively. For each track, it is assumed that an underlying, non-observable Markov chain determines the time-varying (behavioural) states. Each state is associated with a distinct set of parameters for both the von Mises turning angle distribution and the gamma step length distribution. State 1 area-restricted searching (ARS) behaviour consists of relatively small step lengths with frequent turnings, while state 2 patrolling behaviour consists of longer movement steps and fewer turnings (Fig. 1). We included a point mass on zero in the step length distribution in state 1 in order to accommodate the observed zero step lengths (cf. McKellar *et al.* 2015; here ~2% of the data points). White sharks necessarily never stop moving so a zero step length is an artefact of the sampling process, corresponding to sharks moving distances smaller than error measurements of tracking (20 m).

For each track k , $k = 1, \dots, 76$, the Markov chain generating the state sequence is assumed to be non-homogeneous, with time-dependent transition probability matrix given by

$$\Gamma^k(t) = \begin{pmatrix} \gamma_{11}^k(t) & \gamma_{12}^k(t) \\ \gamma_{21}^k(t) & \gamma_{22}^k(t) \end{pmatrix}$$

where $\gamma_{ij}^k(t)$ is the conditional probability of the shark being in state j in the time interval $(t, t + 1)$, given it is in state i during the interval $(t - 1, t)$. For a single bivariate time series of step lengths and turning angles, observed for an individual track k , the likelihood of such a basic model is calculated in the standard way, that is

$$L_k = \delta^k P(\mathbf{z}_k) \left(\prod_{t=2}^{n_k} \Gamma^k(t) P(\mathbf{z}_{tk}) \right) \mathbf{1}, \quad \text{eqn 1}$$

where n_k is the number of data points for track k , the row vector δ^k is the Markov chain initial state distribution (which we will assume to be the steady-state distribution for the given covariate values at time $t = 1$), $\mathbf{1} = (1, 1)^T$ and

$$P(\mathbf{z}_{tk}) = \begin{pmatrix} f_1(z_{tk}) & \mathbf{0} \\ \mathbf{0} & f_2(\mathbf{z}_{tk}) \end{pmatrix},$$

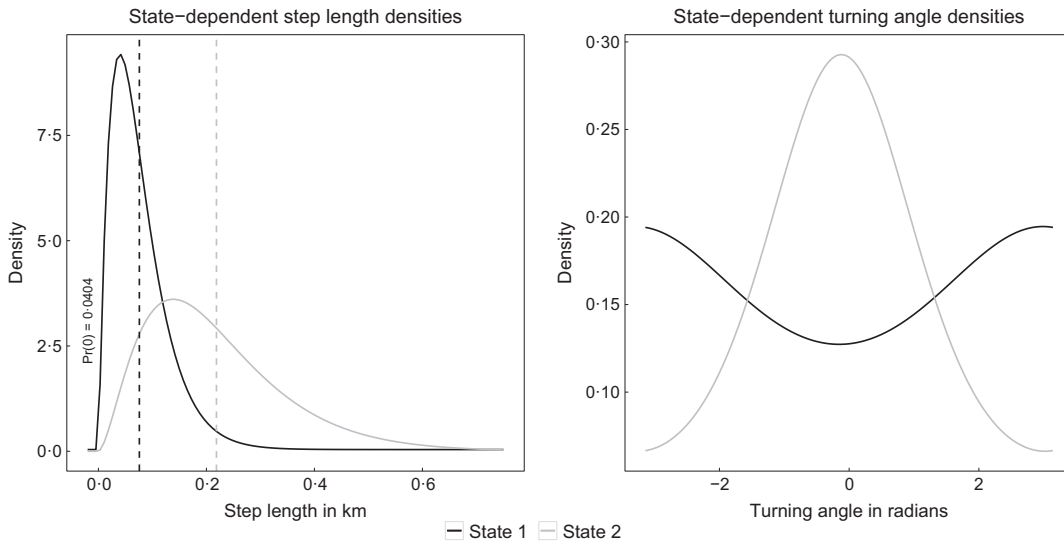


Fig. 1. State-dependent conditional densities of step length and turning angles for tracked white sharks. For the state 1 step length density, $\text{Pr}(0)$ corresponds to the point mass at zero of the zero-inflated gamma. The dashed lines correspond to the mean of the step length distributions.

