

Candice-Jade Parkes

**Behavioural Ethograms & Social Hierarchy
of *Carcharhinus limbatus* (blacktip) During a
Simulated-feeding Scenario within South African
MPA**



UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2021

Candice-Jade Parkes

Behavioural Ethograms & Social Hierarchy of *Carcharhinus limbatus* (blacktip) During a Simulated-feeding Scenario within South African MPA

Mestrado em Biologia Marinha

Masters in Marine Biology

Supervisors:

Dr. Sara Andreotti

University of Stellenbosch, South Africa

Co-supervisor

Dr. Ester Serrao

University of Algarve, Portugal



UNIVERSIDADE DO ALGARVE

Declaração de autoria de trabalho

Declaro ser o(a) autor(a) deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Candice-Jade Parkes

Copyright ©Candice-Jade Parkes

A Universidade do Algarve reserva para si o direito, em conformidade com o disposto no Código do Direito de Autor e dos Direitos Conexos, de arquivar, reproduzir e publicar a obra, independentemente do meio utilizado, bem como de a divulgar através de repositórios científicos e de admitir a sua cópia e distribuição para fins meramente educacionais ou de investigação e não comerciais, conquanto seja dado o devido crédito ao autor e editor respetivos.

Contents

List of Abbreviations	v
Abstract	vi
Resumo	vii
State of the Art	x
Threats in South Africa.....	xii
Sampling Pelagic Organisms	xiv
Underwater Video Surveys	xv
Laser Photogrammetry	xvi
Photo-Identification	xvi
References	xviii
Introduction	1
Social Behaviours & Inter-specific Niche Partitioning	1
Study Species	4
Shark Social Behaviours	5
Objectives	6
Research Methodology.....	6
Study Site	6
Data Collection.....	7
Photographic Identification	8
Laser Photogrammetry	11
Behavioural Analysis	12
Statistical Analysis.....	15
Results	16
Discussion	24
Environmental Variables & Size	24
Behaviours	25
Limitations & Future Research.....	29
Conclusion	30
Acknowledgements	31
Annex 1.....	32
References	36

List of Abbreviations

ICUN – International Union for Conservation

KZNSB – Kwa-Zulu Natal Sharks Board

KZN – Kwa-Zulu Natal

UVS – Underwater Video Survey

BRUVs – Baited Remote Underwater Video surveillance

MPA – Marine Protected Area

USA – United States of America

IUU – Illegal, Unreported, Unregulated

DAFF – Department of Fisheries and Forestry

Abstract

It has become apparent that elasmobranchs form more complex social organisations than previously thought, and recent improvement of new technologies and analysis has provided valuable information into their social behaviour. Here, a simulated-feeding scenario was utilized to investigate the behaviour of *Carcharhinus limbatus* within Aliwal Shoal MPA, by defining and testing species-specific ethograms. Ten behavioural units were identified and grouped in the following categories: i) dominant category: ‘fast turn’, ‘upward swim’, ‘downward swim’; ii) semi-dominant category: ‘parallel swim’; iii) submissive: ‘body tilt’, ‘avoid’, ‘giveaway’, ‘follow’; and iv) neutral category: ‘pass’, ‘patrol’. A total of 1014 individual behaviours were recorded, with ‘fast turn’ representing 39% and ‘avoid’ representing 19%. There were 475 dominant displays, 32 semi-dominant, 331 submissive and 176 neutral displays. Ten individuals were successfully identified using photographic-identification of their dorsal fin. The observed sharks were mostly females, with average sizes of $146.3 \text{ cm} \pm 3.088$ (e.g. sub-adults). The data indicated that size played a significant role in the position of the individual within the hierarchy, with larger individuals showing more displays of dominance and smaller individuals showing more submissive displays. One particularly large female shark, named ‘Broken Tail’, appeared to be consistently more dominant than the other individuals, with also the highest level of re-sightings over the sample period, and the most displays of dominance (33% of the total). Finally, in the few instances where larger species (e.g. *Galeocerdo cuvier* or *Carcharhinus leucas*) were present, the number of blacktip sharks observed-appeared to be less. Although the observations in the presence of other sharks were too few for drawing statistically significant conclusions, these preliminary observations suggest interspecific interactions during a simulated-feeding scenario. Given the influence of size and possibly individual behaviour, the observed structure and hierarchy displayed by the blacktip sharks in this study is likely to have further fitness and survival implications that will require further studies.

Resumo

A conservação de tubarões tornou-se um tema de crescente interesse público, uma vez que o aumento global da pressão da pesca levou ao declínio de quase 90% das populações de peixes nos Oceanos, sendo as populações de elasmobrânquios um dos grupos mais afetados. Nos últimos anos, tornou-se evidente que a grande maioria das populações de Chondrichthyes está a caminho de um declínio global, como resultado da sua vulnerabilidade à pressão da pesca e às mudanças ambientais. Isto pode ser encontrado na sua estratégia de reprodução: a maioria dos Chondrichthyes são espécies selecionadas K, o que significa que as suas características biológicas compreendem baixas taxas de crescimento e de reprodução, longos períodos de gestação produzindo poucas crias, e longos tempos de geração (Cahmi et al 1998, Bornatowski et al 2014). Os tubarões atuam como predadores marinhos fundamentais pelo seu papel de manter o equilíbrio do ecossistema e prevenir a cascata trófica. Ao fornecer serviços como saúde e equilíbrio dos ecossistemas, os elasmobrânquios podem ser usados como bio-indicadores para avaliar o estado de saúde dos oceanos. Alguns são considerados predadores marinhos chave que medeiam, ou previnem, as cascatas tróficas através do seu papel como espécies de topo ou meso-predadoras. Além disso, existe uma tendência para as espécies Chondrichthyes, como os tubarões Blacktips, se agregarem a outros indivíduos de idade, sexo e fase reprodutiva semelhantes, o que os coloca em perigo de extinção da pesca, como espécies alvo ou captura acessória acidental, levando a possíveis cascatas tróficas e extinção de grupos populacionais específicos (Cahmi et al 1998). A remoção simultânea de grupos com fases de vida compartilhadas pode levar a colapsos populacionais e extinções locais. A remoção de grupos de tubarões com idades ou tamanhos específicos pode levar a mudanças na proporção de sexos reprodutores, padrões de acasalamento, abundância populacional, tamanho e estruturas e resultar em perda de biodiversidade, especialmente em áreas com alto endemismo. Tornou-se evidente que os elasmobrânquios, tubarões e raias, formam organizações sociais mais complexas do que se pensava anteriormente. O crescimento de novas tecnologias e análises tem fornecido dados valiosos para a vida dos comportamentos sociais de Chondrichthyan. Embora a maioria da investigação se tenha centrado principalmente nos níveis de repartição de recursos entre as diferentes espécies de tubarões, poucos estudos investigaram as hierarquias sociais encontradas tanto intra como inter especificamente entre os tubarões formando agregações, e que fatores podem influenciar uma posição individual dentro destas organizações sociais. Historicamente, os tubarões têm sido considerados solitários, contudo, evidências recentes têm demonstrado que uma variedade de espécies de tubarões formam

agregações com base em semelhanças em tamanho, sexo ou idade. Isto deve-se a uma maior capacidade de alimentação e os tubarões sofrem mudanças na sua dieta ontogenética durante as suas fases de vida à medida que o seu porte e velocidade aumentam com a idade. As agregações permitem uma maior aptidão física através da proteção dos predadores durante as fases de desenvolvimento dos juvenis, estratégias de alimentação bem sucedidas através de frenesi de alimentação e melhor acasalamento e sucesso reprodutivo. Com o futuro desenvolvimento das tecnologias e análises estatísticas, a amostragem dos organismos pelágicos e a compreensão dos comportamentos tornou-se amplamente disponível. Métodos não invasivos como UVs, fotogrametria e fotogrametria a laser permitiram um aumento no número de estudos de pelágicos, mantendo a distância social e sem causar danos aos indivíduos da amostra. O ecoturismo através de mergulhos com isco tornou-se uma ferramenta útil ao permitir um método não-invasivo de amostragem de comportamentos sociais, ao mesmo tempo que gera uma renda que permite a conservação da espécie. Na África do Sul, um hotspot de diversidade de tubarões, lar de espécies de tubarão, mergulhando como atividade cada vez mais popular entre os mergulhadores ávidos, permitindo oportunidades de pesquisa envolvendo estes organismos pelágicos. Uma visão comum em mergulhos com tubarões são as agregações de *Carharhinus limbatus* (blacktip), com números por vezes superiores a 15 indivíduos, mas em média 5-8 indivíduos. Este estudo permitiu a integração de várias partes interessadas no MPA do Aliwal Shoal incluindo operadores de mergulho, cientistas cidadãos e pescadores; e forneceu os dados necessários para compreender melhor as organizações sociais da espécie. Os dados foram recolhidos entre Março e Junho, após o que se iniciou a conhecida corrida da sardinha que ocorre na costa africana de Southern e os tubarões deixaram a área. Após análise UV, dez unidades comportamentais para identificação e avaliação com base na literatura anterior e avistamentos originais. As unidades comportamentais foram categorizadas como as seguintes: i) dominantes: 'volta rápida', 'nadar para cima', 'nadar para baixo'; ii) semi-dominantes: 'nadar em paralelo'; iii) submissas: 'inclinação do corpo', 'evitar', 'desistir', seguir'; e iv) neutras: 'passar', 'patrulhar'. Foi registado um total de 1014 comportamentos individuais, sendo que 'virar rápido' representa 39% e 'evitar' representa 19%. Havia 475 exibições dominantes, 32 semi-dominantes, 331 submisso e 176 neutras. Dez indivíduos foram identificados com sucesso usando a identificação fotográfica da barbatana dorsal do flanco esquerdo. A identificação fotográfica das barbatanas permitiu o reconhecimento dos indivíduos que retornaram ao local do estudo e sugeriu que o grupo agregado estava bem estabelecido nesta área em particular. O grupo era dominado principalmente por fêmeas e os tamanhos médios representam os dos sub-adultos (146,3 cm \pm 3,088). O tamanho desempenhou um papel

significativo na posição do indivíduo dentro da hierarquia, com indivíduos maiores mostrando mais exibições de dominância e indivíduos menores mostrando exibições mais submissas. A 'Cauda Quebrada' foi nomeada como o domínio feminino da organização, com o maior nível de re-visibilidade durante o período amostral, e a maior parte das exibições de dominância (33% do total). Embora grupos se agreguem com semelhanças de tamanho, ainda existem discrepâncias entre os indivíduos, o que permite a estruturação da hierarquia. Os números de pontas negras foram diminuindo durante os mergulhos em que *Galeocerdo cuvier* ou *Carcharhinus leucas* foram encontrados sugerindo uma outra organização social interespecífica durante um cenário de alimentação simulada. Este estudo mostra que o tamanho desempenha um papel crítico na organização das agregações de Blacktip, o que em última análise leva ao sucesso da aptidão e sobrevivência dos indivíduos. Durante as interações interespecíficas, o número de *Carcharhinus limbatus* diminuiu na presença de *Carcharhinus leucas* (tubarão-touro) e *Galeocerdo cuvier* (tubarão tigre). Isto sugere um nível de organização social não só dentro de uma espécie, mas através de diferentes taxas. Este estudo fornece informações valiosas sobre organizações sociais e pode funcionar como uma ferramenta útil na reavaliação das medidas de conservação necessárias para a proteção da espécie. O impacto visto das atividades de pesca não regulamentadas dentro da MPA, incluindo maxilares partidos, anzóis de pesca e feridas causadas por barcos, requer uma avaliação mais aprofundada e objetivos de gestão para reduzir o conflito visto entre espécies sociais como o *Carcharhinus limbatus* e os pescadores. A conservação das espécies de tubarões é vital para a saúde tanto dos ecossistemas locais como dos oceanos. Outros estudos devem avaliar o papel da personalidade individual, em conjunto com o tamanho, para a posição do indivíduo dentro da hierarquia.

State of the Art

One of the potential causes of Chondrichthyes vulnerability to fishing pressure can be found in their reproduction strategy: most Chondrichthyes are K-selected species, meaning that their biological characteristics comprise low growth and reproductive rates, long gestation periods with the production of few young, and long generation times (Cahmi et al 1998, Bornatowski et al. 2014). In addition, there is a tendency for Chondrichthyes species, such as blacktips sharks, to aggregate with other individuals of similar age, sex, and reproductive stage which further puts them in endangerment from fisheries, as target species or accidental bycatch, leading to possible trophic cascades and extinction of specific population groups (Cahmi et al 1998). Simultaneous removal of groups with shared life-stages can further lead to population collapses and local extinctions. Removal of age or size-specific groups of sharks could lead to changes in the breeding sex ratios, mating patterns, population abundances, size and age structures and result in biodiversity loss, especially in areas with high endemism's (Stevens et al. 2000). The role of social behaviours (i.e. tendencies to aggregate) is therefore a fundamental factor in documenting the risk imposed by fisheries targeting aggregations as this is select against social individuals (Jacoby et al. 2012, Finger et al. 2018). As apex predators, sharks play a crucial role in shaping respective community dynamics through predation and associated risk effects helping to regulate and maintain the balance in marine systems (Daly et al. 2013), therefore their subsequent removal can lead to cascading effects down the food chain. A decrease in shark populations is met with an increase in prey populations which causes ecosystem shifts throughout trophic levels showing that a systematic elimination of one species, a key component of the food web, can destabilize the entire ecosystem. This leads to severe consequences for productivity and derived economic yields which humans are often dependent on for their livelihoods. (Pauly 1995; Bax 1998; Robbins et al 2006). The level of diversity in diet is linked to foraging success of sharks, which implies that there is a limit placed on shark behaviour and is a decisive factor in shaping the feeding strategy of these predators (Yunkai et al 2014; Duffy et al 2015; Paes-Rosas et al 2018). Sharks are typically considered asynchronous opportunistic, or generalist, feeders consuming a diverse array of prey which has led to a highly evolved range of resource use strategies leading to various influences on local communities (Munroe et al 2013). These strategies aim to exploit resource regions that are simultaneously abundant, persistent, and profitable (Au 1991; Compagno et al 2005; Paez-

Rosas et al, 2018). In general, predation studies have focused predominantly on the predator and the rates of predation. However, it has been noted by Polis (1984) that selectivity of predation deserves proportional attention with size being the most obvious factor for selection basis (Bax 1998) stating that “different size classes of a species exploit different sizes and species of prey allowing different size classes to use different ecological niches”. It has been suggested that often a greater extent of diet overlap occurs between different species of similar sized individuals compared to same species with different sized individuals (Bax 1998). This is a result of ontogenetic shifts in habitat use and diet preferences (Wetherbee & Cortes 2004; Guttridge et al. 2009). As predators grow, so their gape and speed increases allowing an increase in range size of available prey to hunt and consume (Okada & Taniguchi 1974; Armstrong 1982; Bax 1998). Feeding occurs in short bursts which is followed by a longer period needed for digestion if feeding is reduced (Wetherbee & Cortes 2004; Motta & Wilga 2001). Most consumed prey are the teleost’s considering they are one of the most abundant taxa and according to Budker (1971) sharks, on average, consume approximately 3-14% of their body weight per week. This value varies depending on species.

Globally, sharks are killed for their meat, fins, gill plates and liver oils (McClenachan & Dulvy 2017; Clarke et al 2006) and, since the early 2000s which saw a peak at 63-273 million catches, rapid declines have been observed due to overfishing (Pacoureau et al 2019). ‘Boom-and bust’ catch patterns because of increased demand for the international shark fin trade have showed serious declines in oceanic and coastal shark populations found in South Africa (Dudley & Simpfendorfer 2006), Gulf of Mexico, Northwest Atlantic (International Commission for the Conservation of Atlantic Tunas 2019) and Australia (Roff et al 2018). As of 2019 according to the International Union for Conservation of Nature (IUCN), amongst the 470 species of sharks, 2.4% are listed as ‘Critically endangered’, 3.2% ‘Endangered’, 10.3% ‘Vulnerable’ and 14.4% ‘Near Threatened’. For species like *Galeorhinus galeus* (common name: Tope shark) which demonstrate a long history of being caught both as bycatch and in targeted fisheries, population declines of 88% over the last 80 years have resulted in the re-classification in the IUCN red list from ‘vulnerable’ to critically endangered’ and face a high risk of extinction in the wild (Pondella & Allen 2008, see <https://www.iucnssg.org/red-list.html> for available IUCN Red List Categories). Deep-water sharks are considered the most vulnerable to fishing efforts (as a result of trawling and destructive off-shore fishing methods), with growth rates 40-60% lower compared to pelagic species and 55-63% lower than coastal species (Garcia et al 2008, Ferretti et al 2010). This raises concerns regarding management

and conservation as by-catch regulations do not always protect local populations making them particularly vulnerable due to their life-history strategies (Das & Afonso 2017).

