

Insights into shark behaviour in the pelagic environment by means of a non-invasive sampling technique

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ABSTRACT

Sharks are apex predators that play a vital role in maintaining ecosystem stability in the pelagic environment, however many pelagic species are experiencing worldwide declines in population numbers as a result of fisheries overexploitation. Consequently, understanding how pelagic sharks interact with novel stimuli may provide insight into their relative vulnerability to fishing-induced mortality and may have significant implications for shark conservation and fisheries management strategies. The inherent challenges that arise when studying large, highly mobile and predatory animals such as sharks raises the need for observational techniques that enable safe, non-invasive *in situ* sampling of shark behaviour. Stereo-baited remote underwater video systems (stereo-BRUVS), typically used on the seabed, have been adapted to a mid-water configuration in order to sample sharks within pelagic environments. In conjunction with an ethogram, which was developed from a combination of behaviours previously reported in the literature and from preliminary review of video imagery, this study used video footage generated by mid-water stereo-BRUVS to examine location-, species- and size-specific differences in the behavioural composition, frequency and timing for silvertip (*Carcharhinus albimarginatus*), grey reef (*Carcharhinus amblyrhynchos*) and silky (*Carcharhinus falciformis*) sharks observed across three geographical locations. These locations were used as a proxy for fishing pressure, as each location varied in their level of fishing protection. Within the scope of this study, size was a strong predictor of behavioural variation, where larger sharks were less diverse and frequent in their behaviours, compared to smaller sharks. Preliminary findings suggest that location and species do play a role in behavioural differences, with some evidence indicating that sharks exposed to fishing pressure are more conservative in their behaviour and that some species are more inquisitive with respect to the mid-water stereo-BRUVS. However, location and species covaried to some degree, thus attributing behavioural differences to either of these two factors must be done cautiously. Additionally, this study provides evidence that mid-water stereo-BRUVS, in conjunction with an appropriate ethogram, are capable of extracting large quantities of behavioural data relevant to the conservation of sharks in the pelagic environment.

Key words: stereo-BRUVS, ethogram, fisheries, conservation, silky shark, grey reef shark, silvertip shark, British Indian Ocean Territory, Palau, New Caledonia

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INTRODUCTION

Apex predators, such as large sharks, occupy the top trophic level within a community, and play a fundamental role in maintaining ecosystem structure and function (Fortin et al. 2005; Knight et al. 2005; Heithaus et al. 2008; Ritchie and Johnson 2009). Consequently, large scale removal of apex predators has been associated with trophic cascades and mesopredator release, resulting in the reduction of ecosystem stability (Myers et al. 2007; Prugh et al. 2009; Ritchie and Johnson 2009; Mclean et al. 2011; Ruppert et al. 2013). Apex predators not only control mesopredator abundance, but also significantly affect their distribution and behaviour (Ritchie and Johnson 2009). For instance, bottlenose dolphins (*Tursiops aduncus*) have been found to reduce their use of shallow, resource-rich habitats and instead rest in safer, less resource abundant deeper habitats to decrease the likelihood of predation by tiger sharks (*Galeocerdo cuvier*) (Heithaus and Dill 2002; Heithaus et al. 2008).

The fundamental ecological role sharks play in maintaining ecosystem stability makes their rapidly declining numbers worldwide of significant conservation concern (Graham et al. 2010). Fisheries overexploitation is the predominant cause of shark declines, with animals captured in both targeted fisheries (52%) and as incidental capture termed bycatch (48%) (Bonfil 1994; Clarke et al. 2004; Jackson 2008; Holmes et al. 2009; Ritchie and Johnson 2009; Carrier et al. 2012; Worm et al. 2013; Clark et al. 2015). Sharks are particularly vulnerable to exploitation on account of their conservative life-history, including long gestation periods, low fecundity and productivity and high maternal investment, in addition to being the latest maturing and slowest reproducing vertebrates (Cortés 2000; Fowler et al. 2005; Gilman et al. 2008; Carrier et al. 2012).

Due to high exploitation rates, many shark species are now classified as ‘at conservation risk’ (Vulnerable, Endangered or Critically Endangered) by the International Union for Conservation of Nature (IUCN) (Fowler et al. 2005; Worm et al. 2013; Dulvy et al. 2014; IUCN 2015). However, determining the exact conservation status of shark species and developing adequate conservation strategies presents a major challenge, as fisheries records remain the only long standing and spatially extensive data available for shark populations. However, these records are often of limited use due to the inaccurate and incomplete nature of catch reports and mortality estimates (Barker and Schluessel 2005; Clarke et al. 2006; Holmes et al. 2009; Worm et al. 2013). Indeed, fishing mortality is likely to be significantly underestimated given high amounts of illegal, unreported and unregulated (IUU) fishing, with

total catch records estimated at be three to four times greater than reported levels (Barker and Schluessel 2005; Clarke et al. 2006; Worm et al. 2013).

The environment which sharks inhabit closely predicts their vulnerability to fishing-induced mortality (Olden et al. 2007; Dulvy et al. 2014). Pelagic (open-ocean) sharks, when compared to coastal and deeper dwelling species, experience increased fisheries exposure and are heavily targeted given their large fins relative to body size (Olden et al. 2007; Dulvy et al. 2014). Moreover, pelagic commercial fisheries are relatively uncontrolled and generate almost 50% of reported shark catches (Bonfil 1994; Jackson 2008). As a consequence, numerous pelagic species are at considerable risk of overexploitation, most notably the silky (*Carcharhinus falciformis*), short finned mako (*Isurus oxyrinchus*), oceanic whitetip (*Carcharhinus longimanus*) and blue (*Prionace glauca*) sharks (Stevens et al. 2000; Cortés et al. 2010).

Conservation-related research on sharks focuses on reducing fishing mortality (Barker and Schluessel 2005) and implementing spatial closures such as marine protected areas (MPAs) (Baum et al. 2010). Behaviour has been less studied in shark conservation but presents a promising avenue (Morris Gosling and Sutherland 2000). Behaviour is typically analysed using an ethogram, which is defined as a descriptive list of behaviours that may focus on a particular functional class, such as social or agonistic behaviours, or can be all inclusive (McDonnell and Haviland 1995). Ethograms represent a standardised method of documenting behaviours both *in* and *ex situ*, allowing for the repeatable categorisation and quantification of the defined behaviours (Gruber and Myrberg 1977; Mench 1998; Sperone et al. 2012; Okuyama et al. 2013; Thompson 2014). Behavioural studies in the marine environment have typically focused on commercially important fish species such as the Atlantic cod (*Gadus morhua*) and salmonids (Guttridge et al. 2009). For sharks, there remains a need to develop ethograms that allow discrimination of inter- and intra-species behavioural patterns (Gruber and Myrberg 1977; Motta and Wilga 2001; Ruckstuhl and Neuhaus 2005). However, due to inherent difficulties of studying large, predatory sharks, behavioural research is scarce.

Shark behaviour has been reported to vary for a number of reasons, including in response to fishing activities (Morris Gosling and Sutherland 2000; Feldheim et al. 2002; Guttridge et al. 2009; Pimiento et al. 2010). For instance, an associative learning study showed that sharks exhibit the potential to learn and adjust their behaviour according to encounters with commercial and recreational fisheries, where negative interactions with fishing gear can result in future cautiousness or active avoidance (Guttridge et al. 2009). Consequently, examining

locations with varying levels of fishing pressure can provide insight into the degree to which sharks modify their behaviour in response to fishing activities (Morris Gosling and Sutherland 2000; Guttridge et al. 2009). Furthermore, species and size have been reported to be two significant predictors of reef shark behaviour (Thompson 2014). Species differ substantially in their physiology, prey preferences, migratory and swimming patterns, size, sensory systems and foraging behaviour (Cappo et al. 2006; Carrier et al. 2012; Thompson 2014). Therefore, species will interact with their environment differently and display varying behavioural patterns. A number of studies have suggested that sharks also exist in size-dependent dominance hierarchies, where size determines the behaviours exhibited, particularly with respect to foraging and diet (Allee and Dickinson Jr 1954; Gruber and Myrberg 1977; Løkkeborg and Bjordal 1992; Lowe et al. 1996; Ruckstuhl and Neuhaus 2005; Lucifora et al. 2009; Thompson 2014), with individuals experiencing different levels of mortality as a result of these behaviours (Adams 1980; Jennings et al. 2001). Understanding species- and size-specific differences in behaviour of targeted shark species may thus provide insight into vulnerability to catchability in both targeted and incidental fisheries, having substantial implications for conservation and fisheries management (Jennings et al. 2001; Uusi-Heikkilä et al. 2008; Spaet et al. 2010).

Characterising shark behaviour is however challenging, particularly *in situ*. Pelagic sharks are usually large, wide-roaming and predatory. As such, direct observations can be expensive and place observers at risk (Bres 1993; Colton and Swearer 2010; Langlois et al. 2010; Jacoby et al. 2011). Underwater visual surveying methods such as stereo baited underwater video systems (stereo-BRUVS) provide an opportunity to observe sharks without these challenges (Langlois et al. 2010). Stereo-BRUVS are a cost-effective, standardised method of quantifying and monitoring the diversity, abundance and size structure of fish and shark assemblages without diver limitations (Cappo et al. 2006; Dorman and Newman 2012). The non-extractive nature of these systems means they can be used in marine protected areas (MPAs) and to gather information on threatened species (Cappo et al. 2006). Furthermore, the increased use of high definition digital footage allows for accurate species and individual identification (Letessier et al. 2015). Stereo-BRUVS also produce permanent records of all behaviours (Cappo et al. 2006). The ability to extract behavioural observations from existing video, over time and space across large numbers of replicates, along with contextual information on species associations, is a potentially powerful tool for behavioural research (Colton and Swearer 2010; Langlois et

al. 2010; Harvey et al. 2012; Letessier et al. 2015). However, the use of stereo-BRUVS in behavioural research has been limited (Thompson 2014; Ryan et al. 2015).

The application of stereo-BRUVS to behavioural analyses is not without challenges. These systems rely on good visibility and have a relatively limited field of view (~10 m linear distance from cameras), restricting continuous observation of individuals, resulting in some behaviours going unobserved (Watson et al. 2005). However, issues with visibility and challenges with sample size are likely to be present in most underwater sampling methods (Nelson 1977). The use of bait also presents bias as it attracts high trophic level animals, however for the purpose of this study, it is of little concern as its use is not dissimilar to the baiting of fishing gear. Finally, mid-water stereo-BRUVS are limited in the number of locations in which they have been deployed, given their relatively recent development (Letessier et al. 2015). Consequently, this study was unable to include replication at the level of exposure to fishing across geographical locations, so any inferences made with respect to the effects of fishing pressure on shark behaviour must be made cautiously, noting that they still contribute to a broader body of evidence and have the potential for prompt new directions of research (Barley & Meeuwig In Review; McAuley et al. 2007; Hillerislambers et al. 2013).

The primary objective of this study was to understand how shark behaviour varies among geographical location, species and size, where geographical location was used as a proxy for fishing pressure. Additionally, this study aimed to evaluate the practicality of using mid-water stereo-BRUVS to document shark behaviour in the pelagic environment. This was achieved by analysing existing data collected by mid-water stereo-BRUVS in the British Indian Ocean Territory (BIOT), Palau and New Caledonia, in conjunction with an ethogram, which was developed from a combination of behaviours previously reported in the literature and derived from preliminary review of video imagery. It was hypothesised that the composition, frequency and timing of shark behaviour would vary significantly among locations and species, with size playing a secondary role.

METHODS

Study sites

Video footage was collected prior to the commencement of this study for the purpose of documenting spatial patterns in the diversity, abundance, and size of pelagic shark and bony fish assemblages. Expeditions were completed at three sampling locations: the British Indian Ocean Territory (BIOT), New Caledonia and Palau (**Figure 1**). The three locations were chosen

as they represent some of the most pristine marine ecosystems globally, but experience varying levels of protection from fishing (Mortimer and Day 1999; Koldewey et al. 2010; UNESCO 2015). At the time of sampling, fishing protection ranged from the fully protected “no-take” MPA in the BIOT in which all fishing is banned, to the Palau Shark Sanctuary in which targeting sharks was banned but pelagic fishing for other species continued, to New Caledonia with its conventional fisheries management (Koldewey et al. 2010; Vianna et al. 2012; Quirk 2013). These differences among locations provide an opportunity to further our understanding of shark behaviour, with the acknowledgement that the conclusions are subject to the limitation of no replication of protection level.

