The influence of kelp density on white shark presence within the Dyer Island Nature Reserve, South Africa

Running Headline: Kelp density and white shark presence

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ABSTRACT

Large-scale and small-scale natural barriers have the ability to mediate the ecological dynamics within a region. In some instances, these barriers greatly influence the presence of predators and prey on spatio-temporal scales. For this study, we aimed to assess how varying densities of sea bamboo (*Ecklonia maxima*), a kelp species found within South African waters, could influence the presence of *C. carcharias*. Using baited remote underwater video systems (BRUVS), thirty-one different *C. carcharias* were identified and a total of 135 hours of video were collected in high, moderate, and low kelp densities to create an organismal sighting index. Generalized linear models illustrated that the best fit model included the main effect of kelp density, with a clear inverse relationship between kelp density and *C. carcharias* sightings. However, although zero sharks were sighted within the high kelp density regions, ten different *C. carcharias* were sighted within the moderate kelp density regions, illustrating that the broad notion that *C. carcharias* do not navigate through kelp ecosystems is false and requires more specificity (e.g. high density kelp areas may result in decrease *C. carcharias* presence). In contrast, kelp density had no significant influence on the presence of five other elasmobranch species detected by the BRUVS. This study demonstrated that highly dense kelp forests (i.e. ≥1 stalk of kelp per 1 m^2) serve as a local natural barrier for large *C. carcharias*; however, the need for a more inclusive analysis (e.g. routine inclusion of current speed and multi-location assessment) is warranted.

Keywords: Sea bamboo, *Ecklonia maxima*, baited remote underwater video systems (BRUVS), elasmobranch, generalized linear model

Introduction

Variations in responses are often related to animal-based physiological requirements that are linked to environmental (e.g. salinity, currents, and temperature; Lessios *et al*. 1999; Barber *et al*. 2000) and geographic barriers (e.g. open ocean distances, deep ocean basins; Vermeij 1987; Gibbs 1998; Bernardi 2000; Riginos & Nachman 2001; Lessios & Robertson 2006). Such large-scale natural barriers have substantial impacts on organismal distribution and can even lead to allopatric divergence (Taylor & Hellberg 2003; Gopal *et al.* 2006; Muller *et al.* 2012).

Although these large-scale barriers may influence genetics, small-scale habitat heterogeneity acts more at the community level in providing ecosystem-specific natural barriers. Such small-scale barriers can have large-scale implications for the ecological dynamics of an environment, and have even been demonstrated to influence the spatial distributions of both predators and prey (e.g. Hammerschlag *et al*. 2010; Guttridge *et al*. 2012). In Bimini, Bahamas, variations in environmental conditions, such as tides, were demonstrated to elicit changes in the presence of sub-adult lemon sharks (*Negaprion brevirostris*), thereby influencing the utilization of shallow-water mangrove-fringed inlets by neonate and juvenile *N. brevirostris* as an anti-predation mechanism (Guttridge *et al*. 2012). Such findings illustrated that mangroves can serve as small-scale natural barriers to larger predators and consequently, are vital to the functional dynamics within this ecosystem (Robertson & Duke 1990; Robertson & Blaber 1992).

Similarly, in areas ranging from the west of Cape Agulhas to northern Namibia, sea bamboo (*Ecklonia maxima*) is the predominant kelp species in shallow water (e.g. 0-8m) ecosystems and can be considered a small-scale natural barrier (Dayton 1985; Tegner & Dayton 2000; Steneck *et al*. 2002). *E. maxima* is a temperate water species and is a highly productive component of the coastal environment (Field *et al*. 1980; Tegner & Dayton 2000). Kelp forests are structurally complex and ecologically delicate, as small disturbances can lead to substantial trophic cascades (Estes & Duggins 1995; Dayton *et al.* 1998; Steneck *et al*. 2002). However, the structure and distribution associated with kelp forests results in a unique habitat that serves as an important foundation for the life of many marine animals (Fricke 1979; Field *et al*. 1980). The distribution of *E. maxima*, is spatially overlapping with the distribution of *C. carcharias* (an apex predator that has a global distribution in both temperate and tropical seas; Anderson & Goldman 1996; Bonfil *et al*. 2005; Bruce *et al.* 2006). Although considerable research on *C. carcharias* behavioral distribution has been conducted (e.g. Compagno 1984; Casey & Pratt 1985; Fergusson *et al*. 2000; Martin *et al*. 2005; Laroche *et al*. 2007, Kock *et al*. 2013; Towner *et al*. 2016), minimal scientific evidence exists to assess the potential 'natural barrier' influence of a kelp forest in relation to the presence or absence of *C. carcharias.*

