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Marine biology

Cryptic habitat use of white sharks in kelp forest revealed by animal-borne video

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Traditional forms of marine wildlife research are often restricted to coarse telemetry or surface-based observations, limiting information on fine-scale behaviours such as predator–prey events and interactions with habitat features. We use contemporary animal-attached cameras with motion sensing dataloggers, to reveal novel behaviours by white sharks, *Carcharodon carcharias*, within areas of kelp forest in South Africa. All white sharks tagged in this study spent time adjacent to kelp forests, with several moving throughout densely kelp-covered areas, navigating through channels and pushing directly through stipes and fronds. We found that activity and turning rates significantly increased within kelp forest. Over 28 h of video data revealed that white shark encounters with Cape fur seals, *Arctocephalus pusillus pusillus*, occurred exclusively within kelp forests, with seals displaying predator evasion behaviour during those encounters. Uniquely, we reveal the use of kelp forest habitat by white sharks, previously assumed inaccessible to these large predators.

1. Introduction

Determining how predator and prey interact with their surroundings is critical to our understanding of ecosystem dynamics and functioning [1]. The structure and complexity of a habitat can mediate the success of predators or response from prey [2], yet predation events are inherently rare and are difficult to observe in the wild, particularly in marine environments [3]. Surface-based observations have described interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) [4–6]. These have revealed that white sharks typically ambush seals at the surface during crepuscular hours as they swim to or from their terrestrial refuges [4]. However, recent studies have identified one key aggregation area where different patterns occur: the Dyer Island Marine Reserve (Gansbaai, South Africa). Unlike elsewhere, white sharks here occupy small areas close to the seal colony throughout daylight hours [7]. Around this island, sharks predominantly display two distinct behavioural states—area-restricted searching or active patroling [8]—and typical predatory behaviour at the surface is rare [6]. Here, seals also exhibit lower stress hormone levels than at other sites [9]. The abundance of kelp at Dyer Island compared to other seal rookeries is considered a possible reason for the observed differences in predator–prey interactions, as kelp is thought to provide refuge for seals

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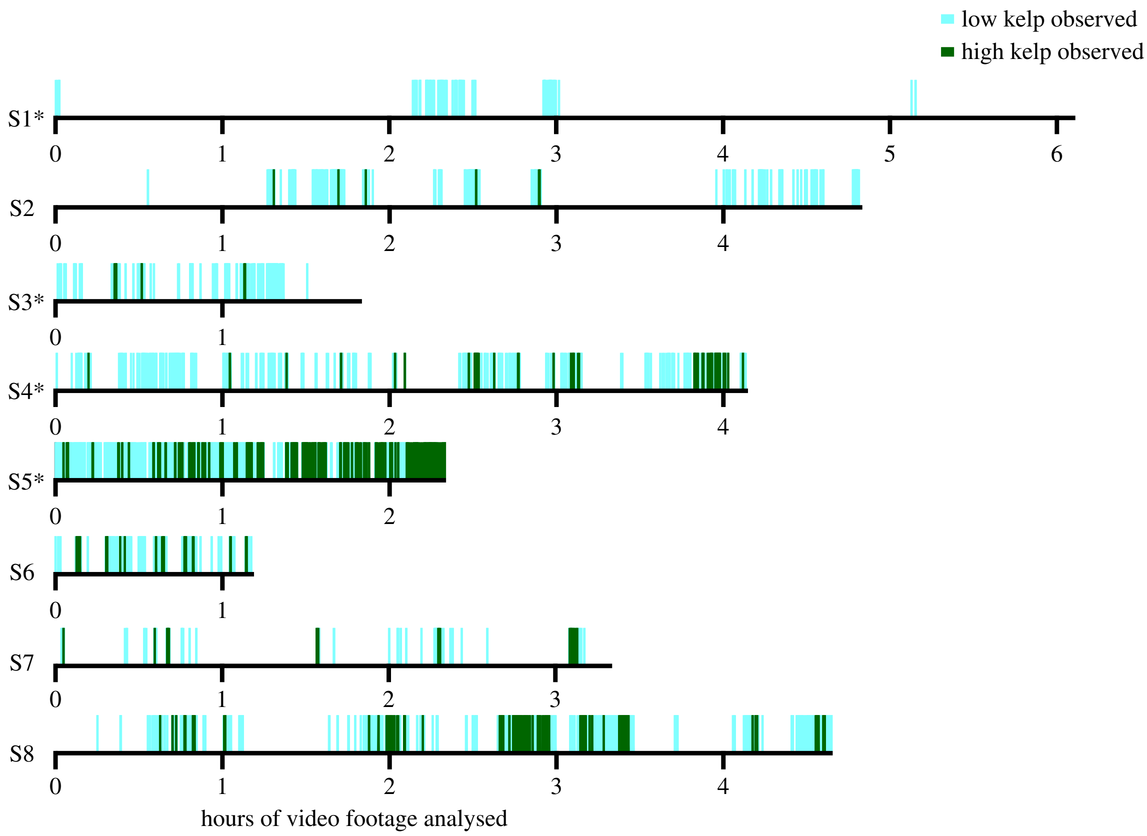

