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Evaluating Behavioural Modelling Predictions in the Blue Shark (*Prionace glauca*) Enables Greater Insight on Habitat Use from Location only Argos Data

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ABSTRACT

The relationship between habitat and behaviour provides important information for species management. For large, free roaming, marine animals satellite tags provide high resolution information on movement, but such datasets are restricted due to cost. Extracting additional biologically important information from these data would increase utilisation and value. Several modelling approaches have been developed to identify behavioural states in tracking data. The objective of this study was to evaluate a behavioural state prediction model for blue shark (*Prionace glauca*) ARGOS surface location-only data. The novel nature of the six SPLASH satellite tags used enabled behavioural events to be identified in blue shark dive data and accurately mapped spatio-temporally along respective surface location-only tracks. Behavioural states modelled along the six surface location-only tracks were then tested against observed behavioural events to evaluate the model's accuracy. Results showed that the Behavioural Change Point Analysis (BCPA) model augmented with K means clustering analysis performed well for predicting foraging behaviour (correct 86% of the time). Prediction accuracy was lower for searching (52%) and travelling (63%) behaviour, likely related to the numerical dominance of foraging events in dive data. The model's validation for predicting foraging behaviour justified its application to nine additional surface location-only (SPOT tag) tracks, substantially increasing the utilisation of expensive and rare data. Results enabled the critical behavioural state of foraging, to be mapped throughout the entire home range of blue sharks, allowing drivers of critical habitat to be investigated. This validation strengthens the use of such modelling to interpret historic and future datasets, for blue sharks but also other species, contributing to conservational management.

Keywords: Blue shark; Behavioural state modelling; Satellite tracking; Foraging behaviour; Habitat use

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1. Introduction

Satellite tracking allows behavioural studies of large, free roaming marine animals, where migration trips are long, out of observational reach and dynamic in three dimensions [1,2]. In addition to providing movement tracks, this technology has the potential to address questions as to what drives the observed movements, and thereby contribute important information to biological, political and conservation issues [3-5]. While satellite tag technology has evolved from initial location only tracks, to recording and transmitting dive profiles and environmental information, the expense of satellite tags acts as a major limiting factor on the number of individuals sampled. Satellite tag sample sizes are six to seven orders of magnitude less than samples from the bycatch data predominantly used for conventional fisheries management policies. Bycatch data is however acknowledged to contain flaws through misreporting, low observer coverage and spatio-temporal biases [6,7]. Combining bycatch data with satellite tagging data can provide 'big data' type approaches, potentially providing a step change for the management of highly migratory marine species [3-5,8-10]. While a persistent restricting factor of expense may not alleviate small sample sizes in satellite tagging studies, validation of data processing methodologies that enable better utilisation of such data sets, would strengthen their application within 'big data' studies and help their contribution to conservational management [11].

The Blue shark (*Prionace glauca*) is the most abundant and widely distributed pelagic shark species [12]. It is the most exploited by-catch in tuna longline fisheries and has a high prevalence in the fin trade [13-15] resulting in observed population declines [16-22]. Effective management of blue sharks requires a global approach defining spatio-temporal patterns in behavior and habitat use [10,23]. Satellite tagging studies provide such data, however only approximately 548 individual blue sharks have ever been tagged [21,24-44]. While this sample size is sourced from throughout the species global range, and appears numerically large, in context to data required for conservational management, additional insight would be beneficial. The restricted sample size of satellite tagging data for this, and other species, highlights the need to develop methodologies to garner additional information where possible from these data sets.

Behavioural modelling provides a methodology to extend the interpretation of two-dimensional movement data. It utilizes the understanding that animals will change their movement patterns in relation to habitat, prey density or other internal or external stimuli [45], which can be detected by characterising the distributions of the movement parameters. Foraging behaviour is of common interest as it represents an important habitat, however, it is rarely possible to observe it directly for marine pelagic animals. Behaviour theory suggests that an animal should maximize its time in productive areas [46], meaning variation in an individual's movement pattern can be interpreted as the switching between different underlying behavioural states [47]. In the marine environment, food resources for pelagic species are highly aggregated and patchy [48]. Studies show that a series of slow, persistent and directionally variable movements (high turning angle and frequency) in one area, can be interpreted as the visible consequence of intensive foraging whereas the opposite indicates directed movement, such as migration [49,50]. Movements that appear as in-between in these states may represent searching [51]. These differences in movement behaviour can enable foraging, searching and transitioning behaviours to be inferred from a two-dimensional time series of positions.

Various modelling methodologies have been developed to identify behaviours from the geometry of movement paths (for example, first-passage time methods [52], Levy flight analysis [53], and state-space models [45,54,55]). Each methodology has strengths and weaknesses, and some are likely more accurate in predicting behavioural states for certain species based on their movement trajectories. More model validation is required, where the predictive ability of a model is evaluated using true/observed behavioural states [56-58]. Validation of a particular model's use, for a particular species, would justify the application of that model to further, similar datasets, increasing information from tracking data for conservational management.

The purpose of this paper was to exploit the novel use of SPLASH tags (www.wildlifecomputers.com) on blue sharks, which uniquely provide spatiotemporally accurate ARGOS dive data and location data, to evaluate a behavioural state prediction model. Validation would justify the prediction model's application to additional location only data sets from Smart Position or Temperature Tags (SPOT tags; www.wildlifecomputers.com), which make up 40% of blue shark satellite tag data globally [43]. Such data provide no insight relative to sub-surface behaviour, unlike the other 60% of data which come largely from Pop-up Satellite Archival Tags (PSAT tags), but are limited to low accuracy location information. Validated application of a behavioural prediction model would not only expand data utilisation in this study but also justify it in other studies where such data are potentially underutilised. Having confidence in predicting behaviour through space and time, allows the identification of environmental parameters associated with such behaviours, helping define critical habitat.