Threats in South Africa

In 1952 the ‘beach protection program’ was introduced into South Africa initiating the installation of 300 km of shark nets across 37 beaches on the Kwa-Zulu Natal coastline. First pioneered in Australia during the 1930s (Reid & Krogh 1992, Dudley et al 2006), shark nets aimed to reduce the risks of attacks on bathers. Large mesh gillnets were introduced into Durban’s coastline following several highly publicised shark attacks on bathers during the 1940s and early 1950s. After the net deployments, shark attacks ceased in these localised areas. The principal mechanism driving the persistence of shark-nets is that ‘fewer sharks in an area result in fewer attacks on people’. However, the nets do not form a protective barrier given they are arranged in a scattered formation and are on average only six metres deep. For this reason, sharks can swim under the nets into the ‘protected’ areas and majority of individuals are entangled when leaving the enclosed shoreline. The mechanism driving this reduction in attacks is localised depletion of sharks in the vicinity of the nets (Davies 1963, Dudley 1997, Dudley et al 2006). In 1999, an initiative began aiming to reduce the amount of by-catch of ‘harmless’ animals such as whales, dolphins and turtles by replacing nets with drumlines. A drumline consists of an anchored float with suspended baited hooks which lure and capture sharks and resulted in a 47.5% reduction of bycatch of non-target animals (Cliff & Dudley 1993; Guyomar et al 2019). Drumlines, same as shark-nets, aim to reduce the number of sharks in the vicinity of protected beaches, thereby lowering the probability of encounters between sharks and people (Cliff & Dudley 1992; Brazier et al. 2012). Catch rates of four species (*Carcharhinus leucas*, *C. limbatus*, *Sphyrna lewini* & *S.mokarran*) demonstrated significant declines in populations between 1978-2003, as well as declines in the mean and median of three species (*Carharhinus ambionensis*, *C. limbatus* & female *Carcharodon carcharias*) (Dudley et al 2006). According to Dudley et al. (2006) approximately 120 longline vessels are operating illegally in coastal waters of the western Indian Ocean with an expected increase to 200 vessels in 2005 (IOTC 2005). As of 2021, it was estimated that in the Somali waters of the Indian Ocean alone, there are over 700 foreign fishing vessels in operation (Glaser, Roberts & Hulbert 2019). The illegal vessels primarily target hammerhead sharks and guitar fish (*Rhynchobatus djiddensis*) for their fins. Despite international recognition of the vulnerability of shark species and the urgent need for management of fisheries, there is still little effective management of shark stocks at either a national or regional level (Lack & Glenn 2008). Where

management has been implemented it is often indirect, with a focus on finning operation controls rather than controls on catch or mortality. Illegal, Unreported and Unregulated (IUU) fishing is under-reported and misleading in total catch numbers, causing concern as increasing pressures from excessive industrial fleets and sustained harvest of sharks is unrecorded (Bega 2020). IUU exhibits distinct economic, environmental, and social impacts. For example, direct and indirect loss of revenue, by-catch species (unintended catches), ghost fishing (continued entanglement of marine species in discarded nets), habitat destruction (bottom trawling) and reduced food insecurity and loss of livelihoods (SAIIA 2008). According to the Department of Fisheries and Forestry (DAFF), no fishing is permitted in South African waters without a permit, and all vessels should disclose whether they have fresh fish products on board. If vessels are caught disobeying the law, they are eligible to a hefty fine or imprisonment (DAFF 2019). Fennessy (1994) reported large catches of new-born and juvenile *S.lewini* by prawn trawlers on the Tugela Bank causing a mortality of approximately 98% between 1989 and 1992. Size frequency distributions of KZN shark nets has demonstrated that a wide range of sizes of individuals are caught. Data-collection from the KZN shark nets, however, offers long-term high-quality sources of data acting as a fisheries-independent monitoring tool that can be used to understand a wide variety of species in South Africa and aid management of shark resources in the region, despite the nets causing significant damage to already vulnerable shark species of South Africa (Dudley et al 2006).

Within sharks' social aggregations, displays of agonistic behaviours can be observed: this class of behaviours is prevalent in a competitive context, and it can influence the social dynamics and overall evolutionary fitness of single individuals (Ritter & Godknecht 2000; Matich et al. 2020). Agonistic behaviour is common across all animal taxa including elasmobranchs, crustaceans, mammals, birds, reptiles, insects, spiders, amphibians and fishes (Bradbury & Vehrencamp 1998; Martin 2007). Agonistic displays have been documented in a wide variety of species such as the grey reef shark (*Carcharhinus amblyrhynchos*) through prominent 'hunching' or 'arching' of the back during feeding scenarios (McKibben & Nelson 1986; Ritter et al 2000), or for asserting dominance to reaffirm position in the hierarchy as seen in male free-living zebra sharks (*Stegostoma fasciatum*) (Brunnschweiler & Pratt 2008). Squid (*Loligo pealeii*) and cuttlefish (*Sepia officinalis*) have been shown to exhibit hierarchical signalling through polarized light reflections used to convey a hierarchy of threats (Schnell et al. 2016). Whilst many animals produce multiple displays of agonism, the roles of such displays often remain ambiguous. As a result of these well-documented displays in social hierarchies,

both inter- and intra-specific, it is crucial for species to adapt through temporal and spatial utilization to allow coexistence. In order to promote coexistence of competitor species, particularly in the guild of marine predators novel mechanisms of niche and resource partitioning across time, space and/or resources are established (Lear et al 2021). Resource partitioning involves species feeding within the same area, but on different prey items; spatial partitioning occurs where species utilize different areas to forage or hunt the same preys; and temporal partitioning where sympatric species follow a diel feeding pattern utilizing areas at different peak foraging times. Six large coastal shark species inhabiting the waters of the Gulf of Mexico, Florida, USA were examined by Laer et al (2021) and found to show minimal overlap in diel timing of peak activities suggesting the occurrence of temporal partitioning amongst the species.

Overlapping of trophic niches is common in most terrestrial and marine ecosystems, meaning that reducing the competition over food resources is essential in ensuring coexistence of species. In extreme cases, if food resources are scarce sharks may find themselves in competition with intraguild predators. Through the act of resource partitioning species reduce the competition for resources usually through competitive exclusion (Papastamatiou et al. 2006), or through behavioural changes like feeding on different prey in the presence of a particular predator or by modifying foraging routes to avoid conflict. Resource partitioning has been seen both between species and within species (Gallagher et al 2017) suggesting that there is a hierarchical system of feeding in multi-use feeding areas. However, as Brena et al (2018) mentioned sharks may rely on social cues regarding their competitors and establish dominance or tolerance relationships with respect to increasing their likelihood of access to food, for example by submitting to or avoiding larger individuals. Research has primarily focused on *Sphyrnidae* and *Carcharhinidae* as they are predominately found in coastal systems making them more accessible (Klimley 1985; Heupel & Simpfendorfer 2005; Jacoby et al. 2021). Understanding the mechanisms underpinning social behaviours in *Chondrichthyes*, in conjunction with temporal dynamics such as aggregations, is key for assessing the vulnerability of varied species, many of which require urgent conservation efforts in the upcoming years due to persistent anthropogenic threats (Jacoby et al. 2012).

Sampling Pelagic Organisms

Several challenges arise when studying pelagic marine organisms such as sharks due to their generally high mobility, low population numbers and ontogenetic shifts in habitat

utilization (Dulvy et al 2008, Santana-Garcon et al 2014). Mobile oceanic fishes and sharks often occur at low densities and due to lack of data pertaining to their complex relationships within their physical habitats (Morato et al. 2010, Bouchet et al. 2015, Letessier et al. 2015), poor understanding of geographic distributions (Worm & Tittensor 2011, Letessier et al. 2015), high temporal spatio-temporal heterogeneity (Block et al 2005, Letessier et al 2015), and their intricate population dynamics in comparison with lower trophic levels. In fact, there are many logistical challenges to obtain ecologically meaningful and significant data on these organisms (Letessier et al. 2015). Major challenges arise when trying to obtain long-term data as individuals disperse or suffer mortality (Gruber et al. 2001, Finger et al. 2018). Sampling techniques can be categorized into lethal and non-lethal, with most of the data collection on highly mobile marine species being among the lethal categories. The data collection on large pelagic fishes often relies on fishery-dependent practices or extractive fishery-independent techniques which often lead to sampling bias in catchability and size-selectivity (Santana-Garcon et al 2014). Unfortunately, fishery-independent surveys, although more robust in their design but often employ commercial fishing gear, such as gillnets, trawls, longlines, and therefore sampling bias in terms of catchability and size-selectivity still remain (McAuley, Simpfendorfer & Wright 2007, Santana-Garcon et al 2014).

Underwater Video Surveys

Underwater Video Surveys (UVS) are a useful tool in assessing wildlife communities and characterising biodiversity patterns across various spatial and temporal scales. These can be used to assess behaviours observed in site, species-habitat relationships, extent and magnitude of anthropogenic impacts and temporal and spatial variability (Bouchet et al 2018). The mobility of most elasmobranch species presents significant challenges to their assessment and management (Knip et al. 2012, White et al. 2013). UVS provide a standardized alternative, non-extractive, and fishery-independent approach to sampling a wide range of marine species and biodiversity indices (Cappo et al 2003, Santana-Garcon et al 2014). The concept revolves around the idea of using bait to attract individuals into the field view of a camera in which the species coming into view can be identified and counted (Dorman, Harvey & Newman 2012; Santana-Garcon et al 2014). The UVs provide a valuable tool in assessing the behaviours of pelagic sharks and attain data comparable to that of scientific longline surveys (Santana-Garcon et al 2014) whilst removing sampling bias caused by gear selectivity, such as hook size.

Laser Photogrammetry

Morphometrics are important components in furthering the understanding of life-history traits of various species including individual growth rates, physical and sexual maturity (Walters & Whitehead 1990), size class segregations in a population (Cubbage & Calambokidis 1987) and phenotypic differences. However, obtaining such morphometrics on free-ranging organisms is often challenging, compared to the more widely used morphology assessment on dead or captured individuals (Deakos 2010). Laser photogrammetry is a non-invasive method that has been used to estimate the size of free ranging, large marine individual organisms, including whales (Cubbage & Calambokidis 1987), dolphins (Perryman & Lynn 1993), sharks (Klimley & Brown 1983) and rays (Deakos 2010). More specifically, laser photogrammetry has been successfully employed and applied to *Orcinus orca* (Durban & Parsons 2006), *Cephalorhynchus hectori* (Webster et al 2010), *Manta alfredi* (Deakos 2010), *Carcharodon carcharias* (Leurs et al 2015) and *Rhincodon typus* (Rohner et al 2011). In this method, parallel lasers project light of equidistance regardless of the distance from the origin (Rothman et al 2008, Jeffreys et al 2013). The parallel laser beams are of known distance apart and projected onto a target area on the organism thereby creating a ‘scale-bar’ which is photographed (Deakos 2000). The subject should be perpendicular to the axis of the lasers to prevent distortion of the image and inaccurate estimates of the length, making it possible to estimate the size of the individual from the distance between the laser points.

Photo-Identification

Photo-identification offers a non-invasive alternative for estimating population sizes, when sufficient individuals can be recognized based on stable natural markings and features (Gore et al. 2016). By using this method, the amount of induced stress otherwise caused by tagging or artificial markings is avoided (Gore et al. 2016). Photo-ID methods have been used to describe individual growth rates, reproductive cycles, demography analysis, sex difference in aggregation sites, and estimates of population sizes and structures (Sosa-Nishizaki et al 2012). This method has been mostly used for marine cetaceans (Stevick et al. 2001) but has been adapted in the last ten years in elasmobranch studies (Marshall et al. 2011, Sosa-Nishizaki et al. 2012, Araujo et al. 2016). As for any Capture-Mark-Recapture techniques, the photo-ID method also run the risk of identifying false positives or negatives of individuals as markings may change over time or individuals may appear similar (Sosa-Nishizaki et al 2016). The use

of photo-ID has been successful in assessing regional populations of white sharks (*Carcharhinus carcharias*) (Domeier & Nasby-Lucas 2007, Towner et al. 2013, Andreotti et al. 2016, Andreotti et al. 2017, Kanive et al. 2020), nurse sharks (*Ginglymostoma cirratum*) (Castro & Rosa 2005), and whale sharks (*Rhinocodon typus*) (Holmberg et al 2009, Andrejaczek et al. 2016, Araujo et al. 2019). Some photo-ID studies proved to be adequate to apply long-term recognition of individuals, and the collection of data usable in capture-mark-recapture analyses (Forcada & Aguilar 2000, Gore et al. 2016, McCoy et al. 2018); these studies were conducted in areas of elasmobranch aggregations, where the individuals could be consistently identified overtime and showed a certain degree of site-fidelity (Araujo et al. 2016, Brena et al. 2018).

References

- Araujo, G., Snow, S.J., So, C.L., Ponzo, A. (2016). Population structure, residency patterns and movements of whale sharks in Southern Leyte, Phillipines: Results from dedicated photo-ID and citizen science. *Aquatic Conservation Marine and Freshwater Ecosystems* **27**: 391-415. DOI: 10.1002/aqc.2636
- Armstrong, M. J. (1982). The predator-prey relationship of Irish poor-cod (*Trisopterus luscus* L.) and cod (*Gadus morhua* L.). *Journal Conseil International pour l'Exploration de la Mer* **40**: 135-152. doi: <https://doi.org/10.1093/icesjms/40.2.135>
- Andrzejaczek, S., Gleiss, A.C., Pattiaratchi, C.B., Meekan, M.G. (2018). First insights into the fine-scale movements of sandbar shark, *Carcharhinus plumbeus*. *Frontiers in Marine Science* **5**: 2541-2562. Doi: <https://doi.org/10.3389/fmars.2018.00483>
- Bax, N.J. (1998). The significance and prediction of predation in marine fisheries. *Journal of Marine Science* **55**: 997-1030. doi: 1054–3139/98/060997
- Bornatowski, H., Braga, R.R., Vitule, J.R. (2014). Threats to sharks in a developing country: the need for effective simple conservation measures. *Nature & Conservation* **12**: 11-18. doi: doi.org/10.4322/natcon.2014.003
- Cahmi, M., Fowler, S.L., Musick, J.A., Brautigam, A., Fordham, S.V. (1998). Sharks and their relatives – Ecology and Conservation. IUCN/SSC Shark specialist Group. IUCN **5**: 39. ISBN: 2-8317-0460-9
- Cappo, M., Harvey, E., Malcom, H., Speare, P. (2003). Potential of video techniques to monitor diversity, abundance and size of fish in studies of Marine Protected Areas. *Australian Society for Fish Biology* **1**: 455-464. ISBN 0 646 43022
- Castro, A.L., Rosa, R.S. (2005). Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. *Biology Fish* **72**: 213-221. DOI: 10.1007/s10641-004-1479-7
- Clarke, S.C. McAllister, M., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G., Agnew, D., Pikitch, E.K., Nakano, H., Shivji, M.S. (2006). Global

estimates of shark catches using trade records from commercial markets. *Ecology Letters* **9**(10): 1115-1126. DOI: 10.1111/j.1461-0248.2006.00968.x

Cubbage, J., Calambokidis, J. (1987). Size-class segregation of bowhead whales discerned through aerial stereophotogrammetry. *Marine Mammal Science* **3**: 179-185. DOI: <https://doi.org/10.1111/j.1748-7692.1987.tb00160.x>

Daly, R., Froneman, P.W., Smale, M.J. (2013). Comparative feeding ecology of Bull Sharks (*Carcharhinus leucas*) in the coastal waters of the Southwest Indian Ocean inferred from stable isotope analysis. *PLoS ONE* **8**: e78229. doi.org/10.1371/journal.pone.007822X

Davis, D.H. (1963). Shark attack and its relationship to temperature, beach patronage and the seasonal abundance of dangerous sharks. Oceanographic Research Institute Investigational Report 6, Durban South Africa

Domeier, M.L., Nasby-Lucas, N. (2007). Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Marine Biology* **150**: 977-984. DOI: 10.1007/s00227-006-0380-7

Dorman, S.R., Harvey, E.S., Newman, S.J. (2012). Bait effects in sampling coral reef fish assemblages with stereo-BRUVs. *PLoS ONE* **7**: e41538-e41545. DOI: 10.1371/journal.pone.0041538

Dudley, S.F. (1997). A comparison of the shark control programs of New South Wales and Queensland (Australia) and KwaZulu Natal (South Africa). *Ocean and Coastal Management* **34**: 1-27. DOI: 10.1016/S0964-5691(96)00061-0

Dudley, S.F., Simpfendorfer, C.A. (2006). Population of 14 shark species caught in the protective gillnets off Kwa-Zulu Natal beaches, South Africa, 1978-2003. *Marine and Freshwater Res.* **57**: 225-240. DOI: 10.1071/MF05156

Duffy, L., Olson, R., Lennert-Cody, C., Galvan-Magana, F., Bocanegra, N., Kuhnert, P. (2015). Foraging ecology of silky shark *Carcharhinus falciformis*, captured by tuna purse-seine fishery in the eastern Pacific Ocean. *Marine Biology* **162**: 571-593. doi: 10.1111/jfb.13241

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martinez, J., Musick, J.A., Soldo, A., Stevens, J.D., Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **180**: 459-482. DOI: 10.1002/aqc.975

Durban, J.W., Parson, K.M. (2006). Laser-metrics of free-ranging killer whales. *Marine Mammal Science* **22**: 735-743. DOI: 10.1111/j.1748-7692.2006.00068.x

Fennessy, S.T. (1994). Incidental capture of elasmobranchs by commercial prawn trawlers on the Tugela Bank, Natal, South Africa. *South African Journal of Marine Science* **14**: 287-296. DOI: <https://doi.org/10.2989/025776194784287094>

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* **13**: 1055-1071. DOI: 10.1111/j.1461-0248.2010.01489.x

Finger, J.S., Guttridge, T.L., Wilson, A.D., Gruber, S.H., Krause, J. (2018). Are some sharks more social than others? Short- and long-term consistencies in the social behaviour of juvenile lemon sharks. *Behavioural Ecology and Sociobiology* **72**(1) 17-27. DOI:10.1007/s00265-017-2431-0

Garcia, V.B., Lucifora, L.O., Myers, R.A. (2009). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Philosophical Transactions of the Royal Society of Biology* **275**: 83-89. DOI: <https://doi.org/10.1098/rspb.2007.1295>

Gore, M.A., Frey, P.H., Ormond, R.F., Allan, H., Gilkes, G. (2016). Use of photo-identification and mark-recapture methodology to assess basking shark (*Cetorhinus maximus*) populations. *PLoS ONE* **11**(3): e0150160. doi:10.1371/journal.pone.0150160

Guttridge, T.L., Gruber, S.H., Gledhill, K.S., Croft, D.P., Sims, D.W., Krause, J. (2009). Social preferences of juvenile lemon sharks, *Negaprion brevirostris*. *Animal Behaviour* **78**: 543-548. doi: 10.1016/j.anbehav.2009.06.009

Holmberg, J., Norman, B., Arzoumanian, Z. (2009). Estimating population size, structure, and residency time for whale sharks *Rhinocodon typus* through collaborative photo-identification. *Endangered Species Res* **7**: 39-53. DOI: 10.3354/esr00186

International Commission for the Conservation of Atlantic Tunas. (2019). Report of the 2019 ICCAT Shortfin Mako Shark Stock Assessment Update Meeting. (ICCAT)

IOTC (Indian Ocean Tuna Commission) (2005). Information on shark finning fisheries. IOTC-2005-S9-08[EN]. IOTC, Victoria, Seychelles

Jacoby, D.M., Sims, D.W., Croft, D.P. (2012). The effect of familiarity on aggregation and social behaviour in juvenile small spotted catsharks (*Scyliorhinus canicular*). *Journal of Fish Biology* **81**: 1596-1610. DOI: <https://doi.org/10.1111/j.1095-8649.2012.03420.x>

Jeffreys, G.L., Rowat, D., Marshall, H., Brooks, K. (2012). The development of robust morphometric indices from accurate and precise measurements of free-swimming whale sharks using laser photogrammetry. *Journal of the Marine Biological Association of the United Kingdom* **92**(2): 309-320. DOI:10.1017/S0025315412001312

Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., Tobin, A., Moloney, J., 2011. Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. *Marine & Freshwater Research* **62**: 658–667. DOI: 10.1071/MF10136

Laer, K.O., Whitney, N.M., Morris, J.J., Geiss, A.C. (2021). Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. *Proceedings in Royal Society Publishing* **288**: 1-8. DOI: <https://doi.org/10.1098/rspb.2021.0816>

Letessier, T.B., Bouchet, P.J., Meeuwig, J.J. (2015). Sampling mobile oceanic fishes and sharks: implications for fisheries and conservation planning. *Biological Reviews* **92**(2): 627-646. DOI: 10.1111/brv.12246

Leurs, G., O’Connel, C.P., Andreotti, S., Rutzen, M., Von Noordegraaf, H. (2015). Risks and advantages of using surface laser photogrammetry on free-ranging marine organisms: a case study on white sharks *Carcharodon carcharias*. *Journal of Fish Biology* **86**(6): 1713-1728. DOI: 10.1111/jfb.12678

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akcakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S.N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* **22**: 1424-1442. DOI: 10.1111/j.1523-1739.2008.01044.x.