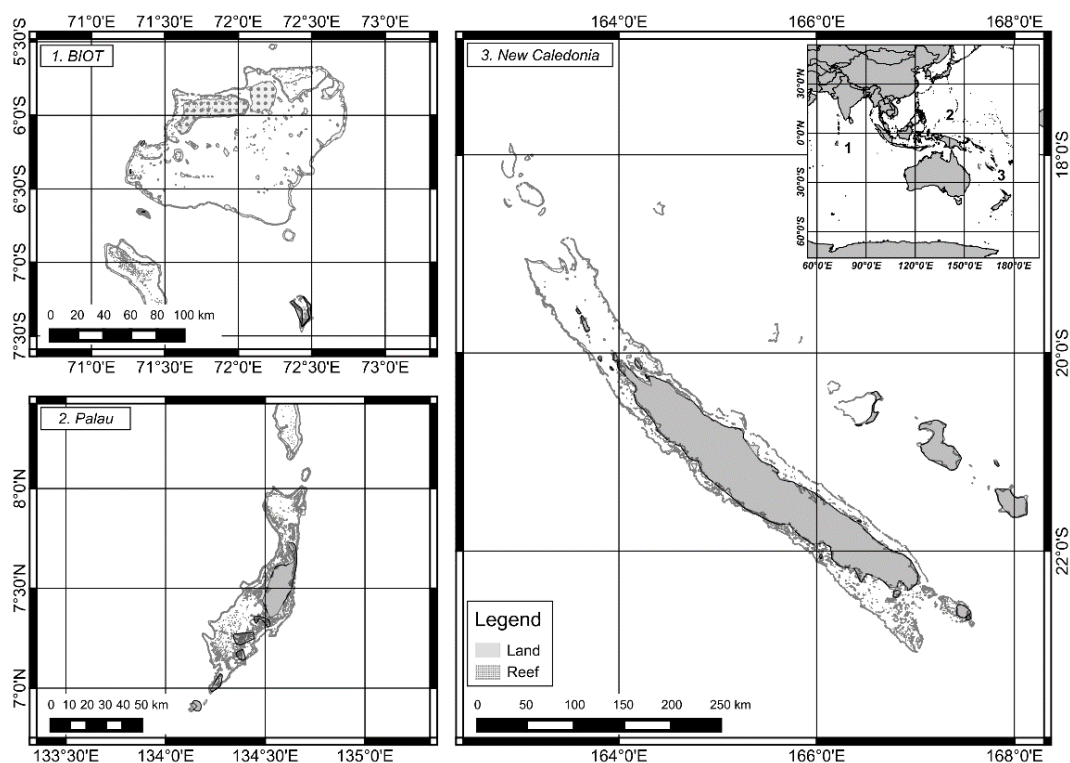


Figure 1 – Map of 1. The British Indian Ocean Territory, 2. Palau and 3. New Caledonia, with the insert illustrating the geographical positioning of each location. Grey and dotted represent land and reef, respectively. Courtesy of D.Tickler.

Administered by the United Kingdom, the BIOT is located in the geographical centre of the Indian Ocean and is currently the world’s largest fully protected MPA (638,556 km²) (Seaward et al. 1999; Koldewey et al. 2010; Sheppard et al. 2012). Prior to being declared a no-take MPA in April 2010, the BIOT supported pelagic longline and purse seine fisheries that mainly targeting tuna, but in which pelagic sharks were bycatch (Koldewey et al. 2010). Although the BIOT is classified as a no-take MPA, a recent report by the Indian Ocean Tuna Commission (IOTC) suggested that illegal fisheries continue, with several threatened shark species being

caught, including blacktip (*Carcharhinus melanopterus*), silvertip (*Carcharhinus albimarginatus*) and grey reef (*Carcharhinus amblyrhynchos*) sharks (Clark et al. 2015).

The Republic of Palau has an economic exclusion zone (EEZ) of approximately 459,000 km² in the Western Pacific Ocean, which has previously supported international fishing fleets that target tuna and other pelagic species (Woesik et al. 2012). At the time of sampling, Palau's EEZ was classified a shark sanctuary, where targeted fishing of all sharks was prohibited (Quirk 2013). However, sharks continued to be caught as bycatch and illegal fisheries remained an ongoing enforcement challenge, thus affording moderate protection for sharks (Quirk 2013; Vianna et al. 2016). Since the time of sampling, the Palauan Congress established the Palau National Marine Sanctuary Act, which banned all foreign commercial fishing in the EEZ, creating a national MPA (Quirk 2013).

New Caledonia is located 1,500 km east of Australia in the South Pacific Ocean, occupying an area of approximately 18,575 km² (Douillet et al. 2001). At the time of sampling, the majority of fishing in New Caledonia occurred in reef and lagoon waters, with targeted families including Carangidae (jacks mackerels and scads), Scombridae (mackerels and tunas) and Serranidae (basses and groupers), although direct pelagic fisheries remained in operation (Harper et al. 2009).

Deployment of mid-water stereo-BRUVS

Prior to deployment, each individual stereo-BRUVS, or rig, was calibrated following recommended guidelines (SeaGIS 2008; Letessier et al. 2015). Rig calibration was conducted in a controlled environment in the University of Western Australia swimming pool, using the standard 3-dimensional (3D) calibration cube (1x1m), as described by SeaGIS (2008). Videos from the pool were then uploaded into EventMeasure to generate calibration (CAL) files, resulting in each stereo-BRUVS having an individual CAL file, which was loaded alongside video footage during video analysis to ensure accurate length measurements (SeaGIS 2008).

Five mid-water stereo-BRUVS were deployed in a longline configuration with 200 metres between each rig (Letessier et al. 2015). Each longline had a series of devices in place to ensure its successful retrieval, including a bright coloured flag to aid visual location and a radar reflector and waterproof GPS to track the drifting equipment. Stereo-BRUVS were suspended at 10 m depth by a system of mid-water and surface buoys, weights and an elasticised bungee cord to reduce wave shock and enhance footage quality (**Figure 2a**) (Bouchet and Meeuwig 2015). Each rig comprised of either paired GoPro Hero 3 (2012) or paired Hero 4 (2015)

cameras mounted 95 cm apart, on a horizontal stainless steel frame (**Figure 2b**). The cameras were mounted with an inward convergent angle was 8° to maximise field of view (127°) and ensure adequate overlap for length measurements (Letessier et al. 2015). A non-flexible bait arm extended 1.8 m from the centre of the horizontal frame, with a bait canister filled with 1 kg of mashed pilchards (*Sardinops sagax*) fastened to its end. To allow later synchronisation of left and right cameras, a temporal sequence was established using a clapperboard.

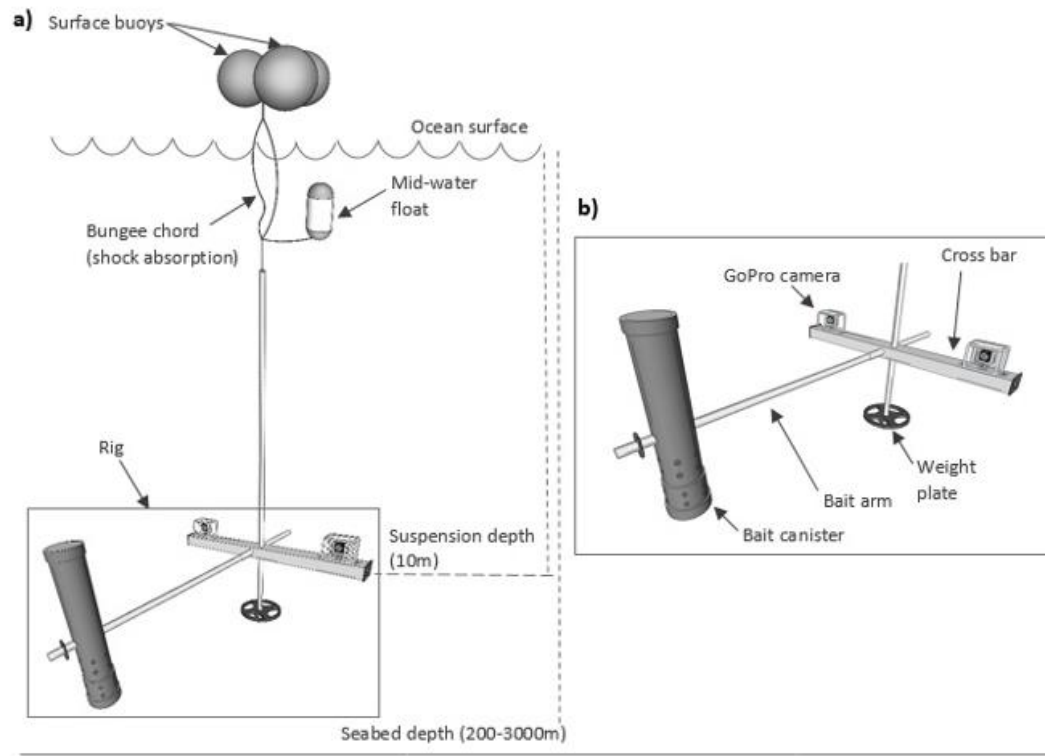


Figure 2 –Schematic diagrams of (a) the configuration of a deployed mid-water stereo-BRUVS and (b) a standard mid-water stereo-BRUVS. Adapted from P.Bouchet.

Data selection

Video footage for this study was selected from a large meta-dataset of 726 mid-water stereo-BRUVS deployments across the BIOT, Palau and New Caledonia. These videos were previously analysed to identify all animals to the lowest taxonomic level possible and generate a conservative measure of relative abundance, MaxN, the maximum number of individuals of the same species appearing in the field of view at any one time on a given sample (Harvey et al., 2007). A total of 698 sharks were identified, representing seven species from five families, and were present at 25.3% of deployments.

Video footage to be used in this study was extracted based on the following focal species being present: silvertip (*Carcharhinus albimarginatus*), grey reef (*Carcharhinus*

amblyrhynchos) and silky (*Carcharhinus falciformis*) sharks. All three species are considered top order predators based on their trophic level, they are caught in commercial and recreational fisheries and exhibit relatively high vulnerability and low resilience to fishing pressure (Froese and Pauly 2016). A subset of data was then selected to ensure a range of deployments were included (i.e. a range of species and abundances), where video footage from only a single stereo-BRUVS was selected from each longline to ensure independence of samples. The final set of videos consisted of 35 mid-water stereo-BRUVS deployments.

Video conversion and analysis

All videos were converted from MP4 to XVID format using Xilisoft video conversion software. Video analysis was then conducted using EventMeasure, a software program that enables precise length measurements and recording of behavioural ‘events’ (SeaGIS 2008; Letessier et al. 2015). Videos were analysed for the full duration of the deployment, from the moment the rig settled in the water column to the beginning of the rig retrieval. During video analysis, each time a shark entered the camera’s field of view, a fork length measurement (tip of the snout to the fork of the tail) along with any unique identifying markers such as fighting or mating marks, hooks or unique body markings were recorded and individuals were coded by species, followed by a unique three digit reference number (E.g.: *Carcharhinus falciformis* = FAL001). To define unique individuals amongst the records, sharks were firstly identified by unique markings and fork length. Secondly, unique individuals were distinguished by their co-occurrence on imagery. The total number of individuals assigned per mid-water stereo-BRUVS deployment represented a realistic estimate of each deployments original MaxN (**Appendix 1**). This individual assignment process identified a total of 168 individuals across 35 deployments, including 17 individuals for which length measurements were unachievable either due to camera angle or distance from the stereo-BRUVS. Individual behaviours were recorded based on an ethogram, which was developed from a combination of previously defined behaviours described by Martin (2007), Myrberg Jr and Gruber (1974) and Thompson (2014), and new behaviours observable on a subset of pre-reviewed videos not included in the final analyses (**Table 1**). New behaviours were added to the ethogram if they were distinctive and could be clearly defined.

Table 1 – Ethogram developed to classify behaviours of sharks occupying the pelagic environment, consisting of a combination of previously identified behaviours (indicated by superscript), with new definitions being developed for behaviours of interest where previous research could not be sourced. BL = body length and Hz = frequency per second. Adapted from ^aMartin 2007; ^bMyrberg and Gruberg 1974; ^cThompson 2014.

Class	Behaviour	Definition
Entries/Exits	Enter	First point at which the shark is visible in both camera's fields of view
	Exit	Last point at which the shark is visible in both camera's fields of view
Direct behaviours	Approach	Approaching the stereo-BRUVS to within 2-3 BL, as if to make contact, before veering away
	Bite ^c	Closure of jaw on receiver, bait arm or animal and contact with teeth
	Charge ^a	Fast (2-3+ BL/s) approach towards the stereo-BRUVS, often terminated by veering away on a perpendicular course within a distance of 1-2 BL
	Feeding	Consumption of bait (released from bait canister)
	Nictitating ^c	Closing of the nictitating membrane >30% of the eye
	Nudge	Contact with the bait canister with snout or head
	Ramming ^a	A shark using its rostrum to forcefully strike the bait canister, often causing it to retreat or recoil
	Indirect behaviours	Circling
Head shake ^a		Rhythmic, exaggerated lateral shaking of the head, usually rapid (>2 Hz) and through an arc of >30°
Head snap		Singular, exaggerated lateral whip of the head
Hunch ^b		Arching of the back with the tail slightly lowered and head slightly raised, so that the body forms an reversed "U" shape
Jaw gape ^{a, c}		A slow, exaggerated opening of the jaw (\pm approximately 30-90°, estimated as the angle formed at the mouth commissure), conspicuously wider than during ram ventilation
Patrolling ^b		Relatively straight-line swimming pattern, with usual swimming position
Pectoral fin depression ^a		A sustained (>5 s), bilateral lowering of the pectoral fins from usual swimming position
Rapid, tight pattern swimming (RTSP) ^a		Fast (2-3+ BL/s) swimming marked by sudden and frequent changes in direction
Rapid withdrawal ^a		Rapid movement of the shark away from the stereo-BRUVS at ≥ 3 BL/s, initiated by several strong tail beats followed by a long glide covering ≥ 5 m

Behavioural responses: composition, frequency and timing

Video analysis allowed for the quantification of three behavioural responses. Behavioural composition was derived from the total number of displays of each behaviour type per individual. The frequencies of four behaviours: direct and indirect behaviours, where direct behaviours are those that involve bait-associated interactions and indirect are behaviours that do not, along with approaches and nictitating frequency were examined as they are predicted to provide substantial information about the level of agonistic intent (Thompson 2014). Finally, five behavioural timing metrics were calculated (**Table 2**) as they were predicted to provide information on variations in an individual's propensity to take "risks" and likelihood to investigate novel stimuli (Coleman and Wilson 1998; Dingemans and Reale 2005).

Table 2 – Summary of behavioural timing metrics, measured from when the mid-water stereo BRUVS settled at ten metres within the water column.