2. Methods

2.1 Tagged blue sharks (*Prionace glauca*) and data processing

As described in detail by Elliott et al. [43] between 2012 and 2015, nine SPOT tags (model 196) and six SPLASH tags (model 289 and 316) (www.wildlifecomputers.com) were attached to the dorsal fins of 15 blue sharks in New Zealand. Two mature females, two mature males, one juvenile male (< 190 cm in fork length) and one juvenile female (< 180 cm in fork length) were SPLASH tagged. Seven mature males, one mature female, and one juvenile male were SPOT tagged. SPOT and SPLASH tags both provide ocean surface ARGOS locations of sharks (location only data) while SPLASH tags also provide dive data (depth and temperature), both of which are transmitted opportunistically, every time the shark's dorsal fin (and thus the tag) breaks the water's surface. Data were processed and filtered as described in Elliott et al. [43] resulting in two forms of data output: time-stamped surface location only tracks of blue sharks and subsurface dive data associated with SPLASH tag tracks.

Elliott et al. [43] identified five common dive patterns which were used to infer blue shark behavioural states from SPLASH tagged blue sharks. U, VU and UV dives are inferred to represent foraging. V and W dives are to represent searching, and ZZ or no diving is to represent travelling. Dive data from SPLASH tags are time-stamped, indicating the actual occurrence time of a dive shape and thus the inferred behavioural event, even though such data is transmitted at a later surface time and location. To identify approximate locations of dive events, the time of occurrence was tracked back along the surface location track (as the crow flies), based on the average swim speed of that shark and available locations of the same or similar time, thus interpolating the location of inferred dive events as best possible. No behavioural/dive event greater than 24 hours from a surface location was retained in this interpolation process. Interpolated events were used as 'known' behavioural events, to test the validity of the model's predicted behaviour states from the surface location-only aspect of SPLASH tag tracks.

2.2 Modelling of surface location only data from SPLASH tags

A behavioural change point analysis (BCPA) and K-means clustering as described by Zhang et al. [59] were used. This approach extends the state-space BCPA model developed by Gurarie et al. [54,60]—a likelihood-based means of detecting latent structural changes in parameters (e.g. intra-fix speed and relative turning angles (RTA)) underlying locational time-series data. K-means clustering is a common statistical approach to group similar observations or events.

Filtered Argos locations (as per Elliott et al. [43]) longitude and latitude, were converted into a plain project system (New Zealand Transvers Mercator 2000) in ArcMap 10.2 [61]. The intra-fix speed and relative turning angles were then calculated and used as inputs for the BCPA model. Behavioural bouts were characterized by BCPA based on the changes in the temporal autocorrelation structures in data and means of speed and RTA were calculated for each individual bout. The number of behavioural states was determined using maximum likelihood estimation. The bout means were then grouped by K-means clustering analysis, and a multi-exclusive behavioural state was assigned to each individual bout. All locations within the bout, were assigned with the same behavioural state.

2.3 Validating the model—modelled surface location behavioural states contrasted with 'known' dive events

To evaluate the BCPA modelled behavioural states for SPLASH tag surface location tracks, a simple question was asked in comparison to the 'known' and interpolated behavioural events from SPLASH tag dive data. When a 'known' dive behaviour event from SPLASH tag data is present, in the same location/time (within 3 hours) as a BCPA modelled state, does the modelled state match the 'known' event? The number of correct modelled 'known' matches for each behaviour, was divided by total matches along a track, thus quantifying the BCPA model's ability to predict blue shark behaviour, based solely on surface location tracks.

2.4 Model application to additional location-only SPOT tag tracks and association of environmental variables with blue shark behaviour

Movement data from nine additional, surface location-only blue shark satellite tag tracks (SPOT tags), were processed through the BCPA model, in the same fashion as that of SPLASH tag surface location-only data. To understand how environmental variables may be associated with behavioural states, modelled behavioural states from SPOT tag data were mapped along with modelled states from SPLASH tag surface location-only data, as well as inferred behaviour events from SPLASH tag dive data.

A generalized linear model (GLM) was run in R [62] using the package 'stats' to test the influence of independent predictor variables, on the behavioural state response of blue sharks. Behavioural states have been categorised into travelling, searching and foraging. Using spatiotemporal information relative to each behavioural state location, satellite derived environmental variables of ocean depth, weekly mean sea surface temperature (SST), weekly mean chlorophyll A (9km daily resolution NASA L4 MODIS), ocean current magnitude (25 km daily resolution AVISCO), and distance from shore were obtained through the STAT program (www.seaturtle.org), and two shark-related variables (shark swim speed and shark ID), collectively formed the predictors that were put through 13 different GLM models. Models were run for three binomial comparisons of behavioural state responses (forage vs travel, forage vs search, search vs travel), comprising different combinations of predictor variables, including those where correlated variables were excluded and/or certain data series were transformed (log). Akaike Information Criterion (AIC) values were compared between the 13 models and the model with the lowest AIC was selected as the final model. The output from this model was used to determine the impact predictor variables had on response variables, so that the potential association of habitat type to behavioural state, could be investigated. Raw datasets of predictor variables associated with behavioural states were analysed manually, to determine means and if statistically significant differences were present via F and T-tests. This provided greater insight as to potential habitat types associated with blue shark behavioural states.