Figure 1. Repeated usage of kelp forest by white sharks as observed in AVED footage. All observations of low (teal) and high (dark green) density kelp forest over time of video analysed per shark are shown. All white sharks encountered kelp forest, with seven of eight entering areas of the densely covered canopy. *Video deployments that could be matched to motion sensor logs. (Online version in colour.)

Table 1. Summary of all deployments of animal-borne cameras on white sharks at Dyer Island and Geyser Rock during 2014 and their representative time spent in kelp forest habitat.

shark ID	date	size (cm)	sex	video analysed (h)	kelp observed (incidence)	kelp observed (h)	kelp observed (%)	contact with kelp	seal encounters
1	3 May 2014	305	F	6.1	71	0.09	1.44	0	0
2	7 May 2014	365	F	4.8	168	0.25	5.22	1	0
3	7 May 2014	350	M	1.8	105	0.21	11.82	0	0
4	11 May 2014	305	M	4.3	267	1.17	27.47	1	0
5	11 May 2014	305	F	2.3	240	1.41	60.08	31	10
6	12 May 2014	290	F	1.2	98	0.29	24.27	1	0
7	13 May 2014	275	F	3.3	72	0.20	6.10	0	0
8	13 May 2014	290	M	4.7	319	1.28	27.56	3	0
all sharks total				*28.5*	*1340*	*4.9*	*163.96*	*36*	*10*

from white sharks [6–9], in a similar way that it does for sea otters in California [10]. However, the hypothesis that kelp provides an unsuitable habitat, or barrier for white sharks in South Africa has not been tested, because previous research was limited to surface-based observations [6] and coarse telemetry positions [7,8]. Recent advances in the field of biologging have made it possible to explore cryptic behaviours of a wide range of species by collecting visual data from animal-attached video systems and behavioural data through animal motion sensing via 'animal-borne video and environmental data collection systems' (AVEDs [3,11]). Here, we used AVEDs to examine the cryptic interactions between white sharks and Cape fur seals in this region in an attempt to understand the role kelp forests play in the foraging behaviour of white sharks.

2. Material and methods

We tagged eight white sharks ranging from 275 to 365 cm total length with high-resolution camera/motion sensor AVEDs (*CATS-Cam, Customized Animal Tracking Solutions; CaféCam, Monterey Bay Aquarium Research Institute*) near a Cape fur seal colony on Geyser Rock, in the Dyer Island Marine Reserve, near Gansbaai, South Africa during May 2014 (Department Environmental Affairs permit RES2014/34). Sharks were attracted to a