McAuley, R.B., Simpfendorfer, C.A., Wright, I.W. (2007). Gillnet mesh selectivity of the sandbar shark (*Carcharhinus plumbeus*): implications for fisheries management. *ICES Journal of Marine Science* **64**: 1702-1709. DOI: <https://doi.org/10.1093/icesjms/fsm136>

McClenachan, L., Cooper, A.B., Dulvy, N.K. (2016). Rethinking trade-driven extinction risk in marine and terrestrial megafauna. *Current Biology* **26**: 1640-1646. DOI: <https://doi.org/10.1016/j.cub.2016.05.026>Munroe, S.E., Simpfendorfer, C.A., Heupel, M.R. (2013). Defining shark ecological specialisation: concepts, context, and examples. *Reviews in Fish Biology and Fisheries* **24**: 317-331. doi: 10.1007/s11160-013-9333-7

Okada, S., Taniguchi, A. (1974). Size relationship between salmon juveniles in inshore waters and their prey animals. *Bulletin Faculty Fisheries* **22**: 30-36. doi: 10.1577/T08-244.1

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.M., Marshall, A.D., Pollow, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J.S., Kindsvater, H.K., Dulvy, N.K. (2019). Half a century of global decline in oceanic sharks and rays. *Nature* **589**: 567 – 575. DOI: <https://doi.org/10.1038/s41586-020-03173-9>

Paez-Rosas, D., Auriolles-Gamboa, D., Alva, J., Palacios, D. (2012). Stable isotopes indicate differing foraging strategies in two sympatric otariids of the Galapagos Islands. *Journal of Experimental Marine Biology and Ecology* **425**: 44-52. DOI: 10.1016/j.jembe.2021.05.001

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution* **10**: 430-441. doi: 10.1016/s0169-5347(00)89171-5

Pondella, D.J., Allen, L.G. (2008). The decline and recovery of four predatory fishes from the Southern California Bight. *Marine Biology* **154**: 307-313. DOI: <https://doi.org/10.1007/s00227-008-0924-0>

Reid, D.D., Krogh, M. (1992). Assessment of catches from protective shark meshing off New South Wales beaches between 1950 and 1990. *Australian Journal of Marine and Freshwater Research* **43**: 283-296. DOI: <https://doi.org/10.1071/MF9920283>

Robbins, W.D., Hizano, M., Connolly, S.R., Choat, J.H. (2006). Ongoing collapse of coral-reef shark populations. *Current Biology* **16**: 2314-2319. doi: 10.1016/j.cub.2006.09.044

Roff, G., Brown, C.J., Priest, M.A., Mumby, P.J. (2018). Decline in coastal apex shark populations over the past half century. *Community Biology* **1**(223): 1-11. DOI: <https://doi.org/10.1038/s42003-018-0233-1>

Santana-Garcon, J., Braccini, M., Langlois, T.J., Newman, S.J., McAuley, R.B., Harvey, E.S. (2014). Calibration of pelagic stereo-BRUVs and scientific longline surveys for sampling sharks. *Methods in Ecology and Evolution* **5**(8): 824-833. DOI: <https://doi.org/10.1111/2041-210X.12216>

Rohner, C.A., Richardson, A.J., Marshall, A.D., Weeks, S.J., Pierce, S.J. (2011). How large is the world's largest fish? Measuring whale sharks *Rhincodon typus* with laser photogrammetry. *Journal of Fish Biology* **78**: 378-385. DOI: 10.1111/j.1095-8649.2010.02861.x.

Webster, T., Dawson, S., Slooten, E. (2010). A simple laser photogrammetry technique for measuring Hector's dolphins (*Cephalorhynchus hectori*) in the field. *Marine Mammal Science* **26**: 296-308. DOI: <https://doi.org/10.1111/j.1748-7692.2009.00326.x>

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A. (2000). The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476-494. DOI: <https://doi.org/10.1006/jmsc.2000.0724>

Torres, A., Abril, A.M., Clua, E.E. (2020). A time extended (24h) Baited Remote Underwater Video (BRUV) for monitoring pelagic and nocturnal marine species. *Journal of Marine Science & Engineering* **8**: 2-8. DOI:10.3390/jmse8030208

Water, S., Whitehead, H. (1990). Population and growth parameters of Galapagos sperm whales estimated from length distributions. *Rep. Int. Whaling Community* **40**: 225-235.

Wetherbee, B.M., Cortes, E. (2004). Food consumption and feeding habits. *Biology of Sharks and Their Relatives* 223-244. doi:10.1201/b11867-11

White, J., Simpfendorfer, C.A., Heupel, M.R. (2013). Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology* **448**: 281-288. DOI: <https://doi.org/10.1016/j.jembe.2013.08.004>

Yunkai, L., Gong, Y., Xinjun, C., Xiajie, D., Jiangfeng, Z. (2014). Trophic ecology of sharks in the mid-east Pacific Ocean inferred from stable isotopes. *Journal of Ocean University of China* 13: 278-282. DOI: 10.1007/s11802-014-2071-1

Behavioural Ethograms & Social Hierarchy of *Carharhinus limbatus* (blacktip) During a Simulated-feeding Scenario within a South African MPA

Candice-Jade Parkes¹, Sara Andreotti², Ester Serrao³

¹*University of Algarve, Faculty of Science and Technology, Gambelas 8005-139, Faro, Portugal*

²*Evolutionary Genomics Group, Department of Botany and Zoology, Private Bag XI, Stellenbosch University, Stellenbosch 7600, South Africa*

³*CCMAR — CIMAR Laboratório Associado, Univ. Algarve, Gambelas, 8005-139, Faro, Portugal*

Email: candicejade@parkesbdtc.com

Keywords: ethogram, sharks, hierarchy, behaviour, social

Introduction

Shark conservation has become a topic of growing public interest as the global rise in fishing pressures has led to nearly 90% decline in fish populations, with elasmobranchs populations being one of the groups most affected (Stevens et al 2000; Myers & Worm 2003; Paez-Rosas et al 2018). Of the 400 known shark species, 117 of these reside in South African waters representing all major families (Ebert et al. 2021). Elasmobranchs are a highly charismatic group of organisms, accounting for more than 1 000 species of sharks and rays dating back 400 million years during the Palaeozoic Era (Das & Afonso 2017). Some are considered key marine predators playing a crucial role in preventing trophic cascades through their role as top or meso-predatory species (Myers et al 2007; Baum & Worm, 2009; Heithaus et al. 2012; Das & Afonso 2017). Also, due to their role in maintaining ecological balance and ecosystem health (Pace et al. 1999, Das & Afonso 2017), elasmobranchs can be used as bio-indicators to assess the health state of the oceans (Stevens et al. 2000; Bansemer & Bennett 2010). Despite recent efforts for increasing the protection status of some elasmobranch species, through legislation and more sustainable fishing practices, a recent study published in journal Nature reveals that since 1970, ‘global abundance of oceanic sharks and rays has declined by 71% owing to an 18-fold increase in relative fishing pressure’ (Pacoureaux et al. 2019).

Social Behaviours & Inter-specific Niche Partitioning

Recent and growing evidence supports the idea that some shark species form structured social networks during which they partake in complex social behaviours (Guttridge et al. 2009, Jacoby et al. 2010, Mourier et al. 2012, Findlay et al. 2015), however, there is still little existing literature on feeding habits and social interactions within species-specific group aggregations. During various times of the year different species will migrate, interact and forage together resulting in polyspecific associations. Au (1991) suggested that the primary reason for these associations is the search for food amongst sharks as abundance and distribution are primarily determined by food availability amongst others (Compagno et al. 2005; Klarian et al. 2018; Paez-Rosas et al. 2018). Aggregations have been observed in both solitary and social species and is usually a result of individuals being attracted to a common resource or due to synchronised patterns of daily or seasonal activities (Schilds et al. 2019). *Carcharodon carcharias* (white sharks) have shown non-random associations and observed sex-dependant co-occurrence variations are linked to intraspecific competition for resource (Schilds et al. 2019). In several species like *Carcharodon carcharias*, *Carcharhinus plumbeus*, and

Carcharhinus limbatus aggregative behaviours has been underpinned by temporal changes such as higher water temperatures and is considered the primary driver (Schilds et al. 2019, Cattano et al. 2020). Other drivers of aggregated movement include seasonal changes such as photoperiod, or biotic factors such as seasonal prey availability (Kaijura et al. 2016) Whilst most sharks have been perceived as solitary, recent studies have shown many species to exhibit both aggregation and social groupings (Clue et al. 2013, Bouveroux et al. 2021). In general, sharks tend to aggregate into groups of similarities in size (for protection against larger predators), age (for predatory reasons as a result of ontogenetic diet shifts) and sex (for breeding purposes) It has been suggested that often a greater extent of diet overlap occurs between different species of similar sized individuals compared to same species with different sized individuals (Bax 1998). This is a result of ontogenetic shifts in habitat use and diet preferences (Wetherbee & Cortes 2004; Guttridge et al; 2009). As predators grow, so their gape and speed increases allowing an increase in range size of available prey to hunt and consume (Okada & Taniguchi 1974; Armstrong 1982; Bax 1998). Due to the elusive behaviour of most elasmobranchs, social behaviours are rarely studied, however grouping is known to be a common phenomenon (Bass et al 2016, Pini-Fitzsimmons et al 2021). As a result of this aggregative behaviour of shark species whilst feeding on a common prey source, an establishment of social hierarchies is often observed. In 1974, Myrberg & Gruber studied the behaviour of bonnethead sharks, *Sphyrna tiburo*, under semi-natural conditions, to investigate the organizational patterns within the social structure of the colony. It was found that the bonnetheads showed a clear, yet subtle social organization and dominance hierarchy based on ‘straight-line and size-dependent influences. In recent years, there has been some discrepancies amongst studies focusing on social behaviours of sharks, and this particular field still remains majorly unexplored, especially in uncontrolled environments. In 2018, Finger et al. investigated the role of individual personalities in the social behaviour of wild juvenile lemon sharks (*Negaprion brevirostris*) in Bimini, USA. The results suggested reduced plasticity and highlights individuality as a key explanatory variable influencing the social dynamics of the juvenile lemon sharks. Expanding such research to wild populations would help determine the importance and role of individual personalities to sharks’ interactions and social organization patterns. Juvenile lemon sharks have also shown to preferentially group based on body size, with larger individuals showing stronger dominance tendencies compared to smaller sharks (Guttridge et al. 2011). The nature of these social interactions is dynamic across space and time, because the observed individuals can grow, increase their experience and thus change their position within a group, ultimately altering group composition and context (Sih et al 2009,

Pini-Fitzsimmons et al 2021). Grouping of elasmobranchs is often based on both social congregation (i.e., reproduction; e.g. *Carcharias taurus* & *Heterodontus portusjacksonii* & *Scylorhinus canicula*) (Bass et al. 2016; Furst 2011) and non-social aggregations (ie. attraction to limited resources, e.g. *Carcharodon carcharias* & *Galeocerdo cuvier* & *Carcharhinus limbatus*) (Sims et al. 2000; Clua et al 2013; Pini-Fitzsimmons et al 2021). The use of social network analysis has become beneficial in analysing social behaviours of elasmobranchs: for example, it has been used to determine the impact of captive male behaviour on females of differential social status in sexually segregating benthic sharks (Jacoby et al. 2010; Jacoby et al. 2012) and to quantify the interactions in juvenile *N. brevirostris* using their body length and potential relatedness, to show non-random assortment of individuals (Guttridge et al. 2011).

Within Aliwal Shoal MPA, *Carcharhinus limbatus* (blacktip), *Carcharhinus leucas* (bull), and *Galeocerdo cuvier* (tiger) sharks are found throughout the same general area all year round, thus suggesting a certain degree of spatial overlap. Interference competition may be a considerable driver in the activity patterns and behaviours of the blacktip due to their smaller size (Plumlee & Wells 2016). Whilst adults do not have common natural predators, like most *Carcharhinid* sharks, juveniles are susceptible to predation by other larger sharks. Laer et al. (2021) also suggested that blacktips, due to their small size, may reduce their activity during peak activity times of higher order predators. This allows competitors of lower trophic levels to decrease their probability of being detected by a predator during those times. As a result of slightly different microhabitats used for foraging and refuging, temporal partitioning results in spatial separation of lower order trophic competitors allowing them to avoid dominant species. Blacktips have been found to show plasticity in their diel rhythms of feeding, which changes in response to the presence of predator, prey, or competitor species (Laer et al. 2012). This may be a key mechanism in allowing the species to succeed in a variety of environments, and also acts as a stronger buffer to environmental impacts, compared to that of shark species with stricter diel patterns (Laer et al 2021). However, it has been noted by Polis (1984) that selectivity of predation deserves proportional attention with size being the most obvious factor for selection basis (Bax 1998) stating that “different size classes of a species exploit different sizes and species of prey, allowing different size classes to use different ecological niches”. It has been suggested that often a greater extent of diet overlap occurs between different species of similar sized individuals compared to same species with different sized individuals (Bax 1998). This is a result of ontogenetic shifts in habitat use and diet preferences (Wetherbee & Cortes 2004; Guttridge et al. 2009). As predators grow, so their gape and speed increases

allowing an increase in range size of available prey to hunt and consume (Okada & Taniguchi 1974; Armstrong 1982; Bax 1998). Feeding occurs in short bursts which is followed by a longer period needed for digestion if feeding is reduced (Wetherbee & Cortes 2004). Most consumed prey are teleost's and according to Budker (1971), sharks consume approximately 3-14% of their body weight per week, on average. This value varies depending on species.

Study Species

Carcharhinus limbatus (blacktips) are considered meso- predators and are a cosmopolitan species found throughout tropical and subtropical waters, primarily in waters shallower than 30 m depth with favoured habitats being drop-offs near coral reefs, island lagoons and muddy bays. Prevalent along the eastern coast of the southern African coastline (Dudley & Cliff 1993, Almojil et al. 2018), they are a common sighting on baited-shark dives and along the reef systems in the area (Almojil et al. 2018). They are characterized by their black-tipped pectoral, dorsal and tail fins with a robust, stream-lined body and long pointed snout (Ritter et al. 2000, Huber et al. 2006, Motta et al, 2012). Their maximum reported lengths are 2500 mm, whilst males reach maturity at approximately 1400 mm and females at approximately 1500 mm (Robins & Ray 1986). They are viviparous, giving birth to 4 to 11 pups every two years (Castro 1996, Keeney et al. 2005, Tavares 2008). Pups are birthed in shallow-water nurseries and usually aggregate during early years to protect themselves against predation (Castro 1996, Keeney et al. 2005). Blacktips often travel in groups, and can display fast movements during feeding (Dudley & Cliff 1996). They are primarily piscivorous feeding only pelagic and demersal bony fish (*Osteichthyes*) including Spanish mackerel (*Scomberomorus maculatus*), grunter (*Pomadasys commersonnii*), sea bream (*Sparus aurata*), kob (*Kobus kob*), ladyfish (*Elops saurus*) and sole (*Solea solea*), also small sharks and rays (*Chondrichthyes*), cuttlefish (*Sepiida*), and rock lobsters (*Palinuridae*) (Compagno, Ebert & Smale 1989). Dudley & Cliff (1993) found that the most important prey species were from the jack and herring families after examining the stomach contents from 1836 black tip sharks caught by the gillnets in South Africa between 1978 to 1991.

Shark Social Behaviours

In recent years there has been growing awareness of the importance of understanding pelagic social behaviours, such as that of sharks, in order to promote conservation measures and raise awareness. Behavioural ethograms have become a common tool in assessing social hierarchies and understanding the importance of individuals roles and positions within these organisations. Whilst resource partitioning is commonly observed, more studies have recently focused on the understanding of the social behaviours of marine organisms. In 1974, Myrberg & Gruber published a study focusing on the behaviour of bonnethead sharks (*Sphyrna tiburo*) in order to provide a detailed ethogram of the species-typical motor patterns, provide insight into factors underlying these patterns and to determine whether these sharks possess any type of social structure. They found that most movement patterns were in relation to intervening variables such as aggression, flight, food deprivation, maintenance, or courtship. Allee & Dickinson (1954) provided a quantitative study on the avoidance responses of 10 smooth dogfish (*Mustelus canis*). Their findings included evidence that smaller individuals avoided larger individuals if there was a clear difference in size. Historically, sharks have generally been considered solitary, however, growing findings suggest that sharks may interact more than previously thought. For example, sickle fin lemon sharks (*Negaprion acutidens*) are considered solitary predators, however, are known to interact with other individuals occasionally during periods of mating, foraging, defence or during their juvenile development stage (Brena et al. 2018). It has become evident that social groupings of elasmobranchs are common (e.g., Bass et al. 2016) as well as complex social behaviours (Sims et al. 2000, Furst 2011, Papastamatiou et al. 2020, Pini-Fitzsimmons et al. 2021). However, formal assessments of elasmobranch behaviours are still in its infancy and is often further hindered by the elusiveness of the species (Jacoby et al. 2011, Pini-Fitzsimmons et al. 2021). The provisioning of elasmobranchs through acts of eco-tourism, such as baited-shark dives, can be used as an affordable tractable avenue to study sociality in various species (Newsome et al. 2004, Sperone et al. 2010, Pini-Fitzsimmons et al. 2021). In previous research it has been suggested that size may be the most influential factor when assessing an individual's position within a hierarchy (De Vries et al. 2006, Sims et al. 2000, Brena et al. 2018, Pini-Fitzsimmons et al. 2021). Commonly observed behaviours include 'gaping', 'tail slap', 'parading', 'biting', 'parallel swimming', 'avoid' and 'give way' to name a few (Sperone et al. 2012, Brena et al. 2018). When applying previously defined ethograms to current studies, it is necessary that ethograms are adapted to the study species as not all species of elasmobranchs display the same types of behavioural units.