Time metric	Acronym	Definition
Time of first arrival	TFA	Total time from stereo-BRUVS settlement to first entry
Time of first behavioural display	TFA	Total time from individual's first entry to first behavioural display, excluding entries and exits
Span	Span	Total time from first entry to last exit. Represents total time spent within the surrounding area
Total time in field of view	TTFoV	Total time between an animal's entry and exit. Represents total time spent in the camera's field of view
Mean total time spent in field of view	mTTFoV	Mean total time in field of view

Statistical analysis

A chi-squared contingency test (χ^2) was first conducted in Microsoft Excel 2015 to determine if behavioural composition varied between measured and unmeasured sharks, where a non-significant result indicates that the behaviour of measured individuals can be used as a representative sample for the whole dataset. Consequently, unmeasured sharks were excluded from the following analyses. Subsequently, all data were analysed using PRIMER 6 with the PERMANOVA+ add-in. Additional visual representations of data were achieved using Microsoft Excel 2015 and R Studio 2015. Within all analyses, each stereo-BRUVS deployment was treated as a replicate, but were not grouped into sites as there was no consistent spatial structure across locations.

Due to the unbalanced nature of this study's dataset and the potential covariation between location and species, where some species were absent from some locations and particular species were strongly associated with a given location, it was not possible to examine differences in these two factors within the same analysis. The data were thus analysed in two ways. First, location differences were tested within each species independently using one-way permutational analyses of covariance (PERMANCOVAs) with fork length as a covariate. Second, species differences were examined within the BIOT using PERMANCOVAs with fork length as a covariate, as the BIOT was the only location in which all three species occurred in adequate abundance. Permutational methods are a widely accepted and robust method of analysing composition, frequency and timing data, as they make few assumptions about the form and distribution of the data (Clarke and Warwick 2001). They are robust to non-normally distributed and unbalanced datasets with high zero counts, whilst allowing for the addition of covariates (Clarke and Warwick 2001).

One-way PERMANCOVAs, with fork length as a covariate, were used to test differences in behavioural composition, frequency and timing among locations within each species and among species within the BIOT. For the analysis of behavioural composition, the counts of behaviours for each animal were square-root transformed to moderately reduce the influence of common behaviours and increase the influence of rare behaviours. Resemblance matrices were computed on Bray-Curtis with an additional dummy variable (+d). A dummy variable was included as joint zeros were present in the data and, in its absence, the resemblance matrix would express such joint zeros as "undefined" (Clarke and Warwick 2001; Birt et al. 2012). Dummy variables additionally reduce the influence of outliers (Clarke and Warwick 2001). Euclidean distance matrices (+d) were calculated for each of the four behaviours for which frequency was individually evaluated. Finally, behavioural timing metrics were tested individually using PERMANCOVAs, based on Euclidean distance resemblance matrices (+d) on untransformed data, as time was measured on a single scale. Within the PERMANCOVAs, where fork length was non-significant ($p > 0.05$), it was removed from the analyses and permutational analyses of variance (PERMANOVAs) were computed for either location or species. If fork length reported significance ($p < 0.05$) and no difference among locations or species was detected, distance based linear models (distLM) were utilised to determine fork length's final significance. Where significances were detected, post-hoc analyses using Tukey's pairwise comparisons were used to compare means between pairs of locations or

species. To enable post-hoc analyses on size, fork length was classified into three size classes; small (<1 m), medium (1–1.5 m) and large (>1.5 m).

RESULTS

Video footage from 35 mid-water stereo-BRUVS deployments at three geographical locations was analysed. A total of 4389 behavioural observations (including entries and exits) were made for 168 individual sharks from the three species (silvertip (n=60), grey reef (n=65) and silky (n=43) sharks) (**Table 3**). Only one silky shark was observed in New Caledonia, so it was removed from the analyses.

Table 3 – Species information as a function of location, including number of total behavioural observations recorded (excluding entries) (No. obs), total number of behavioural types (no. type), number of total individuals (No. indiv), number of measured individuals (No. mindiv), mean fork length and standard error (\pm SE) and size range.

Location	Common name	No. obs	No. type	No. indiv	No. mindiv	Length mean \pm SE (cm)	Size range (cm)
BIOT	Grey reef	386	8	26	22	147.9 \pm 21.0	74.5 - 259.4
	Silky	76	3	15	13	203.6 \pm 32.9	133.8 - 256.3
	Silvertip	1528	14	49	46	149.1 \pm 20.3	71.2 - 294.7
Palau	Grey reef	22	1	6	3	149.3 \pm 43.0	138.3 - 162.2
	Silky	232	5	27	25	149.3 \pm 24.7	95.1 - 242.3
New Caledonia	Grey reef	621	15	33	32	121.9 \pm 18.5	68.1 - 250.3
	Silky	1	0*	1	1	171.3	171.3
	Silvertip	166	5	11	9	153.6 \pm 19.4	63.2 - 245.6

*A count of zero (0) for behavioural types means this individual only displayed an entry.

The 167 sharks included 151 (89.9%) individuals for which fork length measurements were taken, varying from 63.2 cm to 294.7 cm with a mean of 148.3 cm \pm 50.7 (SD). PERMANOVAs revealed that silvertip and grey reef sharks exhibited no significant differences in size between locations, however silky sharks were significantly larger within the BIOT, compared to Palau (N = 43, df =1, p = 0.0002; PERMANOVA) (**Figure 3**). Within the BIOT, where all three species were present, silky sharks were significantly larger than both silvertip (p = 0.0008; Tukey) and grey reef (p = 0.001; Tukey) sharks.

For the 151 measured individuals, a total of 1035 behavioural observations (excluding entries and exits) were recorded from a suite of 17 behaviours. The remaining unmeasured individuals (n = 17) generated 323 behavioural observations (excluding entries and exits). There was no difference in the behavioural composition of measured and unmeasured individuals ($X^2_{0.05,4} = 3.1$, p = 0.54). Behavioural composition for all 167 sharks was dominated

by approached (47.2%), patrolling (13.3%), nictitating (13.3%) and nudging (10.3%) (**Figure 4**).

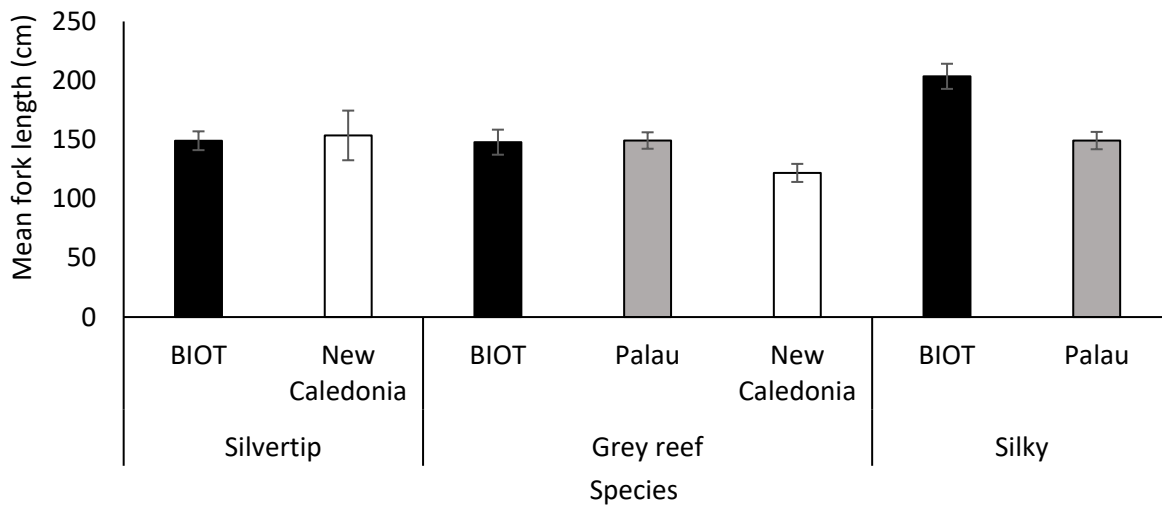


Figure 3 – Mean fork length \pm standard error (SE) for three species across their corresponding geographical locations. Note that the single individual silky shark recorded in New Caledonia has been omitted from this figure.

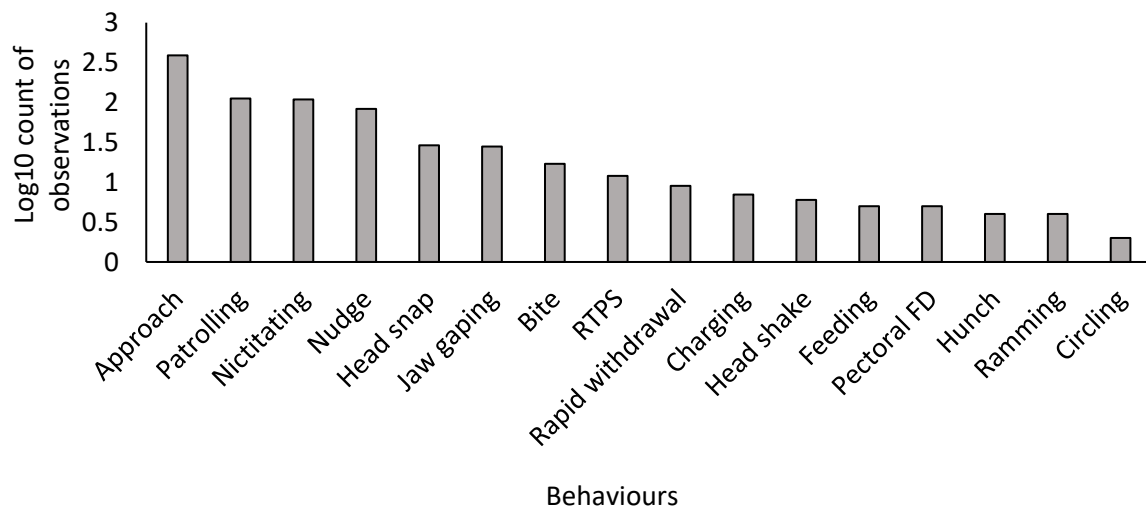


Figure 4 – Log transformed counts of behavioural observations for all 167 individuals over 35 deployments within the British Indian Ocean Territory, Palau and New Caledonia.

Location differences

Behavioural composition

Location-specific variations in behavioural composition were examined within each species independently. Silvertip sharks displayed all 16 behaviours defined in the ethogram across the BIOT and New Caledonia. Behavioural composition varied significantly between these locations ($N = 60$, $df = 1$, $p = 0.003$; PERMANOVA), where silvertip sharks within the BIOT exhibited more diverse behavioural composition and were dominated by approaches, compared

to their conspecifics in New Caledonia, whose composition largely consisted of patrolling (Figure 5).

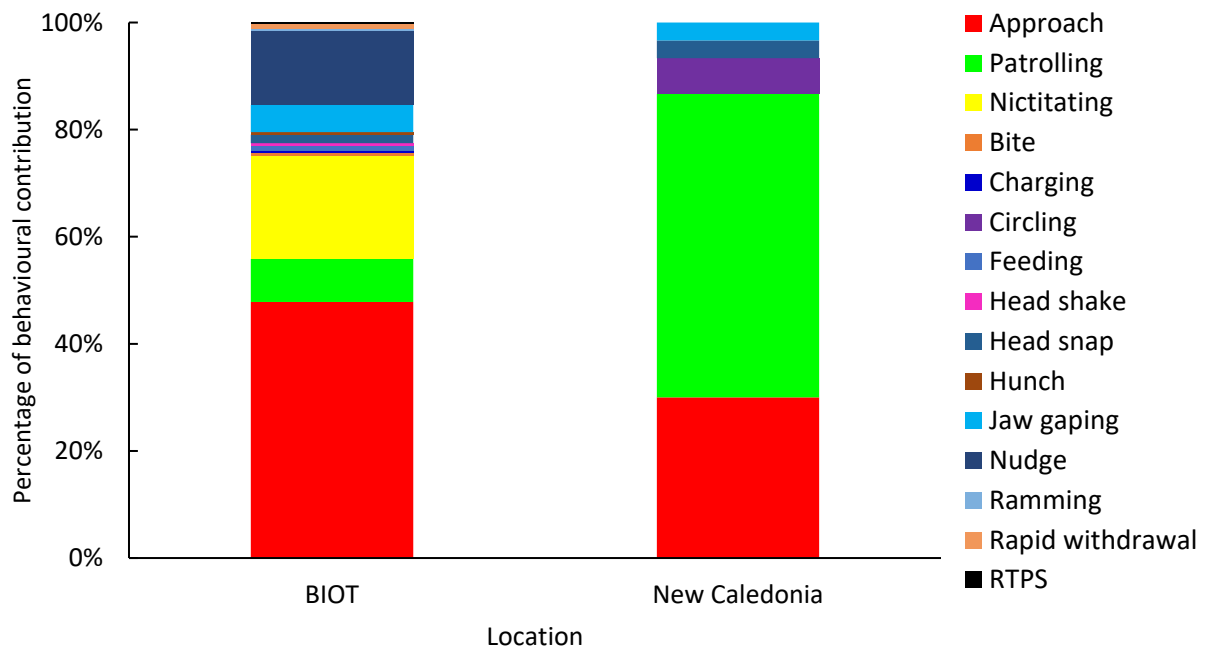


Figure 5 – Percentage contribution of behaviours for silvertip sharks within the British Indian Ocean Territory (BIOT) and New Caledonia. RTPS represents rapid tight swimming pattern. Note no silvertip sharks were observed within Palau.

Grey reef sharks only exhibited seven of the 16 defined behaviours at three locations, and no location differences in behavioural composition were detected ($N = 65$, $df = 2$, $p = 0.21$; PERMANCOVA). Silky sharks were only present at BIOT and Palau and exhibited five defined behaviours, and were also consistent in their behavioural composition between the two locations ($N = 43$, $df = 1$, $p = 0.60$; PERMANCOVA).

