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Spatiotemporal abundances and habitat use of the new species of shark *Carcharhinus humani* within the iSimangaliso Marine Protected Area (Kwa-Zulu Natal, South Africa), with considerations on zonation effect

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Abstract

Sharks are one of the most evolutionarily distinct and functionally diverse vertebrate radiation. The International Union for Conservation of Nature estimated that one-quarter of sharks are threatened with extinction, making them the most threatened vertebrate lineage after amphibians. Conservation efforts for this group have historically been hindered by the paucity of data regarding their ecology and biology, imputable to resource limitations and inherent intricacies related to researching highly-migratory species in the marine environment. As a result, almost half of global sharks and rays are classified as Data Deficient by the IUCN, hence excluded by the list of priorities of many regional conventions and fisheries commissions, which are a fundamental precursor to potential species-specific protection. *Carcharhinus humani*, is a newly described and data deficient species of whaler shark, occurring in the Western Indian Ocean. This research project aimed at building baseline ecological data on this species within the iSimangaliso Marine Protected Area (KZN, South Africa), using Baited Remote Underwater Video Surveys (BRUVs). Spatiotemporal structuring of *C. humani* population was inspected for the first time incorporating sexual-based segregation over a study period of two years. Average lengths of individuals occurring in this area were measured. Preferences of substrate type and depth ranges were surveyed and included in a mixed-model analysis assessing the effect of the different protection levels present in the MPA. This study revealed that *C. humani* constitutes a resident population within the iSimagaliso MPA, as females can be sighted all year around. Males seem to arrive in the area during the warmer months, supporting the hypothesis that this species mates in summer. Preferences were displayed for sandy substrates, and individuals were more commonly sighted at depth ranges of 26-35 m. Finally, protection level was one of the main factors influencing Human's whaler sharks distribution, as they tended to aggregate in no-take zones, especially during the alleged mating season. This study represented the first step in the process of departing *C.humani* from the Data Deficient classification, setting the basis for future research on this species.

Contents

Introduction

Understanding habitat use and seasonal dynamics of marine species is critical for successful management and conservation strategies at multiple spatial scales (Ferretti et al., 2010; Block et al., 2011; Bird et al. 2018). The first global assessment of the International Union for Conservation of Nature (IUCN) estimated that one-quarter of sharks were threatened with extinction, thereby classified as critically endangered, endangered or vulnerable according to the criteria of the IUCN Red List of Threatened Species (Dulvy et al., 2014). This makes sharks the most threatened vertebrate lineage after amphibians (Hoffman et al., 2010; Dulvy et al., 2014). Pacoureau et al. (2021) recently documented an alarming, ongoing, worldwide depletion in shark populations, estimating a decline in abundance of 70.1% (95% credible interval, 62.8–77.2%) over the half-century from 1970 to 2020. In particular, in the Indian Ocean, an overall decline of 84.7% (95% credible interval, 75.9-92.1%) was indicated. Decades of ecological research have shown that changes in predator abundance lead to far-reaching consequences for ecosystem structure, functioning, and resilience (Paine et al., 1969; Duffy et al., 2002), making the protection of shark populations a critical aspect of marine conservation. Despite the evident urge of adopting and implementing protection measures for this animal group, the management procedures and conservation efforts are often hindered by a deficiency of information about the species of interest (Heithaus et al. 2008, Heupel et al. 2015). This study aims at building baseline ecological data for *Carharhinus humani*, a recently described species of whaler shark classified as Data Deficient by IUCN.

1.1 Human's whaler shark, a new species

Despite the concerns conveyed by scientists such as Mace (2004) and Ebert et al. (2015) about the future of systematic disciplines, chondrichthyan taxonomy has undergone somewhat of a renaissance in recent decades (White et al., 2018). More than 260 new species of chondrichthyan fishes were formally described since 2002, thus more than 20% of the extant species of sharks and rays have been described in the last two decades (White, 2012). The family *Carcharhinidae*, commonly known as whaler sharks, are one of the most species-rich and economically important groups of sharks in fisheries globally, particularly in commercial and small-scale coastal fisheries (White and Sommerville 2010; White et al., 2018). Due to the sheer biological and economic importance of this group, it's essential to have a strong taxonomic foundation to work upon, both in terms of conservation and fisheries management. Within this family, *Carcharhinus* Blainville is the most speciose genus, with about 34 species currently considered valid nominal species and one undescribed species (White et al. 2014). Recent taxonomic investigation of this genus and in particular of the *dussumieri-sealei* subgroup, resulted in the resurrection of two species previously not considered valid, and the description of a new species: *Carcharhinus humani* (White et al., 2018). *Carcharhinus humani* (Human's whaler shark), was described by White and Weigmann in 2014, after decades of erroneous classifications. This species was previously considered to be conspecific with *C. sealei* (Blackspot shark) from the western Indian Ocean. The *sealei* complex has also been commonly confused with *C. dussumieri* throughout its range, particularly in the Arabian Sea region. The first details on Human's whaler sharks were provided by Wheeler (1960) using a name with complicated history, *C. menisorrah*, later resolved by Garrick (1982). Notwithstanding the tortuous nomenclature this species has gone through, it can be readily readily distinguished from its closest relatives, *C. dussumieri* and *C. tjutjot*, in having basal cusplets on upper anterolater teeth, first dorsal fin apically narrow and falcate (vs. broadly triangular and not falcate), and more vertebrae (total centra 152–167 vs. 113–138, precaudal centra 74–85 vs. 55–70) (White and Weigmann, 2014). The differentiation from *C. sealei* is not only based on morphological characteristics, most notably the colouration of the second dorsal fin, but also on not-overlapping distributions. *Carcharhinus humani* occurs in the Western Indian Ocean from the Socotra Islands, off Kuwait in the Persian/Arabian Gulf, down the east coast of Africa to KwaZulu-Natal, South Africa, while *C. sealei* is absent from the Western Indian Ocean (White and Weigmann, 2014). Ultimately, *C. humani* is the only member of the genus *Carcharhinus* in the Western Indian Ocean with a prominent black spot on the second dorsal fin, while all the other fins have white or almost translucent edges. Little to no information is provided by literature on the life history and ecology of *C. humani*, therefore classified as being Data Deficient on the IUCN Red List (Pollom et. al, 2019). Bass et al. (1973) estimated that this species is born at 35-45 cm and attains a maximum size of 90 cm, however important data such as size at sexual maturity is currently not available. Fundamental biological and environmental research pertaining to distribution and abundance of *C. humani* is still needed to effectively develop and manage conservation initiatives around this species, as well as other species connected to it via trophic relationships (Garla et al., 2006).