3. Results

3.1 Tagged blue sharks (*Prionace glauca*) and data received

Fifteen blue sharks were satellite tagged, 9 with

SPOT tags and 6 with SPLASH tags. SPOT tags transmitted data for periods between 66 and 505 d (mean ± SD = 250 ± 144 d) and SPLASH tags between 200 and 343 d (255 ± 63 d), spanning latitudes of 0.1° and 43.1° S and between longitudes of 160.1° E and 150.8° W. Also, SPLASH tags transmitted 3923 hours of dive data, used to infer 373 foraging, 94 searching and 83 travelling events (**Table 1**), each of which were interpolated along reciprocal surface location tracks from SPLASH tags (**Figure 1** inset illustrates a sample of data (see Elliott et al. [43] for an in-depth summary)).

Table 1. Behaviour events were identified throughout each shark track from SPLASH tag dive data.

Shark id (Maturity/ sex)	Track duration (d)	# Foraging events	# Searching events	# Travelling events
16 (mM)	267	99	31	7
17 (mF)	206	47	7	22
68 (jF)	200	40	21	27
69 (jM)	200	27	1	12
70 (mM)	315	48	11	7
71 (mF)	343	112	23	8
Total	1531	373	94	83

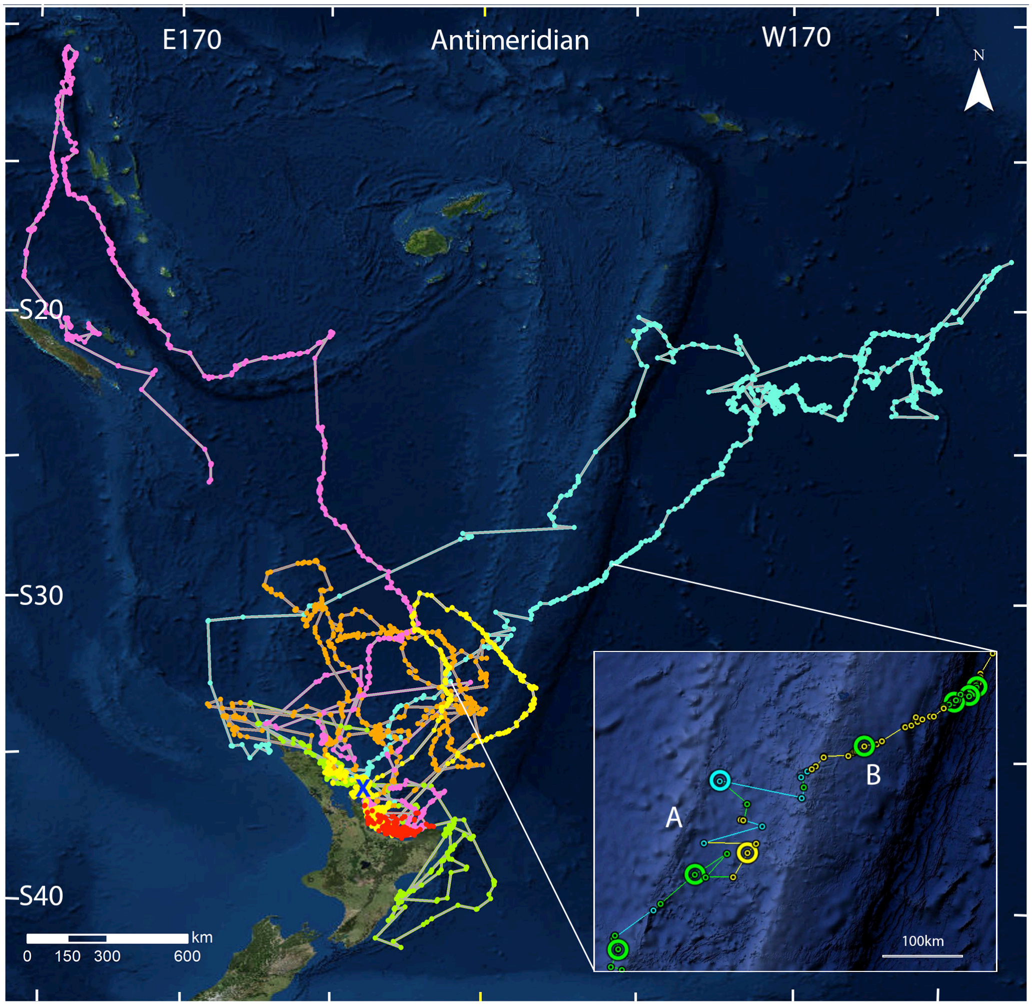

Figure 1. Satellite location-only tracks of 6 SPLASH tags that were later modelled using BCPA method to predict behavioural states of sharks using turning angle and speed. Blue X indicates release location of all sharks. **Inset map** is an expansion of part of SPLASH tag 71's location-only track, showing results once the prediction model and 'known' behavioural events from dive data were overlapped. 'Known' behavioural events from dive data (large circles) overlaid on BCPA predicted behavioural states (small circles) to validate model performance. Green = Foraging, Yellow = Search, Blue = Travel. The letter 'A' indicates three examples of matches based on colour codes of behaviours; 'B' indicates an example of a non-match.

3.2 Modelling of behavioural states in surface location-only data from SPLASH tags

Surface location-only information from all six SPLASH tag tracks was successfully processed through the BCPA K-means model from Zhang et al. [59]. Filtering the data before input removed on average 20% (range 10-26%) of original, raw Argos locations. Most deleted locations were duplicate locations with zero time or distance difference, therefore little information was removed from data sets. The BCPA model output for all six location tracks showed three alternating behavioural states throughout each track's duration. Consistent with behaviour modelling theory and supporting literature, specific animal behaviours were associated with each state defined by relative turning angle (RTA) and speed.