In this study, we aim to address two key scientific objectives: (1) to assess if differing densities of sea bamboo (*Ecklonia maxima*) can influence *C. carcharias* sightings and (2) to determine if there is a relationship pertaining to *C. carcharias* presence with respect to several additional explanatory variables. Based on previous findings, we hypothesized that *C. carcharias* sightings would be best dictated by kelp density, with high (i.e. ≥1 stalk of kelp per 1 m^2) and moderate kelp (i.e. <1 stalk of kelp per 1 m^2 to >1 stalk of kelp per 6 m^2) densities being sufficiently difficult for *C. carcharias* to navigate through yielding a significantly greater quantity of *C. carcharias* sightings in the low kelp density (i.e. ≤1 stalk of kelp per 6 m^2) regions. Furthermore, several additional explanatory variables (i.e. the presence or absence of other elasmobranchs and baited remote underwater video systems [BRUVS] redeployment) will be assessed to determine if the main effects or interactive effects of these variables have a significant influence on *C. carcharias* sightings. More specifically, results from a previous South African study illustrate that elasmobranchs were the most common prey category for *C. carcharias* with a <250 cm precaudal length (PCL; Cliff et al., 1989) and for this reason, it is hypothesized that sightings of potential *C. carcharias* prey (i.e. other elasmobranchs) may also yield significant increases of *C. carcharias* sightings. In addition, on certain occasions BRUVS will be redeployed in the same location. This re-deployment would result in continued olfactory plume dispersal and maximizing the overall area covered by the plume. Therefore, it is hypothesized that BRUVS redeployment may have a significant impact on *C. carcharias* sightings as this approach may increase the likelihood of overlap between the olfactory plume and *C. carcharias* movements.

Materials and Methods

Kelp Density Experiment

Regions around Dyer Island Nature Reserve (Kleinbaai, South Africa; 34°41'S; 19°25'E; Fig. 1) were selected as the designated study sites due to the overlapping spatial distributions of *Carcharodon carcharias* and varying densities of *Ecklonia maxima*. Several of these regions were surveyed to determine their approximate surface and sub-surface kelp densities by using a 5 m research vessel as a reference and a 1.0 m^2 PVC frame with an attached GoPro Hero 3 HD 1080p camera. Frames were randomly deployed 10 times within each perspective kelp bed in a selected zone (see Fig. 1c to see zone designations) and the mean kelp density per kelp bed was calculated. For a kelp bed within a zone to be characterized as a deployment site, the following criteria were required: the kelp bed was a minimum of 25 m x 25 m, at least 75% of the kelp bed boundaries were exposed to open water rather than a region of differing kelp density (e.g. a moderate density kelp bed that existed within the confines of a high density kelp bed could not be used for experimentation), and kelp bed location must be characterized as feasible for routine BRUVS deployment (e.g. minimal wave exposure). The kelp beds of interest were thus categorized as either low density (i.e. ≤1 stalk of kelp per 6 m^2), moderate density (i.e. <1 stalk of kelp per 1 m^2 to >1 stalk of kelp per 6 m^2), or high density (i.e. ≥1 stalk of kelp per 1 m^2).

To make subsurface observations, custom made 61 cm x 46 cm BRUVS were constructed out of 5 cm diameter PVC piping that was reinforced with a 1 cm diameter steel dropper bar, a GoPro Hero 3 1080p camera, and a 60cm bait canister that contained 2.25 kg of natural fish chum (i.e. comprised of minced skipjack tuna – *Katsuwonus pelamis*). In the center of the BRUVS, a 15 m long steel cable was attached to a surface buoy to permit deployment, locating and retrieval (Fig. 2).