with $f_i(\mathbf{z}_{tk})$ denoting the conditional density of the observation \mathbf{z}_{tk} , made at time t , given that the current behavioural state is i . The conditional density is simply the product of the state-dependent densities of the von Mises and the gamma/zero-inflated gamma distribution, respectively. Thus, we assume that step lengths and turning angles are conditionally independent, given the states. The above matrix product expression for the likelihood is a consequence of applying a recursive scheme called the forward algorithm, which is a powerful HMM tool and one of the main reasons for the popularity of these models (Zucchini & MacDonald 2009). Even for fairly large n_k , the evaluation of the likelihood usually requires only a fraction of a second, rendering parameter estimation via numerical maximum likelihood feasible in most cases. We allowed the state transition probabilities to be functions of up to three covariates: presence/absence of chum, shark total length (in metres) and time of day (h). More specifically, we use an indicator variable x_{1kt} to denote the presence/absence of chum at occasion t of track k , a variable x_{2k} to denote the total length (m) of the shark associated with track k , and two trigonometric functions with period 24 h, $\sin(\frac{2\pi t}{288})$ and $\cos(\frac{2\pi t}{288})$, to account for the diel pattern. As we model data collected at regular time intervals, with observations every 5 min, the 24-h periodicity is represented by 288 time points.

To account for heterogeneity across tracks caused by individuals being observed in different environmental and general behavioural contexts, we additionally incorporated random effects in the state transition probabilities. The full model is as follows:

$$\begin{aligned} \text{logit}(\gamma_{ii}^k(t)) = & \epsilon_{i,k} + \beta_{1,i}x_{1kt} + \beta_{2,i}x_{2k} + \beta_{3,i}\sin\left(\frac{2\pi t}{288}\right) \\ & + \beta_{4,i}\cos\left(\frac{2\pi t}{288}\right) \end{aligned} \quad \text{eqn 2}$$

for $i = 1, 2$ and $k = 1, 2, \dots, 76$. Here $\epsilon_k = (\epsilon_{1,k}, \epsilon_{2,k})$ are bivariate random variables, with one realization for each shark track (track lengths varied from 2 to 9 h). Such random effects are often

assumed to be Gaussian. However, such an assumption is restrictive, the resulting models can be difficult to interpret, and computational problems arise in the estimation because each continuous-valued random effect adds an integral to the likelihood (cf. Altman 2007). Therefore, we implemented a discrete random effects model within the HMM (Maruotti & Rydén 2009). We assume that $\epsilon_k = (u_{m,1}, u_{m,2})$ with probability π_m^k for $m = 1, \dots, M$, with $\sum_{m=1}^M \pi_m^k = 1$. Each possible outcome of the bivariate random effects distribution and associated transition probability matrix corresponds to one particular movement pattern exhibited during a track. The probabilities π_m^k , also referred to as the mixture proportions, denote the expected proportion of tracks that correspond to the m -th movement pattern. In order to assess how the covariates affect the state-switching dynamics of the M random effects groups, we computed the stationary distribution at each time t for given values of the covariates, as described by Patterson *et al.* (2009). In this manner, we obtain the marginal probability of each state throughout the day for the M groups under different values of the random effects and covariates. To examine differences in observed movement patterns by sexes, we allowed for the mixture proportions to depend on sex in the following manner,

$$\text{logit}(\pi_m^k) = \alpha_m + \eta_m x_{sk}, \quad \text{eqn 3}$$

for $m = 1, \dots, M$, where $x_{sk} = 1$ if the shark associated with track k is male, and $x_{sk} = 0$ for female. In other words, we assumed that some of the M possible state-switching dynamics may be exhibited more often by females than males, and vice versa. We also considered the state transition probabilities as a function of sex but it was not selected for inclusion by the Akaike information criterion (AIC). The value of M , giving the number of possible values of ϵ_k , is chosen based on the AIC. Assuming independence of the individual tracks, the log-likelihood of the model has the following form:

$$l = \log L = \sum_{k=1}^K \log \left(\sum_{m=1}^M L_{k,m} \pi_m^k \right),$$

where $L_{k,m}$ is calculated exactly as in eqn (1), but with the values $u_{m,1}$ and $u_{m,2}$ plugged in for $\epsilon_{1,k}$ and $\epsilon_{2,k}$, respectively, in the state transition probabilities, as defined by eqn (2); that is, $L_{k,m}$ is the likelihood for track k assuming that it was generated by the m -th of M possible state-switching processes, corresponding to the different values for the discrete random effects.

Further, we can use the values of $L_{k,m}$ and π_m^k to classify each track into one of the M random effects groups. Using Bayes' theorem, we compute the probabilities p_m^k of the m -th state-switching process having given rise to each track k in the following manner:

$$p_m^k = \Pr(\epsilon_k = (u_{m,1}, u_{m,2}) | \mathbf{z}_{1k}, \dots, \mathbf{z}_{n_k} k) = \frac{L_{k,m} \pi_m^k}{\sum_{m=1}^M L_{k,m} \pi_m^k}$$

For each track k , classification is then done by selecting the value of m that gives the maximal probability among $\{p_1^k, \dots, p_M^k\}$.