1.2 Data deficiency in shark research

The IUCN's Red List categories are used internationally by governments for assessing the conservation status of species and for prioritizing conservation actions upon these species (Lamoreux et al., 2003; De Grammont and Cuaròn, 2006; Mace et al., 2008; Viè et al., 2008). Under these categories, 'Data Deficient' species are defined by IUCN as ones where "there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status" (IUCN, 2001). As a result, Data Deficient species are excluded from priority species lists set by regional conventions and fisheries commissions, which are a fundamental precursor to potential species-specific protection (Bland et al., 2014). However, many recently resolved species complexes may be exposed to fisheries and hence the newly described 'Data Deficient' species might already be highly threatened (Iglèsias et al., 2010; White and Last., 2012). Historically, scientists and conservationists were hindered from focusing on these species by resource limitation (Bland et al., 2015), as policy-makers are often disincentivized to support scientific investigation of the species under this category (Parsons, 2016). As a result of these dynamics, along with the inherent intricacies related to research activities of marine, migratory species, almost half of global sharks and rays are Data Deficient (46.8 %, n = 487) (Walls et al., 2020). Recent studies (Walls et al, 2020) attempted at mitigating the uncertainty in global estimates of extinction rates created by data deficiency developing categorical regressions based on relevant biological and ecological traits. Despite it being a cost-effective solution to this shortcoming (Bland et al., 2015), the authors indicated the importance of having baseline information, such as life history data and population assessments, from which to elaborate predictive models until data availability and resources allow for fully comprehensive IUCN assessment of these species.

1.3 Survey methodologies and the three Rs issue

Our knowledge of the biology and ecology of sharks and other highly mobile fish species relies largely on fishery-dependent data from commercial and recreational fisheries (Myers and Worm, 2003; Oliver et al., 2015). Catches made by net, hook and line, trawl, or trapping can provide valuable information, especially when biological samples are required (Jaiteh et al., 2014; Santana-Garcon et al., 2014a). However, invasive sampling techniques are becoming ethically less acceptable with growing concerns over the status of some threatened, endangered, and protected species, as well as individual animals welfare. Although the process of incorporating the three Rs (i.e. Replacement, Reduction, Refinement) into wildlife research is slow (Draper and Bekoff, 2013), the benefits of non-invasive methods are being recognized, such as increased research quality (Lindsjo et al., 2016). Extractive methods are often harmful and can result in direct mortality at capture or cryptic morbidity and eventual mortality after release. Serial depletion (i.e., the continued removal of individuals when sampling with extractive methods) can bias future sampling and is undesirable for long-term monitoring. Fishery-dependent methods can also introduce sampling biases due to gear selectivity and heterogeneous fishing efforts that discriminate among species, sizes, and habitats (Murphy and Jenkins, 2010; Simpfendorfer et al., 2002). Moreover, the effects of capture, handling, and marking on the health, behavior, and welfare of the individual, was proven to have potential impacts on research data (Mulcahy, 2003; Cattet et al., 2008). Refined research methods may therefore decrease confounding effects in study results (Powell and Proulx 2003). Non-extractive (i.e., nondestructive) visual methods using scuba divers or cameras have become widely used alternatives to fishing methods when collecting data on marine fishes. These techniques include for example underwater visual censuses (UVC) (Brock, 1954), and remotely operated camera systems (e.g., “camera traps). Marine scientists have increasingly adopted the use of camera technology alongside the rapid technological advancements in imaging systems of the 20th century, precisely since the 1980s (Mallet and Pelletier, 2014). Over the last decade, the use of video sampling has increased greatly as the size and cost of video cameras have decreased dramatically, particularly in the consumer market (Struthers et al., 2015). Furthermore, remote video techniques can access depths and habitats inaccessible to divers (Goetze et al., 2011) and have been used to avoid the behavioral biases of fish (Watson and Harvey, 2007) and sharks (McCauley et al., 2012) toward divers. They have also been used to sample for longer time periods through the day and night (Myers et al., 2016). A major advantage of video techniques is that images and video footage can be stored as a permanent digital record. This represents a prime example of application of the Reduction principle, as the same footage can provide a large amount of different information according to the aims of the study and the species of interest, inflicting minimum disturbance to the ecosystem. Unfortunately, practical referral to the concept of the 3Rs in peer-reviewed wildlife research literature is still uncommon (Lindsijo et al., 2016), but there are several possibilities to transfer the 3R principles to shark research, including replacement with non-invasive research techniques, reduction with optimized experimental design, and refinement with better methods of capture, handling, and release. Few precedents of intervention of ethical committees in shark scientific investigations already exist (Russel, 2013), promising a future with a more systematic and thoughtful implementation of the 3Rs principle in wildlife research.

1.3.1 BRUVs

Baited remote underwater video systems (Cappo et al., 2000, 2003, 2004, 2006; Harvey et al., 2007) involve the use of video cameras that are deployed underwater with a bait canister in the field of view. The initial bait plume attracts animals into the field of view, as does the "berley effect" of feeding activity on the bait canister (Cappo et al., 2000). This method also records animals that do not actively interact with the canister and are indifferent to the bait attractant, but resident in the field of view (Cappo et al., 2006; Harvey et al., 2007; Watson et al., 2005). Among the advantages of using BRUVs, there is their minimal impact on the ecosystem, their potential to overcome some of the biases associated with the use of extractive techniques or the presence of scuba divers, and their provision of a permanent digital record (Harvey et al., 2004; Whitmarsh et al., 2017). The use of bait to attract animals was proven particularly suited for sampling large carnivorous species targeted by fisheries and those with special conservation needs (Cappo et al., 2003; Goetze and Fullwood, 2013; Goetze et al., 2015; Langlois et al., 2012), without precluding the sampling of species from other trophic groups (Dorman et al., 2012; Hardinge et al., 2013; Harvey et al., 2007; Watson et al., 2005). BRUVs are becoming widely adopted and have been used to sample assemblages across a variety of depths and habitats. Comparative studies surveying a variety of sharks using BRUVs and longline surveys (Bond et al., 2012; Espinoza et al., 2014; Goetze and Fullwood, 2013), provided similar estimates of shark abundance (Brooks et al., 2011; Santana-Garcon et al., 2014a). Furthermore, this technique is suitable for covering large spatial scales with multiple replication, as simultaneous deployment of BRUV stations is possible. BRUVs have been used to map the patterns of habitat association and relative abundance of common reef sharks across entire biomes (Espinoza et al., 2014). This application demonstrates that BRUVs are a powerful and cost-effective method for assessing spatial and temporal changes in the diversity, relative abundance, and length structure of sharks and fishes. In recent years, the reduction in size and cost of hardware that has occurred with the development of action cameras has made the technique relatively cost efficient (Struthers et al., 2015). For these reasons, BRUVs have become the most popular form of video-based sampling method for sharks, rays and fishes (Whitmarsh et al., 2017).

Materials and methods

2.1 Study site

The study was conducted in the offshore portion of the iSimangaliso Marine Protected Area. This World Heritage site extends in KwaZulu-Natal from the South Africa-Mozambique border in the north to Cape St. Lucia lighthouse in the south. The expansion of 10 700 km2 makes this the largest MPA in the South African network, covering a wide variety of habitats mainly distinguished by the nature of the substrate. These include: rocky reefs, mixed rocky and sandy bottoms, coral reefs, sedimentary bottoms, as well as submarine canyons along the edge of the continental shelf.