State 1 was characterised by fast (mean speed = 3.33 ms^{-1}, σ' = 1.89 ms^{-1}) and comparatively straight (mean RTA = 57°, σ' = 6.34°) movement trajectories, suggestive of 'persistent travelling' or 'transit' behaviour.

State 2 was defined by slow swimming speeds (mean speed = 0.74 ms^{-1}, σ' = 0.14 ms^{-1}) and moderately low variation in direction (mean RTA = 48°, σ' = 6.94°). Searching behaviour was the label given to what could also be commonly labelled 'unknown' or 'in-between' state of transit and foraging.

State 3 was classified by similarly slow swimming speed (mean speed = 0.76 ms^{-1}, σ' = 0.17 ms^{-1}) but highly tortuous (mean RTA = 105°, σ' = 18.94°) movements. In this state, shark locations were highly localized and restricted in area; represented commonly in the literature as foraging (**Table 2**).

Individual sharks mean RTA and speed values support the prediction of three distinct behavioural states. However, shark 68 had a travelling state that was far slower than other sharks. The common mean values across all six sharks (except the aforementioned difference) gave confidence in labelling modelled behaviour states 1, 2 and 3 respectively, as Travelling (blue), Searching (yellow) and Foraging (green) (plotted as small circles of respective colours in **Figure 1** inset as an example).

The proportion of locations classified in each of the three behavioural states was relatively similar between four of the sharks: 16, 17, 69, 71 where state 1 (travelling) accounted for between 2-6% of all locations, state 2 (searching) between 65-76% and state 3 (foraging) between 19-28%. Sharks 68 and 70 had far more locations representing travelling behaviour in comparison to foraging, and searching, respectively (**Table 2**).

Table 2. Six SPLASH tag surface location-only tracks modelled by the BCPA methodology identified three behavioural states based on relative turning angle (RTA) and speed of inter-location legs.

Shark id (Maturity/ sex)	Track duration (days)	#Locations pre-filter	#Locations post-filter	%Locations in travel (mean RTA/Speed)	% Locations in search (mean RTA/Speed)	% Locations in forage (mean RTA/Speed)
16 (mM)	267	959	783	6 (55/2.60)	65 (43/0.64)	29 (98/0.58)
17 (mF)	206	823	633	5 (78/3.50)	73 (49/0.60)	22 (103/0.60)
68 (jF)	200	458	336	25 (39/0.90)	69 (58/0.65)	6 (142/0.69)
69 (jM)	200	370	277	2 (48/6.30)	70 (39/0.91)	28 (87/0.93)
70 (mM)	315	795	719	24 (74/2.20)	46 (53/0.76)	30 (98/0.80)
71 (mF)	343	929	773	5 (48/4.50)	76 (45/0.90)	19 (105/1.00)
Total	**1531**	**4334**	**3513**	**Mean 11.2(57/3.33)**	**66.5(48/0.74)**	**22.3(105/0.76)**

3.3 Evaluating the model

Using the time stamp that accompanied 'known' dive events, the approximate location of each was plotted in ArcGIS along respective shark tracks (a subsample represented in **Figure 1** inset, as big circles coloured the same as modelled behaviour states, being the small circles). The interpolated dive events lay over Argos locations or linear legs/bouts between locations, both of which had BCPA modelled behaviour state colour coding (reciprocal to inferred behaviours from dive events). Simple colour comparison of a BCPA modelled state location, when a 'known' dive behaviour event was present, within three hours of a track location, enabled the predictive ability of the BCPA model to be tested (all comparisons represented in **Figure 2**).

BCPA model predictions matched behavioural event states on average 86.2% of the time (σ' = 13.37) for foraging, 52.6% (σ' = 28.71) for searching and 63.3% (σ' = 28.95) for travelling states (**Table 3**). The results indicate that the method performed well in predicting foraging behaviour and reasonably well for travelling. Searching behaviour was not as well predicted.

Table 3. Results from behaviour event overlay validation of BCPA model ability.

Shark id (maturity/ sex)	**% of BCPA Foraging validated correct by events**	**% of BCPA Searching validated correct by events**	**% of BCPA Travelling validated correct by events**
16 (mM)	92	59	50
17 (mF)	69	22	60
68 (jF)	100	67	93
69 (jM)	83	100	100
70 (mM)	100	34	55
71 (mF)	73	34	22
Mean	**86.2**	**52.6**	**63.3**