The model formulation allows for a numerical optimization of the likelihood, that is a simultaneous estimation of all model parameters via maximum likelihood, which we conducted using R (R Core Team 2014). For each model, we considered several sets of initial values in the numerical maximization and as a result are confident that we found the global maxima of the respective likelihoods. A forward selection approach was implemented and covariates included according to the AIC of the corresponding models. We assumed fixed effects for the covariates across the M values of the random effects. All plots were generated using the *ggplot2* and *ggmap* packages in R.

Results

Between September 2010 and April 2014, we tracked 14 individuals for a total of 468 h, 5 males and 9 females (Table 1). Individuals ranged in size from 290 to 450 cm TL and were tracked on multiple days over periods of 2–9 h for a total of 76 tracking bouts.

Males and females differed in their habitat use, with females using habitat closer to the bay in addition to Dyer Island and Geyser Rock, while males spent more time directly off Dyer Island (Fig. 2). Model results showed clear geographic patterns of sharks being in state 1 (area-restricted searching (ARS)) in certain habitats (Fig. 1). These habitats include the channel between Dyer Island

and Geyser Rock, the edge of the kelp forest NW of Geyser Rock, and areas adjacent to the beach where fish abundance is high. However, overlaying location of chumming by dive boats identified clear overlap between the presence of chum and sharks being in state 1 (Fig. 2). While tracking, surface predation attempts on seals were observed 9 times, five of which were for an individual in state 1, and four for individuals in state 2.

Using AIC, we settled on a model with $M = 3$ pairs of random effects, that is three different state-switching patterns (Fig. 3). We expanded this model to test the influence of covariates on the state-switching dynamics. Again using AIC, the transition probability matrix in the final model depended on the covariates chum and time of day, and mixture proportions were functions of sex (eqn 3, Table 2). According to the fitted model, if chum is present, there is an increase in probability of remaining in state 1 (ARS) when in state 1, and an increase in probability of switching from state 2 to state 1 when in state 2, which overall results in a substantial increase in state 1 occupancy. Regarding the diel pattern, only the results for the time period from about 7:00 to 19:00 are meaningful – outside of these hours there were not enough individual tracks and observations to infer the state-switching behaviour. The results indicate that, for each of the three random effects groups, the marginal probability of individuals occupying state 1 is highest during the early morning and decreases throughout the day, reaching a minimum at about 18:00–19:00. In contrast, the marginal probability of individuals occupying state 2 (patrolling) is highest in the evening.

The three random effects groups account for the heterogeneity in tracks observed, in part due to sample size and duration of tracks. In particular, the estimated random effects groups presented here are a reflection of the observed behaviour and state-switching patterns of the data set used for the analysis. On some occasions, sharks were only observed in state 1 or state 2 throughout the

Table 1. Tracking criteria from 14 white sharks tagged and tracked at Dyer Island and Joubertsdam in Gansbaai, from 03 September 2010 until 11 April 2014

Shark ID	Sex	TL (cm)	Start date	End date	Tracking segments	Tracking hours	Mean (\pm SD) in hours
WSF1	F	420	3/9/2010	17/10/2010	12	60-75	5.06 \pm 2.02
WSF2	F	400	5/9/2010	29/09/2010	6	25-08	4.19 \pm 2.36
WSF3	F	350	22/11/2010	13/12/2010	7	33-83	4.85 \pm 2.27
WSF4	F	290	26/01/2011	3/3/2011	11	55-00	4.91 \pm 2.16
WSM1	M	420	11/4/2011	12/5/2011	9	75-20	8.37 \pm 2.84
WSM2	M	350	15/05/2011	21/05/2011	3	18-50	6.17 \pm 0.12
WSF5	F	350	11/7/2011	20/07/2011	8	32-50	4.06 \pm 2.24
WSM3	M	300	15/11/2011	16/11/2011	2	13-00	6.50 \pm 4.50
WSM4	M	450	16/02/2012	12/3/2012	7	57-05	6.44 \pm 2.17
WSF6	F	340	7/9/2012	12/10/2012	7	27-50	3.93 \pm 1.81
WSF7	F	440	3/11/2012	19/11/2012	5	20-00	4.00 \pm 0.95
WSM5	M	430	12/5/2013	3/6/2013	9	33-30	3.73 \pm 1.48
WSF8	F	430	9/10/2013	10/10/2013	2	7-00	3.50 \pm 1.10
WSF9	F	380	11/4/2014	18/04/2014	4	8-88	2.22 \pm 1.36
Total						468:04	