Behavioural frequency

Each within-species analyses revealed that direct and indirect behavioural frequencies, along with nictitating frequency, did not vary significantly between locations. Location differences in approach frequency varied depending on the species considered, with no difference found between locations within grey reef ($N = 65$, $df = 2$, $p = 0.73$; PERMANCOVA) or silky ($N = 43$, $df = 1$, $p = 0.53$; PERMANCOVA) sharks. Within silvertip sharks, individuals within the BIOT displayed significantly higher frequencies of approaches, compared to their conspecifics in New Caledonia ($N = 60$, $df = 1$, $p = 0.04$; PERMANCOVA; **Figure 6**).

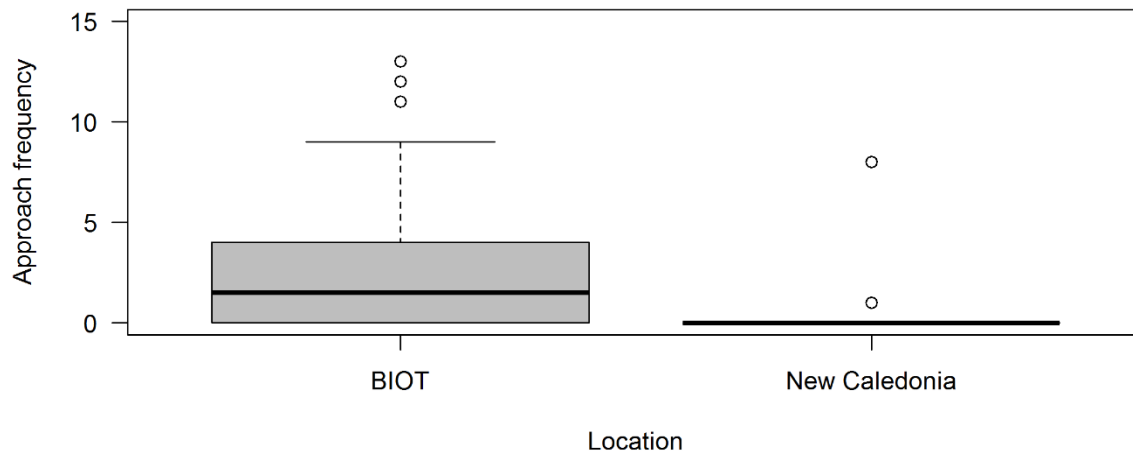


Figure 6 – Variations in silvertip shark approach frequency between the British Indian Ocean Territory (BIOT) and New Caledonia. For the purpose of graphical representation, two outliers of 53 and 24 approach displays within the BIOT were removed.

Behavioural timing

Location differences in behavioural timing varied depending on the species considered. Silvertip sharks in New Caledonia remained in the camera’s field of view (TTFoV) for significantly longer than their conspecifics within the BIOT, whilst also demonstrating significantly longer span and time to first behavioural display (TFA) (**Figure 7**). Grey reef sharks in New Caledonia exhibited significantly earlier time of first arrival compared to their conspecifics in the BIOT ($p = 0.0001$; Tukey) and Palau (0.004 ; Tukey). Furthermore, New Caledonian grey reef sharks demonstrated longer spans than their conspecifics within the BIOT ($p = 0.0004$; Tukey) and marginally longer span than conspecifics within Palau ($p = 0.05$; Tukey) (**Figure 7**). Behaviour timing of silky sharks was consistent across all locations (**Figure 8**).

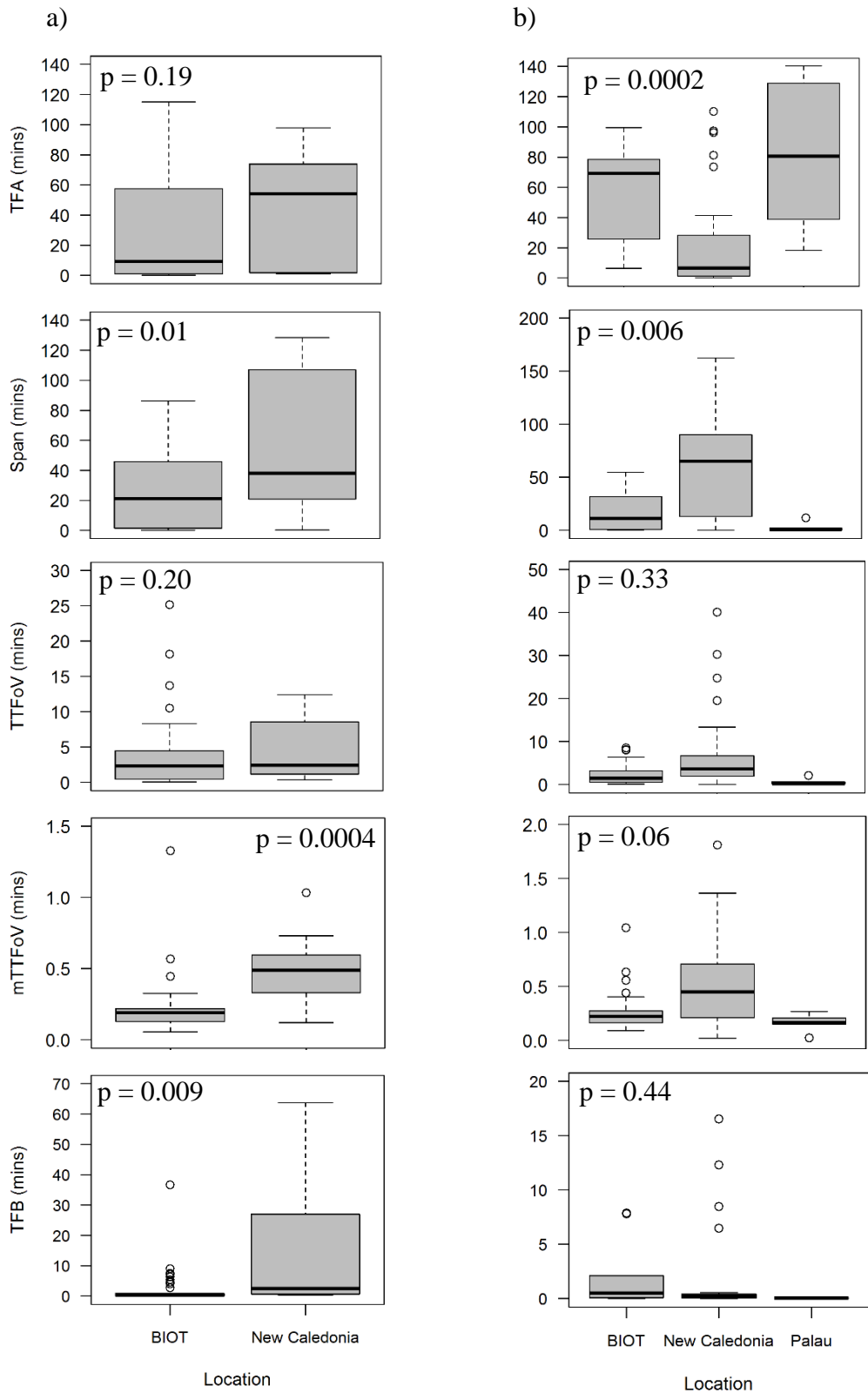


Figure 7 – Variations in behavioural timing tested by one-way permutational analysis of covariance (PERMANCOVA) by location effects within **(a)** silvertip sharks (left column) and **(b)** grey reef sharks (right column), including time of first arrival (TFA), span, total time in field of view (TTFoV), mean time in field of view (mTTFoV) and time from first entry to first behaviour (TFB). BIOT represents the British Indian Ocean Territory.

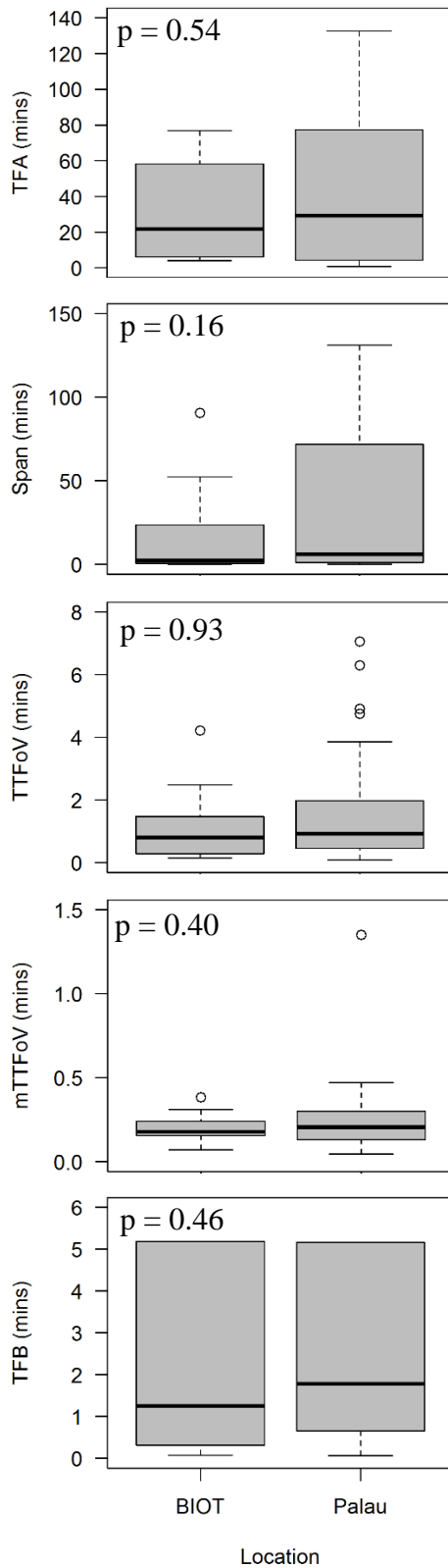


Figure 8 – Variations in behavioural timing by silky sharks tested by one-way permutational analysis of covariance (PERMANCOVA) between the British Indian Ocean Territory (BIOT) and Palau, including time of first arrival (TFA), span, total time in field of view (TTfOV), mean time in field of view (mTTfOV) and time from first entry to first behaviour (TFB).

Species differences

Behavioural composition

Behavioural composition varied significantly between all three species within the BIOT ($N = 90$, $df = 2$, $p = 0.003$; PERMANCOVA). Silvertip sharks displayed significantly more diverse behavioural composition than both grey reef ($p = 0.01$; Tukey) and silky ($p = 0.0004$; Tukey) sharks, with no difference was detected between the latter two species ($p = 0.18$; Tukey) (**Figure 9**).

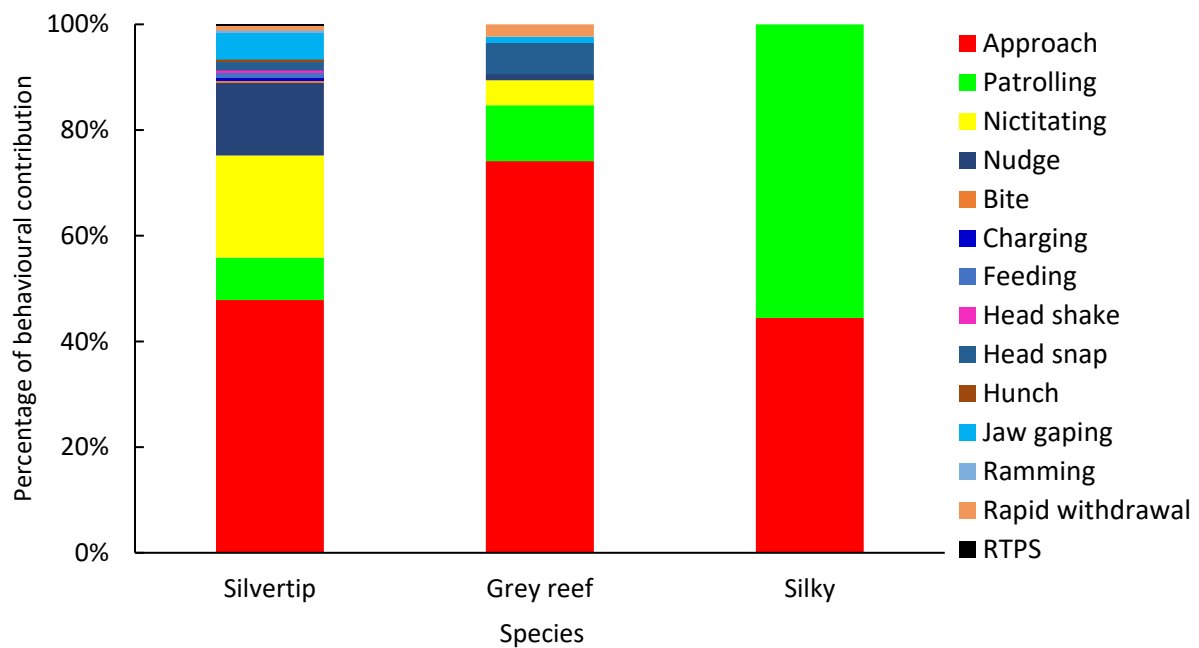


Figure 9 – Percentage contribution of behaviours of three species: silvertip, grey reef and silky sharks within the British Indian Ocean Territory (BIOT). RTPS represents rapid tight swimming pattern.