2.1.1 iSimangaliso MPA zonation

The iSimangaliso Marine Protected Area is formed by an inshore and an offshore area. The regulation governing the MPA can be schematized in a three-levels fashion. The first level of protection allows controlled pelagic linefishing and spearfishing activities, and covers two zones of the park, namely iSiman-

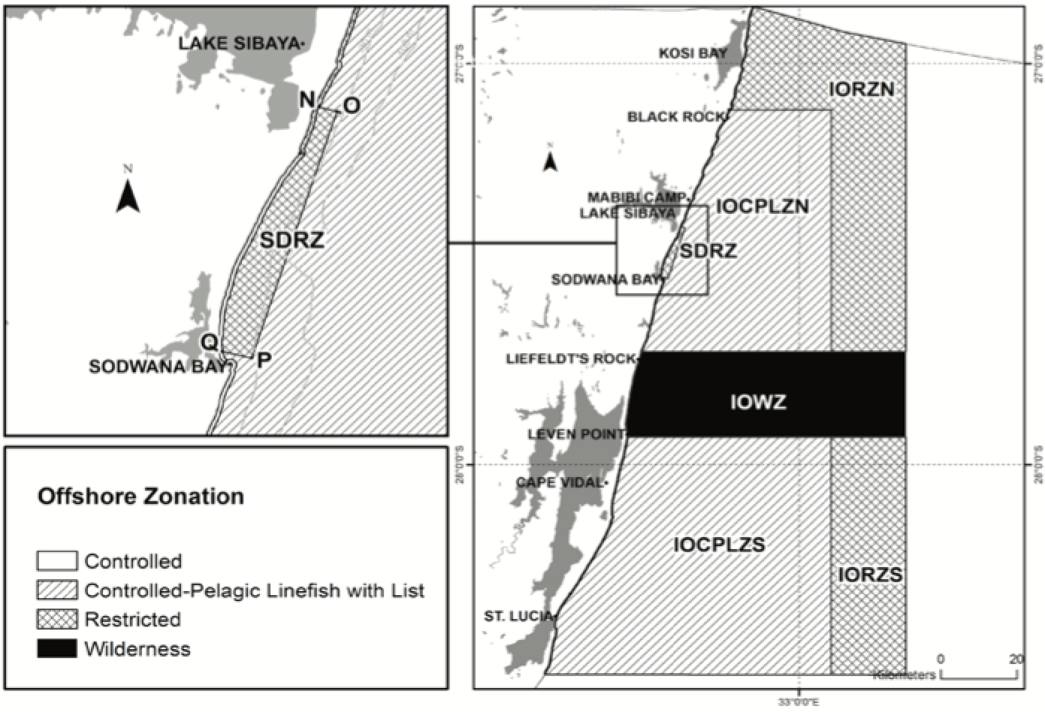


Figure 2.1: Map of the iSimangaliso Wetland Park including the designated study Areas within the various levels of protection of the MPA

galiso Offshore Controlled Pelagic Linefishing Zone North (IOCPLZN) and iSimangaliso Offshore Controlled Pelagic Linefishing Zone South (IOCPLZS). The second and third levels of protection regulate three Offshore Restricted Zones, and one Offshore Wilderness Zone (IOWZ) respectively, making all of them no-take areas. The Restricted Zones regulation allows controlled recreational SCUBA diving activities, while the Wilderness Zone regulation allows SCUBA diving activities for scientific research purposes only. For the aim of this study, one zone per each regulation level was selected according to logistical criteria. Hence, the sampling took place in the iSimangaliso Offshore Controlled Pelagic Linefishing Zone North (IOCPLZN), in the Sodwana Diving Restricted Zone (SDRZ), and in the iSimangaliso Offshore Wilderness Zone (IOWZ) (**Figure 2.1**).

2.2 Sampling design

Over a two-year period (October 2020—September 2022), a total of 558 BRUVs were successfully deployed at 327 sites within the iSimangaliso MPA, in 5 different study areas of equal length (15km), covering the coastline delimited by Leven Point southerly and Black Rock northerly. More specifically, Area 2 and 4 are situated in the IOCPLZN, Area 1 corresponds to the SDRZ, while Area 5 is located in the IOWZ. Area 3 is divided between IOCPLZN and IOWZ (**Figure 2.2**). Each BRUV drop represents a replicate at a site, and between one to three (mean = 1.7) drops occurred per site. Area 3 and Area 4 both lack seasonal replicates as sampling started in May and March 2022

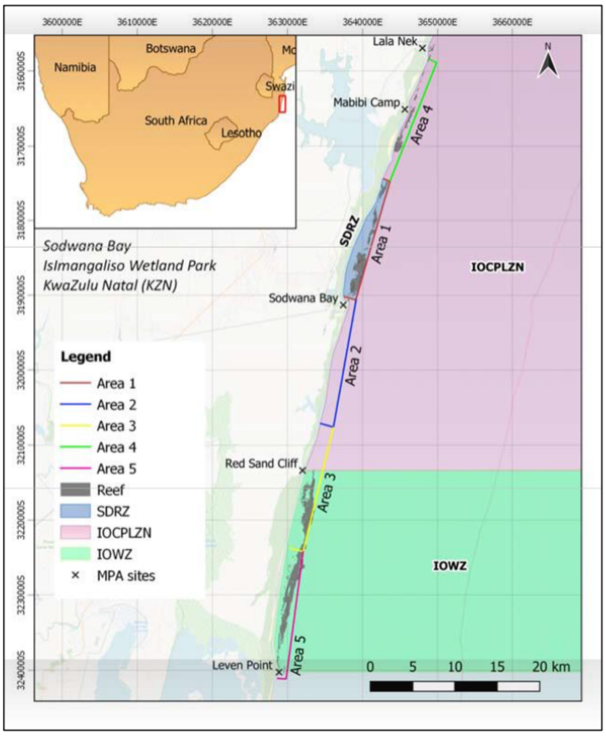


Figure 2.2: Map of the iSimangaliso Wetland Park including the designated study Areas within the various zones (SDRZ,IOCPLN,IOWZ) of the MPA

respectively. At least two seasonal replicates in each level of protection were sampled. Ultimately, a total of 255 BRUV drops occurred in the summer-fall and 303 BRUV drops in the winter-spring. Sites were systematically placed in order to be distributed in the whole study area (**Figure 2.3**). Deployments occurred in sets of three BRUV drops on the same latitude along the shore but at different depth categories. Depths of sampled sites ranged between 8.0 m and 33.7 m (mean = 21.8 m, standard deviation (SD) = 6.2 m). Three depth categories were set as: shallow (8-15 m), intermediate (16-25 m), and deep (25-35 m). All sites were a minimum of 350 m apart but no more than 500m apart, this was to avoid overlapping bait plumes during multiple deployments and to ensure that each site could be monitored for boat traffic. Efforts were made to sample across all habitat types (reef, sandy, and mixed substrates) within each area, but this was not possible without fail due to the intrinsic features of each region that did not always display all habitat types.