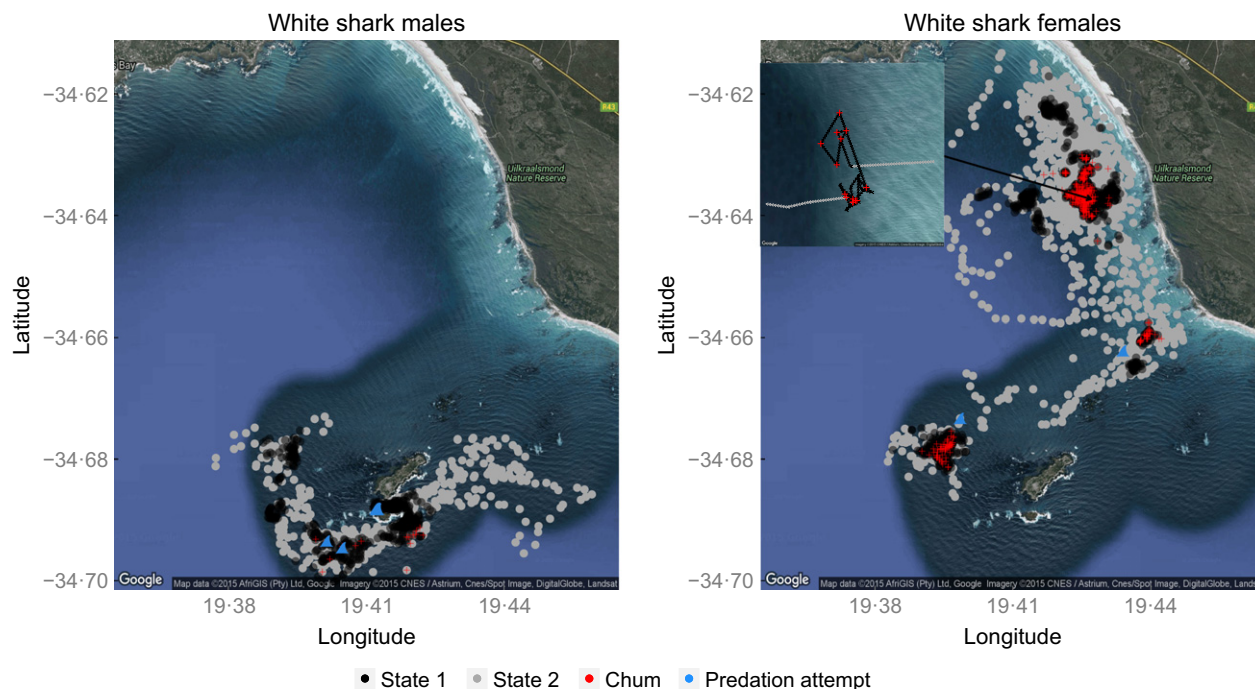


Fig. 2. Active tracks of white sharks ($n = 14$) within Gansbaai, South Africa. Locations have been colour coded based on whether the HMM allocated the individual to state 1 or 2 behaviour at that time. The location of shark ecotourism operations (crosses) and observed predation attempts on seals by tracked sharks (dorsal fins) are also shown. Tracks have been split by sex.

track (i.e. no switching), although most were observed to occupy both states with different degrees of state-switching and dwell time in each state. As such, the random effects groups account for the possibility that shorter or longer lengths could exhibit different state-switching patterns and any biases in covariate effect that could be attributed to the pooling of tracks of varying durations. In the absence of chum, the first random effects group (RE1) is characterized by a higher probability of inhabiting state 2 than state 1 across all times of day (i.e. corresponding tracks comprise a substantial amount of patrolling-type movement, Fig. 3). Random effects group 2 (RE2) represents the other extreme, where the marginal probability of inhabiting state 1 is higher than state 2 throughout most of the day (i.e. corresponding tracks involve mostly ARS behaviour). Random effects group 3 (RE3) lies in-between these extremes, with a lower degree of state-switching through most of the day, higher probability of state 1 through the morning, and higher probability of state 2 in the evening (Fig. 3). A period of time corresponding to a higher marginal probability of state 1 than state 2 (or vice versa) does not indicate that the tracks in that period will only correspond to state 1, but more generally reflects a higher occurrence of state 1 behaviour. Tracks assigned to RE1 or RE2 may contain multiple state switches, while tracks assigned to RE3 switched states sparingly, if at all. In the presence of chum, the relative roles of the three random effects groups remain the same, but the probabilities of being in state 1 are generally much higher (Fig. 3). The mixture proportions for the random effects groups for

females are 0.67 (RE1), 0.11 (RE2) and 0.22 (RE3), and for males 0.17 (RE1), 0.18 (RE2) and 0.65 (RE3). The large difference in mixture proportions between sexes for RE1 indicates that females generally spend more time in state 2 than males. The difference in mixture proportions for RE3 indicates that males remain more often in either of the two different movement strategies than females (Fig. 4). As mentioned previously, female and male sharks differed in their use of habitats. While we would like to have incorporated an effect of habitat into the model, there were insufficient data in some habitats to make appropriate inferential statements. Although there were some differences in the geographic distribution of RE groupings, there was also considerable overlap making it unlikely that habitat was driving the results (Fig. 4). There was no difference in track duration for the track segments classified as RE1, RE2 or RE3 (Kruskal–Wallis, chi-squared = 2.91, d.f. = 2, $P = 0.23$).