To commence experimentation, three BRUVS were deployed simultaneously, one in each kelp density region. When possible and weather permitting, the BRUVS were re-deployed in the same location. All videos were subsequently analyzed by one observer, to maintain consistency among video footage analysis and data collection (Bernard &

Götz 2012). To keep the deployment duration of all BRUVS standardized and prevent bias in statistical analysis, when a BRUVS was flipped during a trial (e.g. by waves or a shark) the behavioral observations associated with the other two BRUVS were discarded at the time of BRUVS inversion. During post-hoc video analysis, the researcher recorded: species, estimated quantity of *C. carcharias*, and re-sighting frequency where possible. To identify individual *C. carcharias* and to determine if an individual returned over the experimental timeframe, distinctive characteristics (e.g. presence/absence scars, tags, pigmentation patterns, and dorsal fin notch characteristics) were used, a technique that has been successfully implemented in previous studies (Anderson et al. 2011, O'Connell et al. 2014, 2017).

Sighting data collected throughout experimentation were binomial, where researchers focused on identifying whether *C. carcharias* were sighted (e.g. scored as 1) or not sighted (e.g. scored as 0) within a trial and kelp density region. These data were multi-dimensional and therefore a logistic regression was used to analyze the binomial sighting data (see Table 1 and 2 for variable description). The logistic regression model is shown as the following form:

$$\ln(p/1-p) = \beta o+\beta iXi$$

where p = the probability of a *C. carcharias* sighting, (p/1-p) = odds of a *C. carcharias* sighting; βo = constant; Xi = vector of explanatory variables; βi = parameter estimate for the i^{th} explanatory variable. Forward selection was used to determine the best fit model for the data, starting with a null model of which subsequent models were created by adding one or several explanatory variables to determine their effect on the response variable (i.e. *C. carcharias* sighting). Model selection criteria included: Akaike Information Criteria (AIC), and behavior of model residuals using a quantile-quantile (Q-Q) plot, and associated p-values. The response variable was whether or not a *C. carcharias* was sighted during a trial. The explanatory variables were: kelp density (T), the presence or absence of other elasmobranchs (E), research season (R), and BRUVS redeployment (B). There were three kelp density categories, high (≥1 stalk per 1m^2), moderate (<1 stalk of kelp per 1m^2 to >1 stalk of kelp per 6m^2) and low (≤1 stalk per 6m^2). The second explanatory variable was binomial, where the researcher recorded the lack (i.e. recorded as 0) or the presence (i.e. recorded as 1) of other elasmobranchs throughout a trial. The third explanatory variable was binomial, where the first research season (May-October 2014) was scored as 0 and the second research season (June-August 2015) as 1. Lastly, when feasible, researchers conducted two BRUVS trials within one day. During some of these occasions, researchers re-deployed BRUVS in the same location. Therefore, this explanatory variable was binomial, where BRUVS were either deployed for the first time (i.e. recorded as 0) or re-deployed in the same location (e.g. recorded as 1).

It is important to note that no *C. carcharias* sightings occurred within the high density kelp region throughout experimentation. Therefore, to permit data interpretability for areas where zero sightings were recorded, data were transformed by adding one sighting to each kelp density category (i.e. one sighting was added to low, moderate, and high densities, respectively; O'Connell et al., 2014, 2017).

Results

Kelp Density Experiment

Over two consecutive years (May-October 2014 and June-August 2015) a total of 135 hours of camera observations were collected during 19 total days at sea. During this period, twenty-one trials (45 hours of deployment within each region) were conducted within each kelp density region. For each trial, BRUVS deployment lasted 2-3 hours (mean ± s.d.: 2.14 ± 0.30 hrs). During these trials, *C. carcharias* were present only within low (19 trials) and moderate (6 trials) kelp densities (Fig. 3b). The quantity of positively identified *Carcharodon carcharias* within a trial ranged from 0-5, with a combined trial total of 21, 10, and 0 different *C. carcharias* sighted within the low, moderate, and high kelp densities, respectively (Fig. 3a).

For model selection and upon initial inspection, research season (R) was found to have no significant influence ($p=0.52$) on response variables. This justified data aggregation over the two research seasons and the subsequent dropping of this variable from model formulation. For *C. carcharias* sightings, the best fit model (A2) included the main effect of kelp density (T; $p<0.001$) and contained an AIC of 47.21 (Table 1). The coefficient and associated p-value with the selected model demonstrate that the influence of low kelp density had a significantly positive ($p<0.001$; Table 2) relationship with *C. carcharias* sightings within a trial in comparison to high kelp density. Moderate kelp density also had a positive relationship with *C. carcharias* sightings within a trial in comparison to high kelp density; however, this relationship was not significant ($p=0.07$). Based on model coefficients, the low density kelp region resulted in a greater frequency of individual *C. carcharias* sightings per trial in comparison to the moderate kelp density region (Table 2; Fig. 3b).

