KATHERINE MASON

APPLYING PHOTO-IDENTIFICATION TO BRUVS TO INVESTIGATE THE ABUNDANCE AND DRIVERS OF REEF SHARKS IN THE CAYMAN ISLANDS

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2018/2019

KATHERINE MASON

APPLYING PHOTO-IDENTIFICATION TO BRUVS TO INVESTIGATE THE ABUNDANCE AND DRIVERS OF REEF SHARKS IN THE CAYMAN ISLANDS

Mestrado em Biologia Marinha

Supervisors:
Dr. Mauvis Gore
Co-supervisor
Professor Dr. Karim Erzini

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2018/2019

“Applying photo-identification to BRUVS to investigate the abundance and drivers of reef sharks in the Cayman Islands”

Declaração de autoria de trabalho / Declaration of work authorship

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

I declare to be the author of this work, which is original and unpublished. Authors and works consulted are duly cited in the text and are contained in the list of references included.

(Katherine Mason)

Declaração de direitos autorais / Declaration of copyright

Abstract

Baited Remote Underwater Video Systems (BRUVS) are an increasingly popular method of surveying marine life such as sharks, due to their ease of use, low cost and non-invasive nature; important when sampling threatened and protected species. BRUVS generate relative abundance indices, most often by counting the maximum number of individuals recorded at one time (MaxN). This study counted the total number of individuals (Nind) per survey using photo-identification to differentiate between sharks. Individuals were also assigned sex and maturity. Relative abundance was compared across the factors associated with each site, in order to gain insight into the drivers of abundance. BRUVS were deployed at 84 sites around Grand Cayman and Little Cayman Islands, during October and November 2018, each for a minimum of 2 hours. Seventy sharks were recorded across 45 sites, belonging to four reef shark species and one unidentified species (identified to genus level). The Caribbean reef shark (*Carcharhinus perezi*) and the nurse shark (*Ginglymostoma cirratum*) were the most abundant species. Longer deployment times (120 v 60 min) were found to significantly increase both MaxN and Nind abundance estimates. Significantly more species were recorded with longer time. The mean time for *C. perezi* and *G. cirratum* to arrive and to reach Nind was beyond 60 min. Photo-ID allowed 97% of sharks to be identified to species level and 85% of these as individuals. A significantly higher relative abundance of *C. perezi* were found on Little Cayman but not at inner lagoon sites, whilst there was a higher relative abundance of *G. cirratum* at deep sites. Depth and zone were significant predictors of species composition, with depth being significant to species and maturity composition. The results demonstrate that the longer deployment time improves abundance estimates and the application of Nind through photo-ID allows for finer-scale analysis. Nind estimates, combined with evaluation of drivers, can be used to explore which factors affect shark abundance of each species, at different maturity stages and for each sex. This can provide valuable information for conservation plans and marine protected area development.

Keywords: Baited remote underwater video systems; relative abundance; photo-identification; Cayman Islands; reef sharks

Resumo

Os Sistemas de Vídeo Subaquático Remoto com Isco (BRUVS) são um método cada vez mais popular de pesquisa de vida marinha, como tubarões, devido à sua facilidade de uso, baixo custo e natureza não invasiva; importante na amostragem de espécies ameaçadas e protegidas. O BRUVS pode ser usado para gerar índices de abundância relativa, geralmente contando o número máximo de indivíduos registrados ao mesmo tempo (MaxN). O número total de tubarões individuais (Nind) pode ser contado por meio de identificação com foto. Recursos diferenciados são observados e comparados nas implantações. Ao remover a subestimação potencial do uso do MaxN, a precisão das estimativas de tamanho da população pode ser melhorada. O BRUVS também pode ser usado para classificar sexo e atribuir maturidade a indivíduos. Os fatores associados a cada local podem ser analisados para explicar as variações na abundância de tubarões. A abundância relativa de grupos demográficos pode ser explorada para estabelecer quais fatores são os fatores mais importantes desses grupos. A intensa pesca histórica no Caribe pode ter afetado as populações locais de tubarões, e Cayman reforça a proteção de todas as espécies de tubarões em toda a sua Zona Econômica Exclusiva (ZEE), desde 2015.

O BRUVS foi implantado em 84 locais em Ilhas Grand Cayman e Little Cayman no Caribe, durante outubro e novembro de 2018, cada um por um período mínimo de 2 horas. Os locais das pesquisas foram espalhados pelas ilhas e variaram em profundidade de 0,3 a 25 m, cobrindo uma variedade de habitats. Nind foi determinado usando identificação com foto e os tubarões foram identificados ao nível das espécies e atribuídos sexo e maturidade sempre que possível. As estimativas de Nind foram comparadas ao MaxN por dois períodos de implantação (60 e 120 min). O número registrado de espécies foi comparado entre os períodos. A hora de chegada e de Nind foram comparadas entre as duas espécies mais abundantes. A diferença na abundância relativa entre os locais foi explorada em relação aos fatores associados a cada local. Os fatores foram ilha, zona de recife (lagoa interna ou recife externo), habitat, profundidade e proteção (parque marinho ou nenhum). As diferenças na composição das espécies foram testadas nos locais em relação a esses fatores e as parcelas foram usadas para visualizar padrões. Os indivíduos foram agrupados dentro das espécies por sexo e maturidade e posteriormente testados quanto a diferenças

entre locais em relação a esses fatores. Esses testes indicaram se havia ou não grupos significativos e quais fatores eram mais importantes para os agrupamentos.

Setenta tubarões foram registrados em 45 locais, pertencentes a quatro espécies de tubarões de recife e uma espécie não identificada (identificada ao nível de gênero: *Carcharhinus* spp.). O tubarão-de-recife (*Carcharhinus perezi*) e o tubarão-enfermeiro (*Ginglymostoma cirratum*) foram as espécies mais abundantes, com tubarão Blacktip (*C. limbatus*) e tubarão-limão (*Negaprion brevirostris*). Verificou-se que tempos de implantação mais longos (120 v 60 min) aumentam significativamente as estimativas de abundância de MaxN e Nind para *C. perezi* e *G. cirratum*. Significativamente mais espécies também foram registradas com mais tempo. No entanto, as estimativas de Nind não foram significativamente maiores que as estimativas de MaxN. O tempo médio para *C. perezi* e *G. cirratum* chegarem e chegarem a Nind foi superior a 60 minutos e nenhuma diferença significativa foi encontrada entre as duas espécies. A identificação com foto permitiu que 97% dos tubarões fossem identificados em nível de espécie e 85% deles fossem identificados como indivíduos. Uma abundância relativa significativamente maior de *C. perezi* foi encontrada em Little Cayman do que em Grand Cayman, mas não nos locais das lagoas internas, enquanto mais *G. cirratum* estavam em locais profundos, em vez de rasos. As duas espécies mais raras foram registradas apenas em zonas internas. A profundidade e a zona foram preditores significativos da composição das espécies nos locais, enquanto outros fatores não tiveram efeito significativo. *C. perezi* foi fortemente associada a locais profundos e na zona externa, enquanto *G. cirratum* foi mais associado a todas as profundidades. Grupos demográficos de sexo e maturidade de cada espécie foram testados, mas nenhum fator foi considerado significativo. A profundidade foi um preditor significativo de espécies e composição de maturidade. *C. perezi* maduro foi separado por associação apenas aos locais profundos, enquanto *C. perezi* imaturo foi dividido entre locais profundos e médios. Por outro lado, *G. cirratum* maduro foi agrupado mais próximo aos locais rasos e médios, e indivíduos imaturos de *G. cirratum* foram registrados em locais, independentemente da profundidade.

Conforme previsto, os resultados demonstraram que as estimativas de abundância eram maiores com o tempo de implantação mais longo. Embora esse fosse o caso das métricas MaxN e Nind, não havia diferença significativa entre as duas métricas. Foi levantado a hipótese de que, com um tempo de implantação mais longo, indivíduos diferentes teriam mais tempo para entrar no quadro, aumentando assim a contagem de Nind, mas provavelmente não a contagem de MaxN. No entanto, o comportamento dos tubarões registrados neste estudo determinou que, quando mais de 3 indivíduos da mesma espécie apareciam, esse acontecia com mais frequência, diminuindo a vantagem da identificação individual. BRUVS são limitados como método ao usar MaxN como uma métrica de abundância; fornece apenas informações sobre abundância relativa e demonstrou não se relacionar diretamente com a abundância verdadeira. Com a pesquisa registrando apenas um total de quatro espécies, era de se esperar que um aumento no número de espécies registradas com o tempo de implantação adicional fosse marginal, porém testes estatísticos provaram que houve um aumento significativo. O tempo médio de chegada e Nind para *C. perezi* e *G. cirratum* ocorreram após 60 minutos, indicando que mais tubarões e espécies aparecem além do tempo de implantação padrão de 60 minutos. Neste estudo, os benefícios dos BacPacs adicionais da bateria superaram o aumento do tempo de análise e o custo adicional. O tempo estendido da pesquisa seria vantajoso onde as restrições do trabalho de campo permitirem. A identificação com foto foi considerada bem-sucedida tanto na lagoa rasa quanto no ambiente de recifes ao redor das Ilhas Cayman, com espécies exibindo amplas características distinguíveis. Isso permitiu uma diferenciação confiante. A baixa visibilidade tornou mais difícil distinguir *C. limbatus*. O BRUVS também permitiu a atribuição de sexo e maturidade. Isso não era possível para indivíduos com baixa visibilidade ou quando havia uma visão limitada da área do clasper. Portanto, menos tubarões foram sexados em comparação com outros métodos de pesquisa, como o palangre. O sucesso da identificação com foto diminuiria em ambientes com pouca luz e baixa visibilidade, ou se o comportamento de uma espécie exigir uma distância mantida da isca. Para combater a visão ruim do clasper e melhorar as estimativas de maturidade, o BRUVS estéreo deve ser considerado para adicionar outro ângulo da câmera. Não foram registradas fêmeas maduras pertencentes a *C. perezi* ou *G. cirratum*. Isso pode ser devido ao tamanho conservador de indivíduos do sexo feminino e mais investigações devem ser realizadas, incluindo a revisão das gravações do BRUVS dos anos anteriores. Isso foi observado em outras espécies de tubarões, como o tubarão-baleia (*Rhincodon typus*). Verificou-se que Little Cayman tem uma abundância relativa maior de *C. perezi* e todas as espécies em geral que Grand Cayman, de acordo com pesquisas anteriores, e foram encontradas em locais mais profundos: comparáveis às

pesquisas nas Bahamas. A profundidade e a zona foram responsáveis por mudanças na composição das espécies entre os locais e, ao explorar as diferenças entre os estágios de maturidade, a profundidade foi o fator mais importante. Diferentes estágios de maturidade de cada espécie utilizaram diferentes profundidades. Essa é uma consideração importante ao estudar as espécies como um todo e as informações adicionais podem fornecer informações valiosas para planos de conservação e desenvolvimento de áreas marinhas protegidas. Observações do método de amostragem são que o BRUVS foi implantado apenas durante o dia e durante uma estação do ano. Isso poderia ser expandido para incluir períodos crepusculares, entre estações e anos, para rastrear possíveis variações de abundância interanuais e anuais.

Em conclusão, o estudo encontrou mérito na implementação de um período de registro mais longo, resultando em maior número de abundância e mais espécies registradas. A identificação com foto pode fornecer estimativas de abundância sem as implicações de técnicas de amostragem invasivas. O MaxN não permite que os tubarões sejam diferenciados dos anteriores, mas Nind permite, permitindo análises em escala mais fina. A identificação com foto foi bem-sucedida para as espécies registradas no BRUVS nas Ilhas Cayman. A profundidade e a zona foram responsáveis por afetar a composição das espécies nos locais. Enquanto alguns indivíduos foram sexados e receberam maturidade, isso não teve 100% de sucesso. O BRUVS estéreo deve ser considerado para desenvolver análises demográficas da população. Indivíduos pertencentes a diferentes estágios de maturidade associados a diferentes locais com base na profundidade. Essa é uma consideração importante para os planos de proteção. Pesquisas futuras podem ser expandidas por amostragem em diferentes momentos do dia, períodos crepusculares e durante temporadas adicionais. Alterações na abundância relativa podem ser rastreadas ao longo dos anos, permitindo a análise de um conjunto de dados maior. Isso também poderia permitir o rastreamento de indivíduos espacial e temporalmente. Cayman Brac deve ser incorporado à metodologia de amostragem, para abranger a totalidade das Ilhas Cayman.

Palavras-chave: Sistemas de vídeo subaquático remotos com isca; abundância relative; identificação com foto; Ilhas Cayman; tubarões de recife

Table of Contents

Index of Figures

Chapter 2

Appendicies

Index of Tables

Chapter 1

Chapter 2

Appendicies

List of Abbreviations

BRUVS: baited remote underwater video systems
GPS: global positioning system
MaxIND: maximum number of individuals within a single survey
MaxN: maximum number of individuals observed within a single frame
MeanCount: mean count of individuals
Nind: total number of individuals within a single survey
nMDS: non-metric multidimensional scaling
NVC: no visible clasper
T1st: time of first arrival
TITO: time in – time out
TL: total length (cm)

CHAPTER 1: INTRODUCTION

1. Chondrichthyans

Sharks have existed on this planet for millions of years, the first fossils dating back to the Devonian period (Janvier and Pradel, 2015). However, there is now increasing concern surrounding the survival of elasmobranch species. Populations are in rapid decline, due to anthropogenic pressures, namely mass overfishing (as both target species and by-catch) and habitat degradation (Myers and Worm, 2003). This is compounded by their K-selected life history characteristics (Stevens *et al.*, 2000), making population recovery challenging.

Chondrichthyes are a class made up of ≃ 1200 species (Fowler *et al.*, 2005). There are two major subclasses: Holocephali (chimaeras) and the larger subclass Elasmobranchii (sharks, skates and rays). Sharks make up approximately 500 of these species (Ferretti *et al.*, 2010). Chondrichthyans are predatory fish and a significant proportion of large sharks and some rays are situated at or near to the top of marine food webs (Field *et al.*, 2009). Many of these sharks feed on a wide range of prey, from plankton to whales, leading to sharks interacting strongly within food-web models (Bascompte *et al.*, 2005). There is also a large range of meso-predatory elasmobranchs that fall prey to larger sharks (Field *et al.*, 2009).

Larger sharks exert a top-down control on ecosystems, influencing and structuring entire biological marine communities (Myers and Worm, 2003; Stevens *et al.*, 2000). The decline in these larger shark species affects entire ecosystems: reducing natural mortality of their prey and causing knock-on effects to abundance, distribution and behaviour of other animals. The removal of sharks from an ecosystem can also result in complex community changes, including trophic cascade (a shift from coral to algal-dominated reefs), meso-predatory release, and ensuing declines in commercial fish species (Ferretti *et al.*, 2010).

Sharks are directly exploited for their fins, meat, skin, liver-oil, teeth and cartilage (Rose, 1998). They are also caught incidentally in fishing gear, such as trawl nets and long lines, as “by-catch”. Dulvy *et al.* (2014) estimated that nearly one third of chondrichthyan fish species are vulnerable to extinction. Despite growing awareness and concern, shark mortality rates may still exceed reproductive rates in many regions (Worm *et al.*, 2013). Their life history characteristics, such as late sexual maturity, low fecundity and slow growth, dictate minimal ability to recover after depletion (Ferretti *et al.*, 2010; Stevens *et al.*, 2000). Additionally, there are threats from illegal, unreported and unmanaged (IUU) fisheries (Field *et al.*, 2009), which are not accounted for in shark catch estimates.