We computed $L_{k,m}$ for $k = 1, \dots, 76$ and $m = 1, 2, 3$ along with the mixture proportions for female and male sharks, and used the values to assign each of the 76 tracks to a random effects group. Individual sharks were tracked on multiple days and could be assigned to different random effects groups on different days (Fig. 5). Individuals appeared to consistently use the same RE grouping despite being tracked over multiple days throughout a month period. Furthermore, we observed predation on seals while sharks were in either of the groups. In other words, foraging could occur during any of the states or random effects groups so we observed both ‘ARS’ and

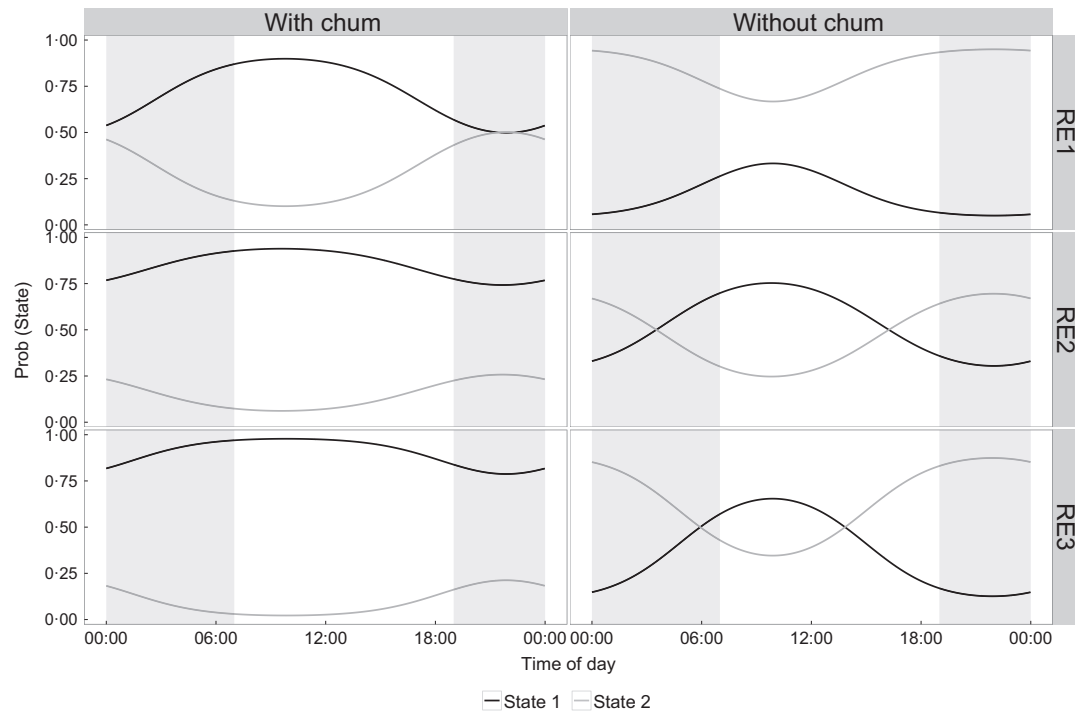


Fig. 3. Probability of being in state 1 or state 2 throughout the day for each random effects group given values with or without the presence of chum.

Table 2. Log-likelihood and AIC values obtained for the mixed hidden Markov models with different possible numbers (M) of random effect outcomes and forward selection of covariates and mixture proportions dependent on sex. The best-fit model is in bold

M	Log-likelihood	AIC	Δ AIC
1 (no covariates)	-2301.671	4625.342	14.13
2 (no covariates)	-2292.043	4612.086	0.874
3 (no covariates)	-2288.606	4611.212	0
4 (no covariates)	-2286.537	4613.074	1.862
3 (chum)	-2275.309	4588.618	4.144
3 (chum, time of day)	-2270.302	4586.604	2.130
3 (chum, time of day, size)	-2268.885	4587.770	3.296
3 (chum, time of day, π_m (sex))	-2267.237	4584.474	0

'patrolling hunting modes'. The decoded states confirm that females, overall, spent more time in state 2 than males ($\approx 56\%$ vs. 46%). In general, about 53% of observations were classified as state 2 and 47% classified as state 1. According to the decoded states, there were 109 state switches out of 2887 possible ones ($\approx 3.78\%$) for females, and 50 state switches out of 1621 ($\approx 3.08\%$) for males.