The remaining explanatory variables; the presence or absence of other elasmobranchs within the study site (p=0.39) and BRUVS redeployment (p=0.39), were found to have no significant influence on *C. carcharias* presence during the study period.

Other Elasmobranch Sightings Relevant to Kelp Density

Throughout experimentation, a variety of different elasmobranchs were identified: leopard catsharks (*Poroderma pantherinum*), common smooth-hound sharks (*Mustelus mustelus*), puff adder shysharks (*Haploblepharus edwardsii*), pyjama sharks (*Poroderma africanum*), and/or dark shysharks (*Haploblepharus pictus*). These elasmobranchs were present within low, moderate and high kelp densities for 20, 21, and 15 trials, respectively. Based on the model selection, there was no significant relationship between the interaction of 'other elasmobranch' sightings and kelp density with respect to *C. carcharias* sightings (e.g. A7; p=0.58; Table 1).

Discussion

This study examines how variations in *Ecklonia maxima* densites may alter the spatial utilization patterns of large juvenile to adult *Carcharodon carcharias.* Although the footage captured during each trial was uni-directional, a limitation when using one GoPro per BRUVS that can contribute to the significant undercounting of shark quantities (Kilfoil et al. 2017), the results suggest that high *E. maxima* densities have the ability to significantly modify large *C. carcharias* fine-scale spatial distributions. But, the results are not consistent with our original hypothesis, as *C. carcharias* were routinely detected in mid-kelp densities. This finding illustrates that *C. carcharias* can utilize ecosystems with moderately spaced kelp and that increasing kelp density may be a characteristic influencing and/or limiting *C. carcharias* movements. Beyond kelp density, there was no detectable influence of the remaining explanatory variables (i.e. the presence or absence of other elasmobranchs, BRUVS redeployment, and research season) on *C. carcharias* sightings.