Objectives

This research paper will provide preliminary data for future research and aimsto investigate the social hierarchy within a subsample of *Carcharhinus limbatus* (blacktip) during a simulated feeding scenario in Aliwal Shoal Marine Protected Area, South Africa. Specific research objectives are : i) identify behavioural units based on existing literature and post-examination of underwater videos taken during sampling; ii) Assess the influence of size of individuals on the position of the individual within the hierarchy; iii) Assess the influence of number of blacktips in an aggregation against another species such as *Galeocerdo cuvier* or *Carcharhinus leucas*.

Research Methodology

Study Site

The Aliwal Shoal Marine Protected Area (30°15'S 31°00'E) lies 45 kilometres south of Durban (South Africa), alongside the town of Umkomaas (30.2007° S, 30.7838° E), in the West Indian Ocean. This MPA can be described as a marginal environment, acting as a host to fauna of tropical, subtropical and warm-temperate reefs. Benthic communities are comparable to hard coral diversity found in high-latitude reefs such as Australia (Olbers et al. 2008). The climate of the Kwa-Zulu Natal coastline is subtropical and humid (Boucher 1975, Olbers et al 2009) with summer rainfall. This results in a large amount of terrestrial and freshwater runoff into the sea. The average water temperature ranges between 16 -24 °C. Common sightings on SCUBA include sharks, dolphins, turtles and an array of reef species. The Protected Area encompasses a total area of 670km², extending for approximately 18.3km along the coastline between the Umkomaas and Mzimayi river mouths, and 7km out to sea. To reduce conflict between users and various stakeholders, the MPA was zoned into two Restricted Zones and one Controlled Zone allowing recreational activities to take place whilst still maintaining the primary objective of conservation and protection of threatened ecosystems. The Restricted Zone comprise the Produce Restricted Zone and the Crown Area Restricted Zone. The remainder of the MPA is represented by the Controlled Zone. The offshore reef system ranges from depths 5 m to 28 m and prevailing wind and current directions determine the length and direction of drift-dives. The area is renowned for its rich marine biodiversity, supporting large predatory sharks such as blacktip sharks (*Carcharhinus limbatus*) and a variety of other shark species are commonly encountered including tiger sharks *Galeocerdo cuvier*, and zambezi *Carcharhinus leucas*.

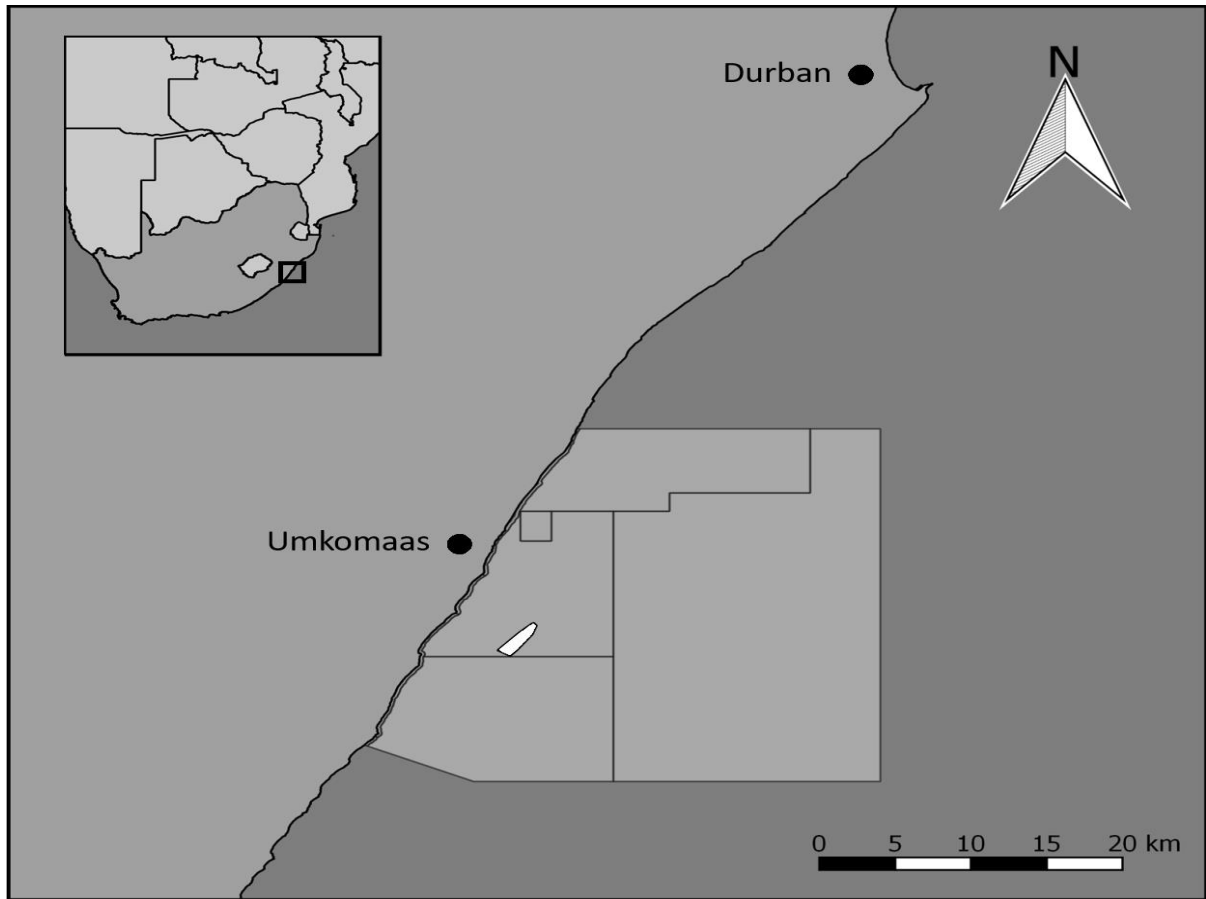


Figure 1. Map showing the Aliwal Shoal MPA on the south coast of Kwa-Zulu Natal, South Africa

Data Collection

Data were collected between March 2021 and July 2021, during isolated baited-shark dives in the absence of other dive operators, to reduce the influence of human presences on the shark behaviour as suggested by Smith et al. (2010), Schlaff et al. (2014), and Richards et al. (2015). A total of four dives were conducted every week, and each dive lasted between 50 and 60 minutes. A simulated scavenging scenario, similar to Sperone et al. 2012, comprised the placement of two drums that enclosed natural fish chum composed of locally sourced sardines (*Sardinops sagas*). The number of sharks was recorded every 15 minutes, and the sex of the sharks encountered was determined by the presence (males) or absence (females) of claspers. The size of each individual shark was estimated by expert observer and, whenever feasible, also measured with laser photogrammetry. Data were recorded as total number of sightings per length class. GPS co-ordinates of dive location, wind speed and the time of bait deployment was also recorded. All dives were conducted in the same study site and interactions observed

between *Carcharhinus limbatus*, *Carcharhinus leucas* and *Galeocerdo cuvier* were found in the proximate area.

Photographic Identification

To identify individual sharks a non-invasive method of photographic identification was used. Following an opportunistic approach, images of the entire shark and the left-flank of the dorsal fin were captured to determine if the markings were unique enough to identify the different individuals. All photographs were taken with a Sony A6000 compact digital camera. The zoom function was not used, and photographs were taken at eye-level to the shark. When underwater, any prominent scars or features found on the shark's body were recorded to assist with the short-term identification of the individuals. Images were standardized using Adobe Photoshop with dimensions 18 cm x 20 cm at a resolution of 240 pixels. An adapted 'Matrix Photographic Identification method was used whereby a transparent 20 cm x 6 cm grid was overlaid onto each image and used to categorize three sections of the fin (Figure 2). Categorization was based on level of colouration, i.e., the amount of black pigmentation, individual markings, and notches, as used in identification for other marine species such as rays (Marshall & Pierce, 2019), turtles (Jean et al 2010) and penguins (Burghardt et al, 2007). Categorization of black pigmentation was classified into the following:

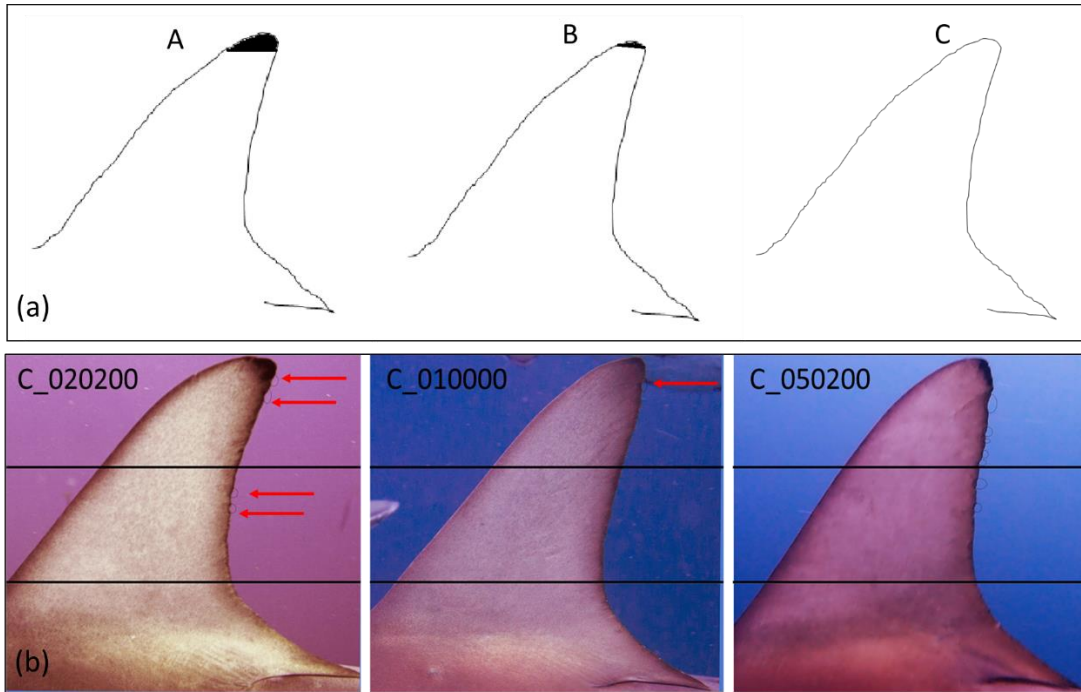





Figure 2. (a) Illustration showing level of pigmentation used to classify *Carcharhinus limbatus* individuals. A – 100% black pigmentation on the tip of the fin; B – 50-75% black pigmentation on the tip; C – Absence of black pigmentation on the fin (b) notches categorization (see also Table 1).

Photographs were assigned a unique code and loaded to the baseline database for Blacktip sharks in Aliwal Shoal MPA alongside date of capture and relevant re-sightings. This database can be used to determine whether individuals repeatedly occupy the area, or whether new individuals arrive into the group. This will form a baseline set of fin photographs to be used for future research. To allow simplification and time-efficiency of analysing new photographs, the classification system separates individuals based on their level of dorsal fin pigmentation (A: 75-100%, B: 50-75%, C: 0-50%). The photograph is then divided into three sections, after-which the number of notches (defined as an indentation or incision on the fin edge) in each section is manually counted. Once new photographs are uploaded, they are compared to the existing individuals of the database, hence why standardization of photographs is critical. It is critical to the success of the database of photo-ID to ensure accurate representations of individuals and understanding of population structures. Example of unique code or ‘fingerprint’ for individuals in each colouration category (Table 1.):

Table 1. Unique photo-id examples and explanations assigned to sharks

Unique Photo-ID Code	Explanation	Photograph
C_000101_A	<p>Section 1: 00 notches Section 2: 01 notch Section 3: 01 notch Colouration A: 100% black fin tip</p>	
C_020000_B	<p>Section 1: 02 notches Section 2: 00 notches Section 3: 00 notches Colouration B: 50-75% black fin tip</p>	
C_000401_C	<p>Section 1: 00 notches Section 2: 04 notches Section 3: 01 notch Colouration C: 0-49% black fin tip</p>	

Laser Photogrammetry

To attain accurate data for size estimation of the sampled sharks, a non-invasive identification method using laser photogrammetry was used before commencing the behavioural investigations. A laser photogrammetry system (20mW; Marine Design Engineering Ltd) was used to project two high-powered green laser dots onto the base of the dorsal fin of each shark, and an image of the two-green dots on the sharks was then recorded by a housed GoPro camera set at a linear angle, mounted on the laser. Lasers were calibrated daily before dives at varying distances (3, 5, 8 m from a target) to ensure accuracy of readings (Rohner et al. 2015). For this process, two markers were adhered to a wall at 30 cm apart, after which the researcher aimed the laser at a 45° angle to align the laser points to the marked points, then moved backwards at increased distances to ensure accurate collaboration. Laser points were set at 30 cm apart and used to extrapolate the total length of the individual sharks from the captured images (Figure 3). When underwater, laser is pointed at a 45° angle onto the shark as at eye-level the laser points will not be emitted for safety and protection of the eyes of both sharks and divers. A photograph suitable for photogrammetric analysis needed to have the shark at a perpendicular angle with the laser points clearly visible.

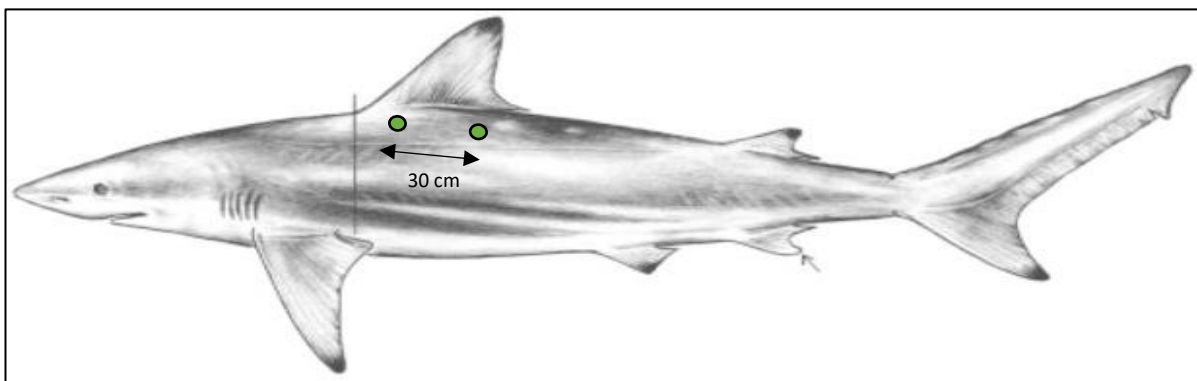
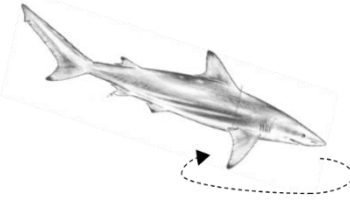
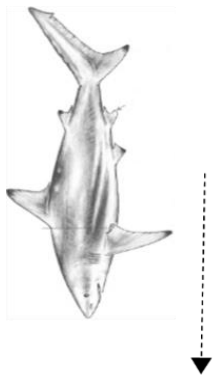

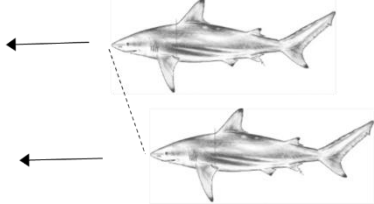
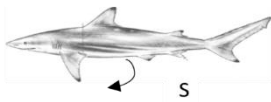
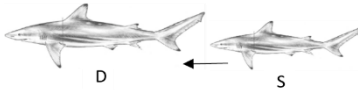
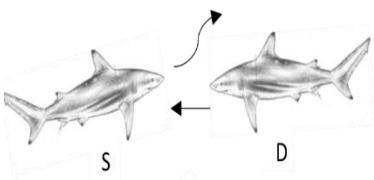
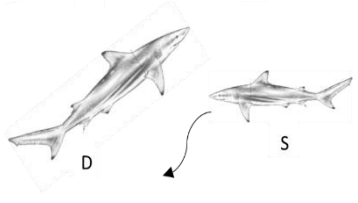
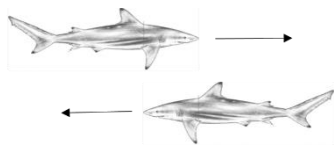



Figure 3. Diagram showing laser points 30 cm apart aimed at lower part of dorsal fin to be used for laser photogrammetry of sharks (Image source: Grace, 2001)

Behavioural Analysis

For the purpose of this study, the theory of using UVS as a sampling method was adapted to include the use of a bait-ball to attract the sharks into the area, after which a stabilised diver would start recording from approximately 5-10 m distance (depending on water visibility) using a GoPro Hero 7. This was decided since limitations arise when sampling larger pelagic animals as the sharks may alter the camera angle during feeding-frenzies or movement, or the camera angle may not be wide enough to observe a wide array of behaviours from a birds-eye-view. Behavioural units specific for blacktip sharks were defined based on existing studies on the following elasmobranch species: *Sphyrna tiburo* (Myrberg & Gruber 1974), *Carcharodon carcharias* (Sperone et al. 2012) and *Bathytoshia brevicaudata* (Pini-Fitzsimmons et al. 2021). Behavioural units were defined after reviewing video footage and identifying the most common interactions. The concept of bilaterally depressed pectoral fins, common in requiem shark species as a sign of agonism was omitted since such behaviour patterns may be considered a ‘pseudo-display’ in which the shark attempts to relieve irritations caused by remora (Echeneidae) (Martin 2007). Behaviours were analysed using software Behavioural Observation Research Interactive Software (BORIS) v.8.0.4. Behaviours were divided into four categories: (i). dominant interactions for example “fast turn”, “accelerated upward swim” and “accelerated downward swim”; (ii) semi-dominant interactions, where two individuals would “swim parallel”; (iii) neutral interactions where two individuals would “pass” each other or display “parading” whereby individual swims in a relatively straight-line; and (iv) submissive interactions where subordinate individual would “avoid” an interaction, “give-way” or “follow” a more dominant individual, subordinates also displayed “body tilts” to expose underside to dominant individuals as a sign of submissiveness. Behaviours were marked as point events. Defined behavioural units include:

Category	Behavioural Unit	Code	Description	Diagram
Dominant	Fast Turn	FT	Individual undergoes a 180° change in movement direction (vertically or horizontally), usually followed by accelerated downward or upward swim	
	Accelerated Downward Swim	DS	Individual accelerates in a downward direction of movement away from the bait ball	
	Accelerated Upward Swim	US	Individual accelerates in an upward direction movement towards the bait ball	
Semi-dominant	Parallel Swim	PS	Two individuals swim adjacently to each other after-which one individual may display dominant or submissive behaviours	

Submissive	Body Tilt	BT	Subordinate individual exposes underside of body	
Category	Behavioural Unit	Code	Description	Diagram
	Follow	FO	Subordinate follows on the tail of dominant individual	
	Give-way	GW	Subordinate gives way to dominant individual when encountering same plane of movement	
	Avoid	AV	Subordinate avoids contact with dominant individual by altering direction of swim	
Neutral	Passing	PS	two individuals of various sizes pass each other either swimming towards or away from the bait ball	
	Patrolling	PT	Individual swims in a straight-line motion towards or away from the bait ball, displaying neither dominant or submissive behaviour	

Statistical Analysis

All statistical analyses were performed using R Studio version 3.6.3. Behaviours were analysed in BORIS version 8.0.4.