Discussion

The unique combination of being able to follow the same individuals over multiple different tracking periods, along with simultaneous observations of surface foraging

attempts on marine mammals, allowed us to identify fine-scale individual behaviour and two hunting modes that white sharks may use: area-restricted search and patrolling. Our analysis quantitatively identified changing behavioural states without user subjectivity within individual animals, and identified some of the factors that cause variability in movements. Furthermore, mixed HMMs allowed us to quantify changing behaviour in white sharks that would not have been apparent using traditional movement analysis methods. For example, movement analysis of a smaller number of acoustically tracked white sharks in Gansbaai identified core areas of habitat use but was not able to detect switching behaviours or differences in movements between the sexes (Jewell *et al.* 2014). Of course, movements by marine predators will also include a vertical component and we did not measure swimming depths. Sharks can switch between diving strategies that include prey-specific strategies (e.g. swimming along the bottom to visually locate prey on the surface) or different forms of random walks (e.g. lévy vs. Brownian movements), based on the abundance and distribution of resources in the habitat (Sims *et al.* 2012). White sharks in Australia switch their diving behaviour, likely due to changes in potential prey density (Sims *et al.* 2012).

Movement states and transitions appeared to be a factor of chumming, time of day, sex, individual preferences and potentially habitat. We did not observe any effects of shark lengths on movement patterns although there may well be spatial segregation between smaller and larger

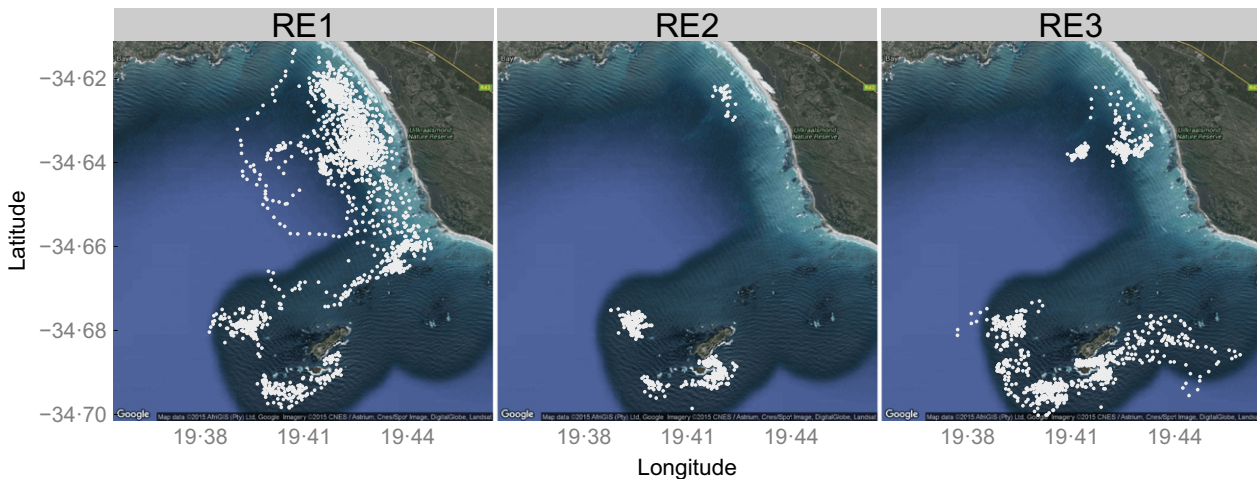


Fig. 4. Spatial distribution of random effects groupings among white sharks tracked in Gansbaai.

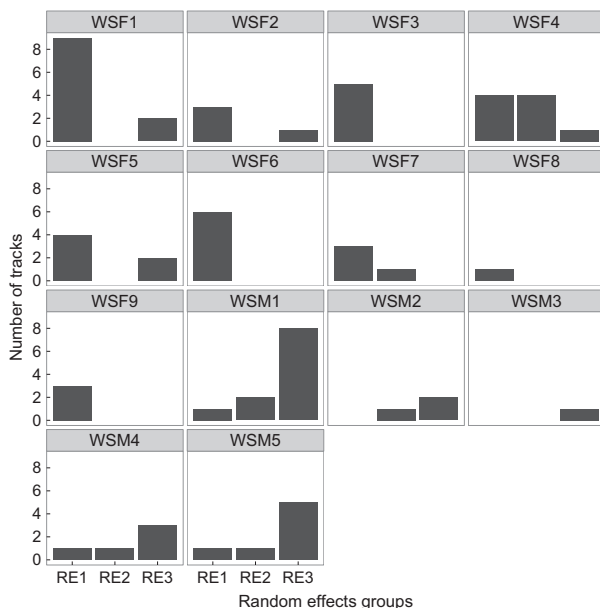


Fig. 5. Bar charts showing which random effects group individual white sharks fit into and how often they were within these groups. WSF are females and WSM are males.