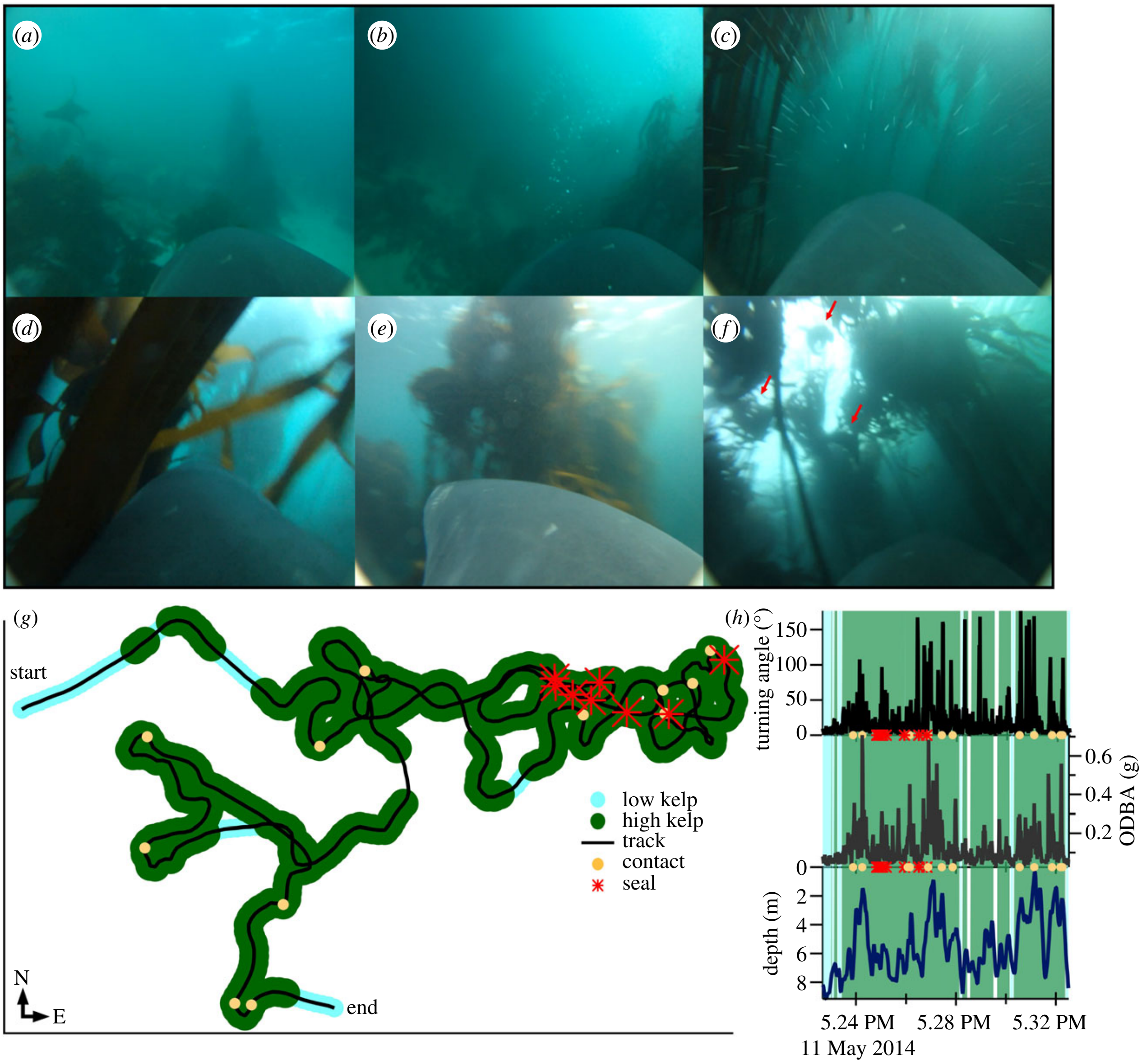

Figure 2. Still-picture frames and a 10-min subsample of pseudo-track and data log of a white shark encountering Cape fur seals in kelp canopy. (*a*) AVED footage of a white shark (Shark 5) encountering Cape fur seals. (*b*) The seals respond to the shark's presence by hunkering to the sea floor and blowing bubble streams as the shark passes overhead or swimming further into the kelp. (*c*) The shark swims through the bubbles, (*d*) then through kelp. (*e*) The shark pursues the seals, making contact with dense kelp fronds at several points and pushing through them. (*f*) At least three Cape fur seals (indicated by red arrows) are seen taking refuge in the canopy area of the kelp forest fronds and successfully avoiding the white shark. (*g*) A 10-min subsample of Shark 5's dead-reckoned pseudo-track within dense kelp forest, including encounters with seals. (*h*) Time-series recordings of turning angle (°), activity (ODBA, g) and depth (m) for the corresponding time period; background colours represent low (teal), high (green) and no (white) density kelp observed. Full tracks (electronic supplementary material, figure S2) and footage (electronic supplementary material) of these interactions are linked at the end of the manuscript. (Online version in colour.)