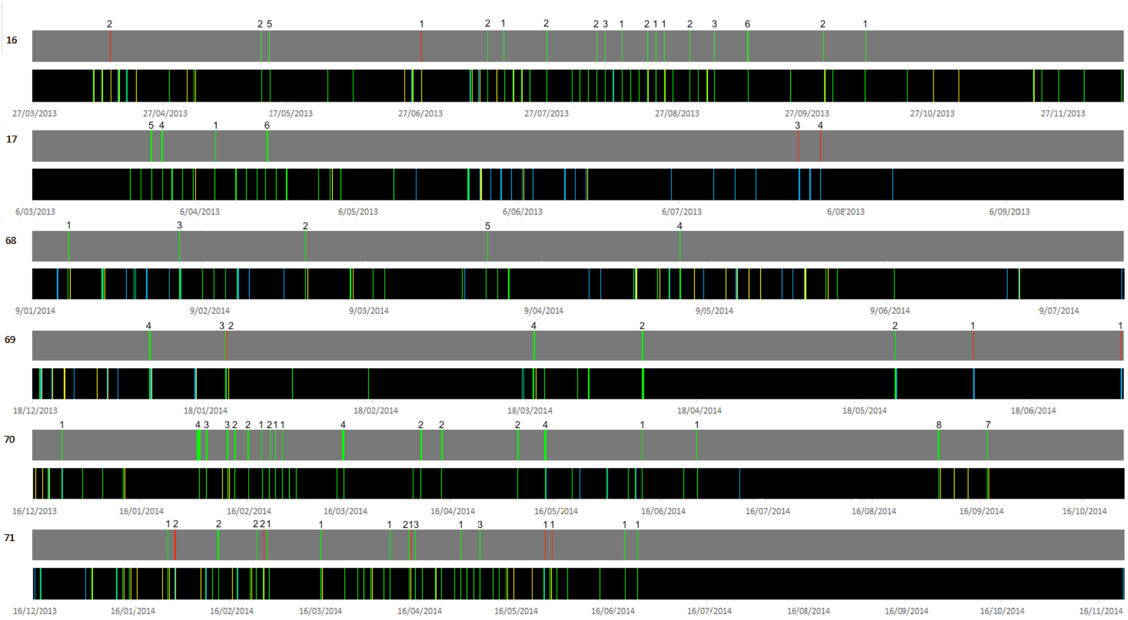

Figure 2. Satellite Time series plots of 6 SPLASH tagged blue sharks (#16, 17, 68, 69, 70, 71). For each shark, the grey row shows only BCPA modelled foraging behaviour locations that had 'known' dive behaviour event data present within three hours of a location. The black row shows all 'known' dive events for each shark, based on SPLASH tag dive data (green = foraging, yellow = searching, blue = travel). If a modelled BCPA foraging behaviour location had supporting evidence, being foraging dive event/s within three hours of the modelled behaviour location, the bar representing that BCPA location (in the grey row) is coloured green (for correct validation). If a foraging event was absent and a searching or travelling dive event was present, the modelled BCPA foraging behaviour bar was coloured red (for incorrect validation). A single bar width represents 3 hours, meaning multiple BCPA location validations may occur within one bar; the sample size of which is represented by numbers above validated BCPA behaviour bars, and which were used to calculate the validation percentage for each shark. Dates for each shark track are on the X-axis, and the shark ID number is on the Y-axis.

3.4 Application of the validated model to additional, surface location-only SPOT tag tracks, to enable association of environmental variables with blue shark behaviour

BCPA processing of nine additional blue shark location-only tracks was justified due to the high validation percentage for foraging behaviour, and respectable predictability for searching and travelling. All nine tracks generated three categories of animal movement with similar turning angles and velocities to the foraging, searching and travelling behavioural states from modelled SPLASH tag location only tracks. Foraging behaviour was of primary focus for further analysis, due to its high validation score but also because it's representative of important habitat. However, searching and travelling behaviours were still modelled for comparative reasons.

BCPA modelling of all 15 location-only tracks from SPOT and SPLASH tags, coupled with behaviour events inferred from SPLASH tag dive data, generated 2049 time-stamped foraging locations for blue sharks. These were distributed throughout the entire horizontal range of blue shark tracks (**Figure 3**). Within the same spatial distribution as foraging locations, 1221 significant bathymetric sea features were identified via Allain et al. [63] and plotted with foraging locations. Significant features included seamounts, knolls, hills, ridges, deep banks, submerged atolls, and other unnamed bathymetric features. Of the 2049 foraging behaviour locations, 2.6% occurred within 10 km proximity (the largest Argos satellite location error radius) of an identified significant sea feature from Allain et al. [63], and only 1.0% within 5 km proximity. Most foraging locations occurred in locations void of identified bathymetric features, or in proximity to those not identified such as trenches (see insets **Figure 3**).

3.5 Using a generalised linear model (GLM) to determine the impact of habitat data on behavioural states

For all three behavioural response comparisons (search/forage, travel/search, travel/forage), the GLM model using a linear combination of all predictor variables giving the lowest AIC value, was used as the final model structure. The GLM suggested that searching and foraging behaviour were influenced