To assess the influence of size of individuals in respect to their position in the social hierarchy a Shapiro-wilks test was used to normalize the data (Shapiro & Wilk 1965), so that any outliers could be removed from the dataset. Then, a method developed by Karl Pearson (1880) involved calculating a Kurtosis score to analyse the shape of the probability distribution, which was completed in Microsoft Excel. Finally, Spearman's rank (Charles Spearman) correlation of 'size of individual' versus 'behavioural units' was analysed and allowed significant results ($p < 0.05$) to be further examined.

To distinguish the individuals from one another all dorsal fin photographs were edited and examined using Adobe® Photoshop® (Thomas & Knoll 1988). Overall mean length standard deviation was calculated for *Carcharhinus limbatus*, five *Carcharhinus leucas*, and one *Galeocerdo leucas* individual. Lengths were estimated using laser photogrammetry and reported as mean standard deviation.

A GGplots (Wickham 2016) was used to represent the overall observed behavioural categories, and visually compare the behavioral differences between different sized individuals.

Finally, a correlation matrix was used to test the significance of the influence of number of individuals of blacktips compared to other species like the bull and tiger shark.

Results

A total of thirty-five dives were conducted over the 22 days during a 3-month period, however, only videos taken from 18 days could be used for analysis. The remaining data were discarded due to poor water visibility and inability to distinguish individuals during analysis. Bait chumming began on arrival at the study site and lasted 15-20 minutes before the first sharks were sighted and divers entered the water. Figure 4. shows the time once the bait ball was deployed $t(0)$ versus the total count of blacktip individuals during the dive duration over a 15-minute interval. Overall, the total sum of blacktip individuals counted over the sample period was 93 at $t(0)$, 121 at $t(1)$, 139 at $t(2)$, 157 at $t(3)$ and 151 at $t(4)$.

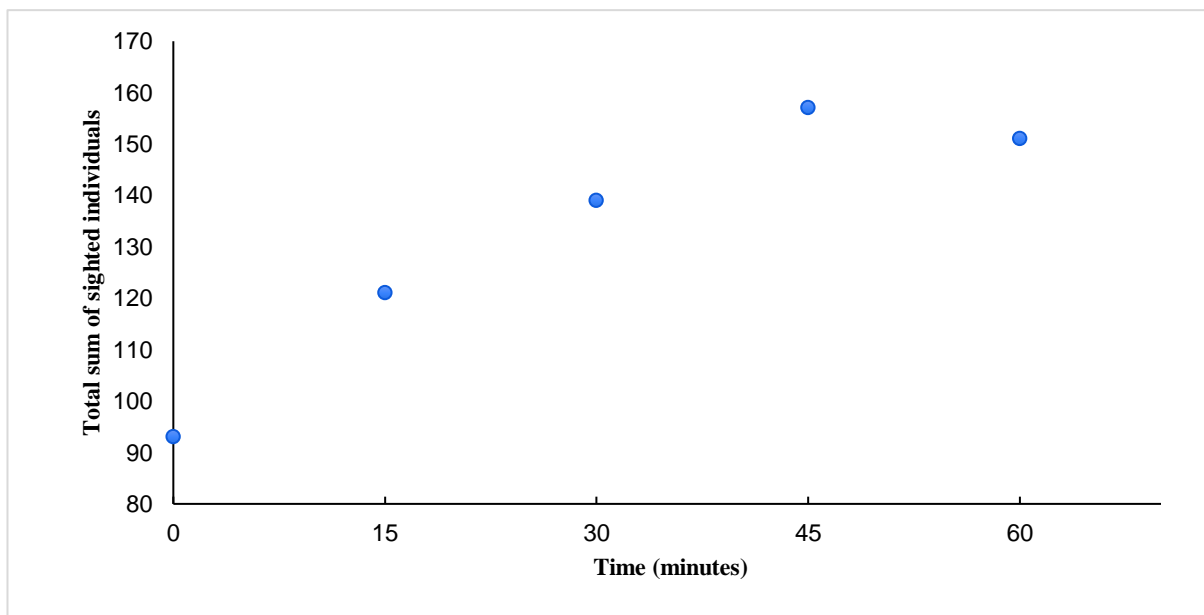


Figure 4. Total sum of sighted individuals observed at 15-minute intervals for dive duration

A total of 1014 individual behaviours were recorded. Dominant display of 'fast turn' was the highest recorded behaviour at 289 observations (29%), followed by submissive behaviour of 'avoid' with 188 observations (19%) (Table 2. & Figure 5.) In total there were 475 dominant displays, 32 semi-dominant, 331 submissive and 176 neutral displays.

Table 2. Total sum of each observed behavioural unit

Category	Behavioural Unit	Σ (total)
Dominant	Fast turn	289
	Upward Swim	80
	Downward Swim	106
Semi-Dominant	Parallel Swim	32
Submissive	Body Tilt	68
	Avoid	188
	Give way	54
	Follow	21
Neutral	Pass	154
	Patrol	22

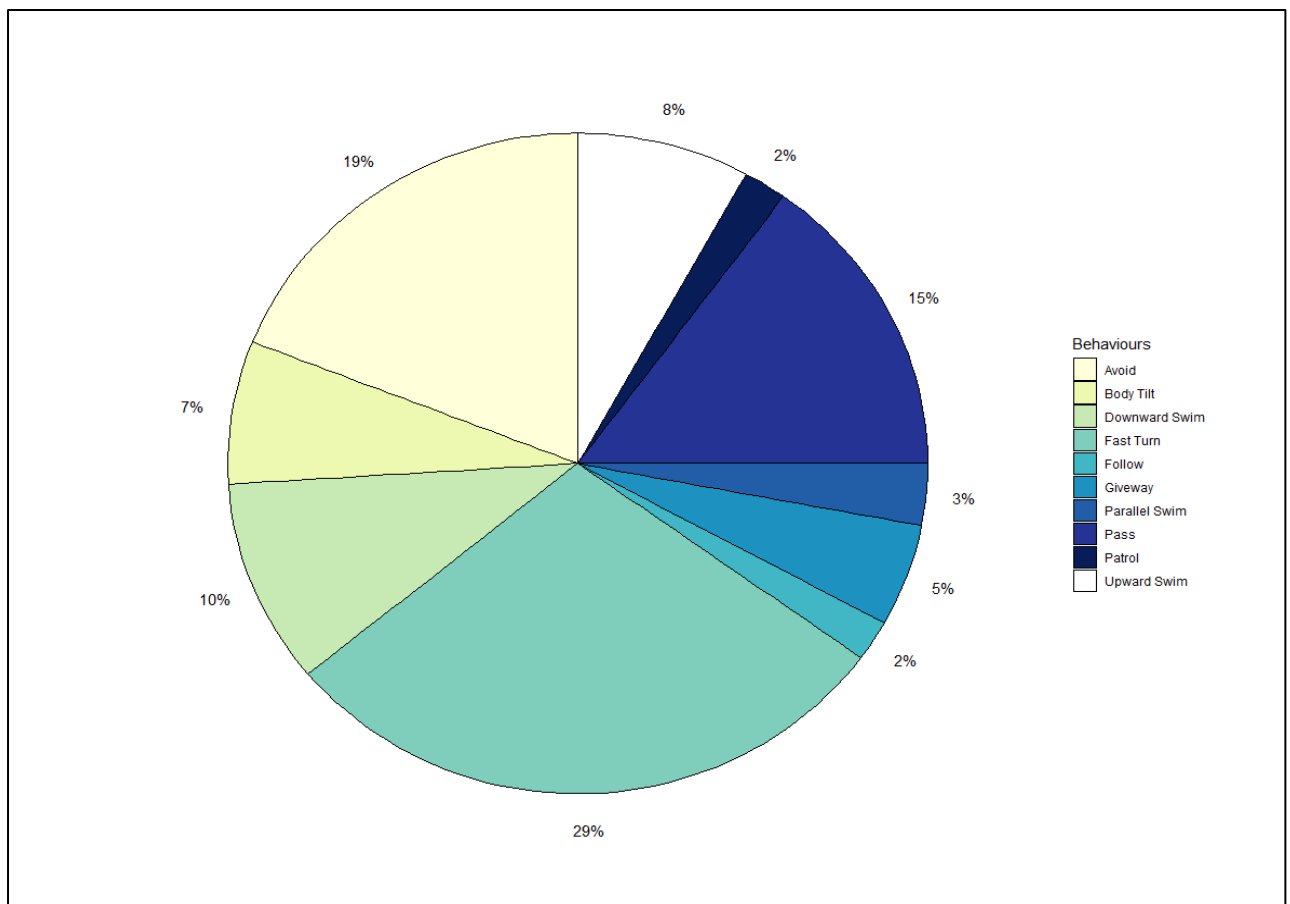


Figure 5. Percentage of each behavioural unit observed during the sample period, n=1014

Within the different behavioural categories, each behavioural unit was observed with a sequential ranking. In the dominant displays: ‘upward swim’ < ‘downward swim’ < ‘fast turn’; semi-dominant displays: ‘parallel swim’; submissive displays: ‘follow’ < ‘give way’ < ‘body tilt’ < ‘avoid’; and neutral displays: ‘patrol’ < ‘pass’ (Figure 6.)

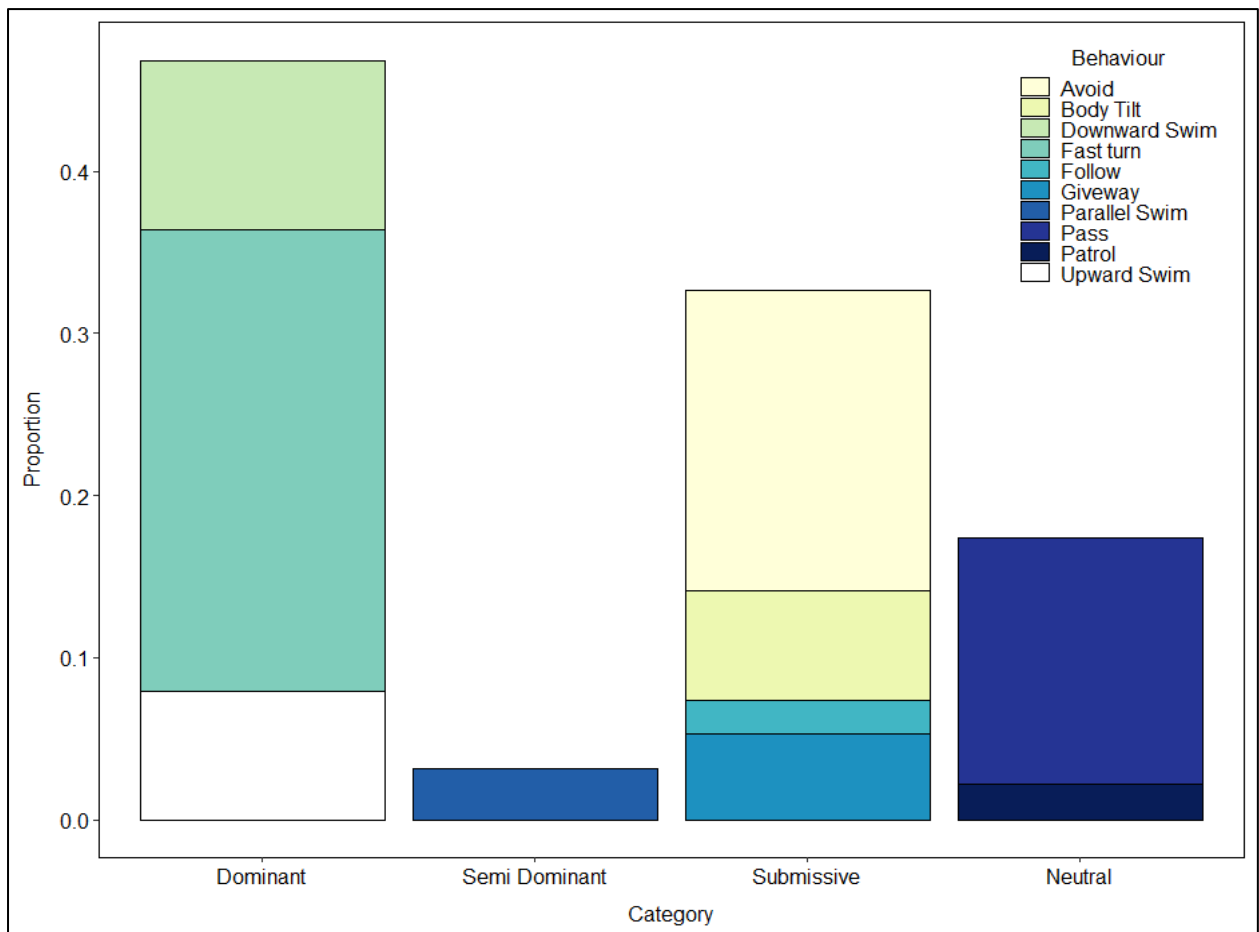


Figure 6. Total proportion of each behavioural unit within the behavioural category (dominant, semi-dominant, submissive, neutral)

Shapiro-Wilks test for normality showed no outliers and normal data, after which a Spearman’s rank correlation test was conducted which yielded 32 out of 110 significant interactions ($p < 0.05$) (Table 3.). Individuals were visually ranked on size (1=biggest, 4=smallest) and behaviours ranked based on level of dominance (1=neutral, 4=dominant) The correlation test suggested larger individuals to display for more dominant behaviour, whilst smaller individuals showed more submissive behaviours. On the 30th of March, the maximum number of significant data correlating ‘size of individual’ to ‘behavioural units’ were recorded. An overall correlation test between ‘number of recorded behaviours and ‘r’ showed a significant relationship ($p < 0.05$) and a moderately strong positive relationship

(rho= 0.731). Observing more behaviours leads to stronger correlation significance between ‘size’ and ‘dominance’.

Table 3. Number of recorded behaviours, spearman's correlation coefficient & significance level of correlation

Date	No. Recorded Behaviours	r	p-value
04/03/2021	31	0.514	0.003
	27	0.461	0.016
11/03/2021	15	0.531	0.042
	13	0.566	0.044
	9	0.653	0.057
	9	0.68	0.044
	20	0.529	0.016
	19	0.587	0.008
17/03/2021	9	0.661	0.052
	4	0.986	0.013
27/03/2021	11	0.891	0.000
	7	0.766	0.044
	7	0.842	0.018
30/03/2021	6	1.00	< 0.05
	5	1	< 0.05
	10	0.837	0.003
	11	0.818	0.002
	7	0.842	0.018
	9	0.777	0.014
	11	0.706	0.015
	23	0.640	0.001
8	0.707	0.049	
06/04/2021	19	0.476	0.039
	12	0.810	0.001
	17	0.676	0.003
	13	0.828	0.000
	20	0.453	0.045

28/04/2021	12	0.802	0.002
	13	0.585	0.035
	10	0.618	0.057
	10	0.653	0.041
	12	0.869	0.000

Visual representation of sized sharks versus number of recorded behaviours showed ‘Shark 1’ (largest individual) displaying the most dominant displays and one semi-dominant, whilst ‘Shark 2’ (smallest individual) showed the least displays of dominance and the most submissive behaviours (Figure 7.) This graph was repeated for all individual observations as inability to recognize individuals across recordings lead to inconsistency when correlating individuals with their sizes and behaviours.