Adding to their essential ecological role, sharks have more recently been credited for their part in generating income for local economies via tourist activities. Shark diving is a growing industry, enabling the observation of sharks and rays underwater either by snorkelling or scuba diving. By 2010, the income generated from these activities (by at least 376 operators in a minimum of 29 countries) consistently outweighed the income generated from landed sharks (Gallagher and Hammerschlag, 2011).

2. Shark monitoring methods

Data collection for chondrichthyans is notoriously difficult, due to the vast scale of their habitat (Baum *et al.*, 2003), which limits scientists' abilities to monitor populations effectively. These limitations, coupled with a low prioritisation of chondrichthyan conservation historically, means there is a relative paucity of ecological data for many species (Dulvy *et al.*, 2014).

There are a plethora of methods used to monitor and sample shark populations in various habitats, including tagging (satellite, acoustic, etc.), fishing (long-lining, gill-netting, etc.) and underwater visual census (UVC). Many studies require sampling a large number of animals, sometimes across multiple taxa, without causing fatalities. Studies also focus on behavioural data, which can be affected by the method of data collection. UVC has been found to have larger behavioural biases than BRUVS (Willis *et al.*, 2000), whilst extractive data collection (such as fatal fishing experiments) can be problematic in protected areas and where species are rare or timid (Brooks *et al.*, 2011; Willis *et al.*, 2000).

2.1. Baited Remote Underwater Video Systems

The use of non-invasive survey techniques, like baited remote underwater video systems (BRUVS), has increased in recent years. Underwater video systems have been used from submersibles in the abyssal zone (Priede *et al.*, 1994), to the more common assessment of fish communities (Pauli *et al.*, 2010), and have in recent years been used to investigate elasmobranch assemblages and communities (Bouchet and Meeuwig, 2015; De Vos *et al*., 2015; Gladstone *et al*., 2012; Heagney *et al*., 2007; Murray *et al*., 2019; Spaet *et al*., 2016).

The methodology accompanying BRUVS studies varies widely, including the number of cameras, use of different bait, soak time (the length of time the BRUVS is left underwater) and depth. Mono- and stereo-BRUVS are predominantly used, with the first being lighter, quicker to set up and easier to deploy, whereas the latter requires specialised gear and more time to prepare for calibration and for analysis (Whitmarsh *et al*., 2017).

Studies found the optimal soak time differs depending on the environment and target species. Most commonly used are lengths of 30, 60 and 90 min (Whitmarsh *et al*., 2017). Those that ran for longer often used additional batteries or power sources (Harasti *et al*., 2016). Studies that compared soak times concluded that shorter periods of 15 min were adequate to capture bottomfish assemblages (Misa *et al*., 2016). Gladstone *et al*. (2012) found 60 – 90 min to be ideal for estuarine environments, and 120 min as optimal for pelagic habitats in tropical or warm-temperate areas (Santana-Garcon *et al*., 2014). Generally, longer time periods are used for shark species (Asher, 2017), as these are less abundant than fish assemblages, with Harasti *et al*. (2016) deploying for 5 h to record white sharks (*Carcharodon carcharias*). However, soak time should be assessed for the individual target species for each study. Therefore, in this study time periods of 60 and 120 min were compared for the number of individuals and species at each site.

There is substantial variation in the distance between consecutive BRUVS, with very few studies using over 550 m (Whitmarsh *et al*., 2017). The distance between BRUVS is often used as a proxy for survey independence. The importance of bait type has been investigated, and oily fish, such as sardines or species easily accessible in the region of the study, are recommended (Walsh *et al*., 2017).

The survey method BRUVS was chosen due to its non-invasive and non-destructive nature, desirable when surveying protected and threatened species. It is also low-cost, relatively easy to build and to deploy; important factors when involving widely distributed species, large areas and long-term programmes (Bernard and Götz, 2012; White *et al*., 2013). Sampling is not size-selective of individuals as in other traditional methods that use hooks or mesh nets. BRUVS also have the advantage of minimising disturbance to animals, which in turn increases data accuracy and allows for large population sampling (Pauli *et al*., 2010). Yet, BRUVS produce similar relative abundance estimates to longline surveys (Brooks *et al*., 2011) and can be deployed at a range of depths and in varying habitats (Cappo *et al*., 2006).

2.1.1 Abundance estimates

BRUVS can be used to estimate the relative abundance of each species present at a specific site or location. The standard and most commonly used metric for measuring relative abundance is MaxN (Cappo, 2010). MaxN is the maximum number of individuals seen within a single frame per species. It is designed to eliminate double counting and the overestimating of abundance. However, this means that each new arrival is assumed to be the same individual as previously, potentially resulting in an underestimation of the total number of individuals (Cappo, 2010; Kilfoil *et al*., 2017). Additionally, when applied to small populations, the values of MaxN may not mirror fluctuations in the wider population, due to sample saturation (Stobart *et al*., 2015), limiting its wider use as a proxy for actual abundance.

BRUVS footage can also be analysed by using mean count (MeanCount), time in – time out (TITO), and time of first arrival (T1st) (Cappo *et al*., 2011). MaxN and MeanCount are abundance estimates, however MeanCount has its own bias by using time intervals, decreasing detection probability (Campbell *et al*., 2015). TITO allows for behavioural analyses such as boldness (Cappo, 2010), and T1st indicates the distance of the animal to the system and/or the attractiveness of the bait (Bassett and Montgomery, 2011). To overcome these biases and to therefore increase the accuracy of abundance estimates, individuals within frame can be individually identified.

2.1.2 Photo Identification

Few studies have attempted to identify and count individuals through photo-identification to estimate actual abundance (Harasti *et al*., 2016; Kilfoil *et al*., 2017). This can be achieved by using distinguishable features such as fin markings and injuries (Domeier and Nasby-Lucas, 2007). Photo-ID has been used on a wide range of taxa, such as cetaceans (Silva *et al.*, 2000), and more recently on elasmobranchs. These include the whale shark (*Rhincodon typus*) using unique spot patterns (Araujo *et al*., 2014), the white shark (*C. carcharias*) and basking shark (*Cetorhinus maximus*) using physical features such as fin markings and injuries (Domeier and Nasby-Lucas, 2007; Gore *et al*., 2016). BRUVS footage often has multiple angles of an individual, enabling the observation of multiple distinguishing features, facilitating identification of individuals in some cases (Sherman *et al*., 2018). Harasti *et al*. (2016) used a combination of markings and size estimates from stereo-BRUVS to identify *C. carcharias* sharks. However, thee sharks were only ever recorded on the one stereo-BRUVS each day and not on neighbouring BRUVS on subsequent survey days. Sherman *et al*. (2018) identified individuals belonging to two batoid species (Superorder: Batoidea) using BRUVS, and examined differences in MaxN estimates to counts of identified individuals (MaxIND, referred to hereafter as Nind). Results demonstrated that MaxIND showed abundances 2.4 and 1.1 times higher than MaxN. However, distinguishing individuals beyond single deployments was not undertaken.

Photo-ID allows for the differentiation between individuals and therefore a count of the total number of individuals on each BRUVS. With enough individuals and "re-sights", it is possible to incorporate mark-recapture methodology, used by Castro and Rosa (2005), producing an estimate of actual abundance within a discrete area during the sampling season. Mark-recapture through photo-ID is a non-intrusive and effective alternative to conventional tagging, allowing for tracking of individuals between BRUVS at the same site, different sites and between islands. Studies have confirmed its accuracy in research, including those with elasmobranchs (Gore *et al*., 2016; Stevick *et al*., 2001). Using mark-recapture data to estimate effective population size has been attempted for some shark species, including the nurse shark (*Ginglymostoma cirratum*), white shark (*C. carcharias*) and the basking shark (*Cetorhinus maximus*) (Castro and Rosa, 2005; Chapple *et al*., 2011; Gore *et al*., 2016). Using a method such as Nind (Sherman *et al*., 2018) to assess and monitor species can provide more accurate abundance estimates for populations where small differences may have significant impact on management and conservation (McConville *et al*., 2009), providing valuable information surrounding the recovery or decline of populations. Repeated sampling using Nind would better represent population fluctuations over time, as the estimates have a higher accuracy overall (Sherman *et al*., 2018).

Furthermore, still photographs from BRUVS foortage can be used to identify sex, assign maturity and estimate size of individual sharks, as carried out by Jaiteh *et al*. (2016). Classifying each individual by sex and maturity allows assessment of potential sexual segregation and tracking movements of certain individuals from within the population. This can give insight into which sites each demographic group utilises, or if they are driven to certain habitats or associate with other site factors, such as depth. The sex and maturity of these sharks can be used to examine whether the same type of individuals are frequenting the site, and which factors are the most important drivers of abundance. Information regarding the abundance and distribution of sharks is central to the development of protection planning and management (Garla *et al.*, 2006).

3. Cayman Islands

The Cayman Islands now enforces protection for all shark species. The Cayman Islands Government (under the National Conservation Law, 2013, Section 17) gave full protection to all sharks and other elasmobranchs throughout its Exclusive Economic Zone (EEZ) in 2015. Monitoring of elasmobranch species and population abundances has been in effect since 2009, to assess whether populations are recovering in Cayman waters.

In the past, it is likely that the Cayman Islands were affected by wider shark population decline in the Caribbean, brought about by intense commercial and recreational fishing (Bonfil, 1997; Ward-Paige *et al.*, 2010). Additionally, during the mid-1900s, the Cayman Islands were the base for a commercial shark fishery covering large areas of the western Caribbean. Nurse and tiger sharks were targeted for their skin and exported for sharkskin leather (Ormond *et al.*, 2017). Before 2009, little was known regarding the species and population numbers of sharks inhabiting the waters around the Cayman Islands. The Caribbean reef shark (*C. perezi*) is one of the least studied carcharhinid sharks; there is a paucity of demographic data and management is generally deficient (Castro *et al.*, 1999). It has been estimated that the abundance of sharks there is perhaps only 20 - 30 % of what might be expected when comparing with large and isolated areas such as the Western Indian Ocean, and are much lower than neighbouring Belize (Clarke *et al.*, 2012; Ormond *et al.*, 2017; Pikitch *et al.*, 2005). Ormond *et al.* (2017) did however estimate the value of the non-consumptive use of sharks in the Cayman Islands to be between US $46.8 million and $62.6 million per year. Management and protection of these species is challenging due to their highly mobile nature (Green *et al.*, 2015; Speed *et al.*, 2016) and the distinct knowledge gap surrounding the spatial ecology of sharks that utilise island habitats.

In the initial stages of the Cayman Islands shark project, information was gathered on species occurrence from both interviews with fishermen and citizen science (Ormond *et al.*, 2017). The results suggested the following frequency of occurrence of shark species around the Cayman Islands, displayed in Table 1.1.

Table 1.1. Shark species encountered in the Cayman Islands with frequency of occurrence and conservation status

Latin Name	Common Name	Occurrence	IUCN Status	Status Reference
Carcharhinus perezi	Caribbean reef	Relatively common	Near threatened	(Rosa *et al.*, 2006b)
Ginglymostoma cirratum	Nurse	Relatively common	Data deficient	(Rosa *et al.*, 2006a)
C. limbatus	Blacktip	Less common	Near threatened	(Burgess and Branstetter, 2009)
Negaprion brevirostris	Lemon	Less common	Near threatened	(Sundström, 2015)
C. longimanus	Oceanic whitetip	Less common	Vulnerable	(Baum *et al.*, 2015)
Galeocerdo cuvier	Tiger	Occasional	Near threatened	(Ferreira and Simpfendorfer, 2019)
Sphyrna mokarran	Great hammerhead	Occasional	Endangered	(Denham *et al.*, 2007)
S. lewini	Scalloped hammerhead	Occasional	Endangered	(Baum *et al.*, 2009)
Rhincodon typus	Whale	Occasional	Endangered	(Pierce and Norman, 2016)
Prionace glauca	Blue	Occasional	Near threatened	(Stevens, 2009)

Ormond *et al.* (2017) reported that *C. perezi* are the most common species to the Cayman Islands over the outer fringing reefs, but *C. limbatus* may also be encountered there, as are *Ginglymostoma cirratum*. *G. cirratum* and to a lesser extent *Negaprion brevirostris* are the main species observed in the shallow lagoons, known locally as “sounds”. As the BRUVS are located in both sounds and fringing reef areas with a maximum depth of ≃ 25m, it is highly unlikely that pelagic species, such as *C. longimanus* and *P. glauca,* would be recorded during this study.

Monitoring of elasmobranch species and population abundances has been in effect since 2009 in Cayman waters (Ormond *et al.*, 2017), using a variety of methods including BRUVS, acoustic tagging and citizen science. BRUVS equipment has been upgraded since then as technological advances have been made. This has allowed for a long-term data set to be acquired, with species presence and relative abundance of each species recorded every year around Grand and Little Cayman. Cayman Brac was initially surveyed prior to this study using BRUVS, but this was discontinued due to logistical limitations.

4. Context of the study

The present study is part of a wider, long-term monitoring program, which has seen the use of BRUVS since 2009. Shark populations have been assessed to investigate whether populations in Cayman waters are recovering since the protection of shark species in 2015. Populations were likely affected and depleted by historical commercial and recreational fishing. The relative ease of using BRUVS, reduced cost and use of simultaneous deployments allow for greater sampling effort and reduced time in the field; important factors in long-term programmes (Bernard and Götz, 2012; White *et al.*, 2013), such as the Cayman Islands shark research project. Originality of this study is credited to the use of photo-ID on a variety of shark species to distinguish between individuals on each BRUVS across all units, sites and two islands, during one sampling season. Using individual identification, and therefore using counts of individuals, can improve the accuracy of abundance estimates. If this method proves successful, it would be beneficial for wider application in further studies. Moreover, with a large enough sampling size, population estimates can be calculated using mark-recapture methodology and population models. This could give further insight into the health of populations and therefore the importance of MPAs and other protection measures for shark species. Additionally, if implemented into long-term monitoring programs, Nind estimates would allow for increased accuracy in tracking population fluctuations temporally. Photo-ID methodology also allows for the tracking of individuals' movements between BRUVS. Notably in past years, four Caribbean reef sharks (two male and two female) fitted with acoustic tags were recorded to swim between islands, with two moving between Grand Cayman and Cayman Brac, covering a distance of approximately 150 km over very deep water (Ormond *et al.*, 2017). Exploratory analysis into the presence of different demographic groups at various sites could aid in gaining insight into drivers of abundance and which factors associated with the sites are of most importance. The use of different sites by the demographic groups are an important consideration when planning protective measures of an entire species.

5. Aims, objectives and hypotheses

5.1 Aims

The major aim of this study is to provide further insight into the presence and abundance of reef shark species at various sites across the Cayman Islands. By testing an alternative abundance metric, it permits us to establish whether shark abundance estimation accuracy can be increased through individual identification. Additionally, testing two different recording periods may display different numbers of individuals. By improving the accuracy of abundance estimates, it is possible to gain further insight into the drivers of shark abundance. Testing characteristics or factors of the sites against abundance counts can indicate whether certain sites are utilised more by different species. By using photo-identification to assign sex and maturity to individuals, we may begin to understand the demographic groups' drive toward particular sites and which factors contribute most to this. In recent years, more effort has been focused on finding alterative methods to traditional abundance metrics, which are prone to underestimation and do not mirror wider fluctuations. Additionally, as management plans are becoming increasingly vital for protecting shark populations, within-species variation should be considered and accounted for.

5.2 Objectives and hypotheses

This study has three main objectives. Firstly, to test whether individual identification affects abundance estimations in conjunction with longer recording time. It would be expected that using photo-ID lead to higher shark counts, especially when combined with an extended time period. Secondly, to determine if and how the abundance of the main reef shark species differs across the Cayman Islands BRUVS sites; investigating abundance versus site factors. Analyses may determine which factors are of most importance to each species. Finally, to explore the drivers of the different demographic groups within each species to certain sites. This could lead to an increased knowledge surrounding the drivers of different individuals belonging to the same species, and could be applied to monitoring and protection plans.