Behavioural frequency

Within the BIOT, all species displayed significantly different frequencies of direct behaviours ($N = 90$, $df = 2$, $p = 0.02$; Tukey) and nictitating displays ($N = 90$, $df = 2$, $p = 0.02$; PERMANCOVA). Silvertip sharks exhibited significantly higher frequencies of both direct and nictitating behaviours, compared to grey reef ($p = 0.01$, $p = 0.02$ respectively; Tukey; **Figure 10**) and silky (both $p = 0.02$; Tukey; **Figure 10**) sharks. Grey reef and silky sharks displayed no significant differences in their frequency of direct behaviours ($p = 0.27$; Tukey) and nictitating displays ($p = 0.28$; Tukey). Species within the BIOT did not vary significantly in their frequency of indirect ($N = 90$, $df = 2$, $p = 0.08$; PERMANCOVA) or approach ($N = 90$, $df = 1$, $p = 0.07$; PERMANCOVA) displays.

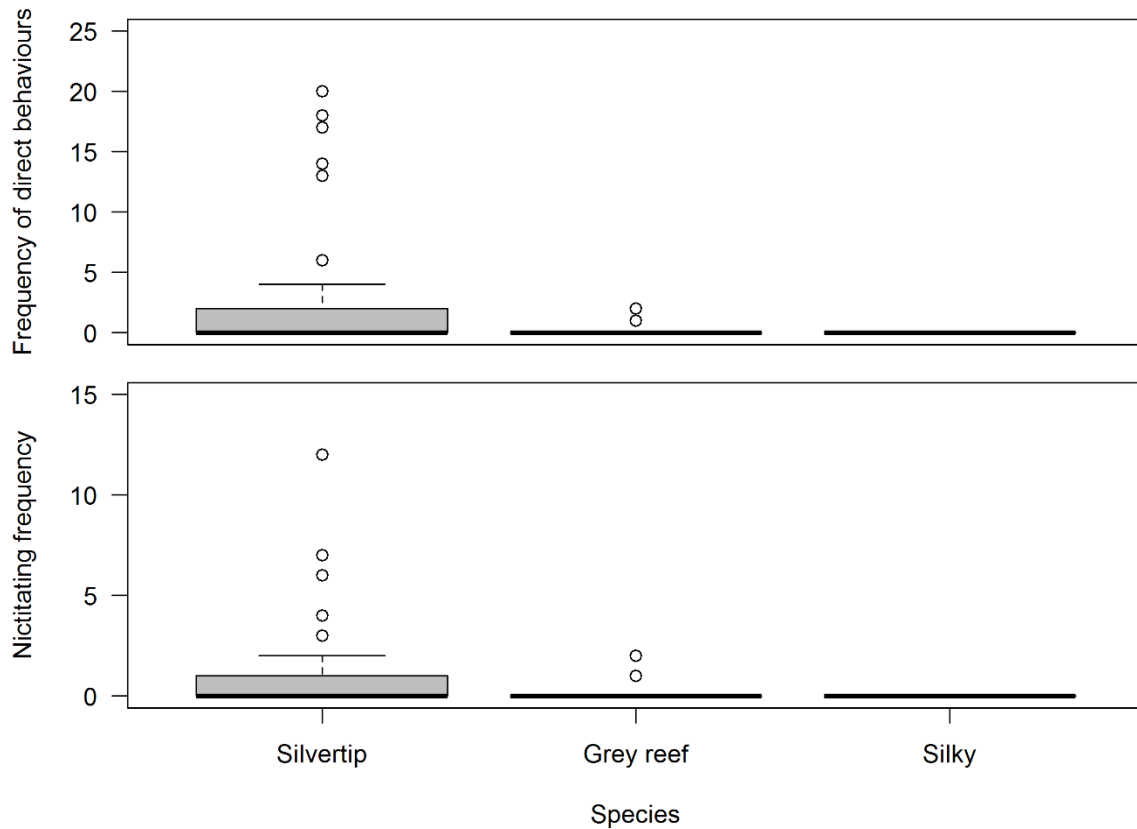


Figure 10 – Variations in direct and nictitating frequency between three species of sharks within the British Indian Ocean Territory (BIOT). For the purpose of graphical representation, an outlier of one silvertip shark exhibiting 19 nictitating displays was removed.

Behavioural timing

Within the BIOT, grey reef sharks exhibited later time of first arrival compared to the other two species with the BIOT, however this was confounded by a significant two-way interaction between species and size ($N = 90$, $df = 2$, $p = 0.03$; PERMANCOVA). No species differences were detected on the remaining four timing responses (**Figure 11**).

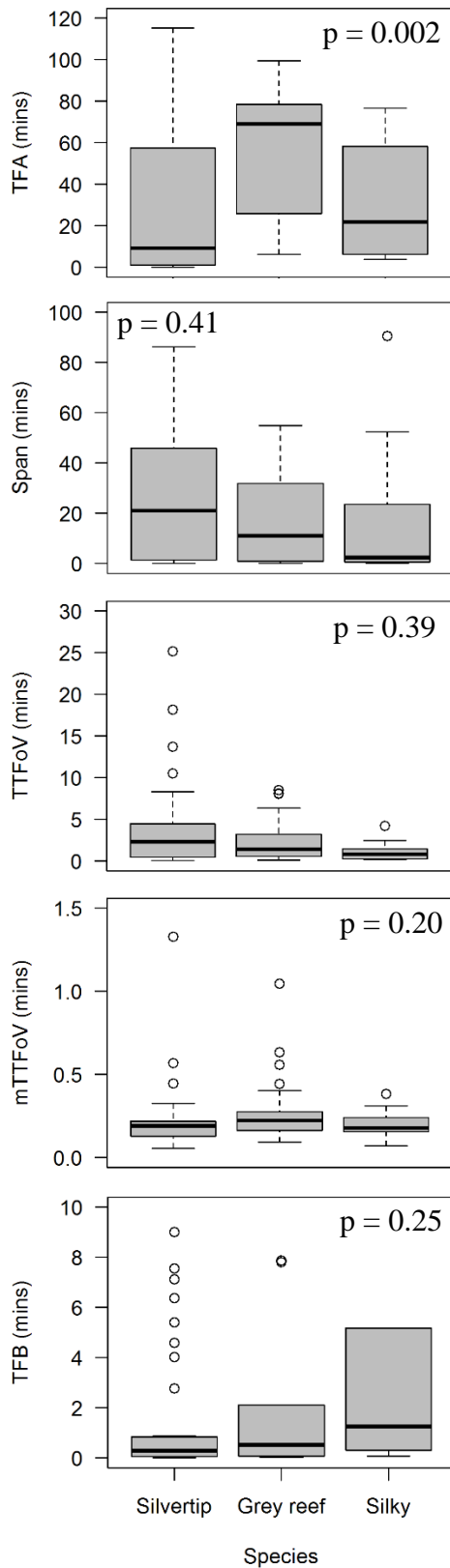


Figure 11 – Variations in species-specific behavioural timing in the three species within the British Indian Ocean Territory (BIOT) (right column), including time of first arrival (TFA), span, total time in field of view (TTfFoV), mean time in field of view (mTTfFoV) and time from first entry to first behaviour (TFB). Tested by one-way permutational analysis of covariance (PERMANCOVA).

Size differences

Behavioural composition

The classification of individuals into size classes resulted in a total of 25 small, 64 medium and 62 large sharks. Size-specific differences in behavioural composition were consistent across all locations and species, where large sharks exhibited significantly less diversity in their behavioural compositions, compared to small ($p = 0.0001$; Tukey) and medium ($p = 0.0002$; Tukey) sharks (**Figure 12**).

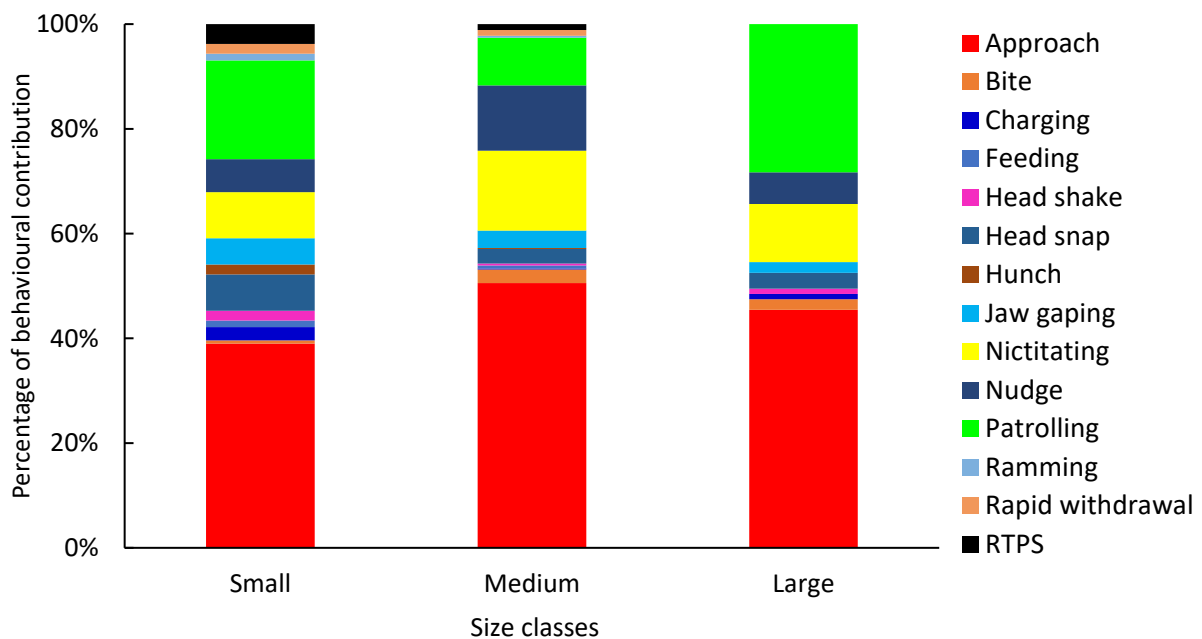


Figure 12 – Percentage contribution of behaviours of all sharks across all three species (silvertip, grey reef and silky sharks) and locations (British Indian Ocean Territory (BIOT), Palau and New Caledonia), as a function of size classes. All size classes were measured through fork length and were categorised as follows: small < 1 m, medium = 1-1.5 m and large > 1.5 m. RTPS represents rapid tight swimming pattern.

Behavioural frequency

Behavioural frequency varied with size depending on the species and location considered (**Table 4**). With one exception, all pairwise comparisons revealed that larger sharks consistently displayed significantly lower behavioural frequencies than both small and medium size sharks, regardless of the behaviour type. Furthermore, small and medium sharks exhibited no significant differences in their frequency of behavioural displays. Indirect frequency in silky sharks were the exception, where large sharks only exhibited significantly lower frequencies of indirect displays compared to medium sharks ($p = 0.003$; Tukey), but not small sharks ($p = 0.39$; Tukey).

Table 4 – Results of fork length as a covariate in independent PERMANCOVAs on direct, indirect, approach and nictitating frequency. Bold represents significance.

Frequency metric	Silvertip				Grey reef			
	df	SS	F	P(perm)	df	SS	F	P(perm)
Direct	1	2.95	1.46	0.24	1	2.51	3.29	0.09
Indirect	1	13.63	6.46	0.01*	1	16.50	10.12	0.002*
Approach	1	6.93	3.59	0.07	1	8.94	6.52	0.01*
Nictitating	1	1.59	1.46	0.24	1	0.19	0.58	0.45

Table 4 continued

Frequency metric	Silky				BIOT			
	df	SS	F	P(perm)	df	SS	F	P(perm)
Direct	1	0.93	6.29	0.01*	1	6.45	4.56	0.04
Indirect	1	6.68	17.91	0.0004*	1	34.23	18.24	0.0001*
Approach	1	4.80	16.61	0.61	1	20.89	11.95	0.0005*
Nictitating	1	0.02	0.60	0.50	1	3.72	4.79	0.03

*Indicates significance result derived from distance based linear modelling (distLM)

Behavioural timing

Silvertip and silky sharks exhibited no significant differences in behavioural timing as a function of size. However, small grey reef sharks exhibited significantly earlier time of first arrival compared to their medium ($p = 0.02$; Tukey) and large ($p=0.0003$; Tukey) conspecifics (**Figure 13**). Furthermore, large sharks exhibited significantly shorter span and total time in the camera's field of view, compared to both small ($p = 0.004$, $p = 0.01$ respectively; Tukey) and medium ($p = 0.005$, $p = 0.02$ respectively; Tukey) sized conspecifics (**Figure 13**).