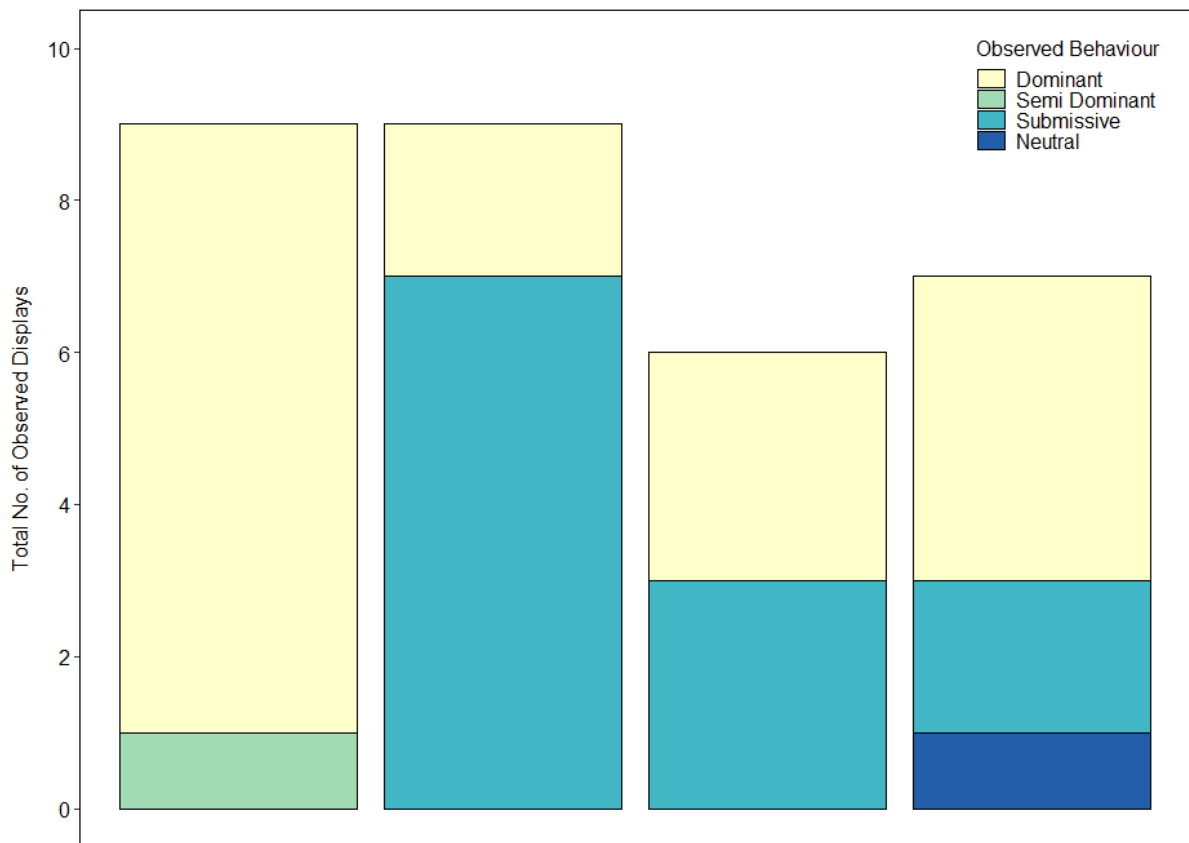


Figure 7. Total number of observed behaviours for each individual shark within a unique video analysis (Shark 1=biggest, Shark 2=smallest)

Overall, group composition remained relatively constant throughout the study period. Ten individuals were successfully identified using fin photographs (Annex 1). Over the sample period, 34 individual blacktips were successfully measured using laser photogrammetry with an overall mean length of 146.3 cm \pm 3.088 confidence interval [40.00; 152.598] and ranged from 115 to 180 cm (Table 4). Kurtosis score of -0.946 was calculated. Aggregations were dominated by females, and only 3 males were sighted during the study period. The length of the 3 observed males were: 136.1, 137.1 and 138.7 cm respectively, falling just below the average length of the females in the group.

5 bull sharks were successfully measured with the laser photogrammetry and had an average length of 173.52 cm \pm 9.856 and total lengths ranged from 160 to 200 cm [CI: 146.156; 200.884]. A kurtosis score of -2.171 was calculated.

Table 4. Total number of sighted individuals, mean and std.deviation in each total length class (cm)

Total length (cm)	No. of sighted individuals (n)	\bar{X} (cm)	σ	No. of Males Present
< 119	3	117.1	1.45	0
120 - 129	3	125.2	1.71	0
130 - 139	7	135.9	3.03	2
140 - 149	7	146.5	3.48	1
150 - 159	4	156.9	1.72	0
160 - 169	6	164.6	3.16	0
170 - 179	4	174.1	2.27	0
Total	34	146.3	17.47	0

An average of 5.458 \pm 1.645 shark sightings were encountered per day. The lowest recorded counts of blacktips during a simulated feeding scenario were when either bull sharks or tiger sharks were present on the dives (Table 5). The correlation between number of blacktips vs number of bull sharks of -0.54 was significant ($p < 0.05$). The correlation between number of blacktips and number of tiger sharks was -0.53 and tested significant (< 0.05).

Table 5. Number of sighted *Carcharhinus limbatus* individuals compared to number of sighted other species (*Carcharhinus leucas* & *Galeocerdo cuvier*)

Date	Number of sighted <i>Carcharhinus limbatus</i>	Number of sighted other species
09/03/2021	2	2 <i>Carcharhinus leucas</i>
10/03/2021	6	1 <i>Galeocerdo cuvier</i>
11/03/2021	4	3 <i>Carcharhinus leucas</i>
18/03/2021	4	2 <i>Galeocerdo cuvier</i>
19/03/2021	4	1 <i>Galeocerdo cuvier</i>
14/04/2021	1	6 <i>Carcharhinus leucas</i>

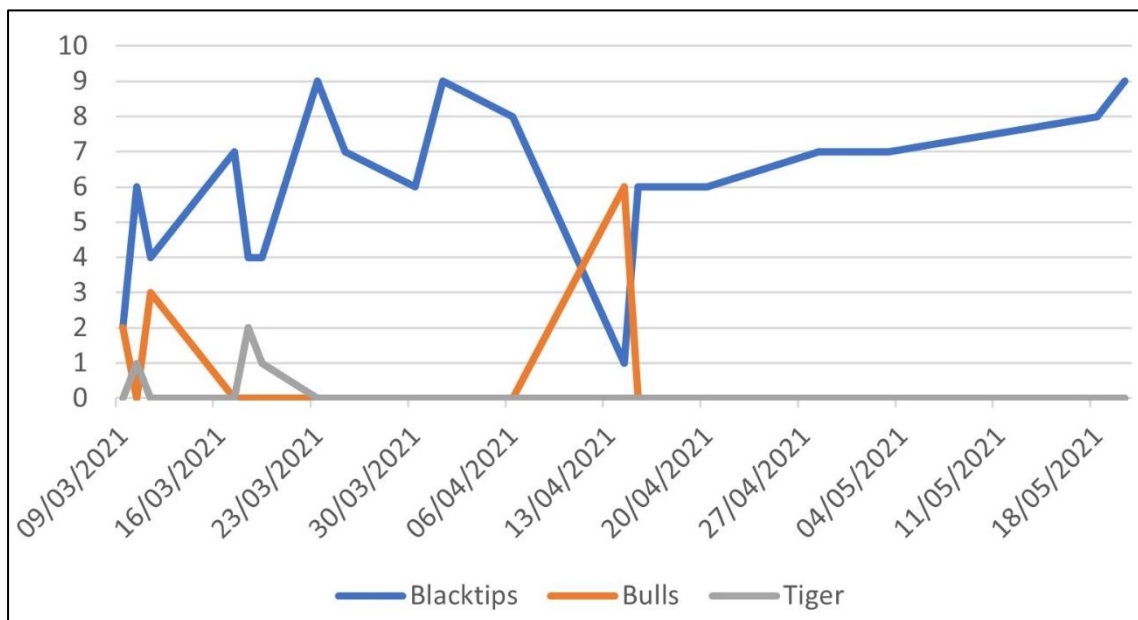


Figure 8. Number of *Carcharhinus limbatus* (blacktips) counted under the presence of *Carcharhinus leucas* (bull) or *Galeocerdo cuvier* (tiger) during sampling duration

One individual, Broken Tail, was named the centralized dominant female of the group. She was present on the maximum number of dives (87.5%) and spent a sizable portion of time in proximity with the bait ball (Figure 8.). She was one of the largest individuals recorded, with a total estimated length of 176 cm. Of the 475 dominant displays observed, Broken Tail accounted for 158 (33%).



Figure 9. Unique fin-id and full-length image of identified dominant individual named 'Broken Tail'

During the beginning of the sample period, an individual female *Galeocerdo cuvier* (\pm 204 cm) was encountered. In this particular scenario, the tiger shark came into the view of the bait ball and surrounded by four blacktips, retained dominance over the feeding scenario by displaying dominant behaviours of 'fast turn' and 'biting' (Figure 9 and Annex 1).



Figure 10. Sequence of events following interaction between *Galeocerdo cuvier* and smaller *Carcharhinus limbatus*. *Galeocerdo cuvier* displays 'fast turn' followed by 'biting' displaying dominance within the feeding scenario

Discussion

During this study, simulated feeding scenarios were used to quantify the social hierarchy and behavioural ethograms displayed in sub-adult to adult *Carcharhinus limbatus* individuals. This study served as preliminary data for future research on the species within South Africa. In addition, this study sought to determine the influence of size on the position of the individual within the hierarchy. Whilst most behavioural studies focus on small coastal species (Guttridge et al. 2009, Mourier et al. 2012, Findlay et al. 2016), there has been growing research into the use of larger pelagic sharks such as white sharks as a model organism (Findlay et al. 2016). Larger studied pelagic sharks tend to be solitary in nature, however, here we use *Carcharhinus limbatus*, a group of sharks known to congregate and tend to form feeding frenzies thereby exhibiting social patterns within coastal environments.

Environmental Variables & Size

Average wind over the sample period was ten knots ranging over a South-West to North-easterly direction. North-easterly winds dominate in Kwa-Zulu Natal over the Spring and Summer, whilst Southerly winds dominate during Winter and Autumn months. Northerly winds tend to be more aggressive in nature, disrupting benthic substrate and cause reduced water visibility (Andzejaczek et al. 2018). During the sample period, visibility was estimated manually through direct observation. On days where visibility was < 10 m, less behaviours could be observed due to the poorer quality of the footage and the increased speed of the sharks, while during dives of > 10 m, clearer observations of a hierarchy were observed. The clearer visibility allowed us to record the blacktips' interactions, in which size became significant to the position of the individual within the hierarchy. Photographic-ID of fins allowed recognition of individuals returning to the study site, and suggested that the aggregated group was well-established in this particular area. The mean length of the sampled population was within the sub-adults category, however, it is possible that the sampling method has influenced observed body size distribution and therefore additional studies would be needed to ensure a more robust result.

Blacktips exhibit a highly defined sense of smell and are hypothesized to be able to detect one part of fish flesh in ten billion parts of seawater (Gardiner & Atema 2010). The

decrease in total number of individuals during the sampling event, (Figure 3) could be a result of disinterest from the sharks, or reduced oil contents dispersed by the sardines-based fish-chum, within the bait ball, which reduces the strength of olfactory stimulus for the sharks. Sharks may become aware of the lack of food availability around the chum causing them to seek prey elsewhere. Despite UVs provided a valuable tool to collect behavioural data, there is a time-limitation in the data collections, which last between 30-60 minutes only. Recording times need to be significantly increased beyond current norms in order to effectively sample low shark population densities and provide an effective alternative to fishery-dependent methods (Torres, Abril & Clua 2020). Short recording durations are primarily limited by power and memory-intensive nature of video data collection. However, recent technologies have enabled the design and deployment of a cost-effective BRUV capable of recording videos up to 24 hours. Torres, Abil & Clua (2020) demonstrated the effectiveness of the 24-hour Baited Remote Underwater Video Surveillance (BRUVs) to sample less abundant shark populations, as well as other rare teleost species.

Behaviours

Ten general behavioural displays were observed for the study duration, with the most frequent displays being Fast Turn (FT; 28.5%, n = 289), Downward Swim (DS 110.4%; n = 106) and Avoid (AV 18.5%; n = 118). It has been noted that sharks may rely on social information regarding one another within the feeding group, thereby establishing tolerance or dominance relationships, with the aim of increasing their chances to access food. As an example, in the presence of larger individuals they might display avoidance of submissive behaviour, to avoid conflict (Brena et al. 2018). In our study, larger sharks displayed motions of accelerated downward swimming and fast turning (e.g. dominant behaviors) towards smaller and less dominant sharks, especially in the vicinity of the food-source. As traveling in a straight line seems to be a more energetically efficient form of movement for the individuals, the higher energetic cost of fast turning should be offset by other benefits, for example magnified foraging success (Wilson et al. 2013; Andrzejczek et al. 2018). These dominant displays, that require energy expenditure, act as a trade-off in increasing the individual's chance of successfully capturing prey. In this study, sharks established relatively stable dominance hierarchies that were related to size but no significant role could be linked

to their sex, also due to the small amount of observed males in the dataset. In more extensive studies by Allee & Dickinson (1954), Myrberg & Gruber (1974), Clua et al. (2013), and Brena et al. (2018) didn't find significant grouping of sharks, based on their sex. The commonly displayed circling behaviour of the group around the bait-ball may represent a strategy that promotes the probability of capturing prey in a truly wild scenario (Brena et al. 2018). The observed dominance hierarchy was seemingly significant, showing a dominant female 'Broken Tail' within the sub-sample of blacktips under investigation. Morphological attributes of individual can pre-determine their distribution within a habitat and may potentially limit conflicts between size or sex classes (Brena et al. 2018). Here, similar to Pini-Fitzsimmons et al. (2021) we find that size plays a key role in the position of the individuals within the hierarchy. Smaller individuals often showed more displays of submissive behaviours (58%; n = 7), whilst larger individuals displayed more significant dominant behaviours (47.1%; n = 8). Unfortunately, most of the individuals' sizes used for these analyses were based on direct observation during video analysis, which is valid for estimating the relative size of the individuals but doesn't allow for a more permanent assessment of the hierarchies. A more accurate assessment could be achieved in the future, through a combined individual identification and laser photogrammetry, as initiated in this study.

It must also be noted that, similar to Sperone et al. (2012) each recorded observation was regarded as unique, due to the challenges associated with the individual identifications of each shark during the data collection, and therefore these results could be also present some biased due to the more prominent presence of few individuals.

As the number of individuals increased, larger sharks spent more time around the bait-ball and reduced the time-gap in which smaller individuals were able to penetrate the area. Sharks may interpret the increased numbers as reduced probability of feeding and therefore try to secure their access to the resource by fine-tuning their spatial position and agonistic interactions. The variation of group numbers across the study period could reflect valuable information regarding the surrounding habitats (e.g., quality and availability of resources) (Laland 2003; Sumpter 2006; Couzin 2009; Brown; Brena et al. 2018). Such interactions during congregations around the bait-ball showed individual levels of both submissive and dominant behaviours, reflecting behaviour-dependent associations which have been reported in other taxa such as birds (Aplin et al. 2013, Brena et al. 2018) and fish (Pike et al. 2008, Croft et al. 2009, Brena et al. 2018). Fewer agonistic displays may be a result of increased side fidelity amongst

individuals in the area. Sharks preferentially tolerate competitors that display similar levels of submissive behaviours which may explain the shark behavioural segregation (Brena et al. 2018). As observed in white sharks (Findlay et al. 2016), patterns of co-occurrence of individuals with similar sizes and same sex tend to occur more frequently during scavenging events (Findlay et al. 2016). Whilst this study may have produced an unavoidable imbalanced sample structure as most individuals were sub-adult females, there is still a level as evidence to detect stratification within the group. Individual behaviour of blacktip sharks, consistent overtime, despite external variables, may also be a key factor to consider for future research. Whilst juvenile lemon sharks have shown consistent individual differences despite group composition, individual social behavioural types play a significant role in the social dynamics of these animals, thereby suggesting a strong impact on their social behaviours in the wild (Finger et al. 2018). The identified dominant female in this study 'Broken Tail' showed the highest number of dominant behavioural units and spent the longest amount of time in close proximity to the bait-ball. The hypothesis stands, as mentioned by Brena et al (2018) that sharks assess their rivals' agonistic displays and avoid dominant individuals which is consistent with the idea that dominant sharks are more isolated within an aggregation compared to the sharks showing intermediate submissive rates. Within the studied blacktip aggregation, when 'Broken Tail' was out of the camera frame, other individuals would venture closer to the bait-ball for inspection, until she arrived again. It has been hypothesized that sharks may be able to assess their rival's behaviour through social information, however, further insight is needed into understanding the correlation between shark behaviour and site fidelity. During the annual Sardine Run which occurs along the South African coastline (June-July), it was noted that the vast majority of the observed group of blacktips had left the study site. 'Broken Tail', however, was still present on each dive throughout this duration, suggesting that she was able to feed enough in the area therefore not requiring the energy expenditure needed to hunt sardines up the coast. This could be another example of her position of dominance in the group. Dominance relationships, observed in various shark species such as sickle fin lemon sharks, are thought to diminish the level of permanent competition between individuals through the establishment of a stable hierarchy (Brena et al. 2018). The relatively stable dominance-tolerance relationships witnessed in shark aggregations could possibly be enhanced through conditioning as the same sharks are often drawn together at a static food source through tourism such as baited shark dives

(Brena et al. 2018). This could provide evidence for the reduced number of statistically significant results as sharks show increasing levels of site fidelity to the study site thereby increasing the level of tolerance relationships and displaying less agonistic behaviours. Individuals that are not accustomed to the baited study site may display more confrontation towards competitors within the hierarchy and as witnessed, become excluded from the group. Sharks, however, preferentially tolerated rivals with similar agonistic displays and thus conclude that a major proportion of sharks might rely on social information to interact with competitors during feeding aggregations. Inter-specific competition was seen during the event of a *Galeocerdo cuvier* individual who entered the feeding zone. As her size was larger than that of the blacktips in the area, she naturally asserted dominance through an attempt of biting a blacktip individual and claimed the area surrounding the bait ball (Figure 9). Although the tiger shark dominated in size, further studies should investigate the influence of blacktip numbers versus the size of individual solitary sharks in the area. During the study period, it was uncommon to witness both *Carcharhinus leucas* and *Carcharhinus limbatus* in the same area. Bull shark dives required longer baiting times as diets usually consist of higher trophic levelled animals such as turtles, birds, dolphins and bony fish (Snelson 1984, Clarke et al. 2006). As a result of their diadromous nature or their ability to adapt to a wide range of salinities, they are able to utilize a wider variety of spatial habitats. This leads to resource-partitioning amongst the shark species within Aliwal Shoal. During dives of visibility < 5 m, bull sharks were more active as they generally prefer to hunt in murky waters where it is harder for their prey to see them (Snelson et al. 1984; Motta et al. 2001; Heupel & Simpfendorfer 2008).