6. References

Araujo, G., Lucey, A., Labaja, J., Lee So, C., Snow, S., Ponzo, A., 2014. Population structure and residency patterns of whale sharks, Rhincodon typus, at a provisioning site in Cebu, Philippines. *PeerJ* **2**, e543. https://doi.org/10.7717/peerj.543

Asher, J., 2017. A Deeper Look at Hawaiian Coral Reef Fish Assemblages: A Comparison of Survey Approaches and Assessments of Shallow to Mesophotic Communities (PhD). *Curtin University, Australia*.

Bascompte, J., Melian, C.J., Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* **102**, 5443–5447. https://doi.org/10.1073/pnas.0501562102

Bassett, D.K., Montgomery, J.C., 2011. Investigating nocturnal fish populations in situ using baited underwater video: With special reference to their olfactory capabilities. *Journal of Experimental Marine Biology and Ecology* **409**, 194–199. https://doi.org/10.1016/j.jembe.2011.08.019

Baum, J., Clarke, S., Domingo, A., Ducrocq, M., Lamónaca, A.F., Gaibor, N., Graham, R., Jorgensen, S., Kotas, J.E., Medina, E., Martinez-Ortiz, J., Monzini Taccone di Sitizano, J., Morales, M.R., Navarro, S.S., Pérez-Jiménez, J.C., Ruiz, C., Smith, W., Valenti, S.V., Vooren, C.M., 2009. Sphyrna lewini. The IUCN Red List of Threatened Species 2009: e.T39385A10190088. *IUCN Red List of Threatened Species.* URL https://www.iucnredlist.org/en (accessed 8.19.19).

Baum, J., Medina, E., Musick, J.A., Smale, M., 2015. Carcharhinus longimanus. The IUCN Red List of Threatened Species 2015: e.T39374A85699641. *IUCN Red List of Threatened Species.* URL https://www.iucnredlist.org/en (accessed 8.19.19).

Baum, J.K., Myers, R.M., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and Conservation of Shark Populations in the Northwest Atlantic. *Science* **299**, 389–392. https://doi.org/10.1126/science.1079777

Bernard, A., Götz, A., 2012. Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. *Marine Ecology Progress Series* **471**, 235–252. https://doi.org/10.3354/meps10039

Bonfil, R., 1997. Status of shark resources in the southern Gulf of Mexico and Caribbean: implications for management. *Fisheries Research* **29**, 101–117. https://doi.org/10.1016/S0165-7836(96)00536-X

Bouchet, P.J., Meeuwig, J.J., 2015. Drifting baited stereo-videography: a novel sampling tool for surveying pelagic wildlife in offshore marine reserves. *Ecosphere* **6**, art137. https://doi.org/10.1890/ES14-00380.1

Brooks, E., Sloman, K., Sims, D., Danylchuk, A., 2011. Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endangered Species Research* **13**, 231–243. https://doi.org/10.3354/esr00331

Burgess, H.G., Branstetter, S., 2009. Carcharhinus limbatus. The IUCN Red List of Threatened Species 2009: e.T3851A10124862. *IUCN Red List of Threatened*

Species. URL https://www.iucnredlist.org/species/3851/10124862 (accessed 8.19.19).

Campbell, M.D., Pollack, A.G., Gledhill, C.T., Switzer, T.S., DeVries, D.A., 2015. Comparison of relative abundance indices calculated from two methods of generating video count data. *Fisheries Research* **170**, 125–133. https://doi.org/10.1016/j.fishres.2015.05.011

Cappo, M., 2010. Development of a baited video technique and spatial models to explain patterns of fish biodiversity in inter-reef waters (PhD). *James Cook University, Australia.*

Cappo, M., Harvey, E., Shortis, M., 2006. Counting and measuring fish with baited video techniques-an overview, in: Lyle, J.M., Furlani, D.M., Buxton, C.D. (Eds.), *Cutting-Edge Technologies in Fish and Fisheries Science*. Presented at the ASFB Workshop Proceedings, Hobart, Tasmania, August 2006, pp. 101–114.

Cappo, M., Stowar, M., Syms, C., Johansson, C., Cooper, T., 2011. Fish-habitat associations in the region offshore from James Price Point – a rapid assessment using Baited Remote Underwater Video Stations (BRUVS). *Journal of the Royal Society of Western Australia* **94**, 303–321.

Castro, A.L.F., Rosa, R.S., 2005. Use of natural marks on population estimates of the nurse shark,Ginglymostoma cirratum, at Atol das Rocas Biological Reserve, Brazil. *Environmental Biology of Fishes* **72**, 213–221. https://doi.org/10.1007/s10641-004-1479-7

Castro, J.I., Woodley, C.M., Brudek, R.L., 1999. A preliminary evaluation of the status of shark species. *FAO Fish. Tech. Paper* **380**, 49.

Chapple, T.K., Jorgensen, S.J., Anderson, S.D., Kanive, P.E., Klimley, A.P., Botsford, L.W., Block, B.A., 2011. A first estimate of white shark, Carcharodon carcharias, abundance off Central California. *Biology Letters* **7**, 581–583. https://doi.org/10.1098/rsbl.2011.0124

Clarke, C., Lea, J., Ormond, R., 2012. Comparative abundance of reef sharks in the Western Indian Ocean, in: *Proceedings of the 12th International Coral Reef Symposium*. Presented at the Reef sharks and coral reefs, Cairns, Australia, 9-13 July 2012, p. 5.

De Vos, L., Watson, R., Götz, A., Attwood, C., 2015. Baited remote underwater video system (BRUVs) survey of chondrichthyan diversity in False Bay, South Africa. *African Journal of Marine Science* **37**, 209–218. https://doi.org/10.2989/1814232X.2015.1036119

Denham, J., Stevens, J., D., Simpfendorfer, C., Heupel, M.R., Cliff, G., Morgan, A., Graham, R., Ducrocq, M., Dulvy, N., K., Seisay, M., Asber, M., Valenti, S.V., Litvinov, F., Martins, P., Lemine Ould Sidi, M., Tous, P., Bucal, D., 2007. Sphyrna mokarran. The IUCN Red List of Threatened Species 2007: e.T39386A10191938. *IUCN Red List of Threatened Species*. URL https://www.iucnredlist.org/en (accessed 8.19.19).

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. https://doi.org/10.1007/s00227-006-0380-7

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S., White, W.T., 2014. *Extinction risk and conservation of the world's sharks and rays.* eLife **3.** https://doi.org/10.7554/eLife.00590

Ferreira, L.C., Simpfendorfer, C., 2019. Galeocerdo cuvier. The IUCN Red List of Threatened Species 2019: e.T39378A2913541. *IUCN Red List of Threatened Species.* URL https://www.iucnredlist.org/en (accessed 8.19.19).

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

Field, I.C., Meekan, M.G., Buckworth, R.C., Bradshaw, C.J.A., 2009. Chapter 4 Susceptibility of Sharks, Rays and Chimaeras to Global Extinction, in: *Advances in Marine Biology*. Elsevier, pp. 275–363. https://doi.org/10.1016/S0065-2881(09)56004-X

Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A., Musick, J.A., 2005. Sharks, rays and chimaeras: the status of the chondrichthyan fishes. *Status Survey, IUCN/SSC Action Plans for the Conservation of Biological Diversity*. IUCN Species Survival Commission (SSC), Shark Specialist Group.

Gallagher, A.J., Hammerschlag, N., 2011. Global shark currency: the distribution, frequency, and economic value of shark ecotourism. *Current Issues in Tourism* **14**, 797–812. https://doi.org/10.1080/13683500.2011.585227

Garla, R.C., Chapman, D.D., Shivji, M.S., Wetherbee, B.M., Amorim, A.F., 2006. Habitat of juvenile Caribbean reef sharks, Carcharhinus perezi, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. *Fisheries Research* **81**, 236–241. https://doi.org/10.1016/j.fishres.2006.07.003

Gladstone, W., Lindfield, S., Coleman, M., Kelaher, B., 2012. Optimisation of baited remote underwater video sampling designs for estuarine fish assemblages. *Journal of Experimental Marine Biology and Ecology* **429**, 28–35. https://doi.org/10.1016/j.jembe.2012.06.013

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**, e0150160. https://doi.org/10.1371/journal.pone.0150160

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J., White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* **90**, 1215–1247. https://doi.org/10.1111/brv.12155

Harasti, D., Lee, K.A., Laird, R., Bradford, R., Bruce, B., 2016. Use of stereo baited remote underwater video systems to estimate the presence and size of white sharks (Carcharodon carcharias). *Marine and Freshwater Research* **68**, 1391. https://doi.org/10.1071/MF16184

Heagney, E., Lynch, T., Babcock, R., Suthers, I., 2007. Pelagic fish assemblages assessed using mid-water baited video: standardising fish counts using bait plume size. *Marine Ecology Progress Series* **350**, 255–266. https://doi.org/10.3354/meps07193

Jaiteh, V.F., Lindfield, S.J., Mangubhai, S., Warren, C., Fitzpatrick, B., Loneragan, N.R., 2016. Higher Abundance of Marine Predators and Changes in Fishers' Behavior Following Spatial Protection within the World's Biggest Shark

Fishery. *Frontiers in Marine Science* **3**, e0200960. https://doi.org/10.3389/fmars.2016.00043

Janvier, P., Pradel, A., 2015. Elasmobranchs and Their Extinct Relatives: Diversity, Relationships, and Adaptations Through Time, in: *Fish Physiology*. Elsevier, pp. 1–17. https://doi.org/10.1016/B978-0-12-801289-5.00001-8

Kilfoil, J., J. Wirsing, A., Campbell, M., Kiszka, J., Gastrich, K., Heithaus, M., Zhang, Y., Bond, M., 2017. Baited Remote Underwater Video surveys undercount sharks at high densities: insights from full-spherical camera technologies. *Marine Ecology Progress Series* **585**, 113–121.

McConville, A., Grachev, I., Keane, A., Coulson, T., Bekenov, A., Milner-Gulland, E., 2009. Reconstructing the observation process to correct for changing detection probability of a critically endangered species. *Endangered Species Research* **6**, 231–237. https://doi.org/10.3354/esr00166

Misa, W., F, X, E., Richards, B., DiNardo, G., T., Kelley, C., Moriwake, V.N., Drazen, J., 2016. Evaluating the effect of soak time on bottomfish abundance and length data from stereo-video surveys. *Journal of Experimental Marine Biology and Ecology* **479**, 20–34. https://doi.org/10.1016/j.jembe.2016.03.001

Murray, R., Conales, S., Araujo, G., Labaja, J., Snow, S.J., Pierce, S.J., Songco, A., Ponzo, A., 2019. Tubbataha Reefs Natural Park: the first comprehensive elasmobranch assessment reveals global hotspot for reef sharks. Journal of *Asia-Pacific Biodiversity* **12**, 49–56. https://doi.org/10.1016/j.japb.2018.09.009

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283. https://doi.org/10.1038/nature01610

Ormond, R., Gore, M., Bladon, A., Dubock, O., Kohler, J., Millar, C., 2017. Protecting Cayman Island Sharks: *Monitoring, Movement and Motive* **15**.

Pauli, J.N., Whiteman, J.P., Riley, M.D., Middleton, A.D., 2010. Defining Noninvasive Approaches for Sampling of Vertebrates. *Conservation Biology* **24**, 349–352. https://doi.org/10.1111/j.1523-1739.2009.01298.x

Pierce, S.J., Norman, B., 2016. Rhincodon typus. The IUCN Red List of Threatened Species 2016: e.T19488A2365291. *IUCN Red List of Threatened Species*. URL https://www.iucnredlist.org/en (accessed 8.19.19).

Pikitch, E., Chapman, D., Babcock, E., Shivji, M., 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Marine Ecology Progress Series* **302**, 187–197. https://doi.org/10.3354/meps302187

Priede, I.G., Bagley, P.M., Smith, A., Creasey, S., Merrett, N.R., 1994. Scavenging deep demersal fishes of the Porcupine Seabight, north-east Atlantic: observations by baited camera, trap and trawl. *Journal of the Marine Biological Association of the United Kingdom* **74**, 481–498. https://doi.org/10.1017/S0025315400047615

Rosa, R.S., Castro, A.L.F., Furtado, M., Monzini, J., Grubbs, R.D., 2006a. Ginglymostoma cirratum. The IUCN Red List of Threatened Species 2006: e.T60223A12325895. *IUCN Red List of Threatened Species*. URL https://www.iucnredlist.org/en (accessed 8.19.19).

Rosa, R.S., Mancini, P., Caldas, J.P., Graham, R.T., Grubbs, R.D., 2006b. Carcharhinus perezi. The IUCN Red List of Threatened Species 2006: e.T60217A12323052. *IUCN Red List of Threatened Species*. URL https://www.iucnredlist.org/species/60217/12323052 (accessed 8.19.19).

Rose, D., 1998. Shark fisheries and trade in the Americas, Volume 1: North America. *TRAFFIC North America, Washington, D.C., USA*.

Santana-Garcon, J., Newman, S.J., Harvey, E.S., 2014. Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. *Journal of Experimental Marine Biology and Ecology* **452**, 82–90. https://doi.org/10.1016/j.jembe.2013.12.009

Sherman, C.S., Chin, A., Heupel, M.R., Simpfendorfer, C.A., 2018. Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? *Journal of Experimental Marine Biology and Ecology* **503**, 80–85. https://doi.org/10.1016/j.jembe.2018.03.002

Silva, C.D., Zeh, J., Madigan, D., Rugh, D., Baraff, L., Koski, W., Miller, G., Silva, C.Q.D., Zeh (contact, J., Madigan, David, Laake, J., Rugh, Dave, Baraff, Lisa, Koski, William, Miller, Gary, 2000. Capture-recapture estimation of bowhead whale population size using photo-identification data. *Journal of Cetacean Research Management* **2**, 45–61.

Spaet, J.L.Y., Nanninga, G.B., Berumen, M.L., 2016. Ongoing decline of shark populations in the Eastern Red Sea. *Biological Conservation* **201**, 20–28. https://doi.org/10.1016/j.biocon.2016.06.018

Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.D., Babcock, R.C., Pillans, R.D., Bradshaw, C.J.A., 2016. Reef shark movements relative to a coastal marine protected area. *Regional Studies in Marine Science* **3**, 58–66. https://doi.org/10.1016/j.rsma.2015.05.002

Stevens, J., 2009. Prionace glauca. The IUCN Red List of Threatened Species 2009: e.T39381A10222811. *IUCN Red List of Threatened Species*. URL https://www.iucnredlist.org/en (accessed 8.19.19).

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. https://doi.org/10.1006/jmsc.2000.0724

Stevick, P.T., Palsbell, P.J., Smith, T.D., Bravington, M.V., Hammond, P.S., 2001. Errors in identification using natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1861–1870. https://doi.org/10.4135/9781412974615.n24

Stobart, B., Díaz, D., Álvarez, F., Alonso, C., Mallol, S., Goñi, R., 2015. Performance of Baited Underwater Video: Does It Underestimate Abundance at High Population Densities? *PLOS ONE* **10**, e0127559. https://doi.org/10.1371/journal.pone.0127559

Sundström, L.F., 2015. Negaprion brevirostris. The IUCN Red List of Threatened Species 2015: e.T39380A81769233. *IUCN Red List of Threatened Species*. URL https://www.iucnredlist.org/en (accessed 8.19.19).