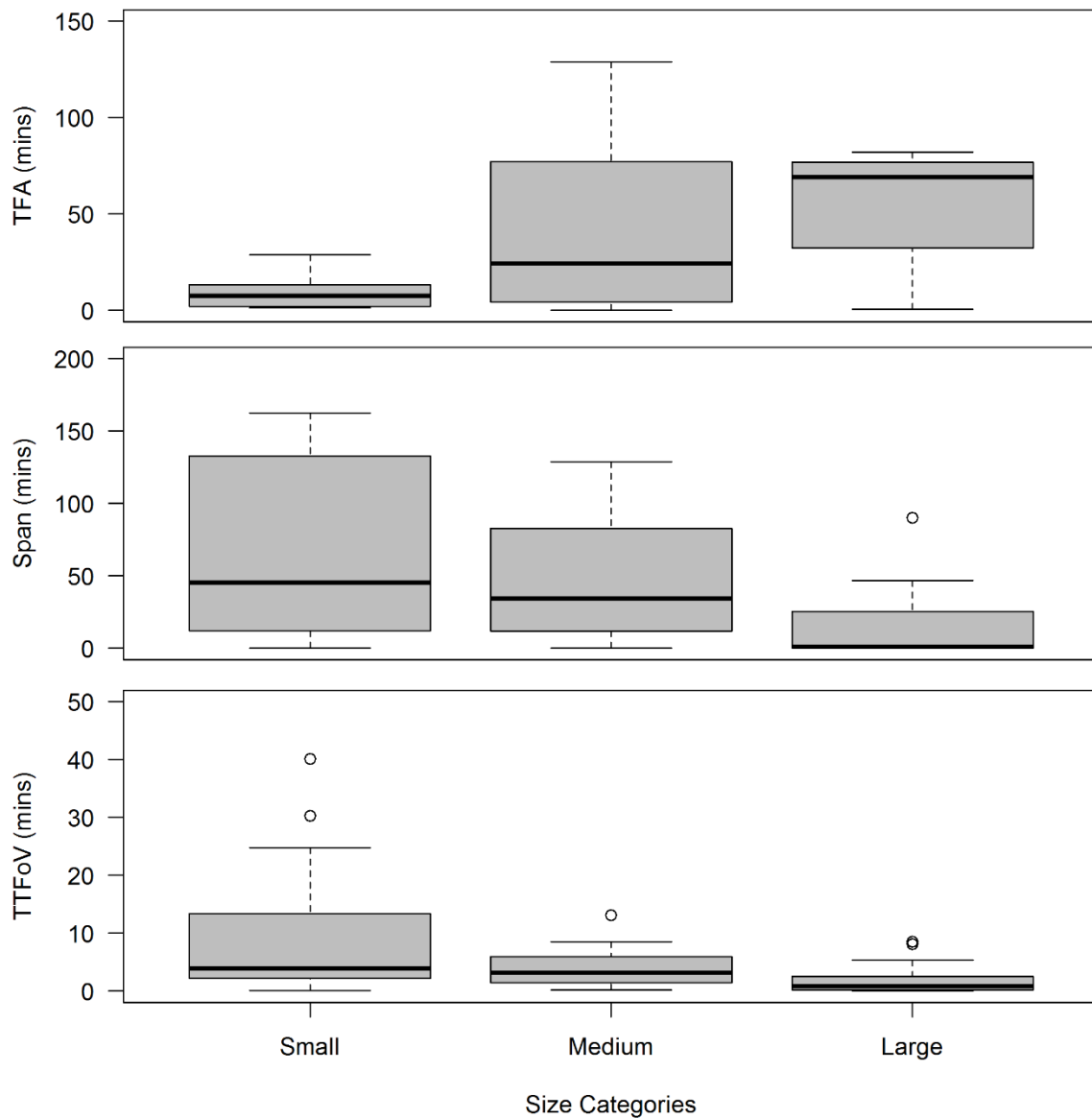


Figure 13 – Size differences in time of first arrival (TFA), span and total time spent in the field of view (TTFoV) for grey reef sharks. All size classes were measured by fork length and were categorised as follows: small < 1 m, medium = 1-1.5 m and large > 1.5 m.

Within the BIOT, smaller sharks, regardless of species, remained in the camera’s field of view for significantly longer than large sharks ($N = 90$, $df = 2$, $p = 0.007$; PERMANOVA) (**Figure 14**). Furthermore, a significant two-way interaction was reported between species and size for time of first arrival ($N = 90$, $df = 2$, $p = 0.02$; PERMANCOVA). Species independent analyses revealed that silvertip ($N = 49$, $df = 2$, $p = 0.63$; PERMANOVA) and silky ($N = 15$, $df = 1$, $p = 0.16$; PERMANOVA) exhibited no difference in timing of first arrival with size. However, grey reef sharks within the BIOT varied significantly in their time of first arrival as a function of size ($N = 26$, $df = 2$, $p = 0.04$; PERMANOVA), where large sharks entered the field of view significantly later than small sharks ($p = 0.02$; Tukey; **Figure 15**).

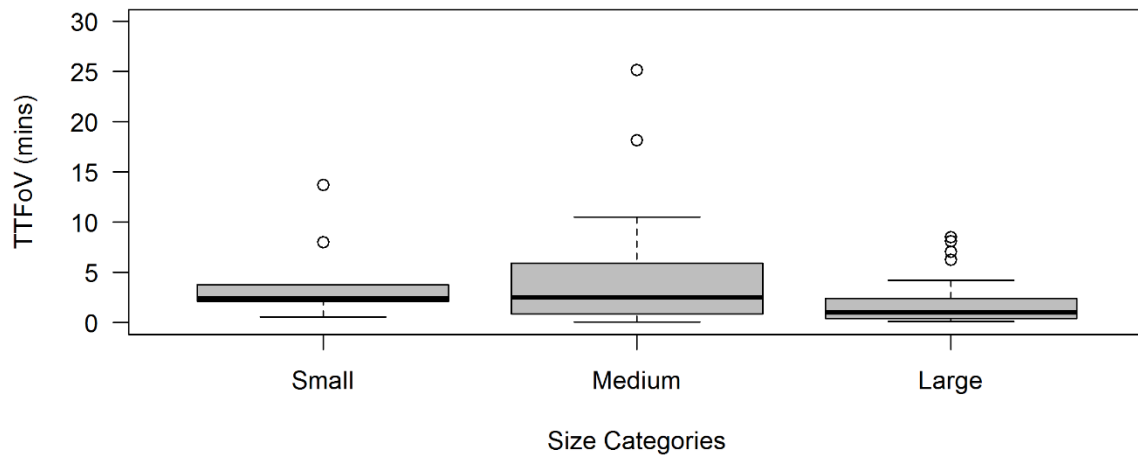


Figure 14 –Total time spent in the field of view (TTFoV) for sharks within the British Indian Ocean Territory (BIOT), as a function of size. All size classes were measured by fork length and were categorised as follows: small < 1 m, medium = 1-1.5 m and large > 1.5 m.

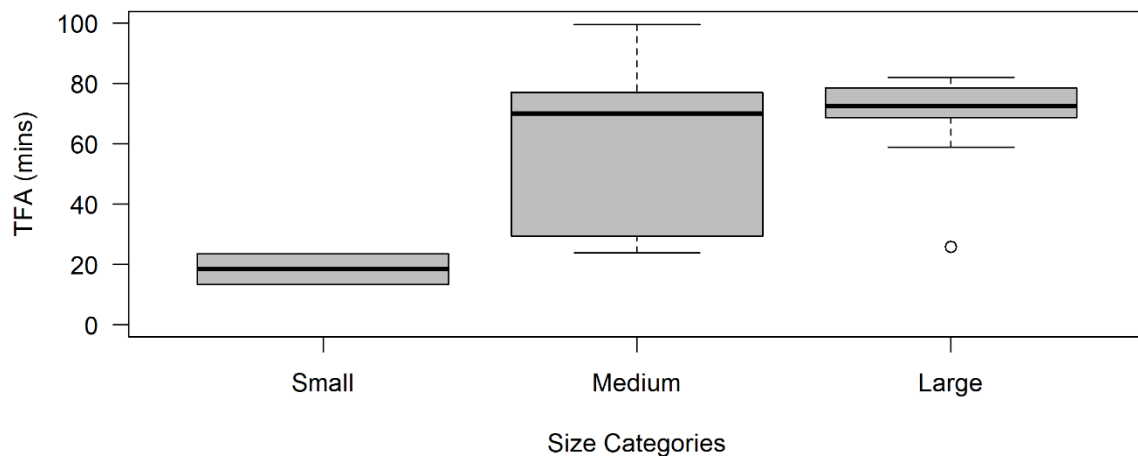


Figure 15 –Size differences in total of first arrival for grey reef sharks within the British Indian Ocean Territory (BIOT). All size classes were measured by fork length and were categorised as follows: small < 1 m, medium = 1-1.5 m and large > 1.5 m.

DISCUSSION

The primary objective of this study was to examine location, species and size differences in the behavioural responses of three species of sharks occupying the pelagic environment. Overall, within the scope of this study, size was found the most consistent predictor of shark behaviour, where when significant, large sharks exhibited consistently fewer behaviours at lower frequencies, compared to small and medium sized sharks, regardless of geographical location or species. Furthermore, larger sharks took longer to investigate the mid-water BRUVS and on average, they remained in the camera's field of view and area surrounding the mid-water stereo-BRUVS for significantly less time than smaller sharks. The effects of location and species on behaviour were less consistent, varying with respect to the metrics considered. This

study also demonstrates that mid-water stereo-BRUVS are capable of extracting large amounts of behavioural data on sharks in the pelagic realm.

Location differences

Silvertip sharks displayed the most consistent behavioural differences between locations, where sharks within the BIOT tended to be more overt in their behavioural displays compared to silvertip sharks within New Caledonia. Furthermore, silvertip sharks within the BIOT exhibited higher frequencies of bait associated behaviours including approaches and nictitating, compared to New Caledonia, where the behavioural composition of silvertip sharks was dominated by a non-direct behaviour, patrolling. It is possible that these behavioural differences are the result of varying levels of fishing pressure between the two locations. Sharks under high fishing pressure may be less likely to engage with novel stimuli as they have potentially experienced negative interactions with fishing gear, causing cautiousness and active avoidance. Prior studies support this theory, suggesting that sharks have the capacity to learn from encounters with commercial and recreational fisheries, where individuals that survive direct encounters with fishing gear are likely to be more cautious or actively avoid novel stimuli in the future (Gilman et al. 2008; Guttridge et al. 2009). Manire and Gruber (1993) also demonstrated learnt net avoidance in juvenile lemon sharks (*Negaprion brevirostris*), where sharks became increasingly more difficult to catch in gillnets with increased capture attempts.

Behavioural timing also varied between locations, however the observed patterns were not consistent with the theory that sharks become cautious or actively avoid novel stimuli where fishing is present. For instance, grey reef sharks within New Caledonia entered the camera's field of view significantly earlier than their conspecifics within the BIOT and Palau. It is possible that this difference in the timing of first arrival is simply due to the higher abundance of grey reef sharks within New Caledonia, compared to the other two locations. Additionally, silvertip and grey sharks in the unprotected waters of New Caledonia remained around the stereo-BRUVS for significantly longer than their conspecifics in the protected regions. Location-specific variables not considered in this study could potentially be driving these differences. Environmental variables such as temperature and habitat have been reported to influence sharks behaviours, for example aggregation size (Economakis and Lobel 1998) and vertical migration (Vianna et al. 2013) in grey reef sharks. However, currently no fine scale environmental data exists at the level of stereo-BRUVS deployments, presenting a current knowledge gap.

Silky shark's behaviour remained consistent across locations. Silky sharks are yet to be the primary focus of in depth behavioural studies, despite being one of the most heavily targeted shark species in pelagic fisheries (Stevens et al. 2000; Simpfendorfer et al. 2002; Cortés et al. 2010). Due to their high vulnerability to overexploitation, future research should focus on examining silky shark behaviour across a variety of different locations, with the aim of gaining a deeper insight into the potential factors influencing their vulnerability to baited fishing gear. Although silky sharks exhibited no behavioural differences between locations, they were significantly larger within the BIOT, compared to their conspecifics within New Caledonia, suggesting that silky sharks may still be experiencing some benefits of the high protection level within the BIOT.

Species differences

Within the BIOT, silvertip sharks displayed significantly more diverse behavioural composition compared to grey reef and silky sharks, and were found to be the most overt with regards to their behavioural frequency, specifically exhibiting approaches, patrolling and nictitating displays. This finding is consistent with a previous study that found silvertip sharks to be particularly overt in their behavioural displays (Martin 2007).

Although this study's findings suggest that silvertip sharks are the most active species, previous behavioural studies have also found grey reef sharks to be one of the more active shark species (Johnson and Nelson 1973; Martin 2007). Behaviours such as hunching and pectoral fin depression play a normal role in social encounters within the grey reef sharks and are considered accurate predictors of defensive behaviour (Johnson and Nelson 1973; Martin 2007). Coleman and Wilson (1998) determined that animals that exhibit bold social interactions such as grey reef sharks are also expected to be bold with respect to engaging with novel stimuli. Such as trend was found in this study, where grey reef sharks were the only species to exhibit pectoral fin depressions and their hunch frequency was twice that of silvertip and silky sharks, although these differences could not be statistically tested due to their low frequency of occurrence.

Species differences in visual, olfactory or auditory sensitivity may also explain differences in behavioural timing between species (Cappo et al. 2006; Thompson 2014; Collin et al. 2015). Løkkeborg & Bjørndal (1992) reported that bait type is one of the most important gear parameters influencing species selectivity of longlines, due to species variations in foraging behaviour and reliance on olfaction. The degree to which this influences sampling by mid-

water BRUVS is currently unknown. Additionally, Bres (1993) found that visual cues are extremely important in triggering agonistic displays in grey reef sharks. Therefore, it is possible that simply the presence of the stereo-BRUVS in the water column, irrespective of the bait used, is enough to trigger agonistic displays in grey reef sharks.

Size differences

This study detected significant changes in shark's behavioural responses as a function of size. On average, large sharks exhibited consistently fewer behaviours in lower frequencies, exhibited later time of first arrival and remained on the camera's field of view for significantly less time, compared to small and medium sized sharks, regardless of species or location. It is important to acknowledge that a significant two-way interaction was detected between species and size on the timing of first arrival within the BIOT, suggesting that there is some covariation between these two factors. However, the same trend in size differences was detected, where larger grey reef sharks entered significantly later than their small conspecifics. The consistent differences in behavioural responses with size detected in this study are consistent with others that have found a strong correlation between body size and behavioural repertoire (Allee and Dickinson Jr 1954; Springer 1967; Gruber and Myrberg 1977; Bres 1993; Schuett 1997; Martin 2007; Lucifora et al. 2009; Sperone et al. 2012). However, few studies have identified factors causing these differences.