Limitations & Future Research

Despite the limited sample size, consistent patterns of individual re-occurrence was observed through reliable photo-identification. Tagging of individuals would provide more robust results, and would bridge the gap between linking the laser photogrammetry results with the observed individual in the video, rather than relying on direct evaluation of size during behavioural analysis. Tagging in other locations will likely uncover other groups of aggregated blacktips and may provide more information about their site fidelity. Increasing the capacity to record and store video will aid in revealing more about factors influencing movements, particularly in foraging behaviours. A longer sample duration will allow a behavioural comparison between seasons and provide further insight into the role of environmental variables such as temperature, visibility and wind speed, on the foraging behaviours. Furthermore, by describing the influence of consistent individual behaviour, and understanding social aggregations through social networks or heterarchy frameworks across a variety of parameters, such as group size or composition, more insight can be gained in uncovering the organizational patterns in animal groups.

Finally, the results of this study show that the behaviour of sharks appears more complex and dynamic than previously understood. Especially for species targeted for human consumption, it will be key to improve our understanding in the role played by shark's inter and intraspecific behaviour, which is deserving of more attention in the future.

Conclusion

This study provides preliminary evidence that size of individual sharks plays a key role in the structuring of social hierarchies during a simulated-feeding scenario. Defining behavioural units of *Carcharhinus limbatus* allows potential for further management of the species, especially within Marine protected Areas where fishing is allowed. Whilst some behaviours are similar to other species of sharks, they still exhibit their own ethograms and therefore it is important to consider the sharks at a species-level rather than use generalizations when implementing conservation measures. Blacktips are considered social sharks, and aggregate into groups to improve feeding efficiency and survival rates based on similarities in size, sex and/or age. This allows improved feeding strategies to take place with the formation of feeding aggregations to enhance prey capture success rates. Although groups aggregate with size similarities, there are still discrepancies between individuals, and this allows the structuring of the hierarchy. Larger individuals tend to display for dominant behaviours, whilst smaller individuals tend to submit to larger sharks, although sometimes may display acts of dominance at a risk of their own. Overall, size and position within a hierarchical system will allow enhanced feeding of the individual and therefore an improved energy expenditure for the individual.

Acknowledgements

I would like to thank my supervisor Dr. Sara Andreotti from Stellenbosch University for all the guidance, support and motivation she provided me with throughout the entire project. She has truly exhilarated my passion and I find her a true role model in this field. A special thank you to Michael Rutzen for his invaluable advice as a shark behaviour expert and for helping me to understand these 'misunderstood' creatures. To Ally Sharp from Adventure Ally for initiating this partnership during unfathomable times and all the interns for their help in data collection. The team of African Watersports including Walter Bernadis and Chad Crowhurst for all the practical fieldwork help, and for fueling my passions into shark conservation.

Annex 1

YouTube links to watch video footage of interesting behaviour observed during research period

- 1) *Galeocerdo cuvier* displaying dominance through ‘fast turn’ and ‘biting’ of *Carcharhinus limbatus* individual: <https://youtu.be/JThFXdoMQxA>
- 2) *Carchinus limbatus* displaying dominant behaviours (‘fast turn’, ;downward swim’): https://youtu.be/_OcDEEFmvUc

If interested in future research, please contact the authors.

Table 2. Dive recordings showing co-ordinates of dive location, time of chumming, end of dive time and wind speed/direction

Date	Lat	Long	Lat End	Long End	Time of Chum	End Dive	Wind
03/03/2021	30° 16' 864"	30°48'555"	30°19'176"	30°47'666"	08:15	09:40	25 NE
04/03/2021	30°16'888"	30°48'540"	30°19'182"	30°47'762"	08:10	09:30	10 S
05/03/2021	30°16'831	30°48'553	30°17'862	30°48'008"	07:20	08:40	10 S
09/03/2021	30°14'994"	30°49'982	30°15'669	30°49'480	08:37	10:00	5 SW
09/03/2021	30°16'886	30°48'534	30°18'020	30°47'878	10:10	11:20	5 SW
11/03/2021	30°16'838	30°48'624"	30°16'8133"	30°48'640	08:30	11:30	15 SW
17/03/2021	30°16'000"	30°48'569	30°17'338"	30°48'461"	08:20	09:30	5 S
18/03/2021	30°17'052	30°48'467"	30°17'490	30°48'323"	10:00	11:20	10 S
19/03/2021	30°16'942	30°48'550"	30°17'490"	30°48'323"	08:00	11:10	0 Wind
23/03/2021	30°17'071	30°48'609"	30°17'943	30°48'318	08:50	11:50	5 S
25/03/2021	30°16'906"	30°48'542"	30°18'140"	30°48'333	08:06	09:06	5 NW
30/03/2021	30°15'912	30°49'264"	30°13'491"	30°50'708"	08:45	11:30	15 NE
01/04/2021	30°16'792	30°48'591"	30°17'541"	30°49'608"	09:26	10:30	0 Wind
06/04/2021	30°17'013"	30°48'507	30°15'602"	30°49'111'	08:10	09:30	20 SW
08/04/2021	30°16'864"	30°48'555"	30°17'009	30°48'925	08:27	09:50	5 NW
14/04/2021	30°16'055"	30°49'706	30°14'762"	30°50'318"	08:42	10:10	10 NE
15/04/2021	30°16'931"	30°48'405"	30°15'191"	30°49'029"	08:32	11:15	5 S
20/04/2021	30°17'005"	30°48'485"	30°15'100"	30°49'512	08:07	11:10	10 SW
30/04/2021	30°16'946	30°48'504	30°17'982	30°48'091	11:48	12:55	0 Wind
03/05/2021	30°17'873	30°49'378	30°16'628	30°49'809	08:38	10:30	10 SW
18/05/2021	30°15'987	30°49'027	30°14'924	30°51'143	09:00	10:10	5 NE
20/05/2021	30°16'892	30°48'517	30°17'462	30°49'531	08:35	09:55	10 NE

Fin Identification Database

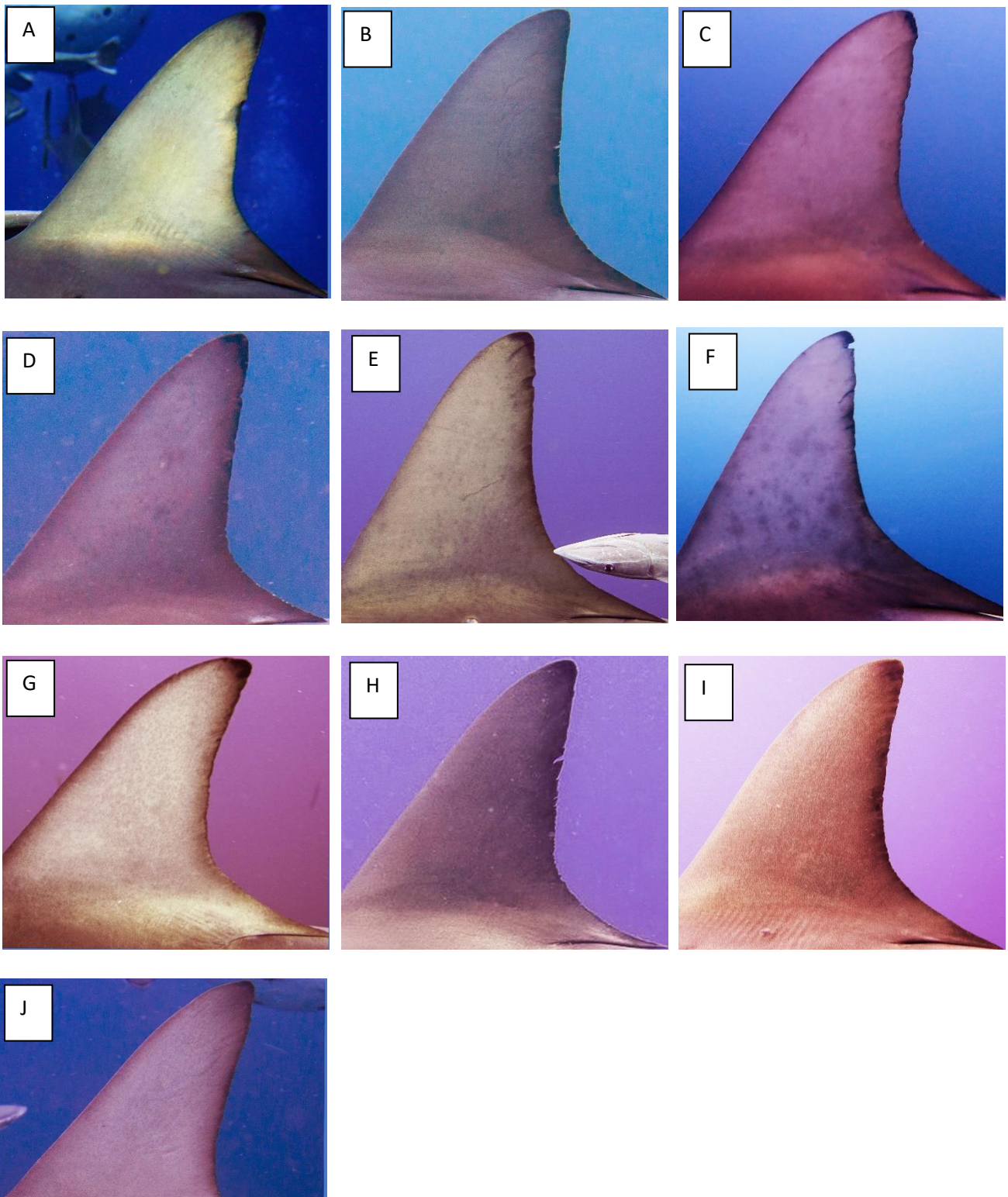


Figure 3. Database of identified fins of *Carcharhinus leucas* individuals. A:C_000101_A, B:C_000401_C, C:C_050200_B, D:C_010101_B, E:C_020000_B, F:C_010200_B, G:C_020200_B, H:C_020503_C, I:C_060600_C, J:C_010000_C



Figure 10. Documentated examples of observed behaviours: Image 1 (Giveaway), Image 2 (Avoid)



Figure 11. Documented incidences of affects of unregulated fishing activities on various shark species occuring within Aliwal Shoal, MPA

References

- Allee, W.C., Dickinson, J.C. (1954). Dominance and sub-ordination in the smooth dogfish *Mustelus canis*. *Physiological Zoology* **27**: 356-364. Doi: 10.1086/physzool.27.4.30152372
- Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A., Sheldon, B.C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecological Letters* **16**: 1365-1372. DOI: 10.1111/ele.12181
- Andrzejczek, S., Gleiss, A.C., Pattriaratchi, C.B., Meekan, M.G. (2018). First insights into the fine-scale movements of sandbar shark, *Carcharhinus plumbeus*. *Frontiers in Marine Science* **5**: 2541-2562. Doi: <https://doi.org/10.3389/fmars.2018.00483>
- Araujo, G., Snow, S.J., So, C.L., Ponzo, A. (2016). Population structure, residency patterns and movements of whale sharks in Southern Leyte, Phillipines: Results from dedicated photo-ID and citizen science. *Aquatic Conservation Marine and Freshwater Ecosystems* **27**: 391-415. DOI: 10.1002/aqc.2636
- Bansemer, C.S., Bennett, M.B. (2010). Retained fishing gear and associated injuries in the east Australian grey nurse sharks (*Carcharias taurus*) implications for population recovery. *Marine & Freshwater Research* **61**: 97-103. DOI: 10.1071/MF08362
- Bax, N.J. (1998). The significance and prediction of predation in marine fisheries. *Journal of Marine Science* **55**: 997-1030. DOI: 1054-3139/98/060997
- Bouveroux, T., Loiseau, N., Barnett, A., Marosi, N.D., Brunnschweiler, J.M. (2021). Companions and casual acquaintances: the nature of associations among bull sharks at a feeding site in fiji. *Frontiers in Marine Science* **8**: 678074. DOI: 10.3389/fmars.2021.678074
- Bouchet, P., Meeuwig, J.J., Salgado Kent, C.P., Letessier, T.B., Jenner, C. (2015). Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. *Biological Reviews* **90**: 699-728. Doi: <https://doi.org/10.1111/brv.12130>
- Bradbury, J.W., Vehrencamp, S.L. (1998). Principles of animal communications. Sunderland, MA: Sinauer Associates Inc. ISBN: 978-0878930456
- Bouchet, P., Meeuwig, J., Huveneers, C., Langlois, T., Letessier, T., Lowry, M., Reese, M., Santana-Garcon, J., Scott, M., Taylor, M., Thompson, C., Vigliola, L., Whitmarsh, S.

(2018). Marine Sampling Field Manual for Pelagic Stereo BRUVS (Baited Remote Underwater Videos). *Field Manuals for Marine Sampling to Monitor Australian Waters, National Environmental Science Programme (NESP)* 105-132. DOI: 10.3354/ab00258

Brown, C., Laland, K.N. (2003). Social learning in fishes: a review. *Fish Fish* **4**: 280-288. DOI: <https://doi.org/10.1046/j.1467-2979.2003.00122.x>

Burghardt, T., Campbell, N., Barham, P.J., Cuthill, I.C., Sherley, R. (2007). A fully automated computer vision system for the biometric identification of African Penguins (*Spheniscus demersus*) on Robben Island. *6th International Penguin Conference*. Accessed 30/06/2021. http://www.cs.bris.ac.uk/Publications/pub_master.jsp?id=2000761

Brunnschweiler, J.M., Pratt, H.L. (2008). Putative male – male agonistic behaviour in free-living zebra sharks (*Stegostoma fasciatum*). *The Open Fish Science Journal* **1**: 23-27. DOI: 10.2174/1874401X00801010023

Cappo, M., Harvey, E., Malcom, H., Speare, P. (2003). Potential of video techniques to monitor diversity, abundance and size of fish in studies of Marine Protected Areas. *Australian Society for Fish Biology* **1**: 455-464. ISBN 0 646 43022

Castro, A.L., Rosa, R.S. (2005). Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. *Biology Fish* **72**: 213-221. DOI: 10.1007/s10641-004-1479-7

Cattano, C., Turco, G., Di Lorenzo, M.D., Gristina, M., Visconti, G., Milazzo, M. (2020). Sandbar shark aggregation in the central Mediterranean Sea and potential effects of tourism. *Aquatic Conservation of Marine and Freshwater Ecosystems* **2021**:1-9. DOI: 10.1002/aqc.3517

Cliff, G., Dudley, S.J. (1992). Protection against shark attack in South Africa 1952-1990. *Australian Journal of Marine and Freshwater Research* **43**(1) 263-272. DOI: <https://doi.org/10.1071/MF9920263>

Clarke, S.C. McAllister, M., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G., Agnew, D., Pikitch, E.K., Nakano, H., Shivji, M.S. (2006). Global

estimates of shark catches using trade records from commercial markets. *Ecology Letters* **9**(10): 1115-1126. DOI: 10.1111/j.1461-0248.2006.00968.x

Clua, E., Chauvet, C., Read, T., Werry, J.M., Lee, S.Y. (2013). Behavioural patterns of a tiger shark (*Galeocerdo cuvier*) feeding aggregation at a blue whale carcass in Prony Bay, New Caledonia. *Marine & Freshwater Behavioural Physiology* **46**: 1-20. Doi: <https://doi.org/10.1080/10236244.2013.773127>

Compagno, L.J., Ebert, D.A., Smale, M.J. (1989). Guide to the Sharks and Rays of Southern Africa. Struik Publishers ISBN 0 86977 880 3.

Couzin, I.D. (2009). Collective cognition in animal groups. *Trends in Cognitive Science* **13**: 36-43. Doi: <https://doi.org/10.1016/j.tics.2008.10.002>

Croft, D.P., Krause, J., Darden, S.K., Ramnarine, J.W., Faria, J.J., James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioural Ecology and Sociobiology* **63**: 1495-1503. DOI: <https://doi.org/10.1007/s00265-009-0802-x>

Cubbage, J., Calambokidis, J. (1987). Size-class segregation of bowhead whales discerned through aerial stereophotogrammetry. *Marine Mammal Science* **3**: 179-185. DOI: <https://doi.org/10.1111/j.1748-7692.1987.tb00160.x>

Davis, D.H. (1963). Shark attack and its relationship to temperature, beach patronage and the seasonal abundance of dangerous sharks. Oceanographic Research Institute Investigational Report 6, Durban South Africa.