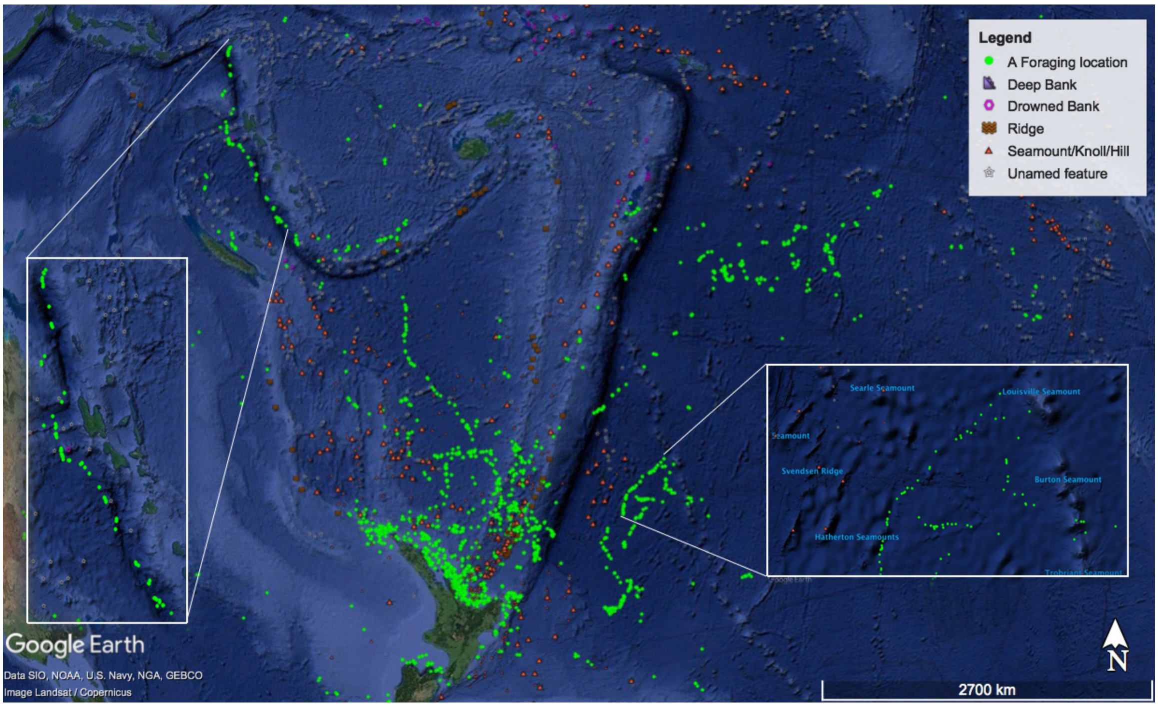

Figure 3. Distribution of all foraging behaviour locations, either predicted through BCPA model or inferred from dive data, plotted with identified major bathymetric features from Allain et al. [63].

similarly by the predictor variables. Chlorophyll A, distance from shore, shark speed and shark ID had less than significant ($p = < 0.05$) impact on determining the behavioural response of searching or foraging states. However, ocean depth, SST and current magnitude did show a significant positive impact on these states. All predictor variables significantly impacted the comparison of response variables traveling and searching, except ocean currents. Similarly, the comparison of travel and foraging states was significantly impacted by all variables, except SST in this case (**Table 4**).

In addition to significant findings from the GLM, mean values derived from raw data for predictor variables, associated with behavioural states, provided further insight on associations. Foraging occurred in areas with significantly lower chlorophyll A ($\mu = 0.181$ mg m^{-3}, $\sigma' = 0.164$) when compared with travelling ($\mu = 0.256$ mg m^{-3}, $\sigma' = 0.227$); $t_{2364} = 10.3$, $p = 2.8e^{-24}$. As did searching behaviour ($\mu = 0.187$ mg m^{-3}, $\sigma' = 0.151$); $t_{2259} = 9.7$, $p = 9.4e^{-22}$. Chlorophyll A did not differ significantly between areas of foraging or searching; $t_{3269} = 1.3$, $p = 0.2$.

Shark speed was significantly slower in foraging locations ($\mu = 3.1$ km h^{-1}, $\sigma' = 4.4$), than in travelling locations ($\mu = 3.7$ km h^{-1}, $\sigma' = 5.4$); $t_{3397} = 3.4$, $p = 6.3e^{-4}$. It was also significantly slower in searching locations ($\mu = 3.2$ km h^{-1}, $\sigma' = 4.5$); $t_{3267} = 2.8$, $p = 5.0e^{-3}$. There was no significant difference in shark speed while foraging or searching; $t_{4567} = 1.0$, $p = 0.3$.

The GLM showed that SST had the variable significance of impact across all comparisons of response variables. When mean values for each response were compared, foraging locations had significantly higher SST ($\mu = 20.3$ °C, $\sigma' = 3.6$), over

Table 4. GLM output indicating the impact of predictor habitat variables on response behavioural states of blue sharks. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Response variables	Predictor variables	Estimate	Standard error	P-value	
Search/Forage	OceanDepth (m)	1.414e-04	3.169e-05	8.05e-06	***
	SST (°C)	2.127e-01	1.661e-02	< 2e-16	***
	CurrentMag (cms^{-1})	1.137e-02	4.887e-03	0.0200	*
	ChlA	6.115e-02	4.428e-01	0.8902	
	DistanceFromShore (km)	–4.368e-05	3.131e-04	0.8890	
	SharkSpeed (kmh^{-1})	8.236e-03	8.170e-03	0.3134	
	SharkID	2.910e-03	1.512e-03	0.0542	.
Travel/Search	OceanDepth (m)	8.996e-05	3.627e-05	0.0131	*
	SST (°C)	–1.411e-01	1.695e-02	< 2e-16	***
	CurrentMag (cms^{-1})	4.898e-03	5.004e-03	0.3277	
	ChlA	2.130e+00	4.214e-01	4.29e-07	***
	DistanceFromShore (km)	8.601e-04	3.296e-04	0.0091	**
	SharkSpeed (kmh^{-1})	3.147e-02	7.695e-03	4.32e-05	***
	SharkID	7.374e-03	1.543e-03	1.77e-06	***
Travel/Forage	OceanDepth (m)	2.408e-04	3.718e-05	9.31e-11	***
	SST (°C)	2.842e-02	1.621e-02	0.0797	.
	CurrentMag (cms^{-1})	1.169e-02	5.497e-03	0.0334	*
	ChlA	1.712e+00	4.090e-01	2.86e-05	***
	DistanceFromShore (km)	1.025e-03	3.410e-04	0.0027	**
	SharkSpeed (kmh^{-1})	3.500e-02	8.248e-03	2.20e-05	***
	SharkID	1.180e-02	1.605e-03	2.00e-13	***

travelling (μ = 19.7 °C, σ' = 3.7); t_{3530} = 4.5, p = 8.2e^{-6}. Searching locations were also significantly warmer (μ = 21.7 °C, σ' = 3.4) than travelling locations; t_{4513} = 18.2, p = 7.9e^{-72}.

Ocean current magnitude also had the variable significance of the impact on response behaviours in the GLM. Results were aligned with analysis of mean values, indicating that foraging locations (μ = 13.3 cm s^{-1}, σ' = 7.8) occurred in weaker current areas when compared with searching (μ = 15.6 cm s^{-1}, σ' = 9.2); t_{3795} = 8.4, p = 4.7e^{-17} or travelling locations (μ = 14.2 cm s^{-1}, σ' = 8.6); t_{3157} = 3.0, p = 2.7e^{-3}.