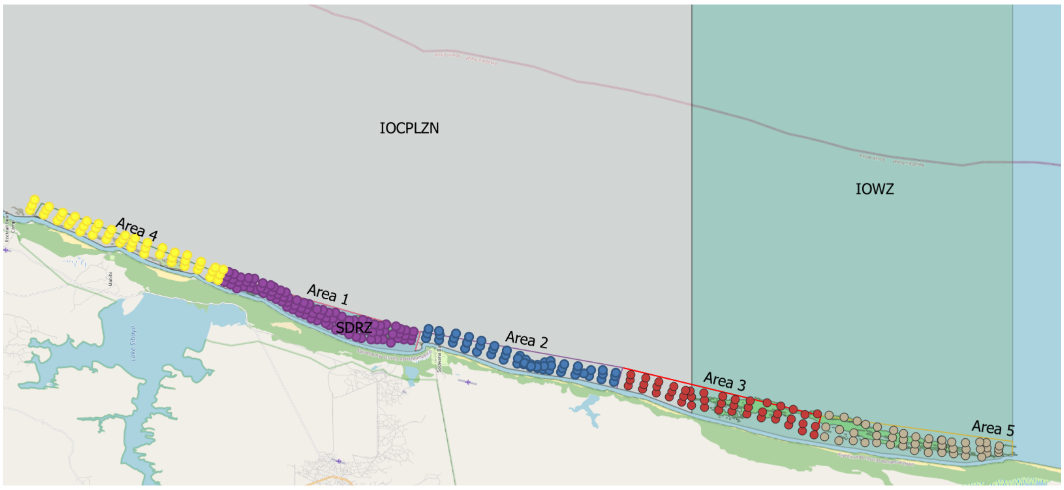


Figure 2.3: Map of the BRUVs deployment sites. Each dot represents one site, the different colors indicate the designated study areas. Different zones of the MPA are indicated in capital letters.

2.3 Baited remote underwater video design

Six stereo-BRUV stations were built from welded stainless-steel tubing following a standard trapezoidal design. Each BRUV was fitted with two GoPros (Hero 4, Hero 5, 7) set to 1080p, 50 frames per second, recording on a linear setting. These were fixed at the extremities of a 70 cm stainless-steel bar and inwardly converged at approximately 5° in order to ensure central view on the bait canister. The PVC bait canister was perforated (180mm x 110mm with 10mm perforations) and located 1 m apart from the lens and 0.6 m from the ground. A stainless steel ring provided attachment to a rope leading to a surface buoy. BRUVs were baited using 1kg of chopped, defrosted sardines (*Sardinops sagax*). Data collection occurred between 07.00 and 11.00, and the number of deployments varied depending on weather and swell conditions. A maximum of four sets of three BRUVs were deployed in a day, although the median was two sets. Each BRUV was deployed for a minimum of 90 minutes. Target deployment time was 60 minutes, the average recording time was 78 minutes. BRUVs were dropped under the surveillance of a trained free-diver ensuring that the steel structure would not damage sensitive spots of substrate such as coral reefs, guiding it on a rocky or sandy patch.

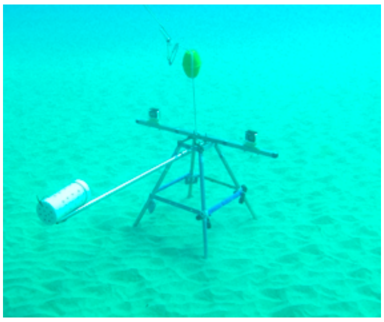


Figure 2.4: A BRUV succesfully deployed on sandy substrate.

2.4 Environmental parameters

For each deployment the exact site location was recorded using Global Positioning System (GPS). Abiotic parameters including the sea surface temperature, swell, depth, visibility, current speed and direction, and habitat type were recorded. A Garmin Colorado 300 GPS (Garmin Ltd) was used to calculate the current flow rate and direction at each deployment site, while the exact depth at which the BRUV was deployed was obtained by a transducer on the research vessel. Water visibility varied between 1 m and approximately 20 m at each site. Sea surface temperatures ranged between 21.2°C and 29.4°C (mean = 24.7°C, standard deviation (SD) = 2.1°C). Habitat types were classified based on the predominant substrate (i.e. over 50For Area 5, corresponding to the Wilderness Zone, the distance of each site from prominent reefs was calculated using QGIS 3.14, based on the bathymetry data acquired from the Oceanographic Research Institute (ORI), as shown in **Figure 2.5**.

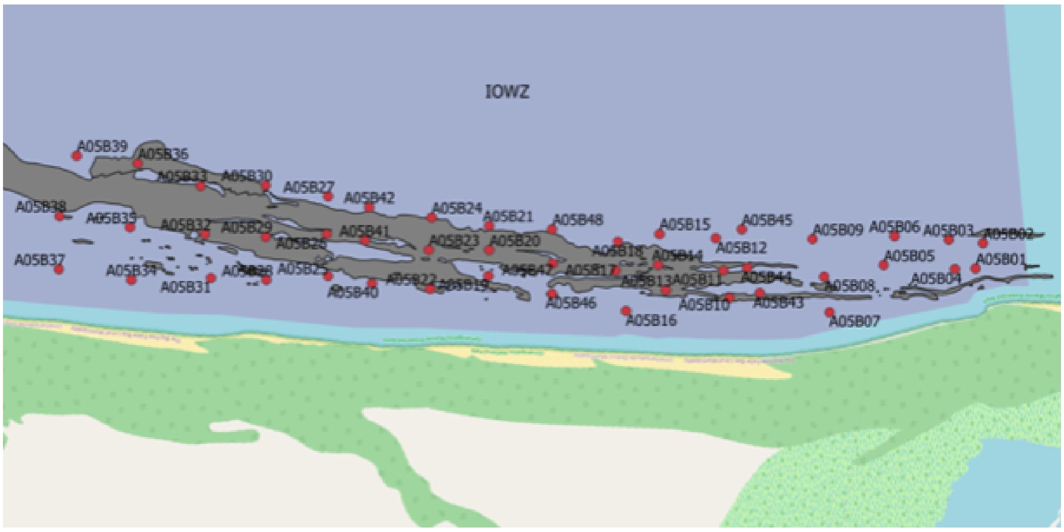


Figure 2.5: Map of deployment sites and bathymetry data of Area 5 from the Oceanographic Research Institute. Gray area represents predominant reefs.