Deakos, M.H. (2010). Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays *Manta alfredi*. *Aquatic Biology* **10**: 1-10. DOI: 10.3354/ab00258

Domeier, M.L., Nasby-Lucas, N. (2007). Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Marine Biology* **150**: 977-984. DOI: 10.1007/s00227-006-0380-7

Dorman, S.R., Harvey, E.S., Newman, S.J. (2012). Bait effects in sampling coral reef fish assemblages with stereo-BRUVs. *PLoS ONE* **7**: e41538-e41545. DOI: <https://doi.org/10.1371/journal.pone.0041538>

Dudley, S.F. (1997). A comparison of the shark control programs of New South Wales and Queensland (Australia) and KwaZulu Natal (South Africa). *Ocean and Coastal Management* **34**: 1-27. DOI: 10.1016/S0964-5691(96)00061-0

Dudley, S.F., Simpfendorfer, C.A. (2006). Population of 14 shark species caught in the protective gillnets off Kwa-Zulu Natal beaches, South Africa, 1978-2003. *Marine and Freshwater Res.* **57**: 225-240. DOI: 10.1071/MF05156

Dudley, S.F., Cliff, G. (2010). Sharks caught in the protective gill nets off Natal, South Africa. The blacktip shark *Carcharhinus limbatus* (Valenciennes). *South African Journal of Marine Science* 13(1); 237-254. DOI: <https://doi.org/10.2989/025776193784287356>

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martinez, J., Musick, J.A., Soldo, A., Stevens, J.D., Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **180**: 459-482. DOI: 10.1002/aqc.975

Durban, J.W., Parson, K.M. (2006). Laser-metrics of free-ranging killer whales. *Marine Mammal Science* **22**: 735-743. DOI: 10.1111/j.1748-7692.2006.00068.x

Ebert, D.A., Winter, S.P., Kyne, P.M. (2021). An annotated checklist of the Chondrichthyans of South Africa. *Zootaxa* **4947**(1): 1-127. <https://doi.org/10.11646/zootaxa.4947.1.1>

Fennessy, S.T. (1994). Incidental capture of elasmobranchs by commercial prawn trawlers on the Tugela Bank, Natal, South Africa. *South African Journal of Marine Science* **14**: 287-296. DOI: <https://doi.org/10.2989/025776194784287094>

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13: 1055-1071. DOI: 10.1111/j.1461-0248.2010.01489.x

Finger, J.S., Guttridge, T.L., Wilson, A.D., Gruber, S.H., Krause, J. (2018). Are some sharks more social than others? Short- and long-term consistencies in the social behaviour of juvenile lemon sharks. *Behavioural Ecology and Sociobiology* **72**(1) 17-27. DOI:10.1007/s00265-017-2431-0

Forcada, J., Aguilar, A. (2000). Use of photo-identification in capture-recapture studies of Mediterranean monk seals. *Marine Mammal Science* 16(4): 767-793. DOI: [10.1111/j.1748-7692.2000.tb00971.x](https://doi.org/10.1111/j.1748-7692.2000.tb00971.x)

Gallagher, A.J., Shiffman, D.S., Byrnes, E.E., Hammerschlag-Peyer, C.M., Hammerschlag, N. (2017). Patterns of resource use and isotopic niche overlap among three species of sharks occurring within a protected subtropical estuary. *Aquatic Ecology* 51: 435-448. DOI: 10.1007/s10452-017-9627-2

Garcia, V.B., Lucifora, L.O., Myers, R.A. (2009). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Philosophical Transactions of the Royal Society of Biology* 275: 83-89. DOI: <https://doi.org/10.1098/rspb.2007.1295>

Gardiner, J.M., Atema, J. (2010). The function of bilateral odor arrival time differences in olfactory orientation of sharks. *Current Biology* 20(13): 1187-1191. DOI: <https://doi.org/10.1016/j.cub.2010.04.053>

Gore, M.A., Frey, P.H., Ormond, R.F., Allan, H., Gilkes, G. (2016). Use of photo-identification and mark-recapture methodology to assess basking shark (*Cetorhinus maximus*) populations. *PLoS ONE* 11(3): e0150160. doi:10.1371/journal.pone.0150160

Grace, M. (2001). *Field Guide to Requiem Sharks (Elasmobranchiomorpha Carcharhinidae) of the Western North Atlantic*. NOAA Technical Report NMFS 153. Available online: <https://spo.nmfs.noaa.gov/sites/default/files/legacy-pdfs/tr153.pdf>

Guttridge, T.L., Gruber, S.H., Gledhill, K.S., Croft, D.P., Sims, D.W., Krause, J. (2009). Social preferences of juvenile lemon sharks, *Negaprion brevirostris*. *Animal Behaviour* 78: 543-548. DOI: 10.1016/j.anbehav.2009.06.009

Guttridge, T.L., Gruber, S.H., DiBattista, J.D., Feldheim, K.A., Croft, D.P., Krause, S., Krause, J. (2011). Assortive interactions and leadership in free-ranging population of juvenile lemon shark *Negaprion brevirostris*. *Marine Ecology Progress Series* 423: 235-245. DOI: 10.3354/meps08929

Guyomard, D., Perry, C., Tournoux, P.U., Cliff, G., Peddemors, V., Jaquemet, S. (2019). An innovative fishing method to enhance the release of non-target species in coastal shark-control programs: the SMART (shark management alert in real-time) drumline. *Fisheries Research* 216: 6-17. DOI: <https://doi.org/10.1016/j.fishres.2019.03.011>

Heupel, M., Simpfendorfer, C. (2005). Quantitative analysis of aggregation behaviour in juvenile blacktip sharks. *Marine Biology* **147**: 1239-1249. DOI: <https://doi.org/10.1007/s00227-005-0004-7>

Heupel, M.R., Simpfendorfer, C.A. (2008). Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology* **1**: 277-289. <https://doi.org/10.3354/ab00030>

Holmberg, J., Norman, B., Arzoumanian, Z. (2009). Estimating population size, structure, and residency time for whale sharks *Rhinocodon typus* through collaborative photo-identification. *Endangered Species Res* **7**: 39-53. DOI: 10.3354/esr00186

International Commission for the Conservation of Atlantic Tunas. (2019). Report of the 2019 ICCAT Shortfin Mako Shark Stock Assessment Update Meeting. (ICCAT)

IOTC (Indian Ocean Tuna Commission) (2005). Information on shark finning fisheries. IOTC-2005-S9-08[EN]. IOTC, Victoria, Seychelles.

Jacoby, D.M., Sims, D.W., Croft, D.P. (2012). The effect of familiarity on aggregation and social behaviour in juvenile small spotted catsharks (*Scyliorhinus canicular*). *Journal of Fish Biology* **81**: 1596-1610. DOI: <https://doi.org/10.1111/j.1095-8649.2012.03420.x>

Jean, C., Ciccione, S., Talma, E., Ballorain, K., Bourjea, J. (2010). Photo-identification method for green and hawksbill turtles – First results from Reunion. *Indian Ocean Turtle Newsletter* **11**: 1-64.

Jeffreys, G.L., Rowat, D., Marshall, H., Brooks, K. (2012). The development of robust morphometric indices from accurate and precise measurements of free-swimming whale sharks using laser photogrammetry. *Journal of the Marine Biological Association of the United Kingdom* **92**(2): 309-320. DOI:10.1017/S0025315412001312

Kajjura, S.M., Tellman, S.L. (2016). Quantification of massive seasonal aggregations of blacktip sharks (*Carcharhinus limbatus*) in Southeast Florida. *PLoS ONE* **11**(3): e0150911. DOI: <https://doi.org/10.1371/journal.pone.0150911>

Keeney, D.B., Heupel, M.R., Hueter, R.E., Heist, E.J. (2005). Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*)

nurseries in the north-western Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular Ecology* **14**(7) 1911-1923. DOI: <https://doi.org/10.1111/j.1365-294X.2005.02549.x>

Klimley, A.P. (1985). Schooling in *Sphyrna lewini*, a species with minimal risk of predation: a non-egalitarian state. *Journal of Comparative Ethology* **70**: 297-319. DOI: <https://doi.org/10.1111/j.1439-0310.1985.tb00520.x>

Knip, D.M., Heupel, M.R., Simpfendorfer, C.A., Tobin, A., Moloney, J., 2011. Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. *Marine & Freshwater Research* **62**: 658–667. DOI: 10.1071/MF10136

Kwa-Zulu Natal Sharks Board. (2021). Shark nets, drumlines and safe swimming. Accessed 07/07/2021. Source <https://www.shark.co.za/Pages/ProtectionSharks-NetsDrumlines>

Lack, M., Sant, G. (2008). Illegal, unreported and unregulated shark catch: A review of current knowledge and action. Traffic: Wildlife trade monitoring network. Available at http://www.trafficj.org/publication/08_IUU_shark_catch.pdf Accessed: 25/09/2021

Laer, K.O., Whitney, N.M., Morris, J.J., Geiss, A.C. (2021). Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. *Proceedings in Royal Society Publishing* **288**: 1-8. DOI: <https://doi.org/10.1098/rspb.2021.0816>

Letessier, T.B., Bouchet, P.J., Meeuwig, J.J. (2015). Sampling mobile oceanic fishes and sharks: implications for fisheries and conservation planning. *Biological Reviews* **92**(2): 627-646. DOI: 10.1111/brv.12246

Leurs, G., O'Connell, C.P., Andreotti, S., Rutzen, M., Von Noordegraaf, H. (2015). Risks and advantages of using surface laser photogrammetry on free-ranging marine organisms: a case study on white sharks *Carcharodon carcharias*. *Journal of Fish Biology* **86**(6): 1713-1728. DOI: 10.1111/jfb.12678

Marshall, A.S., Dudgeon, C.L., Bennett, M.B. (2011). Size and structure of photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Marine Biology* **158**: 1111-1142. DOI: 10.1007/s00227-011-1634-6

Marshall, A.D., Pierce, S.J. (2019). The use and abuse of photographic identification in sharks and rays. *Journal of Fish Biology* **80**(5): 1361-1379. DOI: 10.1111/j.1095-8649.2012.03244.x

Martin, R.A. (2007). A review of shark agonistic displays: comparison of display features and implications for shark-human interactions. *Marine and Freshwater Behaviour and Physiology* **40**: 13-34. DOI: 10.1080/10236240601154872

Matich, P., Plumlee, J.D., Weideli, O.C., Fisher, M. (2020). New insights into trophic ecology of blacktip sharks (*Varharhinus limbatus*) from a subtropical estuary in the western Gulf of Mexico. *Journal of Fish Biology* **98**(2): 470-484. DOI: <https://doi.org/10.1111/jfb.14592>

McAuley, R.B., Simpfendorfer, C.A., Wright, I.W. (2007). Gillnet mesh selectivity of the sandbar shark (*Carcharhinus plumbeus*): implications for fisheries management. *ICES Journal of Marine Science* **64**: 1702-1709. DOI: <https://doi.org/10.1093/icesjms/fsm136>

McClenachan, L., Cooper, A.B., Dulvy, N.K. (2016). Rethinking trade-driven extinction risk in marine and terrestrial megafauna. *Current Biology* **26**: 1640-1646. DOI: <https://doi.org/10.1016/j.cub.2016.05.026>

McCoy, E., Burce, R., David, D., Aca, E.Q., Hardy, J., Labaja, J., Snow, S.J., Ponzo, A., Araujo, G. (2018). Long-term photo-identification reveals the population dynamics and strong site fidelity of adult whale sharks to the coastal waters of Donsol, Phillipines. *Marine Science* **5**: 271-295. DOI: <https://doi.org/10.3389/fmars.2018.00271>

McKibben, J.N., Nelson, D.R. (1986). Patterns of movement and grouping of grey reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science* **38**: 89-110. DOI: 10.1023/A:1007657505099

Motta, P.J., Wilga, C.D. (2001). Advances in the study of feeding behaviours, mechanisms and mechanics of sharks. *Environmental Biology of Fishes* **60**: 131-156. Doi: <https://doi.org/10.1023/A:1007649900712>

Olbers, J., Celliers, L., Schleyer, M.H. (2009). Zonation of benthic communities on the subtropical Aliwal Shoal, Durban, Kwa-Zulu Natal, South Africa. *African Zoology* **44**(1): 8-23. DOI:10.1080/15627020.2009.11407435

Okada, S., Taniguchi, A. (1974). Size relationship between salmon juveniles in inshore waters and their prey animals. *Bulletin Faculty Fisheries* **22**: 30-36. DOI: 10.1577/T08-244.1

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.M., Marshall, A.D., Pollow, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J.S., Kindsvater, H.K., Dulvy, N.K. (2019). Half a century of global decline in oceanic sharks and rays. *Nature* **589**: 567 – 575. DOI: <https://doi.org/10.1038/s41586-020-03173-9>

Papastamatiou, Y., Wetherbee, B., Lowe, C., Crow, G. (2006). Distribution and diet of four species of *carcharhinid* shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series* **320**: 239-251. DOI: 10.3354/meps320239

Pike, T.W., Samanta, M., Lindstrom, J., Royle, N.J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society of Biological Science* **275**: 2515-2520. <https://doi.org/10.1098/rspb.2008.0744>

Plumlee, J.D., Wells, R.J. (2016). Feeding ecology of three coastal shark species in northwest Gulf of Mexico. *Marine Ecology Progress Series* **550**: 163-174. DOI: <https://doi.org/10.3354/meps11723>

Pondella, D.J., Allen, L.G. (2008). The decline and recovery of four predatory fishes from the Southern California Bight. *Marine Biology* **154**: 307-313. DOI: <https://doi.org/10.1007/s00227-008-0924-0>

Reid, D.D., Krogh, M. (1992). Assessment of catches from protective shark meshing off New South Wales beaches between 1950 and 1990. *Australian Journal of Marine and Freshwater Research* **43**: 283-296. DOI: <https://doi.org/10.1071/MF9920283>

Richards, K., O'Leary, B.C., Roberts, C.M., Ormond, R., Gore, M., Hawkins, J.P. (2015). Sharks and people: insight into the global practices of tourism operators and their attitudes to shark behaviour. *Marine Pollution Bulletin* **91**(1): 200-210. DOI: <https://doi.org/10.1016/j.marpolbul.2014.12.004>

Roff, G., Brown, C.J., Priest, M.A., Mumby, P.J. (2018). Decline in coastal apex shark populations over the past half century. *Community Biology* **1**(223): 1-11. DOI: <https://doi.org/10.1038/s42003-018-0233-1>

Rohner, C.A., Richardson, A.J., Marshall, A.D., Weeks, S.J., Pierce, S.J. (2011). How large is the world's largest fish? Measuring whale sharks *Rhincodon typus* with laser photogrammetry. *Journal of Fish Biology* **78**: 378-385. DOI: 10.1111/j.1095-8649.2010.02861.x.

Rothman, J.M., Chapman, C.A., Twinomugisha, D., Wasserman, M.D., Lambert, J.E., Goldberg, T.L. (2008). Measuring physical traits of primates remotely; the use of parallel lasers. *American Journal of Primatology* **70**: 1-5. DOI: 10.1002/ajp.20611

Santana-Garcon, J., Braccini, M., Langlois, T.J., Newman, S.J., McAuley, R.B., Harvey, E.S. (2014). Calibration of pelagic stereo-BRUVs and scientific longline surveys for sampling sharks. *Methods in Ecology and Evolution* **5**(8): 824-833. DOI: <https://doi.org/10.1111/2041-210X.12216>

Schilds, A., Mourier, J., Huveneers, C., Nazimi, L., Fox, A., Leu, S.T. (2019). Evidence for non-random co-occurrences in a white shark aggregation. *Behavioural Ecology and Sociobiology* **73**: 138-149. DOI: <https://doi.org/10.1007/s00265-019-2745-1>

Schlaff, A., Heupel, M.R., Simpfendorfer, C.A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. *Reviews in Fish Biology and Fisheries* **24**: 1089-1103. DOI: <https://doi.org/10.1007/s11160-014-9364-8>

Schnell, A.K., Smit, K.L., Hanlon, R., Harcourt, R. (2016). Cuttlefish perform multiple agonistic displays to communicate a hierarchy of threats. *Behavioural Ecology & Sociobiology* **70**: 346-359. DOI: 10.1007/s00265-016-2170-7

Sims, D.W., Southall, E.J., Quayle, V.A., Fox, A.M. (2000). Annual social behaviour of basking sharks associated with front areas. *Proceedings of the Royal Society of Biological Science* **267**: 1897-1904. DOI: <https://doi.org/10.1098/rspb.2000.1227>

Snelson, F.F., Mulligan, T.J., Williams, S.E. (1984). Food habits, occurrence, and population structure of bull shark *Carcharhinus leucas*, in Florida Coastal Lagoons. *Bulletin of Marine Science* **1**: 71-80. ISSN 0007-4977

Smith, K., Scarr, M., Scarpaci, C. (2010). Grey nurse shark (*Carcharias taurus*) diving tourism tourist compliance and shark behaviour at Fish Rock, Australia. *Environmental Management* **46**: 699-710. DOI: <https://doi.org/10.1007/s00267-010-9561-8>

Sosa-Nishizaki, O., Morales-Bojorquez, E., Nasby-Lucas, N., Gonzalez, E.C., Domeier, M.L. (2012). Problems with Photo Identification as a Method of Estimating Abundance of White Sharks, *Carcharodon carcharias*: An Example from Guadalupe Island, Mexico. *Global Perspectives on the Biology of Life History of the White Shark* **1**(26) DOI: 10.1201/b11532-30

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A. (2000). The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476-494. DOI: <https://doi.org/10.1006/jmsc.2000.0724>

Stevick, P.T., Palsboll, P.J., Smith, T.D., Bravington, M.V., Hammond, P.S. (2001). Errors in identification using natural markings: rate, sources, and effects on capture-recapture estimates and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1861-1870. DOI: 10.1139/f01-131

Sumpter, D.J. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society of Biology* **361**: 5-22. Doi: <https://doi.org/10.1098/rstb.2005.1733>

Tavares, R. (2008). Occurrence, diet and growth of juvenile blacktip sharks, *Carcharhinus limbatus*, from Los Roques Archipelago National Park, Venezuela. *Caribbean Journal of Science* **44**(3): 291-302. DOI: <https://doi.org/10.18475/cjos.v44i3.a4>

Torres, A., Abril, A.M., Clua, E.E. (2020). A time extended (24h) Baited Remote Underwater Video (BRUV) for monitoring pelagic and nocturnal marine species. *Journal of Marine Science & Engineering* **8**: 2-8. DOI:10.3390/jmse8030208

Towner, A.V., Wcisel, M.A., Reisinger, R.R>, Edwards, D., Jewell, O.J. (2013). Gauging the threat: the first population estimates of sharks in South Africa using photo-identification automated software. *PLoSOne* **8**(6): e66035-e66042. DOI: [doi:10.1371/journal.pone.0066035](https://doi.org/10.1371/journal.pone.0066035)

Webster, T., Dawson, S., Slooten, E. (2010). A simple laser photogrammetry technique for measuring Hector's dolphins (*Cephalorhynchus hectori*) in the field. *Marine Mammal Science* **26**: 296-308. DOI: <https://doi.org/10.1111/j.1748-7692.2009.00326.x>

Water, S., Whitehead, H. (1990). Population and growth parameters of Galapagos sperm whales estimated from length distributions. *Rep. Int. Whaling Community* **40**: 225-235.

Wetherbee, B.M., Cortes, E. (2004). Food consumption and feeding habits. *Biology of Sharks and Their Relatives* 223-244. DOI:10.1201/b11867-11

White, J., Simpfendorfer, C.A., Heupel, M.R. (2013). Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology* **448**: 281-288. DOI: <https://doi.org/10.1016/j.jembe.2013.08.004>

White, J., Simpfendorfer, C.A., Heupel, M.R. (2013). Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology* **448**: 281-288.