Collectively the GLM results and comparisons of mean predictor variables suggest that foraging and searching, generally occurred in areas of similar habitat, comprised of lower chlorophyll A, warmer SST and slower animal speeds, when compared to travelling behaviour.

4. Discussion

The long-term monitoring of blue sharks (*Prionace glauca*) with SPLASH tags provides an opportunity to validate behavioural state predictions and extend utilisation of our own, and existing SPOT tag data. Movement models can infer behavioural information from location-only data, however, many require extensive data pre-processing and model training, such as the removal of large outliers, standardisation of intervals between observations, and estimation of the ranges of parameter distributions even with movement data collected by more accurate GPS devices. The method used in this study is conceptually simple, as it identified states of behaviour within the geospatial lifelines of animals by acute changes in the temporal autocorrelation structure of movement metrics. The objective of this study was not to determine the best model for predicting behavioural states in blue sharks, but rather to evaluate the use of one model to demonstrate how, if validated, such a model can enable greater utilisation of rare and expensive satellite tag data. Fishery independent data are several orders of magnitude less abundant than fishery bycatch data for blue sharks, and thus any increase in such data would aid in the management of the species, which in recent times looks most promising through global 'big data' collaborations [10].

The model identified three distinctive behavioural states within the 6 two-dimensional tracks. Most individual sharks shared similar parameters for each of these states. Searching states were the dominant output from the model (66.5% of locations), likely because they were an 'in-between' state. This state has also been labelled as resting and likely comprises mixed behaviours associated with efforts to locate prey [59]. Given the large-scale environment and prey distribution being patchy, it makes sense that this behaviour was dominant. Foraging states (22.3% of locations) were predicted along tracks where expected, according to modelling theory; when the sharks' movements were restricted in an area, moving in tight circles. This supported the prospect of determining what correlation may exist between modelled foraging areas and associated environmental variables, allowing the prediction of important habitats. Travelling states (11.2% of locations) were the least frequently modelled, but were predicted as expected, most often along long, direct routes where a shark moved at the fastest speeds. Overall, the predicted behavioural states from the model were consistent with behaviour modelling theory and the literature [32,64-67].

4.1 Model validation

The simple 'overlay' methodology used to compare 'known' behaviour events, with predicted behavioural states, provided useful validation of the model. Such validation can be rare in modelling, but it is important as it avoids simply applying a model with no actual way of determining its accuracy [56-58]. Although such practice has been applied to GPS tracked animal movements (for example Zhang et al. [59]), and validation of ARGOS data in other species albeit rarely [56-58], to the author's knowledge this is the first study to validate Argos data from blue sharks in this way. This is important as behavioural data for blue sharks is rare, and the prediction of behavioural states from ARGOS data for some marine species has proven inaccurate [56]. ARGOS data may be species-specific as far as its representation of behaviour, relative to the spatio-temporal nature of two-dimensional, surface location tracks. Results in this study reflected that the BCPA behavioural prediction model proved valid for blue sharks. The ability to accurately predict foraging behaviour for the species, throughout its distribution tracked, can assist with management through awareness of critical habitat and potential overlap with fisheries.

A reason for the model's lower predictive probability of travelling and searching states may be related to the dominance of foraging in the 'known' events [43]; making them potentially more likely to overlap spatio-temporally with the more apparent searching or travelling modelled states. 'Mismatches' between searching and foraging are not surprising because searching is likely made up of mixed behaviours, with sporadic foraging events occurring within searching bouts. A lack of foraging persistence during a searching bout would be inadequate for the model to reflect a foraging bout, but on the contrary, an individual foraging event is detectable in dive data. As previously mentioned however, the robust spatio-temporal coverage of the dive event data set provides confidence that an adequate number of each behavioural state was likely captured, providing a strong metric for validation.

4.2 Application of the validated model to additional, surface location-only SPOT tag tracks

The high predictive probability of foraging behaviour for blue sharks (69-100% of locations across individuals), validated the model's use in further analysis of the nine additional location-only tracks from SPOT tags. In doing so, greater insight into blue shark habitat use was possible than what was originally available in this study. Given other pelagic species display similar prey related diurnal vertical migrations (basking shark [68,69], whale sharks [70], tuna [71], sperm whale [72]), and thus likely similar surface location patterns, the model from Zhang et al. [59] or similar, could be validated and applied for comparable benefits, especially as surface location-only Argos tracks are common within studies of pelagic species.

The large number and wide spatio-temporal distribution of these predicted and inferred behavioural events (2049 foraging, 2877 searching, 1839 travelling), enabled an extensive range of habitat and environmental variation to be captured and later investigated for influence on behavioural state. It was evident that blue sharks exhibited all behavioural states, throughout their entire range and calendar seasons. In the context of foraging, as a critical behaviour, the consistent expression of it indicates an absence of specific locations or seasonal timing of foraging habitat. This is important as it suggests a persistent predator impact and potential ecological services provided by the blue shark throughout its entire distribution range in this region. It also suggests persistent exposure to fisheries which often bait using prey of the blue shark.