Within this study, large sharks represented 41% of all sharks sampled, therefore their minimal interaction with the stereo-BRUVS is not a result of low abundance in the populations sampled. Behavioural differences between size classes could be attributed to the direct relationship between body size and maturity. Larger, and therefore more mature, sharks may have learnt to reduce the likelihood of potential risk of injury by actively avoiding novel stimuli. It could also be argued that behavioural differences as a function of size are the result of fishing-induced selection. Uusi-Heikkilä et al. (2008) suggested that fishing-induced selection acts directly upon behavioural traits, where behaviours that increase encounter probably with fishing gear are selected against. Consequently, larger and more mature sharks have evolved with behaviours that reduce exposure to fishing-induced mortality. It remains unclear whether behavioural differences in sharks are due to associative learning, fishing-induced selection or a combination of both.

Ontogenetic dietary shifts in sharks occurring with increases in body size could be another potential explanation of size-specific variations in shark behaviour (Lowe et al. 1996; Guttridge

et al. 2009; Lucifora et al. 2009). Several studies have found that increased body size in sharks results in a shift from small prey such as teleost fishes and crustaceans to larger prey, including other chondrichthyans (Lowe et al. 1996; Lucifora et al. 2009). Therefore, it is possible that the minimal interaction with mid-water stereo-BRUVS by large sharks is due to the relatively small amount of bait being an insufficient inducement to actively engage with the stereo-BRUVS. Several studies have noted the use large mullet or shark flesh as bait on longlines, with the aim of attracting larger sharks (Sumpton, Lane, et al. 2011; Sumpton, Taylor, et al. 2011). This discrepancy between the type of bait used on longlines and that in stereo-BRUVS may potentially explain the inconsistency between the high catch rates in pelagic fisheries, yet the low frequency of observations on stereo-BRUVS.

The inconsistency between low behavioural observations for large sharks on the mid-water stereo-BRUVS and their declining numbers worldwide due to overexploitation in pelagic fisheries raises the need for better understanding of shark demographics (Fowler et al. 2005; Worm et al. 2013; Dulvy et al. 2014; IUCN 2015). Large, mature sharks are integral to marine ecosystem functioning as they control mesopredator abundance, acting as a buffer against trophic cascades (Fortin et al. 2005; Knight et al. 2005; Lucifora et al. 2009; Ritchie and Johnson 2009). Lowe et al. (1996) and Lucifora et al. (2009) conclude that the reduction or removal of even only the largest sharks within an ecosystem is sufficient to destabilise entire ecosystems (Lucifora et al. 2009). The conflict wherein large sharks are fundamental to ecosystem function, whilst also being the most highly targeted animals within pelagic fisheries, indicates that new management strategies need to be implemented. Furthering our understanding of bait preferences between different sized sharks may aid in reducing catchment of large, ecologically important, sharks. Additionally, the use of stimuli that results in aversion behaviour in sharks may be the next step forward to decreasing overall shark bycatch. Several studies have suggested that by stimulating the electrosensory system in sharks, it is possible to repel them from baited fishing gear (Kaimmer and Stoner 2008; Brill et al. 2009; Jordan et al. 2011). For instance, Jordan et al. (2011) suggested that the negative charge created by lanthanide metals that were deployed around baited longlines both repelled sharks and decreased overall bait consumption.

Applicability of mid-water stereo-BRUVS to behavioural studies

This study demonstrates that mid-water BRUVS are a cost-efficient method of extracting large quantities of behavioural data for sharks occupying the pelagic environment similar to data generated for reef shark behavioural studies (Thompson 2014). Stereo-BRUVS represent a

standardised sampling method, which are particularly applicable for behavioural studies on large marine predators such as sharks, negating the need for diver interference and any issues of safety or risk. Furthermore, the use of high-definition Go-Pro cameras allows for accurate individual length measurements to be achieved without the need for invasive methods (Letessier et al. 2015), which is beneficial as it provides accurate information of size-specific differences to vulnerability to catchability and fishing-induced mortality that is fundamental for the development of future fisheries management strategies. Another major advantage of stereo-BRUVS is that they produce permanent records of all recorded footage (Cappo et al. 2006). Some behaviours can be difficult to identify, particularly those which are rapid such as nictitating. The ability to replay video footage substantially increases the range and precision of identification of different behaviours. Finally, the minimal cost associated with deploying mid-water stereo-BRUVS and the ability to standardise all footage means that these systems can be deployed across large spatial scales with comparable results, as evidenced by this study.

Limitations and future considerations

Although this study provides one of the first insights into shark behaviour at a species level in the pelagic environment, the findings must be considered with caution. One of its limitations is the unreplicated nature of fishing pressure across multiple different geographical locations, meaning inferences into the effects of fishing pressure cannot be extrapolated beyond the locations studied here. However, although there are strong arguments in support of adequate replication, there is emerging recognition of the ecological insights to be gained from unreplicated studies, particularly where research is large scale and replication is either unattainable, such as replicating the BIOT MPA, or logistically costly (Barley and Meeuwig In Review; McAuley et al. 2007; Hillerislambers et al. 2013). Another major limitation of large-scale *in-situ* studies is that no degree of sampling effort can guarantee adequate or balanced sample size. Past studies have acknowledged these challenge, concluding that the inherent exclusivity of large, highly mobile and predatory animals such as sharks, has caused researchers to have small or unbalanced sample sizes (Bres 1993; Guttridge et al. 2009). In the case of this study, differences in species' distribution patterns meant that not all species were found at all three geographical locations, limiting the conclusions that could be drawn. In order to fully understand shark behaviour and make more meaningful, informed decisions with regards to conservation and fisheries management practices, future research should concentrate on increasing sampling effort, with the aim of sampling a wider range of geographical locations, along with increasing the number of species, and individuals within those species,

sampled. Furthermore, collecting behavioural data on sharks from different families and varying trophic levels would also enable wider conclusions to be made with respect to overall shark behaviour. Increasing sampling effort is feasible using mid-water stereo-BRUVS as they are a non-invasive, relatively cost-efficient, standardised method of observation (Cappo et al. 2006; Dorman and Newman 2012).

Identifying individuals using mid-water stereo-BRUVS can prove to be challenging, due to repeated movement in and out of the camera's field of view. The protocol used in this study to identify individuals may potentially be limited as it relies on accurate length measurements as one of the primary means of identification. As a consequence, this method may both underestimate and overestimate the number of individuals present, depending on the tendency to assign new records to either existing or new animals. Individual identification is becoming a growing field in shark studies, such as pattern matching to identify individual whale sharks (*Rhincodon typus*) (Arzoumanian et al. 2005). More research is needed surrounding less easily identifiable species such as those used in this study.

The field of shark behaviour would benefit from expanding on the findings of this study by identifying and measuring other factors that could explain variations in shark behaviour. For example, previous studies have examined the effects of habitat, sex and aggregation size on shark behaviour (Hobson 1963; Mucientes et al. 2009). Additionally, understanding the effects of environmental factors measured at the finite scale of stereo-BRUVS deployments would provide invaluable insight into abiotic factors influencing shark behaviour. Additionally, future research might also consider expanding the ethogram used in this study to include social behaviours and behaviours which include other sensory cues such as sound. Underwater videos have been noted to record dolphin communication (Bräger et al. 1999), and therefore stereo-BRUVS hold the potential to record shark behaviours with sound components, such as tail popping (Martin 2007; Smith et al. 2010). The expansion of this study to include a broader range of behaviours will ultimately increase its applicability to different studies, improving our current understanding of the dynamic state of shark behaviour, especially with respect to interactions with novel stimuli such as fishing gear.

Conclusion

Within the constraints of this study, size was found to be a consistent predictor of shark behaviour, where large sharks, irrespective of species or location, were less active than small sharks. Location- and species-differences in shark behaviour were less consistent. This study

highlights the inherent issues associated with measuring the behaviour of large, highly mobile, predatory sharks, particularly with collecting adequate sample sizes. Regardless of these issues, it is apparent that mid-water stereo-BRUVS, in conjunction with an appropriate ethogram, are capable of extracting large amounts of behavioural data for sharks occupying the pelagic environment. By removing diver limitations, and being non-invasive and cost efficient, these systems represent a valuable resource that can be deployed across any geographical location, assisting in improving shark conservation and fisheries management. This study aids in these improvements by providing information on the species- and size-specific vulnerabilities to fishing gear, along with suggestions for strategies to reduce shark bycatch. Shark behaviour in the pelagic environment remains a relatively new field of study, however this study demonstrates how mid-water stereo-BRUVS hold to potential to vastly expand our current knowledge.

REFERENCES

- Adams PB. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.* 78:1–12.
- Allee WC, Dickinson Jr JC. 1954. Dominance and subordination in the smooth dogfish *Mustelus canis* (Mitchill). *Physiol. Zool.* 27:356–364.
- Arzoumanian Z, Holmberg J, Norman B. 2005. An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *J. Appl. Ecol.* 42:999–1011.
- Barker MJ, Schluessel V. 2005. Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 15:325–347.
- Barley S, Meeuwig J. Accepted. The power and the pitfalls of large-scale, unreplicated natural experiments. *Ecosystems*.
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. 2010. Collapse and conservation of shark populations in the Northwest Atlantic. *Science.* 299:389–392.
- Birt M, Harvey E, Langlois T. 2012. Within and between day variability in temperate reef fish assemblages: learned response to baited video. *J. Exp. Mar. Bio. Ecol.* 916:92–100.
- Bonfil R. 1994. Overview of world elasmobranch fisheries. Food and Agriculture Organization Fisheries Department.
- Bouchet PJ, Meeuwig JJ. 2015. Drifting baited stereo-videography: a novel sampling tool for surveying pelagic wildlife in offshore marine reserves. *Ecosphere.* 6:1–29.
- Bräger S, Chong A, Dawson S, Slooten E, Würsig B. 1999. A combined stereo-photogrammetry and underwater-video system to study group composition of dolphins. *Helgol. Mar. Res.* 53:122–128.
- Bres M. 1993. The behaviour of sharks. *Fish Biol. Fish.* 3:133–159.

- Brill R, Bushnell P, Smith L, Speaks C, Sundaram R, Stroud E, Wang J. 2009. The repulsive and feeding-deterrent effects of electropositive metals on juvenile sandbar sharks (*Carcharhinus plumbeus*). *Fish. Bull.* 107:298–307.
- Cappo M, Harvey E, Shortis M. 2006. Counting and measuring fish with baited video techniques - an overview. *Aust. Soc. Fish Biol. Work. Proc.*:101–114.
- Carrier JC, Musick JA, Heithaus MR. 2012. *Sharks and their relatives II: biodiversity, adaptive physiology and conservation*. United States of America: CRC Press.
- Clark M, Pearce DH, Mees CC. 2015. Update on the catch and bycatch composition of illegal fishing in the British Indian Ocean Territory (BIOT) and a summary of abandoned and lost fishing gear. London: Indian Ocean Tuna Commission.
- Clarke KR, Warwick RM. 2001. *Changes in marine communities: an approach to statistical analysis and interpretation*. 2nd ed. Plymouth: PRIMER-E Ltd.
- Clarke SC, McAllister MK, Michielsens CGJ. 2004. Estimates of shark species composition and numbers associated with the shark fin trade based on Hong Kong auction data. *J. Northwest Atl. Fish. Sci.* 35:453–465.
- Clarke SC, McAllister MK, Milner-Gulland EJ, Kirkwood GP, Michielsens CGJ, Agnew DJ, Pikitch EK, Nakano H, Shivji MS. 2006. Global estimates of shark catches using trade records from commercial markets. *Ecol. Lett.* 9:1115–1126.
- Coleman K, Wilson DS. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* 56:927–936.
- Collin SP, Kempster RM, Yopak KE. 2015. How elasmobranchs sense their environment. In: *Physiology of Elasmobranch Fishes: Structure and Interaction with Environment*. p. 19–99.
- Colton MA, Swearer SE. 2010. A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. *Mar. Ecol. Prog. Ser.* 400:19–36.
- Cortés E. 2000. Life history patterns and correlations in sharks. *Fish. Sci.* 8:299–344.
- Cortés E, Arocha F, Beerkircher L, Carvalho F, Domingo A, Heupel M, Holtzhausen H, Santos MN, Ribera M, Simpfendorfer C. 2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Aquat. Living Resour.* 23:25–34.
- Dingemans NJ, Reale D. 2005. Natural selection and animal personality. *Behaviour* 142:1159–1184.
- Dorman SR, Newman SJ. 2012. Bait effects in sampling coral reef fish assemblages with stereo-BRUVs. *PLoS One* 7:1–12.
- Douillet P, Ouillon S, Cordier E. 2001. A numerical model for fine suspended sediment transport in the southwest lagoon of New Caledonia. *Coral Reefs*. 20:361–372.
- Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LNK, Fordham S V, Francis MP, et al. 2014. Extinction risk and conservation of the world's sharks and rays. *eLife Sci.*:1–34.
- Economakis AE, Lobel PS. 1998. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environ. Biol. Fishes* 51:129–139.