individuals (e.g. Jewell *et al.* 2013). Chumming by eco-tourism dive vessels generated a high probability of sharks either remaining in or switching to ARS behaviour. This is not an unexpected result as white sharks tracked off Australia responded to chumming by spending more time at the surface and reducing their core use areas (Huveneers *et al.* 2013). There is mounting evidence that shark eco-tourism can cause changes in behaviour over short time frames (h), but are unlikely to have an impact at longer time scales based on previous studies and ongoing satellite tracking (A. Towner unpublished data; Gallagher *et al.* 2015). However, less clear is how the change in behaviour may influence foraging success or even daily energy expenditure of white sharks, as sharks may spend more time turning and incur additional costs (e.g. Wilson *et al.* 2013).

Acknowledging the lack of night time observations in this study, sharks were also more likely to be performing ARS in the morning through early afternoon. At Seal Island, another South African seal rookery, highest rates of foraging success by sharks occur in the hours following dawn (e.g. Martin *et al.* 2005; Laroche *et al.* 2008). Seals enter and exit the island from predictable sites and the dawn peak is likely due to a combination of juvenile seals (the primary prey item) being present in the water during this period and optimal ambient light conditions for attacking at the surface (e.g. Laroche *et al.* 2008; Martin, Rossmo & Hammerschlag 2009; Martin & Hammerschlag 2012). These conditions lead to white sharks using specific (and presumably optimal) locations to attack, although the behaviour of the sharks prior to surface strikes was not recorded (Martin, Rossmo & Hammerschlag 2009). Foraging attempts and success by sharks on seals are considerably lower at Geyser Rock than at nearby Seal Island, likely due to the extra kelp refuge provided at Geyser Rock (Weisel *et al.* 2015). The added protection provided by kelp causes seal departure locations at Geyser Rock to be more diffuse (i.e. no specific entry/exit point), but there will still be preferable general areas of departure (Weisel *et al.* 2015). Hence, it may still be advantageous for sharks to display ARS movements within key areas during the morning period, but with less emphasis specifically at dawn. The uniquely shaped channel between the islands (Shark Alley) may also offer extended predation opportunities on seals throughout daylight hours, here both predation risk and shark habitat use are notably high (Jewell *et al.* 2014; Weisel *et al.* 2015). As in other areas, selection of ARS sites or predation hotspots is going to be related to a number of factors including prey behaviour, habitat and intraspecific competition (Martin, Rossmo & Hammerschlag 2009).

By assigning tracks to random effects groups, we were able to detect two additional factors that influence white shark movement patterns: sex and individual preference. Sexual segregation in sharks is well known, although less

is known about differences in fine-scale behaviours (e.g. Heithaus *et al.* 2006). For example, female tiger sharks in a subtropical embayment show different microhabitat selection than males, even though they overlap in their overall spatial distribution (Heithaus *et al.* 2006). In South African bays, white sharks display sexual segregation seasonally, but will overlap at other times of the year (Kock *et al.* 2013). In Gansbaai, there was also some spatial segregation between the sexes, with females more likely to use shoreline habitat (similar to False Bay, Kock *et al.* 2013), although individuals will also vary their behaviour within those habitats. Our study shows subtle differences between the sexes with females more likely to perform patrolling behaviour throughout the day. Such fine-scale differences in movements and even hunting tactics between the sexes are seen in other taxa. Male chub would perform sit-and-wait foraging more frequently than females (Katano 1996). Female mantids were more likely to switch hunting modes, especially in relation to prey density, while males tended to remain in one hunting mode (Inoue & Matsuura 1983). However, it is difficult to separate the effects of sex and habitat on movement patterns. Were movements different because of the use of different habitats or specific to the sexes (e.g. if females used the same habitats would their movements be similar)? There was some overlap in habitat use so we believe the differences are driven by sex, but we cannot rule out that habitat was an important driver.

The repeated tracking of individuals over many days showed that patterns of movement will vary between individuals even within each sex. Individual sharks showed a preference for a particular pattern of movement (defined by a random effect group), which they repeatedly used over short time periods (over a month). Individuals may learn a variety of different movement tactics for encountering and catching prey, and they may develop a preference for a particular tactic based on their experiences. We did not track animals for long enough periods to determine whether these behaviours are fixed and cannot define them as true specialization. Variability in short-term strategies should be considered as these may translate to differences in foraging success and potentially even how the predator contributes to changes in prey behaviour (e.g. Heithaus *et al.* 2009). Additional tools (e.g. accelerometers) will be needed to determine the specific function and success (e.g. foraging rates) of different patterns of movement, and whether individual preferences of movement remain fixed over long time periods.