Walsh, A.T., Barrett, N., Hill, N., 2017. Efficacy of baited remote underwater video systems and bait type in the cool-temperature zone for monitoring ‘no-take’ marine reserves. *Marine and Freshwater Research* **68**, 568. https://doi.org/10.1071/MF15165

Ward-Paige, C.A., Mora, C., Lotze, H.K., Pattengill-Semmens, C., McClenachan, L., Arias-Castro, E., Myers, R.A., 2010. Large-Scale Absence of Sharks on Reefs in the Greater-Caribbean: A Footprint of Human Pressures. *PLOS ONE* **5**, e11968. https://doi.org/10.1371/journal.pone.0011968

White, J., Simpfendorfer, C.A., Tobin, A.J., 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. https://doi.org/10.1016/j.jembe.2013.08.004

Whitmarsh, S.K., Fairweather, P.G., Huveneers, C., 2017. What is Big BRUVver up to? Methods and uses of baited underwater video. *Reviews in Fish Biology and Fisheries* **27**, 53–73. https://doi.org/10.1007/s11160-016-9450-1

Willis, T., Millar, R., Babcock, R., 2000. Detection of spatial variability in relative density of fishes:comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**, 249–260. https://doi.org/10.3354/meps198249

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy* **40**, 194–204. https://doi.org/10.1016/j.marpol.2012.12.034

CHAPTER 2: APPLYING PHOTO-IDENTIFICATION TO BRUVS TO INVESTIGATE THE ABUNDANCE AND DRIVERS OF REEF SHARKS IN THE CAYMAN ISLANDS

Katherine Mason[a,*], Mauvis Gore[b, c] and Johanna Kohler[b, c, d]

[a] University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

[b] Marine Conservation International, South Queensferry, Edinburgh, Scotland, EH30 9WN UK

[c] Centre for Marine Biodiversity and Biotechnology, Heriot-Watt University, Edinburgh, Scotland, EH14 4AS UK

[d] Cayman Islands Department of Environment, North Sound, Georgetown, Cayman Islands

*Corresponding author: *kat-mason@hotmail.com*

Abstract

Baited Remote Underwater Video Systems (BRUVS) are an increasingly popular method of surveying marine life such as sharks, due to their ease of use, low cost and non-invasive nature; important when sampling threatened and protected species. BRUVS generate relative abundance indices, most often by counting the maximum number of individuals recorded at one time (MaxN). This study counted the total number of individuals (Nind) per survey using photo-identification to differentiate between sharks. Individuals were also assigned sex and maturity. Relative abundance was compared across the factors associated with each site, in order to gain insight into the drivers of abundance. BRUVS were deployed at 84 sites around Grand Cayman and Little Cayman Islands, during October and November 2018, each for a minimum of 2 hours. Seventy sharks were recorded across 45 sites, belonging to four reef shark species and one unidentified species (identified to genus level). The Caribbean reef shark (*Carcharhinus perezi*) and the nurse shark (*Ginglymostoma cirratum*) were the most abundant species. Longer deployment times (120 v 60 min) were found to significantly increase both MaxN and Nind abundance estimates. Significantly more species were recorded with longer time. The mean time for *C. perezi* and *G. cirratum* to arrive and to reach Nind was beyond 60 min. Photo-ID allowed 97% of sharks to be identified to species level and 85% of these as individuals. A significantly higher relative abundance of *C. perezi* were found on Little Cayman but not at inner lagoon sites, whilst there was a higher relative abundance of *G. cirratum* at deep sites. Depth and zone were significant predictors of species composition, with depth being significant to species and maturity composition. The results demonstrate that the longer deployment time improves abundance estimates and the application of Nind through photo-ID allows for finer-scale analysis. Nind estimates, combined with evaluation of drivers, can be used to explore which factors affect shark abundance of each species, at different maturity stages and for each sex. This can provide valuable information for conservation plans and marine protected area development.

Keywords: Baited remote underwater video systems; relative abundance; photo-identification; Cayman Islands; reef sharks

Introduction

Many shark and ray species are facing rapid population decline due to mass overfishing and habitat loss (Myers and Worm, 2003). These threats are compounded by their K-selected life history characteristics (Stevens *et al.*, 2000), such as low fecundity. Sharks have proven vital to marine ecosystems; many are situated at or near to the top of marine food webs and feed on a wide range of prey (Bascompte *et al.*, 2005; Field *et al.*, 2009). Despite growing awareness and concern, shark mortality rates may still exceed reproductive rates in many regions (Worm *et al.*, 2013) and their life history characteristics dictate minimal ability for populations to recover after depletion (Ferretti *et al.*, 2010; Stevens *et al.*, 2000). This decline affects entire ecosystems and may result in complex community changes including trophic cascade (a shift from coral to algal-dominated reefs), meso-predatory release, and ensuing declines in commercial fish species (Ferretti *et al.*, 2010). Adding to their essential ecological role, sharks have more recently been credited for their part in generating income for local economies via tourist activities. Observing sharks and rays through snorkelling or scuba-diving is a growing industry. By 2010, the income generated from these activities (by at least 376 operators in a minimum of 29 countries) consistently outweighed that from landed sharks (Gallagher and Hammerschlag, 2011).

The Cayman Islands, located in the Caribbean Sea, enforces protection for all shark species throughout its Exclusive Economic Zone (EEZ), since 2015. Monitoring of elasmobranch species and population abundances has been in effect since 2009 in Cayman waters (Ormond *et al.*, 2017), using a variety of methods including BRUVS, acoustic tagging and citizen science. Historical intense commercial and recreational fishing in the Caribbean may be responsible for wider shark population decline (Bonfil, 1997; Ward-Paige *et al.*, 2010). Before 2009, little was known regarding the species and population numbers of sharks inhabiting the waters around the Cayman Islands. Estimated shark abundance is only 20 - 30 % of what might be expected in comparison to large and isolated areas such as the Western Indian Ocean, and much lower than neighbouring Belize (Clarke *et al.*, 2012; Ormond *et al.*, 2017; Pikitch *et al.*, 2005). Ormond *et al.* (2017) did however estimate the value of the non-consumptive use of sharks in the Cayman Islands to be between US $46.8 million and $62.6 million per year.

Data collection for sharks is notoriously difficult, due to the vast scale of their habitat (Baum *et al.*, 2003), which limits scientists' abilities to monitor populations effectively. Management and protection is challenging due to their highly mobile nature (Green *et al.*, 2015; Speed *et al.*, 2016) and the distinct knowledge gap surrounding the spatial ecology of sharks that utilise island habitats. The Cayman Islands are separated by very deep water from continental coasts (Ormond *et al.*, 2017), so understanding the species that use these islands is vital for their on-going protection.

Extractive data collection, as in fishing surveys, can be problematic in protected areas and where species are rare, timid or protected (Brooks *et al.*, 2011; Willis *et al.*, 2000). The use of non-invasive survey techniques, such as baited remote underwater video systems (BRUVS), has increased enormously in recent years. BRUVS were chosen to study the Cayman Island shark populations due to their non-invasive and non-destructive nature, desirable when surveying protected and threatened species. They are also low-cost, relatively easy to build and deploy; important when involving widely distributed species, large areas and long-term programmes (Bernard and Götz, 2012; White *et al*., 2013). BRUVS minimise disturbance to animals, which increases data accuracy and allows for large population sampling (Pauli *et al*., 2010). Yet, BRUVS produce similar relative abundance estimates to longline surveys (Brooks *et al*., 2011), and can be deployed at a range of depths and in varying habitats (Cappo *et al*., 2006).

The soak time of BRUVS widely varies between studies, with the majority recording for 30, 60 or 120 min (Whitmarsh *et al*., 2017). Those that ran for longer often used additional batteries or power sources (Harasti 2016). Studies that compared soak times concluded that whilst 15 - 60 min are ideal for capturing bottomfish assemblages and estuarine environments, longer time periods are used for shark species (Asher, 2017; Harasti *et al*., 2016), as these are typically less abundant.

BRUVS can be used to estimate relative abundance of each species present at a specific site or location. The standard and most commonly used metric for measuring relative abundance is MaxN (Cappo, 2010). MaxN is the maximum number of individuals seen within a single frame per species: designed to eliminate double counting and the overestimating of abundance. However, this means that each new arrival is assumed to be the same individual as previously, potentially resulting in an underestimation of the total number of individuals (Cappo, 2010; Kilfoil *et al*., 2017). Additionally, when applied to small populations, the values of MaxN may not mirror fluctuations in the wider population, due to sample saturation (Stobart *et al*., 2015). BRUVS footage can also be analysed by using mean count (MeanCount), time in – time out (TITO), and time of first arrival (T1st) (Cappo *et al*., 2011). MaxN and MeanCount are abundance estimates, however MeanCount has its own bias by using time intervals, decreasing detection probability (Campbell *et al*., 2015). TITO allows for behavioural analyses such as boldness (Cappo, 2010), and T1st indicates the distance of the animal to the system and/or the attractiveness of the bait (Bassett and Montgomery, 2011). To overcome these biases and increase the accuracy of abundance estimates, individuals within frame can be individually identified.

Few studies have attempted to estimate actual abundance by identifying and counting individuals through photo-identification (Harasti *et al*., 2016; Kilfoil *et al*., 2017). This can be achieved by using distinguishable features such as fin markings and injuries (Domeier and Nasby-Lucas, 2007). Photo-ID has been used on a wide range of taxa, and more recently elasmobranchs. These include the whale shark (*Rhincodon typus*) using unique spot patterns (Araujo *et al*., 2014), the white shark

(*Carcharodon carcharias*) and basking shark (*Cetorhinus maximus*) using physical features such as fin markings and injuries (Domeier and Nasby-Lucas, 2007; Gore *et al.*, 2016; Harasti *et al.*, 2016). BRUVS footage often captures multiple angles of an individual, enabling the observation of several distinguishing features, facilitating identification of individuals in some instances (Sherman *et al.*, 2018).

Photo-ID allows for the differentiation between individuals and therefore a count of the total number of individuals on each BRUVS. Sherman *et al.* (2018) identified individuals of two batoid species and examined differences in MaxN estimates to counts of identified individuals (referred to hereafter as Nind). Results demonstrated that Nind showed abundances 2.4 and 1.1 times higher than MaxN. With enough individuals and “re-sights”, it is possible to incorporate mark-recapture methodology, used by Castro and Rosa (2005), producing an estimate of actual abundance during the sampling season. Studies have confirmed its accuracy in research, an effective alternative to conventional tagging, including those with elasmobranchs (Gore *et al.*, 2016; Stevick *et al.*, 2001). Using a method such as Nind (Sherman *et al.*, 2018) to assess and monitor species can provide more accurate abundance estimates for populations where small differences may have significant impacts on management and conservation (McConville *et al.*, 2009).

Furthermore, BRUVS can be used to identify sex, assign maturity and estimate size of individual sharks, as carried out by Jaiteh *et al.* (2016). Classifying each individual by sex and maturity allows the observation of potential sexual segregation and the use of different sites by different demographic groups. This can be used to examine whether the same types of individuals are frequenting the same sites, and whether factors belonging to each site are important drivers of abundance. Information regarding the abundance and distribution of sharks is central to the development of protection planning and management (Garla *et al.*, 2006).

This study used BRUVS to survey reef shark populations around Grand and Little Cayman during October and November 2018. BRUVS were deployed at depths ranging from 0.3 – 25 m, covering a variety of habitats and reef zones. From the 84 survey sites, sharks were identified to species level and individuals were distinguished via photo-identification, estimating the total number of individuals (Nind) on each survey. Environmental factors (habitat, depth, reef zone) were recorded for each site. BRUVS typically ran for two hours, so abundance counts from the different time periods (60 and 120 min) were compared. For each time period, both MaxN and Nind abundance counts were also compared. Additionally, the time of first arrival and time of Nind for the two main species were analysed and the number of species recorded were compared between the two time periods. The abundance of the two main species (Caribbean reef shark, *Carcharhinus perezi* and nurse shark, *Ginglymostoma cirratum*) were investigated for differences within factors – island, reef zone, habitat, depth and areas of protection. Individuals of *C. perezi* and *G. cirratum* were assigned to demographic groups based on sex and maturity (where possible) and group composition was explored in conjunction with site factors. Information regarding the abundance and distribution of sharks is central to the development of protection planning and management.

Materials and Methods

Study site and sampling.

The Cayman Islands constitute three islands; Grand Cayman, Little Cayman and Cayman Brac, situated in the north-west Caribbean Sea (19.3133° N, 81.2546° W) (Figure 2.1). Midway between Cuba and Jamaica, this cluster of islands are emergent sections of the Cayman Ridge, and run adjacent to the Cayman Trench, ~7 km deep (Ormond *et al*., 2017). A well-developed fringing reef complex borders the islands, surrounded by a coastal shelf, which drops abruptly to considerable depths. In some parts, sandy lagoon areas and seagrass beds (known locally as "sounds") separate the shore and the fringing reef. Mangrove forests often line these shores (Ormond *et al*., 2017). More than 25 years ago, a network of Marine Parks was designated, occupying around 25% of the coastline. Under the Cayman Islands National Conservation Law [2013, section 17], full protection was granted to all shark species throughout Cayman waters in 2015.

BRUVS were deployed during daylight hours in October and November 2018. 84 BRUVS units were dropped at 21 locations around Grand Cayman (*n* = 13) and Little Cayman (*n* = 8) islands (19.3133° N, 81.2546° W), (Figure 2.1). BRUVS used in this study consisted of a plastic crate as the base with dive weights attached inside for stabilisation. A 1 - 1.5 m bait arm, made from PVC or metal pipe extending from the base housed the bait bag. The bait was held in a small, thin mesh bag of either plastic or hessian material, inside a larger plastic mesh bag attached to the arm with zip ties. This was to reduce bait loss by scavenging fish.

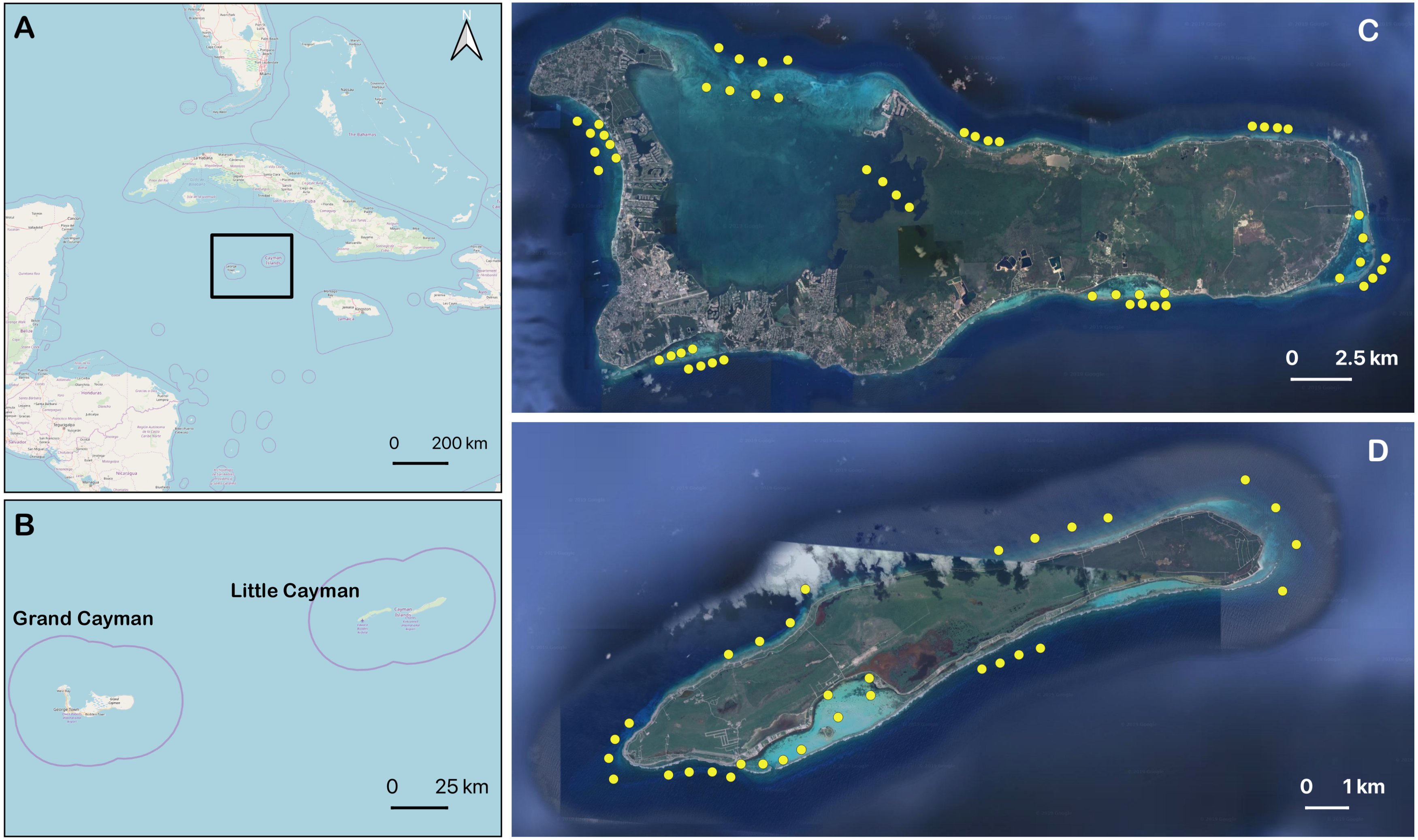


Figure 2.1. Location of the Cayman Islands (a) & (b) in the Caribbean Sea, and sample sites marked as yellow points around (c) Grand Cayman and (d) Little Cayman islands

The bait bag contained ≃ 300 g of oily Atlantic mackerel (*Scomber scombrus*), rated for human consumption, sliced in widths of ≃ 1 cm to promote dispersal of the bait plume. One camera was fixed on top of each crate, aimed horizontally and pointing toward the bait. GoPro Hero 3+ and 4 cameras with wide-angle view, set at 1080 Superview at 25fps, were used in underwater housing. The high definition (HD) videos allowed for the capture of fine detail. Each GoPro had an additional battery BacPac to allow for recordings of 2+ h. Stereo-BRUVS were not used due to cost and time limitations.