- Feldheim KA, Gruber SH, Ashley M V. 2002. The breeding biology of lemon sharks at a tropical nursery lagoon. *Proc. R. Soc. London B Biol. Sci.* 269:1655–1661.
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. *Ecology.* 86:1320–1330.
- Fowler SL, Cavanagh RD, Camhi M, Burgess GH, Cailliet GM, Fordham S V, Simpfendorfer CA, Musick JA. 2005. Sharks, rays and chimaeras: the status of chondrichthyan fishes. Status Survery. Switzerland and Cambridge, UK: IUCN Publications.
- Froese R, Pauly D. 2016. Fishbase.
- Gilman E, Clarke S, Brothers N, Alfaro-Shigueto J, Mandelman J, Mangel J, Petersen S, Piovano S, Thomson N, Dalzell P, et al. 2008. Shark interactions in pelagic longline fisheries. *Mar. Policy* 32:1–18.
- Graham NAJ, Spalding MD, Sheppard CRC. 2010. Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20:543–548.
- Gruber SH, Myrberg AA. 1977. Approaches to the study of the behavior of sharks. *Am. Zool.* 17:471–486.
- Guttridge TL, Myrberg AA, Porcher IF, Sims DW, Krause J. 2009. The role of learning in shark behaviour. *Fish Fish.* 10:450–469.
- Harper S, Frotté L, Bale S, Booth S, Zeller D. 2009. Reconstruction of total marine fisheries catches for New Caledonia (1950-2007). *Fish. Cent. Res. Reports* 17:67–76.
- Harvey ES, Newman SJ, McLean DL, Cappo M, Meeuwig JJ, Skepper CL. 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fish. Res.* 125:108–120.
- Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology.* 83:480–491.
- Heithaus MR, Frid A, Wirsing AJ, Worm B. 2008. Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* 23:202–210.
- Hillerislambers J, Ettinger AK, Ford KR, Haak DC, Horwith M, Miner BE, Rogers HS, Sheldon KS, Tewksbury JJ, Waters SM, et al. 2013. Accidental experiments: ecological and evolutionary insights and opportunities derived from global change. *Oikos.* 122:1649–1661.
- Hobson ES. 1963. Feeding behavior in three species of sharks. *Pacific Sci.* 17:171–194.
- Holmes BH, Steinke D, Warda RD. 2009. Identification of shark and ray fins using DNA barcoding. *Fish. Res.* 95:280–288.
- IUCN. 2015. The IUCN Red List of Threatened Species. 2015.
- Jackson JBC. 2008. Colloquium paper: ecological extinction and evolution in the brave new ocean. *Proc. Natl. Acad. Sci. U. S. A.* 105:11458–11465.
- Jacoby DMP, Croft DP, Sims DW. 2011. Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish Fish.*:2–19.
- Jennings S, Pinnegar JK, Polunin NVC, Boon TW. 2001. Weak cross-species between body

- size relationships and trophic level belie powerful trophic in fish structuring communities. *J. Anim. Ecol.* 70:934–944.
- Johnson RH, Nelson DR. 1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrhah*, and its relationship to attacks on man. *Am. Soc. Ichthyol. Herpetol.* 1973:76–84.
- Jordan LK, Mandelman JW, Kajiura SM. 2011. Behavioral responses to weak electric fields and a lanthanide metal in two shark species. *J. Exp. Mar. Bio. Ecol.* 409:345–350.
- Kaimmer S, Stoner AW. 2008. Field investigation of rare-earth metal as a deterrent to spiny dogfish in the Pacific halibut fishery. *Fish. Res.* 94:43–47.
- Knight TM, McCoy MW, Chase JM, McCoy KA, Holt RD. 2005. Trophic cascades across ecosystems. *Nature.* 437:880–883.
- Koldewey HJ, Curnick D, Harding S, Harrison LR, Gollock M. 2010. Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. *Mar. Pollut. Bull.* 60:1906–1915.
- Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL. 2010. Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. *Aquat. Biol.* 9:155–168.
- Letessier TB, Juhel JB, Vigliola L, Meeuwig JJ. 2015. Low-cost small action cameras in stereo generates accurate underwater measurements of fish. *J. Exp. Mar. Bio. Ecol.* 466:120–126.
- Løkkeborg S, Bjordal Å. 1992. Species and size selectivity in longline fishing: a review. *Fish. Res.* 13:311–322.
- Lowe CG, Wetherbee BM, Crow GL, Tester AL. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environ. Biol. Fishes* 47:203–211.
- Lucifora LO, Garcia VB, Menni RC, Escalante AH, Hozbor NM. 2009. Effects of body size, age and maturity stage on diet in a large shark: Ecological and applied implications. *Ecol. Res.* 24:109–118.
- Manire CA, Gruber SH. 1993. A preliminary estimate of natural mortality of age-0 lemon sharks, *Negaprion brevirostris*. NOAA Tech. Rep. NMFS.
- Martin RA. 2007. A review of shark agonistic displays: comparison of display features and implications for shark-human interactions. *Mar. Freshw. Behav. Physiol.* 40:3–34.
- McAuley RB, Simpfendorfer CA, Wright IW. 2007. Gillnet mesh selectivity of the sandbar shark (*Carcharhinus plumbeus*): implications for fisheries management. *ICES J. Mar. Sci.* 64:1702–1709.
- McDonnell SM, Haviland JCS. 1995. Agonistic ethogram of the equid bachelor band. *Appl. Anim. Behav. Sci.* 43:147–188.
- Mclean DL, Harvey ES, Meeuwig JJ. 2011. Declines in the abundance of coral trout (*Plectropomus leopardus*) in areas closed to fishing at the Houtman Abrolhos Islands, Western Australia. *J. Exp. Mar. Bio. Ecol.* 406:71–78.
- Mench J. 1998. Why It Is Important to Understand Animal Behavior. *ILAR J.* 39:20–26.

- Morris Gosling L, Sutherland WJ. 2000. Behaviour and Conservation. Gosling LM, Sutherland WJ, editors. Cambridge, England: Cambridge University Press.
- Mortimer JA, Day M. 1999. Sea turtle populations and habitats in the Chagos. In: Sheppard CRC, Seaward MRD, editors. Ecology of the Chagos Archipelago. London, England: Westbury Publishing. p. 159–176.
- Motta PJ, Wilga CD. 2001. Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. *Environ. Biol. Fishes* 60:131–156.
- Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW. 2009. Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biol. Lett.* 5:156–159.
- Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007. Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. *Science*. 315:1846–1850.
- Myrberg Jr AA, Gruber SH. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia*:358–374.
- Nelson DR. 1977. On the Field Study of Shark Behavior. *Am. Zool.* 17:501–507.
- Okuyama J, Nakajima K, Noda T, Kimura S, Kamihata H, Kobayashi M, Arai N, Kagawa S, Kawabata Y, Yamada H. 2013. Ethogram of immature Green turtles: behavioral strategies for somatic growth in large marine herbivores. *PLoS One*. 8:1–12.
- Olden JD, Hogan ZS, Zanden MJ Vander. 2007. Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Glob. Ecol. Biogeogr.* 16:694–701.
- Pimiento C, Ehret DJ, MacFadden BJ, Hubbell G. 2010. Ancient nursery area for the extinct giant shark megalodon from the Miocene of Panama. *PLoS One*. 5:1–9.
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS. 2009. The rise of the mesopredator. *Bioscience*. 59:779–791.
- Quirk G. 2013. Does Oceania have the institutional capacity to meet marine spatial protection targets under the Convention on Biological Diversity? *Aust. J. Marit. Ocean Aff.* 5:97–103.
- Ritchie EG, Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12:982–998.
- Ruckstuhl K, Neuhaus P. 2005. Sexual segregation in vertebrates. Ruckstuhl K, Neuhaus P, editors. Cambridge, England: Cambridge University Press.
- Ruppert JL, Travers MJ, Smith LL, Fortin MJ, Meekan MG. 2013. Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS One* 8:1–9.
- Ryan LA, Meeuwig JJ, Hemmi JM, Collin SP, Har NS. 2015. It is not just size that matters: shark cruising speeds are species-specific. *Mar. Biol.* 162:1307–1318.
- Schuett GW. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim. Behav.* 54:213–224.
- SeaGIS. 2008. PhotoMeasure. 2015.
- Seaward MRD, Klaus R, Topp JMW. 1999. The Chagos Archipelago: an introduction. In: Sheppard CRC, Seaward MRD, editors. The Ecology of the Chagos Archipelago. West

- Yorkshire: Westbury Publishing. p. 1–21.
- Sheppard CRC, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Eble J, Fitzsimmons N, et al. 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Natl. Institutes Heal.* 22:232–261.
- Simpfendorfer CA, Hueter RE, Bergman U, Connett SMH. 2002. Results of fishery-independent survey for pelagic sharks in the western North Atlantic, 1977-1994. *Fish. Res.* 55:175–192.
- Smith K, Scarr M, Scarpaci C. 2010. Grey nurse shark (*Carcharias taurus*) diving tourism: tourist compliance and shark behaviour at Fish Rock, Australia. *Environ. Manage.* 46:699–710.
- Spaet JL, Kessel ST, Gruber SH. 2010. Learned hook avoidance of lemon sharks (*Negaprion brevirostris*) based on electroreception and shock treatment. *Mar. Biol.* 6:399–407.
- Sperone E, Micarelli P, Andreotti S, Spinetti S, Andreani A, Serena F, Brunelli E, Tripepi S. 2012. Social interactions among bait-attracted white sharks at Dyer Island (South Africa). *Mar. Biol. Res.* 6:408–414.
- Springer S. 1967. Social organization of shark populations. *Sharks, skates rays*:149–174.
- Stevens JD, Bonfil R, Dulvy R, Walker PA. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.* 57:476–494.
- Sumpton W, Lane B, Ham T. 2011. Gear modifications and alternative baits that reduce bait scavenging and minimize by-catch on baited drum-lines used in the Queensland Shark Control Program. *Proc. R. Soc. Queensl.* 116:23–35.
- Sumpton WD, Taylor SM, Gribble NA, McPherson G, Ham T. 2011. Gear selectivity of large-mesh nets and drumlines used to catch sharks in the Queensland Shark Control Program. *African J. Mar. Sci.* 33:37–43.
- Thompson CDH. 2014. Predicting shark behaviour: the influence of species, size and brain organisation. [Perth, Australia]: The University of Western Australia.
- UNESCO. 2015. Lagoons of New Caledonia: reef diversity and associated ecosystems. 2015.
- Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R. 2008. A behavioral perspective on fishing-induced evolution. *Trends Ecol. Evol.* 23:419–420.
- Vianna GMS, Meekan MG, Meeuwig JJ, Speed CW. 2013. Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. *PLoS One.* 8.
- Vianna GMS, Meekan MG, Pannell DJ, Marsh SP, Meeuwig JJ. 2012. Socio-economic value and community benefits from shark-diving tourism in Palau: A sustainable use of reef shark populations. *Biol. Conserv.* 145:267–277.
- Vianna GMS, Meekan MG, Ruppert JLW, Bornovski TH, Meeuwig JJ. 2016. Indicators of fishing mortality on reef-shark populations in the world's first shark sanctuary: the need for surveillance and enforcement. *Coral Reefs*:1–5.
- Watson DL, Harvey ES, Anderson MJ, Kendrick GA. 2005. A comparison of temperate reef

- fish assemblages recorded by three underwater stereo-video techniques. *Mar. Biol.* 148:415–425.
- Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y. 2012. Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. *Ecol. Evol.* 2:2474–2484.
- Worm B, Davis B, Ketteimer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH. 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Mar. Policy* 40:194–204.

APPENDIX 1 – Original MaxN and estimated no. of individuals, as determined by the individual assignment protocol, for all 35 deployments analysed across three locations. Ratio represents proportion of estimated individuals compared to original MaxN.

Location	Deployment	Species	Original MaxN	Estimated no. of individuals	Ratio
BIOT	CH006	Silvertip	2	3	1.5
BIOT	CH008	Silvertip	1	1	1
BIOT	CH016	Silvertip	7	14	2
BIOT	CH016	Grey reef	1	1	1
BIOT	CH019	Silvertip	2	2	1
BIOT	CH019	Grey reef	1	1	1
BIOT	CH020	Silvertip	1	1	1
BIOT	CH020	Grey reef	1	1	1
BIOT	CH146	Silvertip	3	6	2
BIOT	CH146	Silky	2	5	2.5
BIOT	CH159	Silvertip	3	9	3
BIOT	CH159	Grey reef	2	7	3.5
BIOT	CH159	Silky	1	3	3
BIOT	CH162	Grey reef	1	1	1
BIOT	CH166	Grey reef	1	2	2
BIOT	CH166	Silky	1	1	1
BIOT	CH174	Silvertip	1	1	1
BIOT	CH174	Silky	1	3	3
BIOT	CH178	Silvertip	6	12	2
BIOT	CH178	Grey reef	5	14	2.8
BIOT	CH178	Silky	1	2	2
Palau	PAL013	Grey reef	1	1	1
Palau	PAL022	Grey reef	1	1	1
Palau	PAL026	Silky	1	1	1
Palau	PAL032	Silky	6	10	1.66
Palau	PAL033	Silky	3	4	1.33
Palau	PAL056	Grey reef	1	1	1
Palau	PAL056	Silky	1	2	2
Palau	PAL061	Silky	2	2	1
Palau	PAL072	Grey reef	1	1	1
Palau	PAL100	Grey reef	1	1	1
Palau	PAL100	Silky	1	1	1
Palau	PAL113	Grey reef	1	1	1
Palau	PAL126	Silky	1	1	1
Palau	PAL132	Silky	1	1	1
Palau	PAL141	Silky	1	3	3
Palau	PAL144	Silky	1	1	1
Palau	PAL150	Silky	1	1	1
New Caledonia	NC001	Grey reef	6	17	2.83
New Caledonia	NC011	Silvertip	1	2	2
New Caledonia	NC011	Grey reef	4	7	1.75

New Caledonia	NC012	Silvertip	1	1	1
New Caledonia	NC012	Grey reef	1	1	1
New Caledonia	NC013	Silvertip	1	2	2
New Caledonia	NC013	Grey reef	1	1	1
New Caledonia	NC013	Silky	1	1	1
New Caledonia	NC022	Silvertip	2	2	1
New Caledonia	NC038	Grey reef	1	1	1
New Caledonia	NC040	Silvertip	1	1	1
New Caledonia	NC041	Silvertip	1	1	1
New Caledonia	NC041	Grey reef	4	5	1.25
New Caledonia	NC255	Silvertip	2	2	1
New Caledonia	NC255	Grey reef	1	1	1