As previously stated, movements by themselves cannot be directly correlated with hunting as there are going to be many times when sharks are not foraging. White sharks have shown residency to coastal areas that do not harbour pinnipeds suggesting times of foraging on other prey, or some other function of ARS behaviour (Johnson *et al.* 2009; Bruce & Bradford 2012). We observed actual predation attempts by tracked sharks and these occurred for sharks in either of the three random effects groupings and either movement state (ARS or patrolling). Therefore,

sharks will target seals by either remaining in one location (i.e. essentially sit-and-wait) or by actively patrolling for swimming seals. However, while it is highly likely that individuals will switch between these two hunting modes, we never observed an individual using both ARS and patrolling hunting modes. Of course we could only observe predation on pinnipeds at the surface even though other fishes (teleosts and sharks) are likely to also be an important component of the diet, so predation rates are going to be higher than recorded. Furthermore, there may have been subsurface foraging attempts that we missed.

Hunting mode switching is often explained by different levels of hunger, habitat characteristics, prey density and distribution (Inoue & Matsuura 1983; Kobler *et al.* 2009; Michel & Adams 2009; Higginson & Ruxton 2015). Changes in prey density (seal numbers) and habitat complexity (kelp density) may explain seasonal changes in fine-scale behaviour (although we lacked the sample size to test for seasonal effects). Recent theoretical models predict that active searching becomes more advantageous as prey move slower and/or the energetic cost of predator movements decrease (Higginson & Ruxton 2015; Ross & Winterhalder 2015). Individuals switching hunting modes may be a strategy in itself, and match the predictions of the game theoretic Ambush Search strategy, where a predator alternates ambush with active searching which is predicted to increase the success of systematic searching (Alpern *et al.* 2011). Our results suggest that individual variability in hunting mode, even within the sexes, should also be considered in future predator–prey models. Ambush sites at Dyer Island may be more variable due to kelp refuge at the island, and it would be interesting to compare movement behaviours and/or hunting modes with Seal Island where prey (seal pups) use more predictable entry/exit locations (Martin, Rossmo & Hammerschlag 2009; Weisel *et al.* 2015; De Vos *et al.* 2015). Different hunting modes have also been identified in terrestrial predators although the function of the switching has not been examined (Williams *et al.* 2014; Higginson & Ruxton 2015). Pumas will use both active stalking and sit and ambush to catch prey with the energetic costs of these different strategies varying widely (Williams *et al.* 2014).

Different hunting modes may cause trophic cascades that operate in opposite directions and at different trophic levels (Schmitz 2008). While the importance of hunting mode in marine predators has been raised, it is generally assumed that all individuals will use the same mode (i.e. white sharks ambush all prey, Heithaus *et al.* 2009; Martin & Hammerschlag 2012). To the best of our knowledge, studies have not examined the repercussions of top predators that may switch between hunting modes or where individuals prefer a particular strategy. White sharks in South Africa are likely to exert ecosystem level impacts. Pinnipeds at the rookeries almost certainly adjust aspects of their behaviour to account for the threat of predation from sharks (Laroche *et al.* 2008; Weisel *et al.* 2015; De Vos *et al.* 2015). How the threat of predation actually

alters pinniped population dynamics or foraging success are unclear, but the changes are likely to cascade through the food web as the mammals themselves are upper level predators (e.g. Johnson *et al.* 2006).

We highlight that sharks have essentially two foraging strategies they can use and show individual preference for particular short-term movement strategies. If individuals have preferences for different strategies, and those strategies alter the behaviour of prey in different ways, then not all individuals in the white shark population will be equal in terms of their ecological roles even if they are similar sized. Furthermore, future predictive models will need to consider that top marine predators may still use two modes of hunting, especially those that consider how predators change prey behaviour (e.g. Frid, Baker & Dill 2008; Heithaus *et al.* 2009; Higginson & Ruxton 2015). Theoretical models may be expanded to include the situations where sit-and-wait could be more energetically costly if the animals are having to make frequent turns to remain in one location (Wilson *et al.* 2013; Higginson & Ruxton 2015). While animals are often described as using one form of hunting mode or the other (often at the population level), increasing numbers of studies are showing that in many cases a continuum of modes is likely to exist in wild predators (Cooper 2005).

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Data accessibility

Data deposited in the Dryad Data repository with an embargo on it until December 2018 for the purpose of the author's PhD. <http://dx.doi.org/10.5061/dryad.q90fm> (Towner *et al.* 2015).

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