2.5 Video analysis

All videos were analyzed using VideoLan VLC Media Player 3.0.11.1. Playback speed varied depending on the level of activity and the visibility in the video, with default playback in real time, reduced speed in case of low-visibility of high-activity videos, and speed of 1.2×–1.5× for high-visibility and low-activity videos. Each video was analyzed for 60 minutes starting from the moment of the first contact between the BRUV structure and the bottom. For each video session four indices of relative abundance were calculated, as indicated by Irigoyen et.al (2019):

1. Nmax: the maximum number of *Carcharhinus humani* observed in a single video frame (Ellis 1995; Willis and Babcock 2000). While this is a conservative metric, it is widely used as it minimizes the possibility of re-counting the same individuals (Cappo et al. 2003; Watson et al. 2005).;

2. NmaxIND: the cumulative number of different *C. humani* identified by spot patterns, sex, size, or scars. The relevance of this index in elasmobranch studies was recently described by Sherman et al. (2018). For the estimation of this index, every time a given shark entered the field of view, screenshots of the individual were taken. After visual inspection of all snapshots, the number of unique individuals were determined as NmaxIND;

3. Nocc: the total number of occurrences of *C. humani* in the field of view over the entire video record session.

4. FO: the time expressed in minutes of the first occurrence of *C. humani* in the BRUV footage. When there was no appearance of *C. humani* in

the video, FO was set at 60 min.

Moreover, the duration of each sighting was calculated as the time between the appearance and disappearance of *C. humani* in the same frame. Sex of the individuals was always established based on the presence or absence of claspers, and determined as unidentified (UI) whenever the abdominal side of the shark did not appear in the footage, or in case of visibly immature individuals.

2.5.1 Morphometric measurements

Stereo-video cameras were calibrated prior to field deployments using CAL software from SeaGIS (http://www.seagis.com, Harvey & Shortis, 1998). Paired videos of the same BRUV were analyzed on a large monitor using the program EventMeasure (SeaGIS Pty Ltd). Every *C. humani* was identified and measured to the nearest mm. Fork length (FL) was used, being the distance between the snout and the caudal fin bifurcation. Sharks that did not integrally appear in both cameras were excluded from the survey, as well as those that were too far from the cameras or in a curved position. The average RMS (residual mean square) of the measurements used in this study was 39.6, while the precision of the measurements ranged between 0.01 cm and 0.23 cm.. Overall, 66 out of 204 individuals were successfully measured and basic statistical inspection was performed to establish the average length of the individuals occurring in the area.

2.6 Statistical analysis

All statistical analyses were performed using RStudio 2021.09.0 (RStudio Team 2021).

2.6.1 Seasonality

The effect of seasonality on the abundance and distribution of *C. humani* in the MPA was determined using the Nmax and NmaxIND indexes as response variables. Using the R package 'emmeans' (Russell V. Lenth, 2022) the effect of the Summer (November-February) and Winter (May-August) seasons was studied separately within Areas 1, 2, and 5 and across the whole MPA. Linear model analysis was performed, as well as ANOVA tests. The assumptions were checked using Tukey-Anscombe plots and norm-QQ plots. Finally, the same tests were run for the separate sexes to assess seasonal movements of reproductive nature.

2.6.2 Habitat use

The study of habitat use focused on substrate types and depth ranges. Substrate preference was explored by linear model analysis and three-way ANOVA tests, both in Area 5 and in the whole MPA separately. Area 5 was selected as the most suitable for the study of habitat use since it presents the highest variability in terms of substrate types, along with the highest level of protection, providing an environment with minimized anthropic disturbances. The effect of distance from prominent reefs was tested in Area 5 through a Pearson's correlation and linear model. Depth was initially explored as a continuous variable in a Pearson's test and linear model. Depths were subsequently divided in three categories using the package 'dplyr' (Wikham et al., 2022). Three-way ANOVA was used to determine the effect of depth categories on *C. humani* abundance indexes. Finally, all the effects influencing *C. humani* abundances in Area 5 (i.e. substrate type, depth, distance from prominent reef) were included as fixed effects in the same linear mixed model, while the site number was fitted as random effect using the ‘lme4’ package (Bates et al., 2015).

2.6.3 Zonation effect

Three-way ANOVA was used to compare the effect of the three different protection levels present in distinct zones of the multi-use MPA, namely in the IOCPLZ, SDRZ, and IOWZ. Due to the variety of factors influencing the effectiveness on an MPA (Edgar et al., 2014; Gill et al., 2017; Nash and Graham, 2016), covariates describing the nature of habitats need to be considered when measuring the effects of management strategies in marine systems, as their omission may lead to spurious conclusions (Dulvy et al., 2004; Greenstreet and Rogers, 2006; Nash and Graham, 2016). For this reason, the effect of zonation on Nmax was studied performing a linear mixed effect analysis. The best fit model was selected by comparing the Akaike’s Information Criterion scores from the different models (Hu, 1987). The most parsimonious combination (defined as the simplest model with the lowest AIC score) of fixed effects included: Zone, Substrate Type, and Depth as a covariate. Site number was fitted in the model as a random effect. Likelihood ratio tests using the ANOVA function and χ^2 distribution were used to compare the null model including depth, substrate, and site to a full model containing those factors and zone. The assumptions of linearity and the absence of heteroskedasticity were examined through plotting residuals and the assumption of normality was inspected through visualization of a Q–Q plot.

Results

In total, 563 hours of BRUV data were analyzed. Overall, at least one individual of *C. humani* was recorded in 159 out of 558 BRUVs. Nmax values ranged between 0 and 4 (mean= 0.36, standard deviation (SD) = 0.67). Nocc ranged between 0 and 159 (mean= 6.59, standard deviation (SD) = 18.40). Minimum time of the first occurrence (FO) was 24 seconds, while the maximum was 60 minutes (mean= 30.02 min, standard deviation (SD) = 17.25). Due to the morphology and quick movements of this shark species, NmaxIND barely ever differentiated from Nmax. Sex was the main factor allowing individuals discrimination. 203 individuals were recorded, and 159 successfully sexed. A total of 139 females and 18 males were counted (sex ratio F:M = 7.7:1). Average length for females was 73.2 cm LT, while average length for males was 71.2 cm LT. The smallest *C. humani* measured 57.0 cm, sex was not identified as the individual was assumed to be immature. The largest individual measured 88.1 cm and was determined to be of female sex. Overall, the average length was 72.7 cm (standard deviation (SD) = 62.03).

3.1 Seasonality

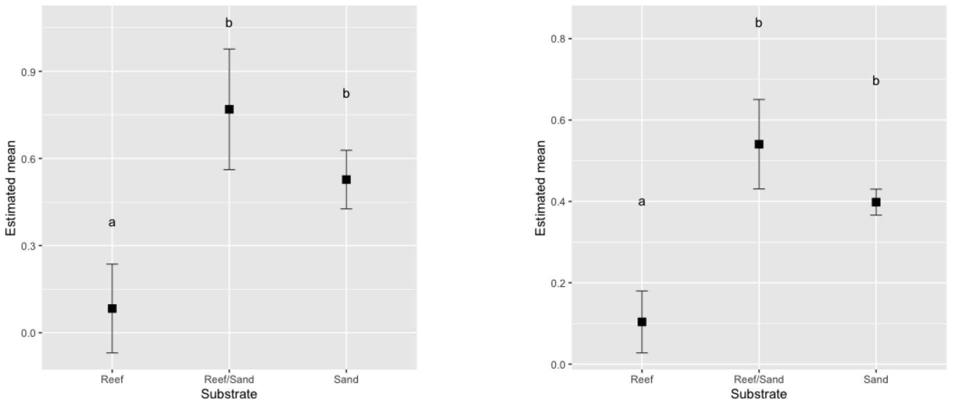
Carcharhinus humani BRUVs derived relative abundance indices did not display evident fluctuations over the period of this study. When all the individuals were included in the analysis, Nmax did not show significant difference in summer and winter seasons in any of the single study areas separately tested, nor in the whole MPA (ANOVA, F = 2.5, p = 0.11). When months were used as the control variable instead of season, some significant differences in Nmax arose in area 1 and 2, as well as in the whole park. Area 5 was the study site with the lowest variability in relative abundance indices, none of the months resulted significantly different from the others. The results of the linear model including the effect of seasons, study areas, and their interaction showed that the interaction between seasons and areas was not significant (ANOVA, F = 0.79, p = 0.45), while areas had a significant effect on the average Nmax