BRUVS survey locations were spread around the islands to cover as much coastline as possible. Deployments on the "inner reef" zone were at depths between 0.3 – 5.5 m in the sounds. Deployments on the outer fringing reef zone were between 6 – 25 m, covering a variety of habitats including sand, seagrass bed, hardpan and coral. Exact BRUVS locations were recorded using a hand-held GPS. Prior to the deployment of each unit, environmental conditions were recorded on-board, such as cloud cover, wind direction and strength, sea state, wave height and swell. BRUVS were manually lowered to the seafloor with a rope attached to a surface buoy. The BRUVS unit was placed onto patches of sand or seagrass, using a viewer to avoid reef. Time of entry was noted and depth was recorded using a hand-held depth sounder. Also logged were bait arm direction, current strength and direction.

Four BRUVS units were deployed per survey location parallel to shore, with a distance of 500 m to 1 km between each to ensure survey independence (Cappo *et al.*, 2003). In once instance, two BRUVS of a set of four were situated 450 m apart due to limited area within the sounds. Cappo (2010) reported that a distance of 300 m still minimised the possibility of large-scale interference of the replicates with each other. Each BRUVS was left to record for a minimum of 120 min. The units were recovered manually using the surface marker buoy. The boat maintained distance from the BRUVS during survey time to reduce effects of boat noise on shark behaviour. Using the GPS locations of the sites, it was determined whether the BRUVS were deployed in a Marine Park protected area. The Marine Parks include a range of complete no-take zones, partial no-take zones and no-diving zones (Cayman Islands Government, 2019). The no-diving zones do not include any other restrictions, including fishing limitations, so these were not counted as protected areas in these analyses.

Video annotation.

All BRUVS footage was analysed manually by two trained experts using media players. Other conditions were recorded, such as visibility, current strength and direction, the success of the BRUVS placement and the relative amount of exposure of the bait bag to current. The time at which each BRUVS settled on the seabed and the time it was retrieved (total seabed deployment time) were documented. The substrate around each BRUVS was categorised by type and quantity at the start of each video. Near, mid and far substrate were allocated by eye, as undertaken in other studies (Espinoza *et al*., 2014; Tickler *et al*., 2017), by dividing the screen into three concentric circles working outwards from the bait bag. Substrate types were allocated percentages of cover. Near, mid and far percentages were averaged and any substrate type that covered 25% or more of the area was included, combined and placed into habitat groups: sediment, seagrass, reef, reef + sediment, hard bottom, hard bottom + reef, sediment + hard bottom. Hard bottom includes hardpan: a hard, impervious, and usually clay layer produced as a result of cementation by precipitation of insoluble minerals. As BRUVS were intentionally placed on sand to avoid causing damage to reef, far habitat was included in analysis to ensure inclusion of any reef structure beyond the sand patches. Far habitat was excluded if obscured by nearer habitat. The depth of each BRUVS was placed into one of three categories: shallow (0 - 7.9 m), mid (8 – 15.9 m) and deep (16 – 23.9 m).

For each shark observed, species, sex and estimated maturity were recorded, alongside the time of arrival into view and the time of departure from view. Any individuals that could not be distinguished as a specific species were pooled at genus level, and will hereafter be referred to as ‘spp’. Sex was established by the visibility and presence/absence of claspers. Males have claspers, and the size of these indicate a maturity stage; claspers shorter than the pelvic fins were classed as immature. Absence of claspers indicates the individual is a female (displayed in Appendix A1). When there was no clear visibility of the clasper area, the sex was undetermined; therefore the individual was classed as No Visible Clasper (NVC).

Maturity was established by size estimates and visualisation of claspers on males. Size was estimated by two annotators; experienced scuba divers who regularly dive with reef sharks. Estimates were made firstly by comparing the total length (TL, from the tip of the snout to the tail in a horizontal plane) of the shark with the known length of the bait bag, striving to measure whilst the shark was situated close to the bag and positioned perpendicular to the bait arm. Secondly, photos were taken of a pole marked with 10 cm increments, at each metre from 1-10 m away from the camera. Screenshots of each shark were taken and the distance away from the camera estimated. The pole length was then compared to the estimated shark TL. Both annotators considered these two lengths and when both measurements were either above or below the length at maturity for that species, a maturity stage was assigned.

Size-at-maturity values for the two most abundant species were taken from literature. *C. perezi* total length at maturity is defined as 150 cm for males and 200 cm for females (Compagno, 1984; Pikitch *et al*., 2005). *G. cirratum* total length at maturity is defined as 180 cm for males and 210 cm for females (Castro, 2000; Pikitch *et al*., 2005). Where claspers were clearly visible past pelvic fins, these were classed as mature males. Any shark larger than the male maturity length without visible claspers was considered female. Any shark not positioned adequately within frame at any point or too far away was excluded from maturity estimations.

Photo-identification.

Individual identification was applied using photo-ID. Frames were taken of each shark when in the field of view while illustrating key identifying features. Any recognisable characteristics were recorded, for example fin shape, abnormal discolouration or pigmentation, cuts or scarring (see Appendix A2). Where necessary, multiple features were used to distinguish between individuals, as seen in studies on *C. carcharias* (Domeier and Nasby-Lucas, 2007). As this study is comparing only those sharks observed within the one sampling season, the likelihood of cuts and marks healing within the season is highly unlikely. If any shark with injuries is re-sighted, it will almost certainly exhibit the same characteristics (Anderson and Goldman, 1996; Gore *et al*., 2016). A photo-ID database for each species was created to enable re-identification of individuals. The identifying features were compared to all other individuals within each and across all deployments. Individuals were marked as “unknown” if they did not swim close to the camera or moved too quickly for detail to be apparent. Any individuals classed as ‘NVC’ were compared to previously identified male and female individuals, which when originally recorded, may have shown the same distinguishing features as well as a clear view of their clasper area. Comparison between individuals could be undertaken with confidence due to the high-resolution images extracted from the videos. If a sufficient number of individuals were re-sighted on subsequent BRUVS, it would be possible to estimate population size using mark-recapture methodology (Pollock *et al.*, 1974).

Abundance.

Photo-ID was also employed for calculations of Nind, and so allowed for comparisons between two abundance estimates on each survey. Firstly, MaxN was calculated; the greatest number of sharks belonging to each species in frame at any one time, along with the time at which MaxN occurred. Subsequently, each shark visiting the BRUVS was identified and the actual number of different sharks was determined. Not all sharks were identifiable. However, this only occurred in circumstances where the shark was the only shark on the entire survey, or it could be definitively differentiated from other sharks on the same survey. MaxN and Nind values were compared with respect to two time periods: 60 min after seabed deployment and 120 min after. This enabled investigation into whether longer deployment time allowed for a higher count of MaxN, more individuals and/or more species.

Statistical analyses.

Shark abundance data recorded across all BRUVS sites was summarised. The number of sites in which a species was recorded was characterised 'Frequency', and the complete sum of Nind was characterised 'Abundance'. The 'Mean Nind' was the sum of all sites with that species present divided by the sum of Nind. The standard deviation evaluated the amount of variation from the 'Mean Nind' for each species. The relative abundance was calculated by dividing the sum of Nind by the total number of sample sites. The probability of encounter was estimated by dividing the number of sites with a species present by the total number of sites.

Standard tests were performed in R software v3.4.2 (R Core Team, 2017). A Shapiro-Wilk test was used to analyse the distribution of data. Most deviated from a normal distribution, mainly due to the abundance of 0 values, therefore non-parametric tests were used where appropriate. Values of $p<0.05$ were considered significant and are denoted in results tables by '*'. *P*-values of <0.001 are denoted in tables by '**'.

MaxN and Nind abundance estimates were compared, between the two main species separately and also between all sharks. These were both compared between the time periods of 60 and 120 min. The Wilcoxon signed rank test with continuity correction was used for both sets of analyses, to account for ties. For these analyses, videos that did not run for 120 min were removed, and for those videos that ran longer, sharks were removed if their arrival was after 120 min. To limit the exclusion of data, videos that ran for 115 minutes were included, and four sharks entering between 120 and 130 min were included. The number of species recorded in the first 60 min versus 120 min was compared. Sharks that could not be identified to species level were removed. As none of the identified sharks were re-sighted, mark-recapture estimates were not undertaken. For time of arrival and of Nind, the data followed a normal distribution and so the two-sample t-test was used to compare between the two main species.

As recording times varied between deployments (mean deployment time ± 1 SD = 126.52 ± 17.72 min) and to include as much data as possible, relative abundance was derived from deployment time and Nind data, standardised to CPUE (Nind sharks/hr^{-1}). The Mann–Whitney U test and Kruskal-Wallis H test were used with continuity correction to analyse the potential effects of environmental and other factors on CPUE data. Dunn's post-hoc test was used to further explore the data where significant differences were found. The p-adjustment method used for multiple comparison corrections was FDR (Benjamini and Hochberg, 1995), as Bonferroni tends to be overly conservative (Perneger, 1998).

PERMANOVAs were used to evaluate differences between species composition amongst various factors. The factors tested were island (Grand Cayman and Little Cayman), zone (inner and outer reef), depth (shallow, mid and deep), habitat type (reef, hard bottom, sediment, seagrass, hard bottom + reef, sediment + hard bottom and reef + sediment) and protection (marine park and none). Individuals were grouped by sex and maturity and differences in the composition of demographic groups were also evaluated. Individuals belonging to the two main species were first grouped by the combination of sex and maturity, and then split into groups of males and females, and groups of mature and immature. These three groupings were tested separately. Pairwise PERMANOVA tests further explored where significant differences were found. The FDR p-adjustment method for multiple comparison corrections was used (Benjamini and Hochberg, 1995). Non-metric multidimensional scaling (nMDS) ordinations using Bray-Curtis dissimilarity were produced, displaying factors that were found to be significant from the PERMANOVAs. The data consisted of a matrix, whereby the rows were the abundance counts of each species and group and the columns were BRUVS sites. Empty samples were removed. The plots were used to visualise potential patterns of groupings across the factors. The MDS plots and PERMANOVA results indicate whether or not there are significant groups and which factors are most important in explaining the groupings. For the analyses investigating demographic groups, only sharks that could be sexed and/or assigned a maturity stage were included. R packages vegan and ggplot2 were used for PERMANOVA and nMDS plots (Oksanen *et al.*, 2018; Wickham, 2016). Pairwise PERMANOVAs were carried out using RVAideMemoire package (Hervé, 2019).

Results

BRUVS Summary.

A total of 83 of the 84 surveys were successful, with the single failed deployment due to camera flooding. From these 83 deployments, a total of 70 sharks were recorded; 68 belonging to 4 species: *Carcharhinus perezi, Ginglymostoma cirratum, C. limbatus* (Blacktip shark) and *Negaprion brevirostris* (Lemon shark), and two were identified to genus level: *Carcharhinus* spp. The total number of sharks belonging to each species is listed in Table 2.1. Overall, 45 BRUVS recorded at least one shark.

Table 2.1. Summary of sharks recorded on BRUVS around Grand Cayman and Little Cayman, in order of descending relative abundance

			Nind				Relative	Probability of
Species	Frequency	Abundance	Mean	SD	Max	Min	Abundance	encounter
G. cirratum	28	36	1.29	0.71	4	1	0.43	0.34
C. perezi	21	27	1.29	0.56	3	1	0.33	0.25
C. limbatus	3	3	1	0	1	1	0.04	0.04
N. brevirostris	1	2	2	0	2	2	0.02	0.01
C. spp.	2	2	-	-	-	-	-	-

G. cirratum was the most abundant species of the survey and was recorded across the most sites (33% of sites). *C. perezi* was the second most abundant species, recorded at 25% of sites.

Abundance estimates and deployment time.

Overall, Nind estimates were 1.13 times greater than MaxN for *C. perezi*, and 1.11 times greater for *G. cirratum* (Appendix B). No significant differences were found for *C. perezi* and *G. cirratum* species when comparing MaxN and Nind abundance values. This was the case for both deployment periods (60 and 120 min) (Table 2.2; Figure 2.2). However, there was a significant increase in MaxN values when comparing periods of 60 and 120 min, for both *C. perezi* and *G. cirratum* species (p=0.002, p<0.001). Additionally, Nind values were significantly higher when comparing 60 and 120 min for both species (p=0.002, p=<0.001). Nind values were also significantly higher during the period of 120 min when including individuals from all recorded species (p<0.001).