Previous studies demonstrate how habitat use can be greatly influenced by small-scale aquatic barriers, such as mangroves (Robertson & Duke 1990; Robertson & Blaber 1992; Guttridge *et al.* 2012). These aquatic plants are often utilized by invertebrates and juvenile fish as nursery habitats, and further serve as refuge from larger predators (Blaber & Blaber 1980; Robertson & Duke 1990; Robertson & Blaber 1992; Laegdsgaard & Johnson 2001; Adams *et al*. 2006; Blaber 2007; Nagelkerken *et al*. 2008). More specifically and similar to the present study, aquatic plants have the ability to serve as small-scale natural barriers and contribute to complex predator-prey dynamics (Jelbart *et al.* 2007; Newman *et al*. 2007). Furthermore, field-based observations indicate that high density kelp regions are an ideal refuge for some prey species (e.g. Cape fur seal – *Arctocephalus pusillus pusillus*) as suggested in earlier studies (Wcisel et al. 2015) and a recent study that linked reduced fecal glucocorticoid metabolite concentrations (i.e. stress) in *A. pusillus pusillus* at Dyer Island to increased refugia (e.g. dense kelp beds) from *C. carcharias* (Hammerschlag et al. 2017). But, with the current methodology and results, it is uncertain as to why the *C. carcharias* in the present study were never sighted in the high density kelp regions. However, one hypothesis is associated with the way the sharks hunt for prey. *C. carcharias* is thought to rely heavily on vision for prey detection (Strong 1996, Martin et al. 2005), thus low density kelp areas will maximize the shark's visual range and hypothetically increase their chances of predation. A second possibility to consider is the obligate ram ventilation breathing mechanism of *C. carcharias* (e.g. Randall 1970, Parsons & Carlson 1998). High density kelp forests may provide a physiological impediment to large *C. carcharias* by preventing adequate respiration. Due to the high energetic demands of *C. carcharias* (e.g. Semmens et al. 2013), the pursuit of prey through these high density kelp regions may not be energetically beneficial. A third explanation for our findings may be related to the habitat transition zone in which this study was conducted. Previous research suggests that habitat transition zones can be beneficial predatory habitats that serve as hunting corridors (e.g. Hammerschlag et al. 2010). Prey species are subjected to peak predation risks when crossing through transition zones, as these zones are often correlated with predictable prey movement patterns and thus a greater probability of predation success (Martin et al. 2005). Off the South African coastline, studies demonstrate that *C. carcharias* often frequent regions that are associated with Cape fur seal (*A. pusillus pusillus*) foraging corridors (Hammerschlag et al. 2006, Martin et al. 2005, Wcisel et al. 2015). Therefore, the predictability of *A. pusillus pusillus* movements through the high refuge area (i.e. high density kelp region) to the offshore foraging sites may result in increased *C. carcharias* quantity in low kelp density or no kelp regions as these sites may result in increased predation success. Interestingly, a recently published study provided data pertaining to *C. carcharias* movements within a kelp forest through the use of an animal-bourne video and environmental data collection system (AVEDs; Jewell et al., 2019). Of the eight sharks equipped with the AVEDs, all exhibited some swimming duration within visual range of kelp, with one 305 cm total length *C. carcharias* spending a substantial amount of navigating through the kelp forest and making contact with the kelp. As observed from our moderate BRUVS data, several *C. carcharias* similarly swam within the kelp regions, bumped into kelp, and on one occasion, the shark was observed to bite the kelp. In this respect, the findings in this study are consistent with Jewell et al. (2019); however, Jewell et al. (2019) mentioned the fact that their focal animals swam within dense kelp areas. Without measurements of kelp density, the density of kelp within these 'dense kelp areas' is unknown and it is further uncertain if these sharks were navigating through corridors within the high kelp density regions. Therefore, the seminal observations of Jewell et al. (2019) support the findings in the present study, but also reveal an inherent need for a more rigorous and comprehensive study examining the inter-relationships between predatory-prey dynamics within a kelp forest, and how measured kelp densities may or may not influence overall *C. carcharias* presence.

Current Speed and Kelp Density

The magnitude of the current with respect to kelp bed densities may vary (e.g. Jackson & Winant, 1983), which may consequently influence olfactory plume dispersal distance and impact the ability of regions with reduced currents to equally attract *C. carcharias.* More specifically, previous studies illustrate how extensive kelp bed regions elicit enhanced hydrodynamic drag (Jackson & Winant 1983) and therefore, currents exhibit differing characteristics (e.g. decreased speed and increased particle deposition) in dense kelp bed regions when compared to similarly sized kelp-free regions. However, anecdotal observations from an Acoustic Doppler Current Profiler (ADCP; Teledyne RD Instruments, Poway, CA, USA; rdinstruments.com) were suggestive that current speeds within zone 4 of our study site were not dictated by kelp density (O'Connell, Pers. Obs.). But, it is uncertain as to the reliability of these results as they were obtained from just one deployment within low, moderate and high kelp density regions. Therefore, different from the present BRUVS survey technique, a more thorough approach would have been to measure current speeds at each BRUVS deployment location during each trial. Such an approach in the present study was impractical due to a substantial amount of logistical constraints (e.g. weather limiting scuba diving possibilities, per day ADCP cost, varying water visibility, and shark presence) and the potential for ADCP presence and scuba divers to negatively influence BRUVS results. However, a more thorough analysis where current measurements are routinely assess within each kelp density region with current meters equipped-BRUVS may yield additional insights into how small kelp beds may or may not influence olfactory dispersal rates, and consequently *C. carcharias* sightings.

Conclusion:

Kelp forests support productive ecosystems and species assemblages that often lead to complex ecological dynamics (Dayton, 1985; Dayton et al., 1998, Steneck et al., 2002). In the present study, the presence of the kelp species, *E. maxima*, affected the sightings of large juvenile to adult *C. carcharias*. However, the findings from this study helped reject the notion that *C. carcharias* do not swim in regions containing kelp and illustrates the importance of kelp density in relation to *C. carcharias* presence. The results are suggestive of how a high density kelp forest may serve as a natural barrier to larger *C. carcharias*; however, continued research that integrates current speed, shark size (e.g. through stereo-BRUVS), and multiple locations to determine the potential broad-scale implications of the present findings will be integral to understanding the complex ecology of these ecosystems.