(ANOVA, $F = 5.15$, $p < 0.001$). The effect of areas was hence inspected in the different seasons, resulting significant in winter, with Areas 1 and 5 showing higher abundance indices values compared to Area 2 (ANOVA, $F = 6.38$, $p < 0.0001$). In summer no significant difference was detected between relative abundance indices across the different areas (ANOVA, $F = 1.04$, $p < 0.35$). When the same tests were run on the male population only, a clear seasonal pattern appeared. Males were exclusively spotted between late September and early May, consequently, Nmax was significantly higher in summer compared to winter (ANOVA, $F = 4.74$, $p = 0.03$). Sixteen out of the eighteen males were found in no-take zones ($n = 12$ in Area 1, $n=4$ in Area 5). However, the effect of the study area was overall not significant (ANOVA, $F = 0.98$, $p < 0.41$), probably due to the small sample size. Female population did not show any significant fluctuation in abundance throughout different seasons, and reflected the trends arisen in the analysis led on the whole population. Visual representation of the results is available in the Appendix.

3.2 Habitat use

From the linear model analysis concerning the substrate type, it emerged that reef habitats had a lower *C. humani* incidence compared to sandy and mixed substrates. This was true both considering Area 5 only (ANOVA, $F = 4.35$, $p = 0.02$), and the whole iSimangaliso MPA (ANOVA, $F = 7.68$, $p < 0.001$), as shown in **Figure 3.1** .

Moreover, Nmax values and the distance from prominent reefs (DFPR) were positively correlated ($R = 0.23$, $p = 0.02$), meaning that at larger distances from prominent reefs, average Nmax values were higher (**Figure 3.2**). This result is consistent with their preference for sandy substrates, however, the time of first occurrence (FO) did not show any significant correlation to

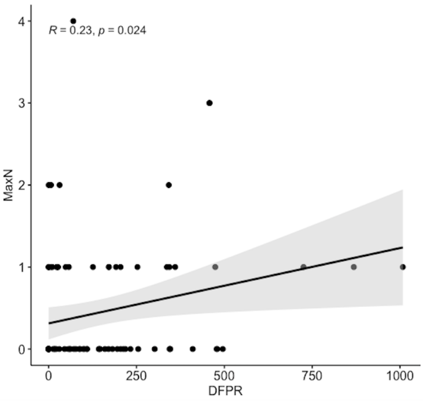


(a) Results in Area 5

(b) Results in the whole MPA

Figure 3.1: Nmax variation at different substrate types

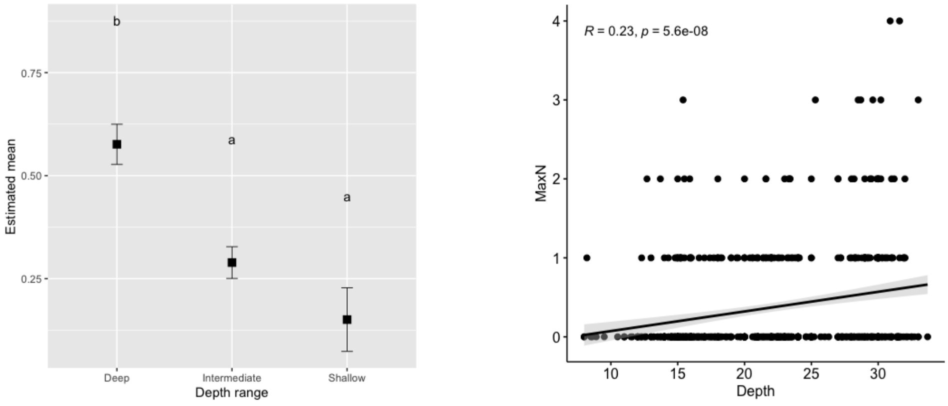
DFPR values (R = - 0.006, p = 0.98).



		MaxN	
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.31	0.12 – 0.51	**0.002**
DFPR	0.00	0.00 – 0.00	**0.024**
Observations	92		
R^2 / R^2 adjusted	0.055 / 0.045		

Figure 3.2: Correlation between Nmax and distance from prominent reef (DFPR)

Depth was strongly correlated to Nmax as well, both in Area 5 (R = 0.27, p <0.01), and in the whole MPA (R = 0.23, p < 0.00001), indicating that *C. humani* display a preference for depths approaching 35 m. Indeed, when treated as a categorical variable, deep deployments had significantly higher *C. humani* incidence compared to shallow depth ones (p = 0.007), but incidence was not significantly higher when compared to intermediate depth ones (p = 0.106). **Figure 3.3** shows the effect of depth on Nmax considering data from the whole MPA, additional graphs for Area 5 results are available in the Appendix.



(a) Nmax at different depth ranges

(b) Nmax and depth correlation

Figure 3.3: Nmax variation at different depths

3.3 Zonation effect

The results of the linear mixed model inspecting the effect of the three different protection levels showed that no-take zones (i.e. IOWZ and SDRZ) had higher average Nmax compared to IOCPLZN, where line fishing is allowed with restrictions. Moreover, the full regression model including the effect of the zone significantly differed from the null model that omitted it (χ^2 (1) = 19.25, $p < 0.0001$). Complete model results are reported in the Appendix.

Discussion

The aim of this study was to provide baseline ecological data on the recently described species of shark *Carcharhinus humani*, classified as Data Deficient in the IUCN Red List. On a regional scale, Data Deficient species are excluded from priority species lists set by regional conventions and fisheries commissions (Bland et al., 2014, 2015). Undoubtedly, identifying spatiotemporal patterns of abundance and habitat association is an essential first step towards the development of effective management and conservation strategies for sharks (Dingle 1996; Speed et al. 2012). Despite the relatively small extension of the study area and the limitations related to non-extractive methods used in this research, this is the first time spatiotemporal structuring has been inspected for *C. humani*, in particular incorporating sexual-based segregation. This study is hence to be considered the starting point of a puzzle that needs to be continued in order to gain more knowledge on this species, possibly with an enhanced focus on its reproductive biology and migratory behaviors.