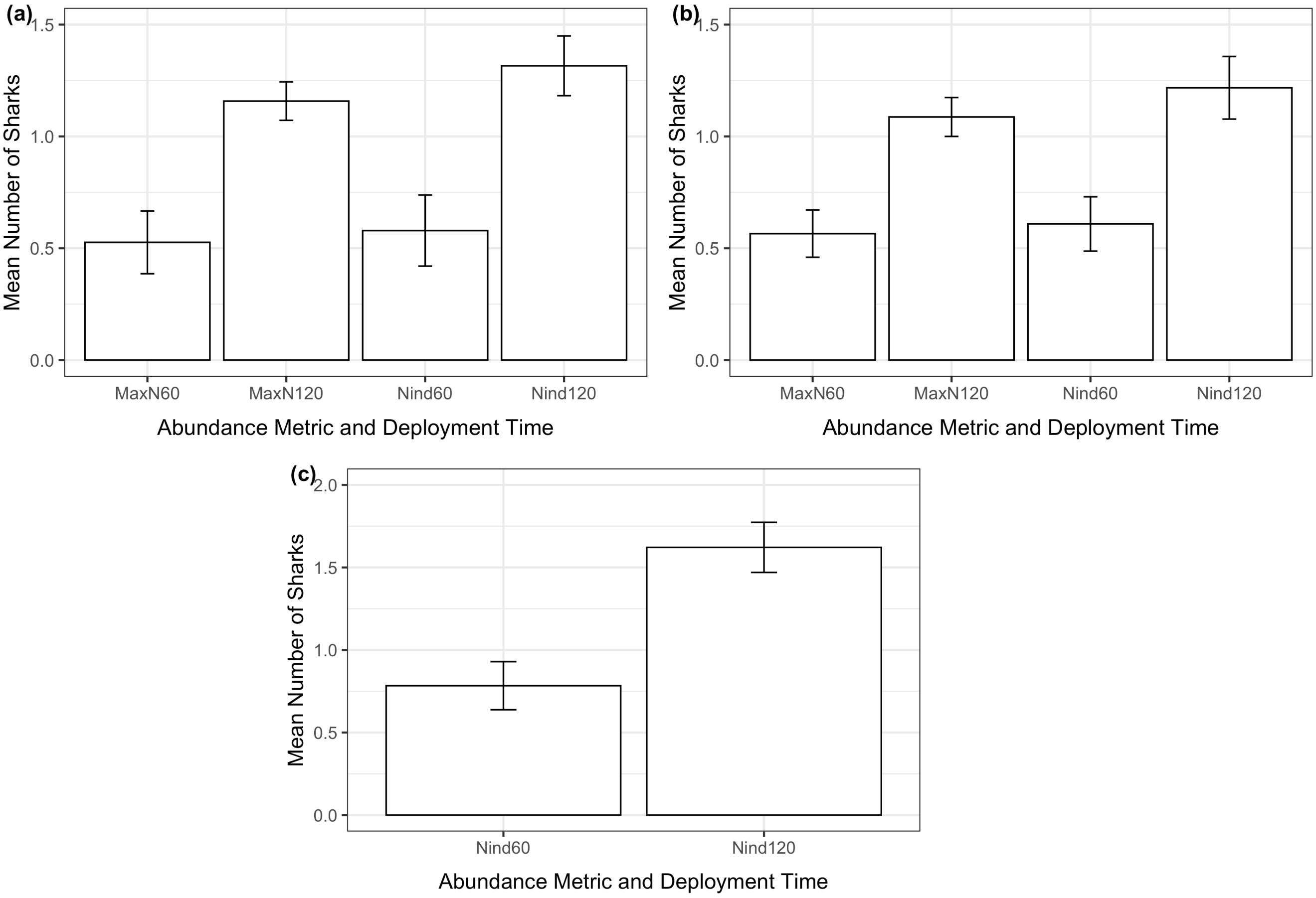


Figure 2.2. The mean number of sharks (± 1 SE) observed on videos with shark presence using MaxN and Nind abundance metrics across deployment periods of 60 and 120 min, for (a) *C. perezi*, (b) *G. cirratum* and (c) all shark species for Nind only

Sample sizes for *C. limbatus* and *N. brevirostris* species were too small for statistical significance to be detected individually.

Table 2.2. The results of Wilcoxon Signed Rank Test (*p* = statistical significance) using continuity correction for the differences between MaxN and Nind abundance estimates and between time periods of 60 and 120 min

Deployment Time (min)	Abundance Estimate	*C. perezi*		*G. cirratum*		All species	
		Z	*p*	Z	*p*	Z	*p*
60	MaxN *vs.* Nind	-0.67	0.5	-0.67	0.5	-	
120	MaxN *vs.* Nind	-1.78	0.074	-1.78	0.074	-	
60 *vs.* 120	MaxN	-3.13	0.0018*	-3.36	0.00079**	-	
	Nind	-3.07	0.0021*	-3.50	0.00046**	-4.34	1.448e-05**

Additionally, the number of shark species recorded during 120 min was significantly higher than during 60 min ($p<0.001$) (Table 2.3).

Table 2.3. The results of Wilcoxon Signed Rank test using continuity correction comparing the number of species recorded between two time periods (60 and 120 min) (*p* – statistical significance)

Deployment Time (min)	Number of species recorded	
	Z	*p*
60 *vs.* 120	-3.97	$7.166e^{-05}$**

Species time of arrival and Nind.

The time taken for the two most abundant species to make their first appearance were analysed and compared. On average, *C. perezi* took 63.25 ± 32.23 min after seabed deployment time to arrive and similarly, *G. cirratum* took 62.63 ± 40.65 min. Additionally, *C. perezi* obtained Nind values on average at 63.16 ± 32.93 min and *G. cirratum* on average at 62.84 ± 40.99 min (Figure 2.4). Two-sample T-tests (Appendix C) showed no significant difference between the two species for both their time of arrival (p=0.95) and their time of Nind (p=0.98).

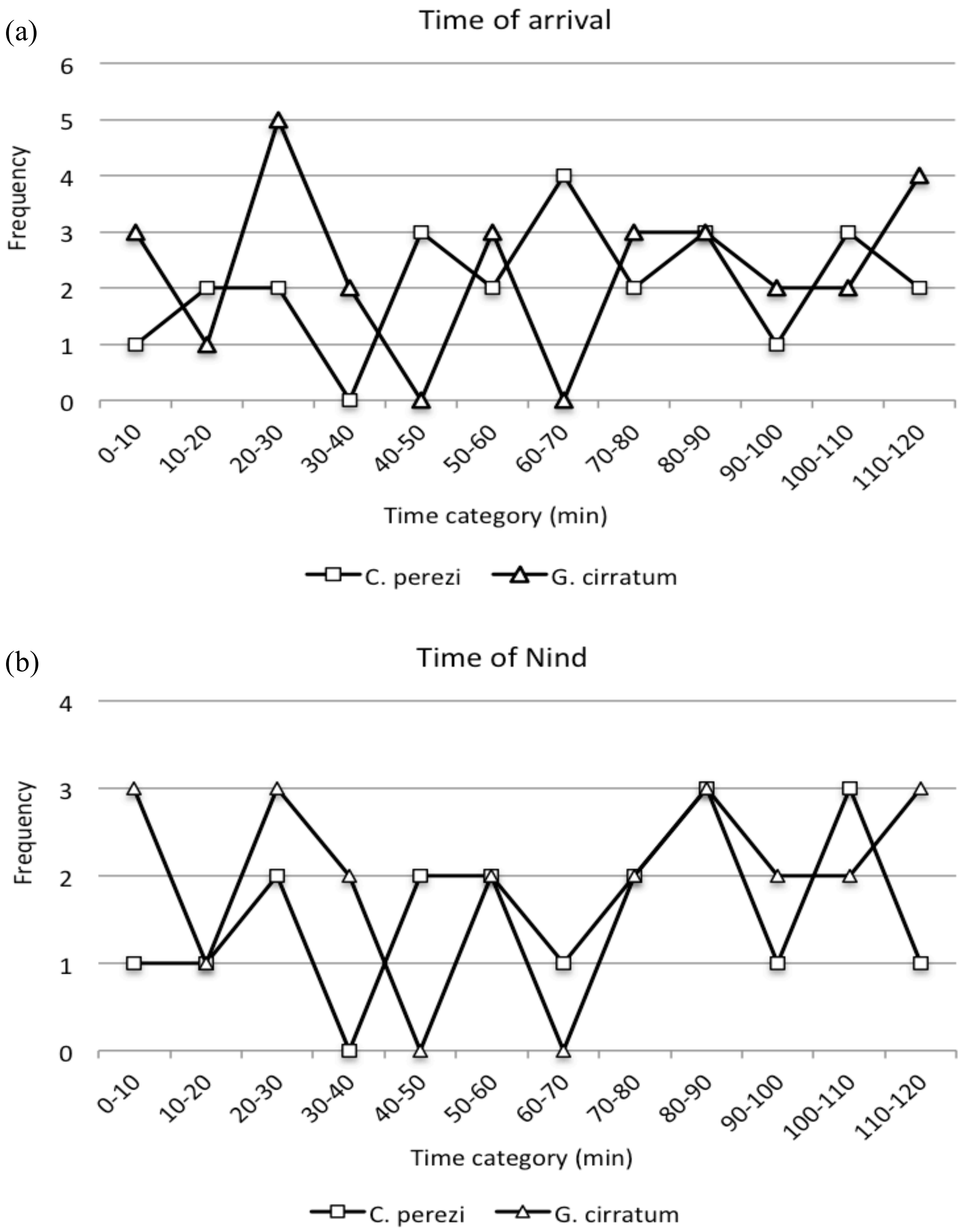


Figure 2.3. Frequency of (a) time of arrival and (b) time of Nind for *C. perezi* and *G. cirratum* species, categorised in 10 min periods

Figure 2.3 (a) displays the different behaviours of the two species; *G. cirratum* arrival time peaks in the 20 – 30 min period, whereas *C. perezi* peaks later at around 60 – 70 min. Both species have individuals arriving towards the end of the 2 h recording period. Figure 2.3 (b) shows more similarity between behaviours; with the time of Nind occurring throughout the entire 2 h period, even within the last ten minutes.

Photo identification.

Of the 68 sharks recorded and identified to species level, 53 could be individually identified. Percentage recognisability per species is displayed in Table 2.4.

Table 2.4. The total number of individuals and individually identifiable sharks of different species observed using photo-ID on BRUVS in the Cayman Islands (83 deployments)

Shark species	Common name	Total no. sharks	No. individually identified sharks	% individually identifiable sharks
C. perezi	Caribbean reef shark	27	19	70.4
G. cirratum	nurse shark	36	31	86.1
C. limbatus	blacktip shark	3	1	33.3
N. brevirostris	lemon shark	2	2	100

All species were relatively easy to recognise for the majority of videos, however *C. limbatus* proved more difficult to differentiate due to low visibility. Individuals belonging to all species often had distinctive markings, colourations and fin shapes, displayed in Appendix A2. Two of the 70 individuals were identified to genus level only (*Carcharhinus* spp.) due to poor visibility and distance from camera. No individually identified sharks belonging to any species were re-identified on a subsequent BRUVS. Therefore, mark-recapture methodology could not be implemented.

Relative abundance and explanatory factors.

BRUVS deployed on the inner zones of Grand Cayman composed 27.8% of all deployments, Grand Cayman outer zones were 33.7%, 9.6% were on Little Cayman inner zones and 28.9% of BRUVS were deployed on Little Cayman outer zones. Sites were categorised into habitat types (reef, hard bottom, sediment, seagrass and combinations), depth classes (shallow: 0 - 7.9 m, mid: 8 – 15.9 m, and deep: 16 – 24 m) and protected areas (marine parks or none) (Figure 2.4).

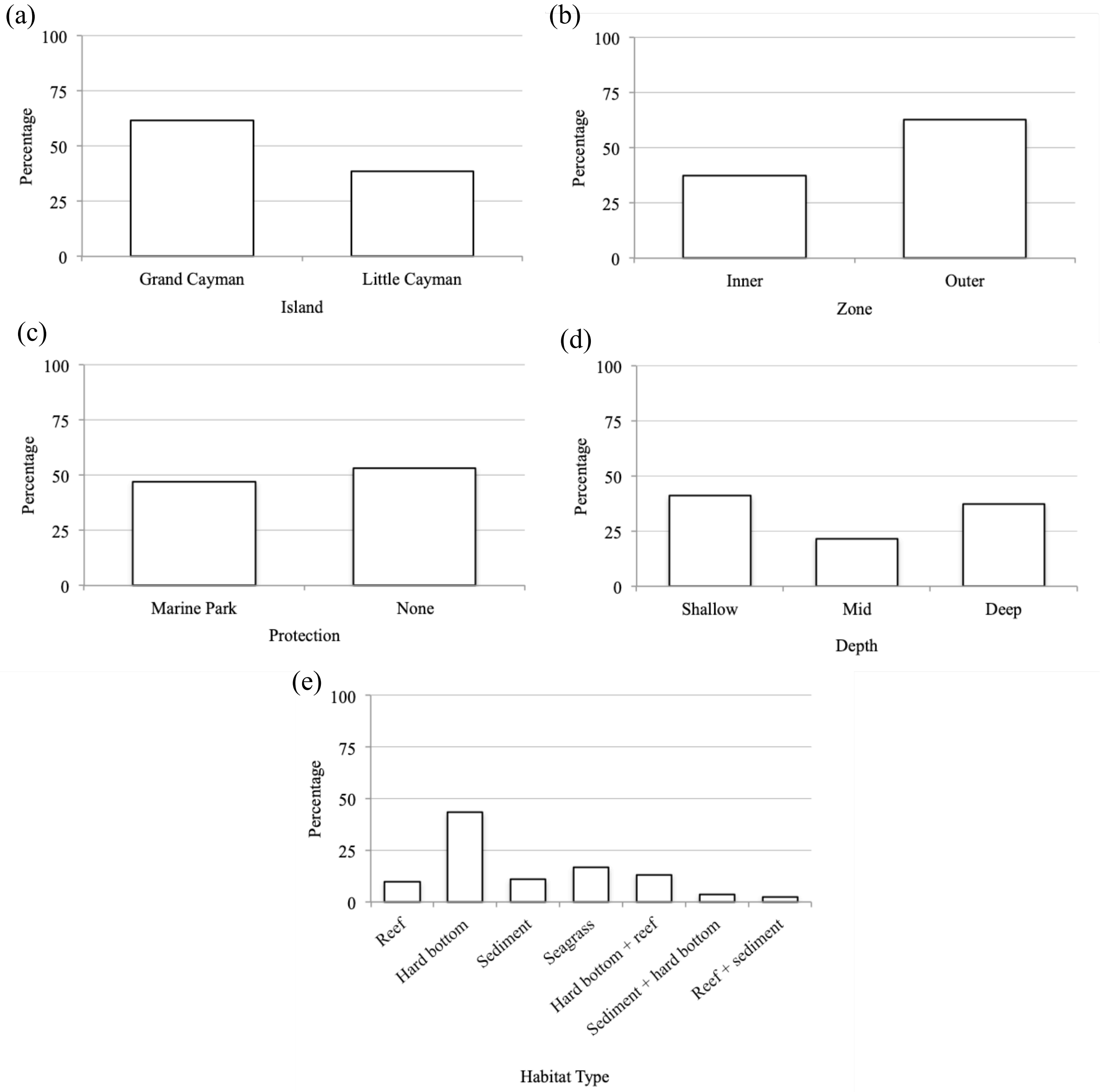


Figure 2.4. Locations and characteristics of BRUVS deployment sites (*n* = 83): (a) island, (b) zone, (c) protection, (d) depth and (e) habitat type

Of the 83 BRUVS, 45 BRUVS recorded at least one shark (Appendix D). *C. limbatus* (*n* = 3) was recorded on Grand Cayman only, within a sound (seagrass, inner zone). In contrast, *N. brevirostris* (*n* = 2) was recorded only on Little Cayman, also within a sound. At these sites, no other shark species were recorded, bar one unidentified *Carcharhinus* species in a Grand Cayman sound. For the two most abundant species, *C. perezi* were present at 21 sites and G. cirratum at 28 sites (Tab. 2.1), both around Grand Cayman and Little Cayman. *C. perezi* were not recorded on BRUVS shallower than 9 m, but were recorded on the deepest BRUVs of 22.5 m. *G. cirratum*, however, were recorded from 1.6 m to the deepest BRUVS at 22.5 m. *C. perezi* were recorded on the outer reef zone only, comprising of habitats of hard bottom and reef, with no sediment or seagrass, whereas *G. cirratum* were recorded on both inner and outer reef zones in a large range of habitats, including hard bottom, reef, sand and seagrass. The relative abundance of the two main species plus all sharks combined (including *C.* spp.) were displayed within and across each explanatory factor, to present the effects on the CPUE (Figures 2.5, 2.6 and 2.7).