research vessel [7] before being fitted with AVEDs (comprising HD video cameras and 12 channels of biologging data), using a minimally invasive stainless steel fin clamp [12,13]. Cameras were programmed to record during daylight hours for a maximum duration of 8 h over a 24–72 h period of deployment. The AVEDs then released from the animals and were retrieved using VHF telemetry at the surface [13].

We categorized habitat and prey encounters by analysing videos in Solomon Coder (version beta 17.93.22 [14]), recording all observations of anchored kelp by occurrence and duration, determining kelp to be of high-density when present and filling 50% or more of the available frame and low-density if less. The presence of seals was also recorded, as were incidences when sharks made contact with or moved between narrow gaps in kelp. To explore these interactions further, we created dead-reckoned pseudo-tracks, derived absolute turning angles every second as a proxy for track tortuosity and calculated overall dynamic body acceleration (ODBA) as a proxy for locomotor activity from tri-axial accelerometer and magnetometer data [15–17].

To determine the significance of differences observed in movement behaviour inside and outside kelp habitats, we implemented a randomization analysis using Kruskal–Wallis rank sum comparison to test for differences in turning angles and ODBA across bootstrap replicates. Each replicate was subsampled (minimum 30 s interval) proportionally to the observed time spent within and outside kelp habitats before statistical differences were tested between habitat groups (Kruskal–Wallis test). Over 1000 iterations, distributions of the test statistic and median rank sum difference (electronic supplementary material, figures S6 and S7) determined the significance of a kelp effect on behaviour by reporting the percentage of randomly sampled replicates exhibiting significant differences. All statistical analyses were conducted within R (*R Core Team* [18]) and are described in greater detail within the electronic supplementary material.

Table 2. Bootstrap results demonstrate the significance of kelp effect on observed behaviours. Large proportions of randomly sampled replicates exhibiting significant differences emphasize a consistent effect of kelp on observed behaviour. Medians and standard deviations are reported for the Kruskal–Wallis statistic and the *post hoc* median rank difference (electronic supplementary material).

			statistic		rank difference	
	shark ID	prop < 0.05	median	s.d.	median	s.d.
ODBA	1	0.037	0.6	1.23	−19.8	32.1
	3	0.550	4.3	4.65	11.8	12.2
	4	0.942	11.9	6.43	49.2	12.8
	5	0.998	20.8	6.83	34.1	5.8
turning angle	1	0.282	2.5	1.73	68.3	26.3
	3	0.704	6.4	5.30	32.3	13.0
	4	—	—	—	—	—
	5	0.732	6.52	4.63	20.6	7.49