4.1 Seasonal abundances and site philopatry

This study suggests a year-round resident population of Human's whaler sharks in the iSimangaliso MPA. While the seasonal difference in the female population abundance was not extreme, the great majority of male observations occurred in summer, suggesting sexual-based segregation philopatry. Demographically segregated populations and seasonally stratified movements are widespread among chondrichthyan species (Speed et al. 2012; Mucientes et al.

2009), and the identification of these characteristics within *C. humani* populations is fairly unsurprising. Natal philopatry, whereby mature females return to their natal region to give birth, is thought to occur in larger sharks of the *Carcharhinidae* family such as blacktip sharks (*Carcharhinus limbatus*, Keeney et al. 2005) and bull sharks (*Carcharhinus leucas*; Tillett et al. 2012); however, natal philopatry has yet to be directly demonstrated in any species of shark. Sexually stratified philopatry was identified in nurse sharks (*Ginglymostoma cirratum*) whereby males returned to a mating site annually in contrast to females which followed a biennial cycle (Pratt and Carrier 2001). Despite the low frequency of occurrence, both a new of the year individual (LT=53.0 cm) and a female in late pregnancy status were spotted in the MPA. This generates the hypothesis that the park may play the role of a nursery area, however a study specifically targeting reproductive physiology and cyclicity of this species could clarify this question. More insights on the reproductive ecology of this species can be deduced by the sex composition of the community throughout the seasons. Females outnumbered males year-round in the area, this may be a result of fine-scale sex-specific differences in habitat use, as found in other species such as *Notorynchus cepedianus* in northern Patagonia (Irigoyen et al., 2018). Even so, several male individuals appeared in the area during the summer seasons between late September and early May. Since it is a long period of time, it is possible that they take advantage of the MPA not only for mating purposes, but as a feeding ground as well, considering that prey abundance is believed to be among the main factors determining distribution of sharks (Speed et al., 2010, Schaff et al., 2014). Satellite tracking studies should be conducted in the iSimangaliso MPA to address this hypothesis and gather information of potential migration routes of the male population. It is also possible that the males arrive in the area prior to the actual mating season in order to display courtship behavior. Interestingly, fifteen out of the eighteen male individuals were sighted in the same BRUV footage where at least one other *C. humani* individual appeared (NmaxIND > 1), and almost in the totality of the cases those were female individuals. In particular, the same pair of individuals (recognized by distinctive scars and darker spots on the skin) appeared together in two different BRUV recordings dated to distinct days, suggesting that cohesive pairs or small groups may be formed during the mating period. Further research on group and courtship behavior is recommended to address this question. These observations, along with the sighting of mating scars on adult female individuals, support the hypothesis that the iSimangaliso MPA most likely constitutes a mating ground for this species during the warmer season. Although this study was successful in providing baseline information, additional research is needed prior to drawing firm conclusions about *C. humani* reproductive cyclicity, sexual segregation, and demographically stratified movement patterns. As reproductive hormones regulate all processes of reproduction (Awruch, 2013), it is suggested that physiological reproductive parameters may provide a more accurate estimate of the different stages of reproductive cycles than morphological characteristics.

4.2 Habitat preferences

The findings of this study indicated that frequency of occurrence and relative abundance of *C. humani* were higher in sandy habitat with little to no coral reef, and at a depth range of 26-36 m. Given the small size of *C. humani*, these results are consistent with the findings of other studies describing interspecific size-based variation in habitat use, whereby small sharks ($<$ 1.00 m LT) are more commonly found inshore in lagoons and larger sharks ([$>$ 1.10 m LT) are more common on deeper fore reefs adjacent to deep water (Pikitch et al. 2005).

As described by Vianna et al. (2013) for *Carcharhinus amblyrhynchos* (Grey reef shark), remaining in sandy habitats could represent an anti-predatory strategy. Other studies of South African sharks (Albano et al., 2021) exploring the relationship between trophic position and habitat preference, state that species covering mid-trophic positions are more abundant in sandy habitat. Despite the lack of knowledge about the species specific feeding behavior and trophic role of *C. humani*, it is comparable in size to other mesopredators, hence confirming the findings of Albano et. al (2021). The use of deep sandy habitat was also described by Fitzpatric et al. (2011) as a strategy to minimize energy expenditure during the day, observing a vertical migration pattern in *Triaenodon obesus* (Whitetip reef shark). In particular, this species has been observed to favor deeper depth ranges (30-35m) during the day and shallower depth ranges (15-20m) at night. This increased vertical migration to shallower water depths at night, compared to little or no vertical movement during the day, suggested that Whitetip reef sharks are nocturnally active and rest during the day (Fitzpatric et al., 2011). The findings by Fitzpatric et al (2011) might be applicable to *C. humani*, supporting the hypothesis that the availability of flat sandy habitats in the iSimangaliso MPA could be utilized by this species during the day to rest. This accounts for the consistent deeper sightings that are reported in this study, as *C. humani* was recorded at higher frequencies in the deep deployment BRUVs. Even if 33.7 m was the highest depth sampled, Smith et. al (1969) reported that this species occurs close inshore in depths of less than 40 m, making it safe to assume that this study included a good representation of their use of the vertical column. Other species comparable in size to *C. humani*, such as *Syliorhinuscanicula* (small-spotted catsharks), have been observed to spend the day in deeper, colder water before foraging in warmer, shallower prey-rich water at night (Sims et al., 2006). However, to gain a more comprehensive understanding of *C. humani* habitat and space-use in the iSimangaliso MPA, future studies should employ additional methods, such as acoustic telemetry, to monitor movement patterns on a 24 hours scale, hence including the nocturnal period.

4.3 MPA zonation effects

Comparing different abundance indices for *C. humani*, allowed this study to obtain insights on the ecological consequences of alternative MPA zone policies within the iSimangaliso MPA. The use of the different zones was contextualized with habitat attributes, as it was demonstrated by Osgood et al. (2019) to be the most efficient way to evaluate the MPAs effectiveness. The findings of this work indicated that the different levels of protection were among the factors driving *C. humani* patterns of abundance. In particular, no-take areas, i.e. the Sodwana Diving Restricted Zone, and the iSimangaliso Offshore Wilderness Zone, were characterized by higher incidence of *C. humani* with respect to the iSimangaliso Offshore Controlled Pelagic Linefishing Zone North. Furthermore, all the males sighted in the MPA during the presumed mating season occured in no-take zones, indicating a positive effect of the protection policies at both ecological and behavioral level. As *C. humani* is not considered to be among the species targeted by local fishermen, these results should be interpreted as an indicator of the ecosystem status and prey availability rather than a direct effect of the restrictions on this species. Indeed, when judging the ecological effectiveness of MPAs policies, trophic cascades are a critical issue that should be kept in mind (Salomon et al., 2001). For this reason, the results of this analysis do not prove the absolute effectiveness of the adopted management policies for all the species inhabiting the area, but provide important insights on their effect on this species of mesopredator. Furthermore, assumptions about the MPA's policies global impact cannot be made due to the lack of data on *C. humani* abundance before their designation; however the findings support the no-take policy effectiveness during the research period. Based on evidence found in this work, it can be concluded that *C. humani* benefits from the fishing restrictions established in SDRZ and IOWZ, however additional research including interspecific interactions is needed to establish the dynamics at the basis of this result.