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Table 1. Analysis of deviance (ANODEV) table for the kelp correlation experiment. The explanatory variables are kelp density (T), other elasmobranchs being present (E), and BRUVS redeployment (B). The dependent variable is the sighting of any white shark (*Carcharodon carcharias*) during post hoc video analysis. The selected model for *C. carcharias* sighting within a particular kelp density is A2 based on a combination of deviance, Akaike Information Criteria, and p-values. 1 in the linear form denotes intercept. Significant models for main effects ($p \leq 0.05$) and interaction terms ($p \leq 0.1$) are in bold.

Number	**Model**	**D**	**Df**	**ΔD**	**Δdf**	***p*-value**	**AIC**
A1	Null	86.05	62	-	-	-	88.05
A2	**1+T**	**41.21**	**60**	**44.84**	**2**	**<0.001**	**47.21**
A3	1+E	85.30	61	0.74	1	0.39	89.30
A4	1+B	85.30	61	0.74	1	0.39	89.09
A5	1+T+E	41.19	59	0.02	1	0.89	49.19
A6	1+T+B	39.18	59	2.03	1	0.15	47.20
A7	1+T+E+T*E	40.11	57	1.08	2	0.58	52.11
A8	1+T+B+T*B	37.36	57	1.82	2	0.40	49.36

Abbreviations: 1 = y-axis intercept, D = residual deviance, df = residual degrees of freedom, ΔD = change in residual deviance between former model and model being considered, Δdf = change in residual degrees of freedom between former model and model being considered, p-value = indicates the level of significance of the explanatory variable added, AIC = Akaike Information Criterion, a model selection criterion.

Table 2. Coefficients, standard errors, z-values and p-values of explanatory variables for best fit model A2 for individual white shark (*Carcharodon carcharias*) sightings within a trial in relation to kelp density. For sighting quantity, data were transformed to "sighting + 1" for each density region to improve the interpretability of the data, as no *C. carcharias* sightings occurred within the high kelp density region. Significant models for main effects ($p \leq 0.05$) and interaction terms ($p \leq 0.1$) are in bold.

Explanatory Variable	Coefficient	Standard Error	Z-Value	p-Value
Intercept	**-2.99**	**1.03**	**-2.92**	**0.003**
Low Density	**5.99**	**1.45**	**4.14**	**<0.001**
Moderate Density	2.08	1.13	1.84	0.07