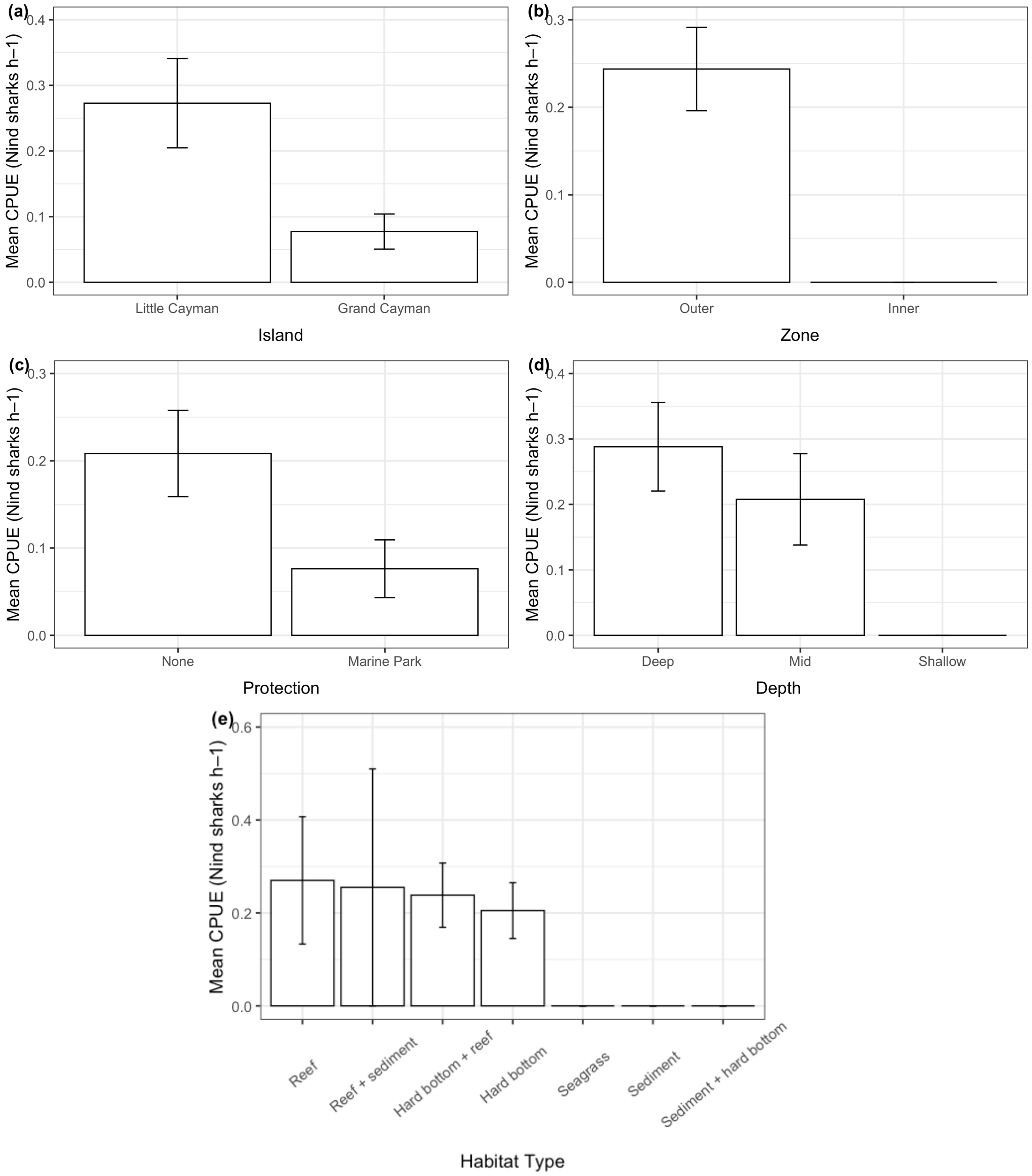


Figure 2.5. Relative abundance (± 1 SE) of *C. perezi* in relation to explanatory factors (a-e)

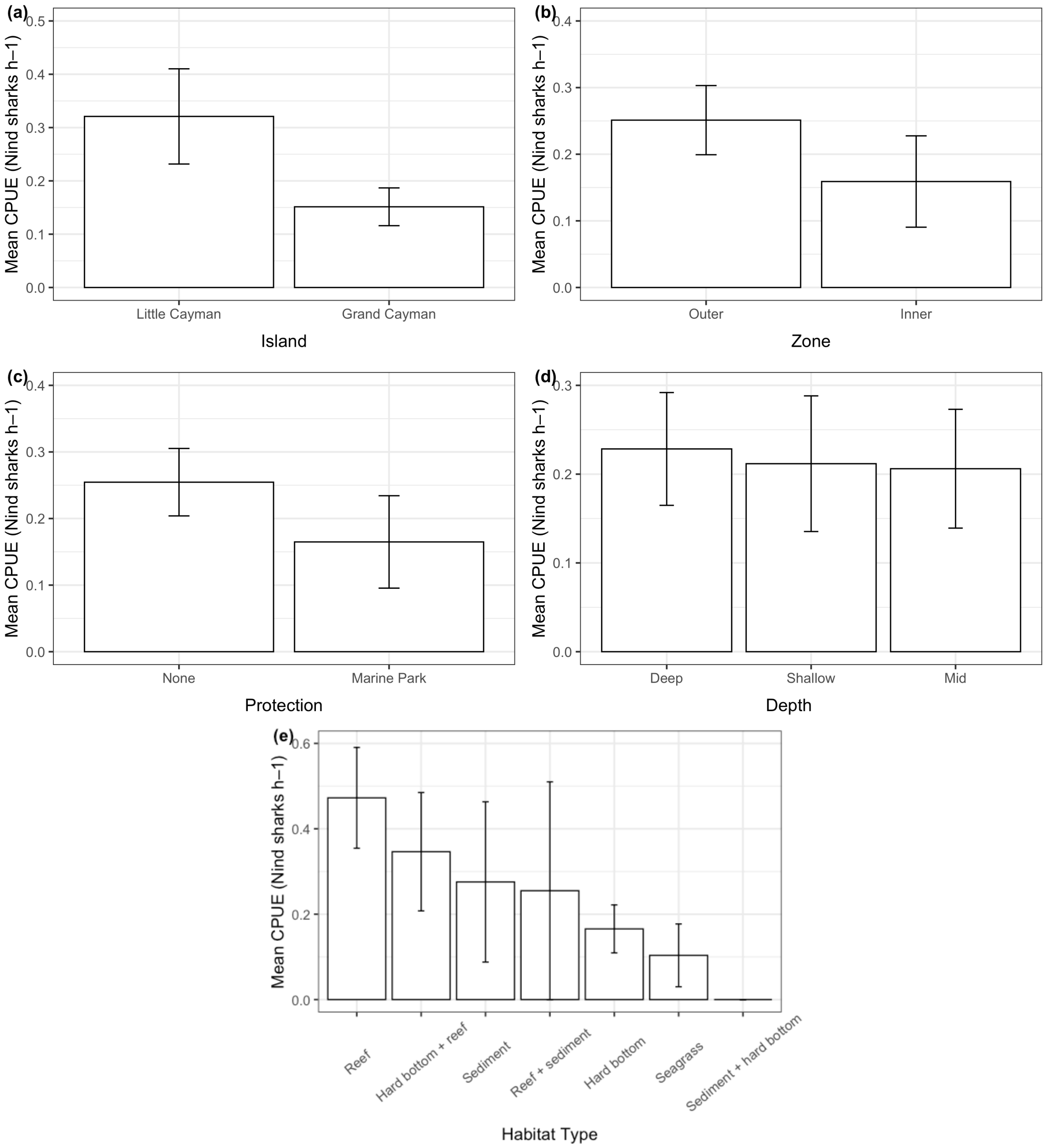


Figure 2.6. Relative abundance (± 1 SE) of *G. cirratum* in relation to explanatory factors (a-e)

The mean CPUE of each species and all sharks combined across all deployments sites is displayed in Table 2.5.

Table 2.5. Mean catch per unit effort (CPUE; Nind sharks/hr^{-1}) across all sites for the two main species and all sharks combined

Species	Mean CPUE
C. perezi	0.15
G. cirratum	0.22
All	0.41

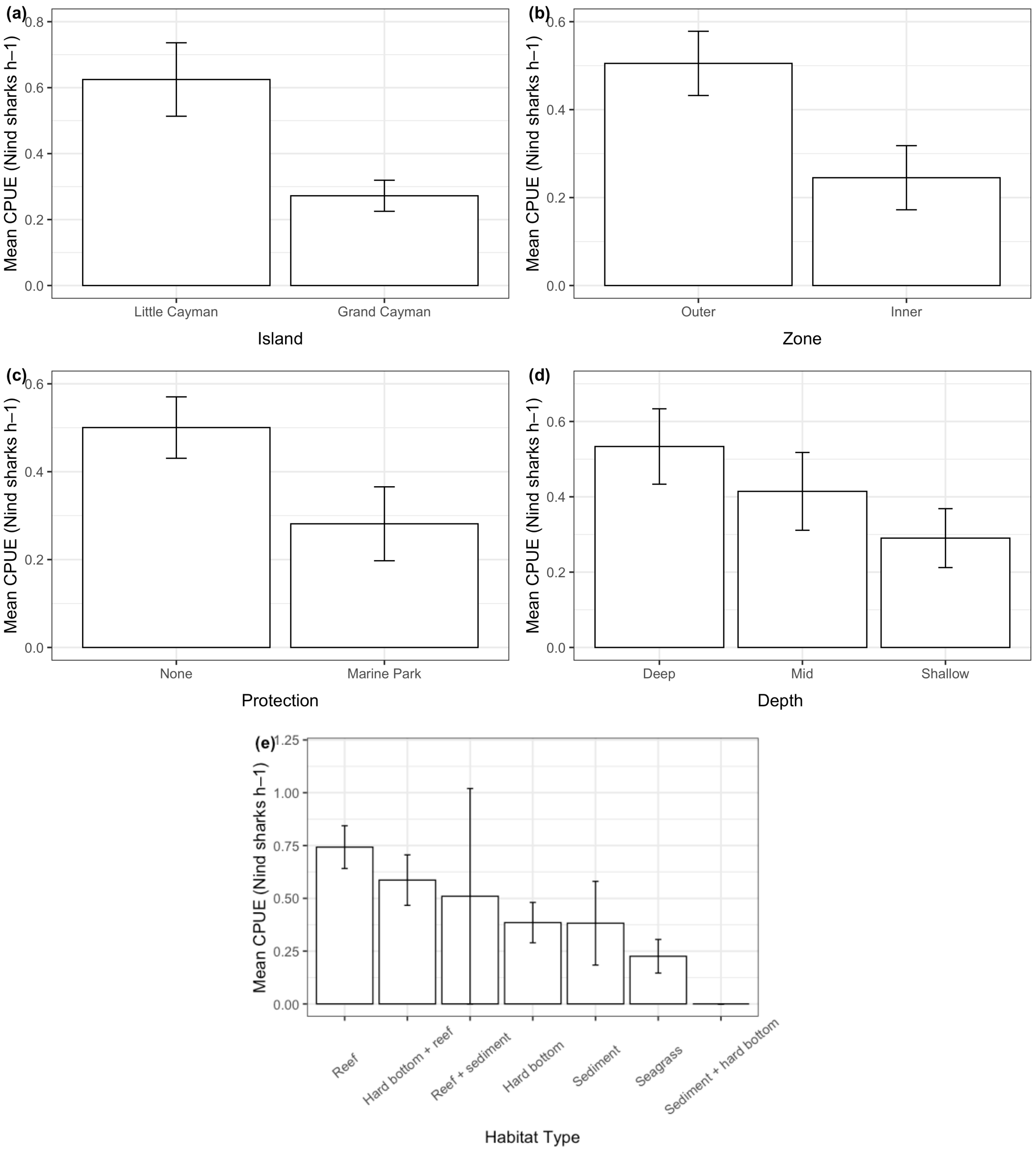


Figure 2.7. Relative abundance (± 1 SE) of all recorded sharks in relation to explanatory factors (a-e)

Explanatory factors were tested using the Mann-Whitney U test and Kruskal-Wallis H test to investigate whether factors had a significant affect on the CPUE of each species and all sharks combined across sites (Table 2.6).

Table 2.6. Results of Mann-Whitney U test and Kruskal-Wallis H test using continuity correction, comparing shark CPUE between explanatory factors for the two most abundant shark species and for all species combined (n – number of surveys; df – degrees of freedom; *p* – statistical significance)

Factors	Species	Mann-Whitney U				Kruskal-Wallis H		
		U	n_1	n_2	*p*	H	df	*p*
Island	*C. perezi*	24	13	8	0.046*	-		
	G. cirratum	59	15	13	0.079	-		
	All	93	24	20	0.00055**	-		
Zone	*C. perezi*	N/A				-		
	G. cirratum	109	22	6	0.017*	-		
	All	157	33	11	0.52	-		
Protection	*C. perezi*	37	16	5	0.84	-		
	G. cirratum	85.5	15	7	0.54	-		
	All	206	32	12	0.72	-		
Habitat Type	*C. perezi*	-				4.9549	3	0.18
	G. cirratum	-				3.7839	5	0.58
	All	-				7.6115	5	0.18
Depth	*C. perezi*	55	14	7	0.68			
	G. cirratum	-				10.711	2	0.0047*
	All	-				0.95074	2	0.62

There was a significant difference in CPUE between the two islands for *C. perezi* (*p*=0.046) and for all recorded sharks combined (*p*=<0.001); Little Cayman had a higher CPUE than Grand Cayman (Figures 2.5 and 2.7). *C. perezi* were only encountered in the outer zones, and there was a significant difference between zones for *G. cirratum* (*p*=0.017), with a higher CPUE recorded in the outer zones (Fig. 2.6). Depth was also significant for *G. cirratum*, with Dunn's post-hoc test revealing significant differences between shallow and deep sites (*p*=0.0034; Appendix E). Marine park protection did not have a significant impact on any species, and neither did habitat type (Table 2.6).

PERMANOVA models were used to test for differences in species composition (*C. perezi* and *G. cirratum* only) across sites associated with different factors (Table 2.7).

Table 2.7. Results of one-way and two-way PERMANOVA models on species composition, testing the effect of island, zone, depth, habitat and protection, and the interactions of significant factors (df - degrees of freedom; SS – sum of squares; Pseudo-F – F value by permutation; *p* - p-value based on 999 permutations)

Factors	df	SS	Pseudo-F	R^2	*p*
Zone	1	1.0931	6.8118	0.15548	0.017*
Depth	2	1.5932	5.2745	0.22662	0.01*
Island	1	0.3002	1.6502	0.0427	0.19
Habitat	5	1.1105	1.2381	0.15796	0.28
Protection	1	0.0033	0.017404	0.00047	0.89
Zone x Depth	2	0.5023	1.6175	-	0.23
Depth x Zone	1	0.0022	0.014	-	0.89

The PERMANOVA models showed that zone and depth were significant for species composition changes (*p*=0.017; *p*=0.01), whilst all others (island, habitat and protection) were not (Table 2.7). The interactions between zone and depth factors however were insignificant. Pairwise tests (Appendix F1) showed that the effect of depth was greatest between shallow and deep locations (*p*=0.006), and also significant between shallow and mid (*p*=0.009). The significant PERMANOVA results are presented on an MDS ordination (Figure 2.8).