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Appendix

Table 5.1: Individuals sighted each month divided by sex

Month	*Female*	*Male*	*UI*
January	13	3	11
February	4	1	0
March	22	1	2
April	13	4	2
May	10	4	5
June	15	0	3
July	12	0	12
August	12	0	4
September	4	3	1
October	3	0	2
November	8	0	0
December	23	2	4

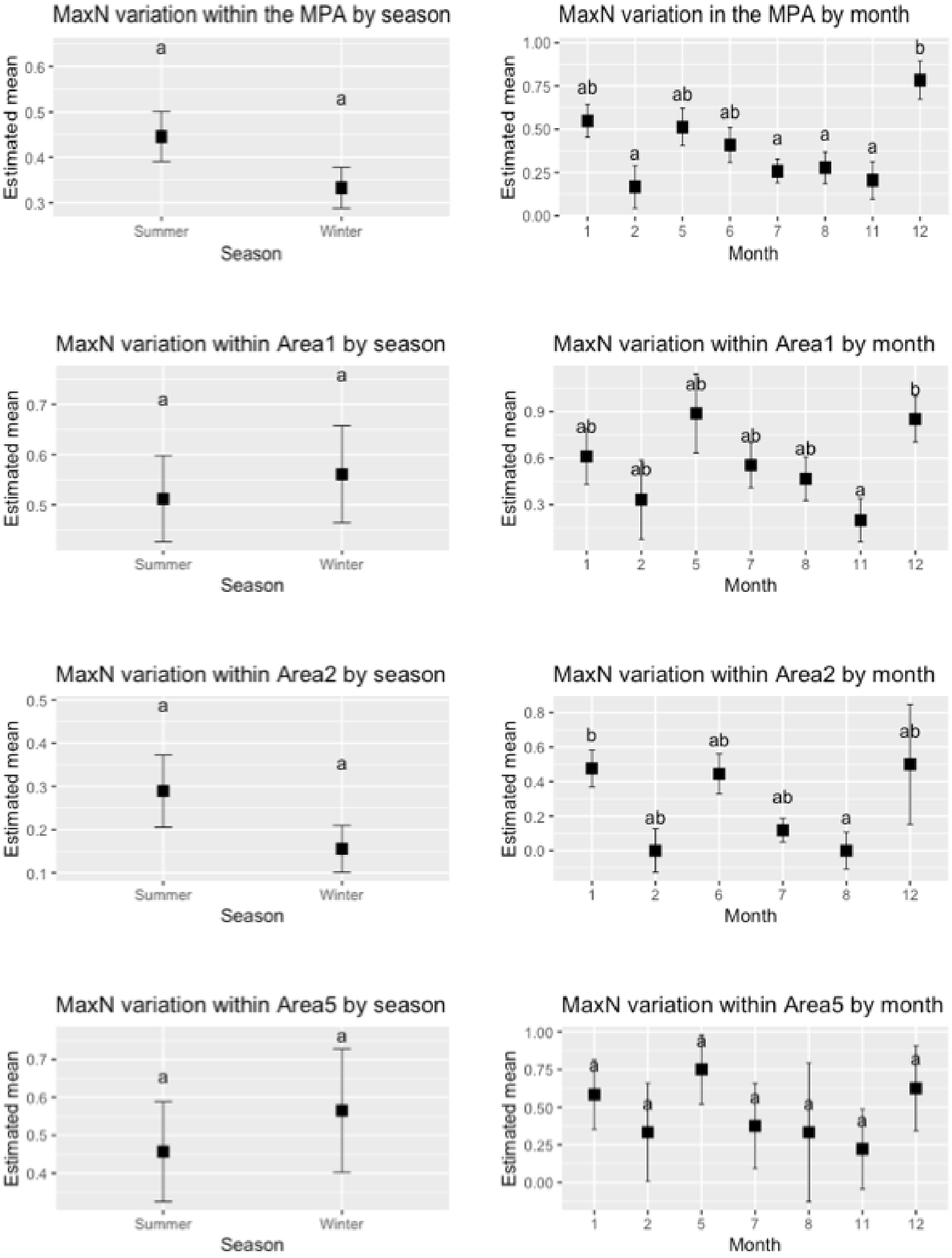
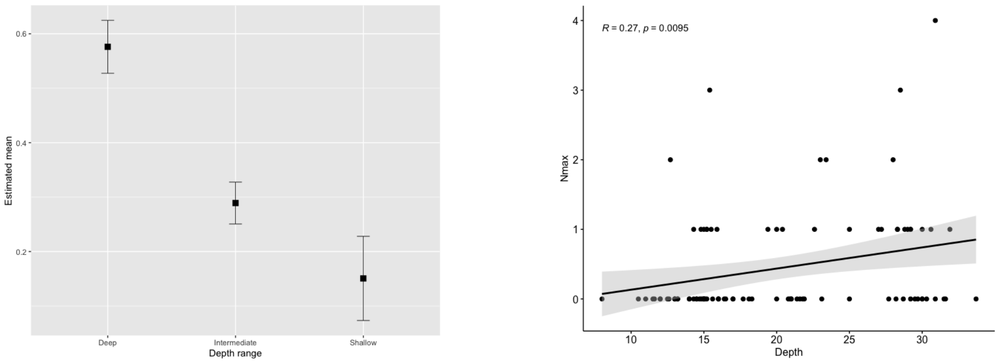


Figure 5.1: Results of seasonality inspection in the designated study areas



(a) Nmax at different depth ranges **(b)** Nmax and depth correlation

Figure 5.2: Effect of depth on Nmax in Area 5

Table 5.2: Null model used in the inspection of zonation effect

Nmax			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.34	-0.59 - -0.09	**0.007**
Depth	0.02	0.01 - 0.03	<**0.001**
Substrate [Reef/Sand]	0.38	0.11 - 0.64	**0.005**
Substrate [Sand]	0.25	0.08 - 0.43	<**0.004**
Random Effects			
σ^2	0.36		
τ_{00}	0.08		
ICC	0.19		
N_{Site}	368		
Observations	506		
Marginal $R^2/Conditional R^2$	0.068/0.243		

Table 5.3: Full model used in the inspection of zonation effect

Nmax			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.69	-0.97 - -0.41	<**0.001**
Zone [IOWZ]	0.34	0.17 - 0.52	<**0.001**
Zone [SDRZ]	0.28	0.15 - 0.42	<**0.001**
Depth	0.03	0.02 - 0.03	<**0.001**
Substrate [Reef/Sand]	0.36	0.10 - 0.62	**0.006**
Substrate [Sand]	0.38	0.20 - 0.56	<**0.001**
Random Effects			
σ^2	0.39		
τ_{00}	0.03		
ICC	0.08		
N_{Site}	368		
Observations	506		
Marginal $R^2/Conditional R^2$	0.108/0.175		