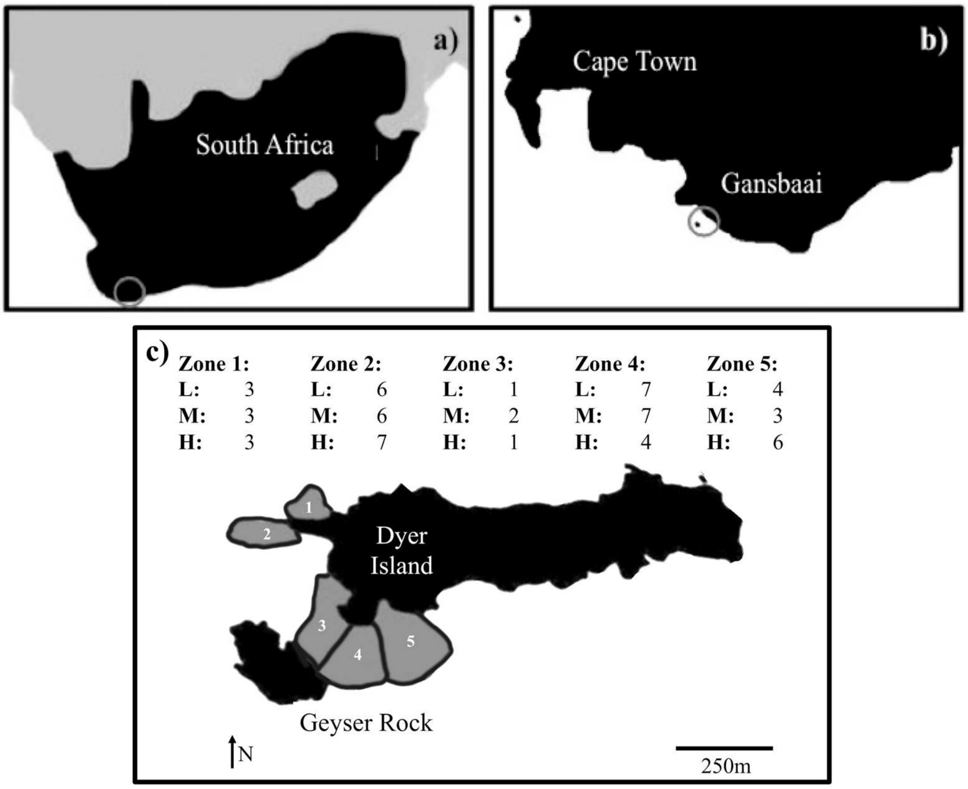

Figure 1. Representation of the sampling locations where kelp density and current speed were measured and thus baited remote underwater video systems (BRUVS) were deployed. c) Specific 'zones' (1-5) where BRUVS were deployed over the course of experimentation. Deployment quantities with respect to zones are written adjacent to the kelp density categories (low [L], moderate [M], and high [H]).

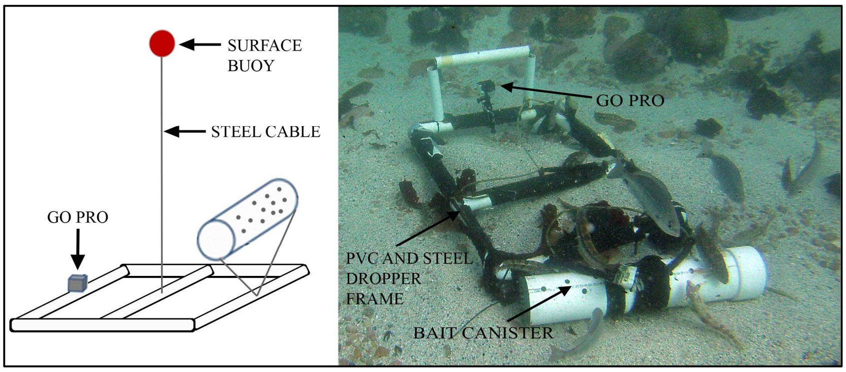

Figure 2. Diagram of the baited remote underwater video systems (BRUVS) deployed for the kelp-correlation experiment.

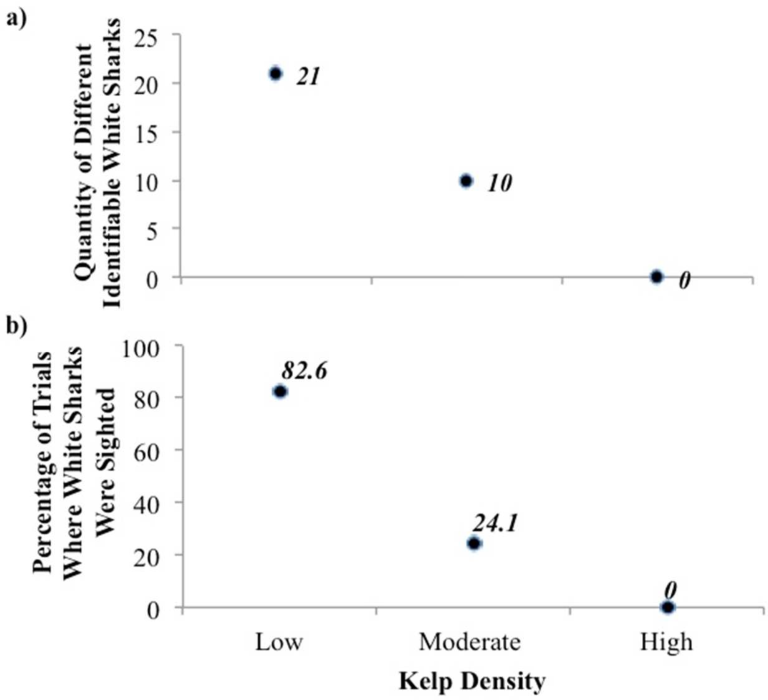

Figure 3. a) The quantity of different white sharks (*Carcharodon carcharias*) observed within each kelp density. b) The percentage of trials of which a *C. carcharias* was sighted in relation to varying kelp densities.