3. Results

A total of 28.5 h of video data from eight sharks (mean of 3.6 h $\pm$ 1.7 (standard deviation); table 1) were analysed and a total of 1340 incidences of kelp presence were recorded, covering 4.89 h (17.20% of total footage, mean of 20.5% $\pm$ 19.1). Technical issues meant activity (ODBA) could only be matched to video in four of these deployments, with pseudo-tracks derived in three of these (electronic supplementary material). Kelp was observed in footage from all eight sharks, ranging from 1 to 60% of individuals' total footage, with seven sharks repeatedly moving into densely covered areas and four sharks making direct contact with kelp fronds or stipes (figure 1), while the eighth (Shark 1) appeared to have left the island system. This was confirmed by the shark's tag being recovered over 50 km away from the study site at a beach in Struisbaai. Two sharks encountered other white sharks while swimming through kelp forest (electronic supplementary material, figure S1). Thirty-six incidences of contact with kelp occurred, with a majority (31) of those recorded from one shark (Shark 5). Ten interactions with seals were recorded, all within dense kelp and all from a single shark (Shark 5). Seals were in groups of one to three individuals and responded to the presence of the shark by blowing bubbles, swimming deeper into kelp or hunkering to the seafloor (figure 2). The shark responded by turning sharply, eventually pushing directly through kelp while increasing activity (electronic supplementary material). No successful predation events were observed in the footage, but ODBA and turning angles differed significantly in the presence of kelp (table 2). Shark 5 consistently exhibited higher ODBA (99.8% of replicates below $\alpha = 0.05$, $\bar{H} = 20.8$) and turning angles (73.2% of replicates below $\alpha = 0.05$; $\bar{H} = 6.52$) inside kelp habitats compared to kelp-free areas. Shark 4 similarly exhibited consistent heightened ODBA within kelp habitat (94.2% of replicates below $\alpha = 0.05$, $\bar{H} = 11.9$) but lacked the magnetometer data necessary for the calculation of turning angles. Kelp had similar effects on Shark 3's movement behaviour, with elevated ODBA in over half of bootstrap replicates (55.0% of replicates below $\alpha = 0.05$, $\bar{H} = 4.3$) and similar levels of increased turning angles (70.4% of replicates below $\alpha = 0.05$, $\bar{H} = 6.35$). Shark 1, which encountered kelp in less than 2% of footage and transited away from the study area, showed no clear effect (ODBA: 3.7% of replicates below $\alpha = 0.05$, $\bar{H} = 0.6$; turning angle: 28% of replicates below $\alpha = 0.05$, $\bar{H} = 2.48$).

4. Discussion

This is the first study, to our knowledge, to document extensive and repeated use of kelp forests by white sharks and to describe predator–prey interactions within this habitat. This kelp foraging behaviour is vastly different from the open-water ambush predation thought to dominate at other coastal aggregation areas [4–6]. Dyer Island is the only pinniped colony in South Africa where white shark presence has been found to increase during daylight hours compared to crepuscular periods [7]. Previous studies have found the incidence of predation and area-restricted search to peak later in the morning at Dyer Island and to occur directly adjacent to the rookery or connected kelp forest [6–8]. Here we confirm the presence of white sharks inside kelp forest, which may serve as an alternative foraging strategy to the traditional ambush predation at twilight. Unfortunately, we did not record successful predations on seals during this study (either outside or inside the kelp), likely because of the rarity of these events on a per individual basis [6,19]. However, the lack of a successful predation should not be considered evidence to the contrary. Indeed, Jorgensen *et al*. [19] only recorded one successful predation event in over 43 days of stomach temperature data in free-ranging white sharks off the California coast. The extent and profitability of kelp foraging in comparison to 'traditional' foraging strategies remains to be determined, but the zero-inflated nature of these datasets will hinder such efforts until much larger datasets are available.

Kelp forests are threatened globally and present in many other temperate locations where white sharks and pinnipeds co-occur [10]. The coverage and density of kelp assemblages change year from year, and future research should reevaluate the role of kelp forest in the foraging ecology of white sharks rather than presume it to be a habitat they avoid. Our findings demonstrate the power of animal-borne video to improve our understanding of the habitat use of large marine predators and reveal interactions within the marine environment that would have remained hidden with conventional telemetry systems.

Ethics. All shark tagging was done under the animal care and use protocols (APLAC) from the Max Planck Institute and Department Environmental Affairs permit RES2014/34.

Data accessibility. Data are available from the Dryad Digital Repository at: https://doi.org/10.5061/dryad.347jg5p [20].

Authors' contributions. O.J.D.J., T.K.C., A.C.G. and S.J.J. conceived the study. T.K.C., O.J.D.J., A.C.G., S.J.J., M.W., S.J.B. and B.A.B. took part in logistical planning of study design, securing of funding, ethical approval and preparation for fieldwork. O.J.D.J., T.K.C., A.C.G. and S.J.J. took part in Fieldwork. O.J.D.J., A.C.G., S.A. and J.H.M. performed Analysis. A.C.G., T.K.C., S.J.J. and S.J.B. provided guidance on the interpretation of results. All authors contributed to writing and drafting the manuscript, approved the final version and accept responsibility for its content.

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