There appeared, through simple proximity correlation, to be no obvious spatial link between foraging and significant bathymetric features like seamounts, which are often associated with pelagic productivity and predator preference. This is interesting as seamounts, in particular, are often considered to be biodiversity hotspots [73,74], that aggregate commercially valuable fish [75]. Because of this, they have been identified as areas of particular interest for conservation and marine-protected areas [76,77]. Associations of this kind are justified for certain species but should be applied with caution. Certain species may not actually prefer such habitat, but due to their abundance and distribution overlapping with fishery location and effort, they may be falsely associated with these features. This could be the case with the blue shark. As an example, Litvinov et al. [78] suggested that seamounts are of particular interest to male blue sharks, where they aggregate, forming 'male clubs'. However, Litvinov et al. [78] also made comparisons using catch per-unit effort fishery data, where the target species, likely tuna, may prefer such a habitat, whilst stating that blue shark aggregations may prefer other places such as features of water structure or gradients. Recent tagging studies, in combination with oceanography revealed that blue sharks counter intuitively showed foraging preference in low surface chlorophyll A, anticyclonic eddies [39], characterised by anomalously warm water, conventionally thought to be ocean deserts void of significant biomass [79]. Such areas differ from conventional seamount 'hotspots' that aggregate commercially valuable fish [75], reflecting how fishery bycatch data may not be able to represent important blue shark habitats. The ability to define critical habitats and areas of bycatch vulnerability, like foraging areas, in a fishery independent way is valuable for the management of highly migratory, marine species like the blue shark [10].

4.3 Using a GLM to determine the impact of habitat data on behavioural states

The GLM provided novel insight into the influence habitat variables can have on behavioural states of blue sharks. The insight was novel firstly because of its location in the South Pacific where no fishery independent data has been recorded for blue sharks before; and because insight came from SPLASH tags, which enabled highly accurate observed and validated behavioural predictions to be mapped. These factors combined, allowed the influence of the environment to be assessed in relation to data directly from blue sharks, through space and time, rather than one-off encounters in fisheries.

Conventional fisheries management has been historically limited to using bycatch data, contrast with environmental variables in an attempt to determine or predict species presence/absence, abundance and distribution in relation to habitat preference. Such data is widely recognised to come with biases however [6], primarily related to effort and location of fleets, and because blue sharks are so commonly caught, presence/absence predictions are nearly always present [80]. While the data set used in the present study's GLM was limited to 15 blue sharks, the tags used and the validation of a behavioural prediction model, generated a robust data set providing novel insight on critical habitat.

When GLM results were coupled with T-test analysis of raw data sets of habitat and other predictor variables, it was evident that foraging and searching generally occurred in areas of similar habitat, comprised of lower chlorophyll A, warmer SST, weaker ocean currents (foraging only) and slower animal speed, when compared to travelling behaviour. Low levels of chlorophyll A are not commonly associated with foraging by oceanic predators. It is often suggested that higher surface chlorophyll A, generated by features like seamounts, especially in oligotrophic regions [81-83], causes greater productivity and likelihood of prey densities, which should catalyse searching and foraging behaviour. Results from the present study suggest this correlation is not the case for blue sharks. Although blue sharks are not filter feeders, which target surface-oriented chlorophyll A densities as they attract zooplankton aggregations [68], there are prey species of blue sharks that do target such chlorophyll A rich habitat [84]. Braun et al. [39] found that satellite tagged blue sharks in the gulf stream also, counter intuitively, showed foraging preference in waters with low chlorophyll A surface expression. Such habitat use was related to anticyclonic eddies (ACE), characterised by anomalously warm water, conventionally thought to be ocean deserts void of significant biomass [79]. Their findings suggested that blue sharks use the core of ACE, which carries warm water down, as conduits to forage more optimally at depths with higher prey densities, where they are usually constrained by their physiological thermal constraints [85]. In the present study, SST was significantly higher on average in foraging and searching locations, than in travelling locations. Foraging locations were also associated with significantly slower ocean current magnitude, which could likely occur within the centre of eddies. Eddy characteristics were not investigated in the present study, however, observations from Braun et al. [39] explain how ACE may be the reason why foraging and searching behaviours in the present study, were associated with areas of lower mean surface chlorophyll A, warmer waters and slower ocean current magnitude when compared with travelling.

It is important to acknowledge that further understanding of prey distribution with eddy type is needed before concluding that eddy type is catalysing better foraging environments, and thus behaviours. However, optimal foraging theory does suggest that conditions which enable a predator to spend greater duration in contact with prey distribution, would be beneficial. The correlation of foraging and searching behaviour with features representative of ACE suggests that they should not be considered barren deserts. ACE move location, grow and shrink, meaning their potential benefit may come and go for the blue shark. This does not mean that the prey associated with the deep scattering layer also moves, but rather that ACE simply enables optimal foraging, and thus it should not be surprising that blue sharks may show spatio-temporal preference for them.

5. Conclusions

The BCPA model [59] was validated for use in predicting foraging behaviour through the entire home range of satellite tagged blue sharks (*Prionace glauca*) in the southwest Pacific. When coupled with habitat information, novel insight on behaviour distribution categorised potential critical habitat quite differently to suggestions from studies using fishery data; predominantly the positive association with surface chlorophyll A [78,86,87]. Because there are pros and cons to both fishery and non-fishery derived data sets, population management of blue sharks would benefit most from the coupling of both through ‘big data’ studies. This study has demonstrated a methodology enabling greater insight from ARGOS satellite tags, enhancing the contribution of such data sets for ‘big data’ studies. This process and the validated model have been specific to blue sharks but can likely be applied to other pelagic predators either directly, or via a similar validation methodology.

Author Contributions

Dr Riley Elliott did all fieldwork, data collection, data processing and writing of the manuscript. Jingjing Zhang processed raw data through the behaviour model and GLM model, and assisted with output interpretation. John Montgomery, Todd Dennis and Craig Radford supervised the research design and co-authored/reviewed the manuscript.

Conflict of Interest

There is no conflict of interest.

Data Availability Statement

Raw data is not publicly available. However, the full PhD thesis can be accessed through the University of Auckland https://researchspace.auckland.ac.nz/handle/2292/53201 and the corresponding author can be contacted for further information.

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