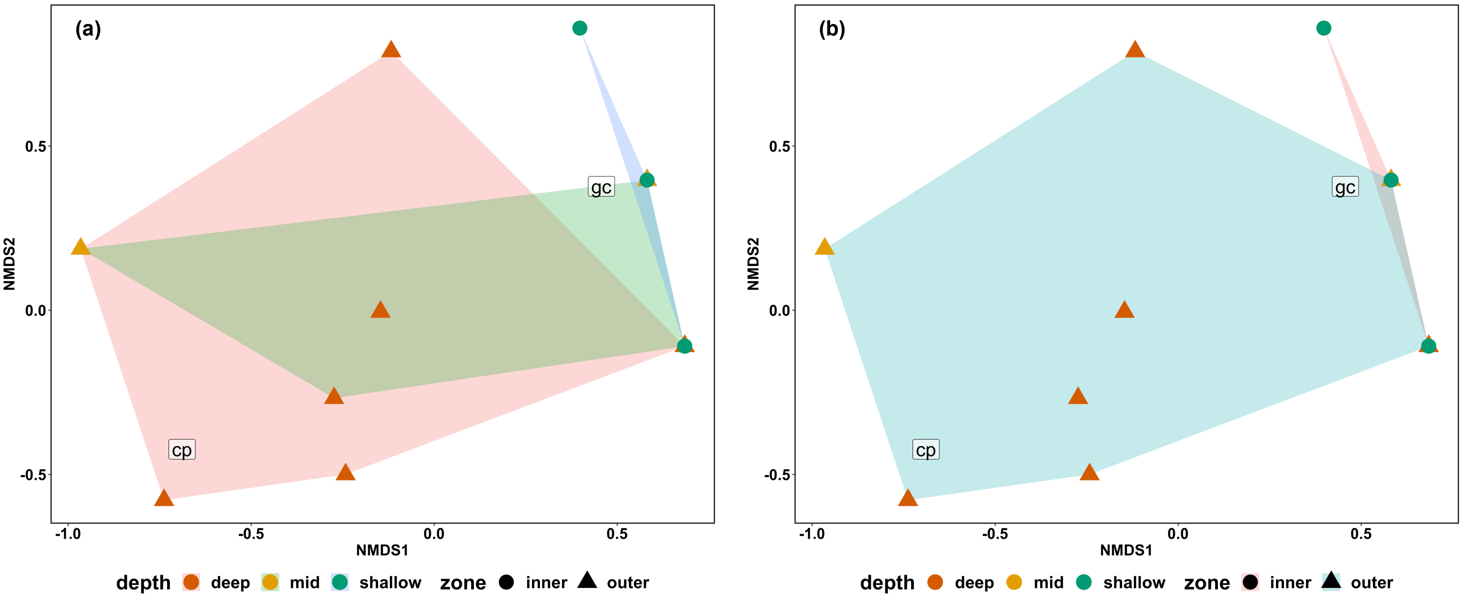


Figure 2.8. MDS ordinations (2D stress = 0.01235) of significant factors affecting species composition across BRUVS sites; Points: shape = zone, colour = depth. Shaded convex polygons denote (a) depth and (a) zone. Labels: “cp” = *C. perezi*, “gc” = *G. cirratum*.

Depth is an important factor for species composition; the shallow locations are grouped together and there is a gradient along the depths from shallow to deep (Fig. 2.8a). *C. perezi* are more closely associated with deeper zones than *G. cirratum*. Shallower depths are associated more with *G. cirratum*. The same is seen for the inner zone (b). Inner zone locations are highly associated with the shallower depths, which is mostly to be expected as the inner zones exhibit the shallowest of depths. Additionally, *C. perezi* were not recorded on the inner zones. MDS ordinations of factors that were not found to be significant from the PERMANOVA models (island, habitat and protection) are displayed in Appendix G1.

Demographic groups and explanatory factors.

Of the 70 sharks, 42 were assigned a sexed (60%). Of the *C. perezi* and *G. cirratum* sharks (*n* = 56), 49 were given maturity stages based on literature values (Table 2.8).

Table 2.8. The number of individuals belonging to the two most abundant species that were assigned a sex and maturity stage using photo-ID

Shark species	No. identified	Male	Female	NVC	Mature	Immature
C. perezi	19	11	5	11	5	18
G. cirratum	31	13	11	12	3	30

PERMANOVA models were used to test species and demographic group composition across sites, by splitting *C. perezi* and *G. cirratum* into four groups each: mature male, mature female, immature male and immature female (Appendix H1). No mature females belonging to either species were recorded on any survey. The PERMANOVA model showed that there was no significant difference in composition for any of the factors. MDS ordinations of all factors are displayed in Appendix G2.

PERMANOVA models were used to test the difference in composition of species and sex (maturity excluded) across sites (Appendix H2). The models showed no significant difference in composition for any of the factors. MDS ordinations of all factors are displayed in Appendix G3. Separate PERMANOVA models were also used to test the difference in composition of species and maturity (sex excluded) across sites (Table 2.9).

Table 2.9. Results of PERMANOVA models on species and maturity composition, testing the effect of island, zone, depth, habitat and protection (df - degrees of freedom; SS – sum of squares; Pseudo-F – F value by permutation; *p* - p-values based on 999 permutations)

Factors	df	SS	Pseudo-F	R^2	*p*
Depth	2	1.5426	3.6035	0.23859	0.019*
Zone	1	0.7397	3.1006	0.11441	0.059
Island	1	0.3666	1.4427	0.05671	0.23
Habitat	5	1.4360	1.1421	0.2221	0.35
Protection	1	0.1943	0.74345	0.03005	0.45

The PERMANOVA models showed a significant difference in composition due to depth (p=0.019). Pairwise tests (Appendix F2) showed that the effect of depth was significant between shallow and deep sites only (p=0.009). PERMANOVA results for the significant factor are displayed on an MDS ordination (Figure 2.9). MDS ordinations of all insignificant factors are displayed in Appendix G4 (Fig. 4).

Depth is an important factor in determining species and maturity group composition across sites; locations of the same depth are mostly grouped together, but are not totally distinct. The shallow sites are associated more with *G. cirratum* than *C. perezi*. Mature *C. perezi* are separated by their association with the deep sites only, whereas immature *C. perezi* are included within mid depth sites. Neither group is associated with shallow sites. Conversely, mature *G. cirratum* are grouped nearer to shallow and mid sites, and immature *G. cirratum* individuals are grouped in the centre of all depths, appearing at a wide range of sites that cover different depths.

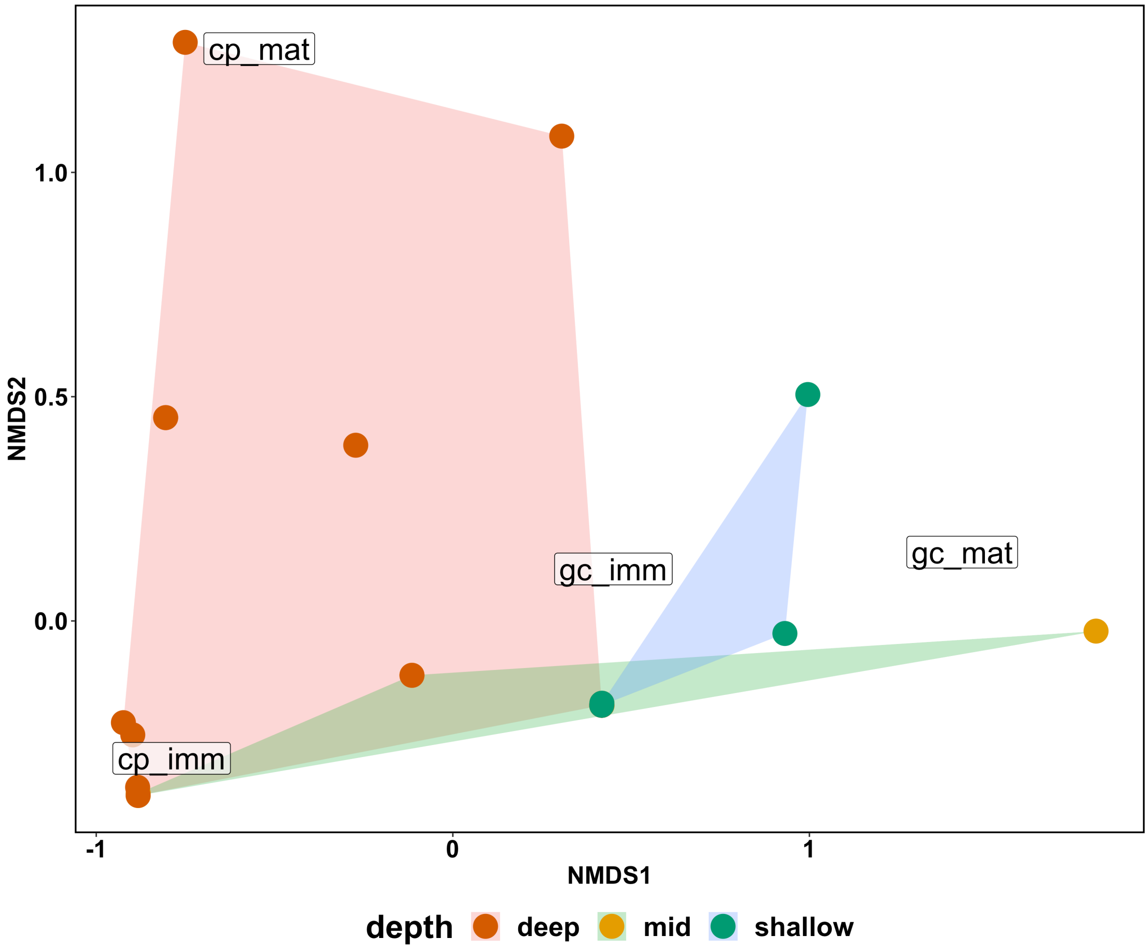


Figure 2.9. MDS ordination (2D stress = 0.0001) of the effect of depth factor on composition of *C. perezi and G. cirratum* in maturity groups; Points and shaded convex polygons denote depth. Labels: "cp_mat" = mature *C. perezi*, "cp_imm" = immature *C. perezi*, *"gc_mat"= mature G. cirratum*, *"gc_imm"*= immature *G. cirratum*

Discussion

This study investigated whether an extended deployment time and identification of individuals through photo-ID increased counts of sharks. Whilst BRUVS have advantages over other sampling methods, such as enabling longer survey times and eliminating behavioural biases caused by scuba-divers (Willis *et al.*, 2000), there are limitations when using MaxN as an abundance metric. MaxN only provides information on relative abundance, not overall population size and has been shown to not relate directly to true abundance (Stobart *et al.*, 2015; Whitmarsh *et al.*, 2018). The results revealed that an extended BRUVS deployment period (120 versus 60 min) generated significantly higher abundance counts, as anticipated. This was the case when using both MaxN and Nind metrics. An example of late shark arrival was a nurse shark (*G. cirratum*) arriving at 2 h 33 min after deployment. The combination of 120 min and Nind gave the highest counts of abundance across all species. The additional time allowed for new individuals to enter the frame at a later stage.

It was hypothesised that there would be significantly more sharks recorded using Nind than MaxN, as MaxN is prone to underestimation (Kilfoil *et al.*, 2017). However, the behaviour of the sharks recorded in this study dictated that on the occasion where there were 3+ individuals of the same species, they most often appeared together, therefore increasing the count of MaxN to match Nind and lessening the effect of individual identification. When used to survey larger populations with higher counts, this situation will be less likely to occur. Additionally, there were significantly more species recorded when using the longer deployment period. This is despite the fact that the two least abundant species (*C. limbatus* and *N. brevirostris*) were recorded on BRUVS with no other species present. Although there was no significant difference found between the two main species for either their time of arrival or time of Nind, both had mean times of over 60 min. This suggests that longer recording times are necessary to gain additional information regarding shark abundance. It is worth considering that the longer the recording period, the more likely it is that Nind will increase as it allows for any new shark to be differentiated from those before, whereas MaxN will not. The additional recording time was made possible by using additional batteries (BacPacs). The data gained from this equipment outweighed the additional analysis time and cost. Extended survey times will be advantageous where fieldwork constraints allow and where additional deployments are not possible. Software packages, such as EventMeasure, can reduce analysis time.

The use of photo-ID methodology was deemed successful for determining Nind, with 68 of the 70 recorded sharks identified to species level; the majority of which (78%) could be identified further as individuals. All species possessed natural and acquired marks, discolourations, fin notches and cuts. *C.* limbatus were more difficult to distinguish, due to high turbidity in the sound. It was noted that *G. cirratum* had a wide range of fin shapes and notches, whereas markings, discolourations and scars were used to distinguish among *C. perezi*. The ability to differentiate between sharks enabled confident Nind counts. However, it is worth noting that not one method of identification fits all species. Moreover, those that could not be identified were too distant, too quick or at a problematic angle. The success of this method may diminish when applied to other environments, such as those with murky water or in low light conditions, or if a species' behaviour dictates a maintained distance from the bait. Brooks *et al.* (2011) found that one species was frequently misidentified using BRUVS, which was only discovered when comparing their longlining data.

Photo-ID also allowed for the assignation of sex and maturity to each individual where possible. However, it was not feasible to assign sex for any immature individuals unless there was a clear view of the clasper area. This led to more NVC individuals than other survey methods like longlining, where confirmation is achievable, described in Brooks *et al.* (2011). No mature females were recorded at any BRUVS sites. This could be attributed to size estimates generally being conservative. An individual was only classed as mature if it was positively larger than the size at maturity, or if claspers were visibly longer than the pelvic fins of males. Therefore, it is possible that more males were sexed successfully. Additionally, size-at-maturity estimates were based on literature values (Castro, 2000; Compagno, 1984; Pikitch *et al., 2005)*, but it is possible that these species exhibited inter-species variation between locations within the Caribbean. There could be other reasons for the lack of mature females. For example they may not respond to the bait plumes as other individuals do. Other species of shark are reported to have fewer females when populations are sampled, such as the whale sharks (*R. typus*) (Rohner *et al.*, 2015). However, the reason for this can only be conjectured at this point. Further investigation should be undertaken to establish if the method requires improvement or whether there are in fact no mature females present on the suvey.

Analysing species presence and relative abundance at each site revealed that there were significantly more individuals belonging to all species around Little Cayman than Grand Cayman. When analysed further, *C. perezi* specifically were significantly more abundant around Little Cayman. This is expected following the review of shark species abundance around the Cayman Islands by Ormond *et al.* (2017). However, *G. cirratum* were more evenly spread between the two. These two species were found to inhabit a different range of sites from each other. *C. perezi* only utilised the outer reef zones and not the inner lagoon zones. This relates to the depth at which this species was recorded; individuals were not seen at any of the shallower BRUVS sites. This reflects findings in the wider Caribbean (Brooks *et al.*, 2011; Pikitch *et al.*, 2005); *C. perezi* were most abundant on the deeper wall sites and not in the shallow lagoons. Whilst *G. cirratum* were found in significantly higher numbers on the outer reefs, they did appear in the inner lagoon areas across multiple sites, and were recorded at a depth range of 1.6 - 22.5 m. Yet, there was a significantly higher relative abundance of this species at the deep site than the shallow site.

There were no significant differences in abundance for any species between protected Marine Parks and unprotected areas. This has not been the case in a plethora of other studies (Espinoza *et* al., 2014; Jaiteh *et al.*, 2016), however these Marine Protected Areas are often located in regions where sharks are still fished extensively. Therefore our result is not all that surprising; sharks are highly mobile and travel large distances, likely swimming between different areas around the islands. Furthermore, all waters within the EEZ are protective of shark species; therefore the differences between areas are not as extreme. Habitat was also found to have no significant effect on abundance. However, *C. perezi* were not recorded at any sites with predominantly seagrass or sediment (the prevalent habitat type in the inner reef zones), whereas *G. cirratum* were present at a wider variety of habitats. Whilst there were not enough individuals to carry out statistical analysis on the two rare species, *C. limbatus* were only detected in the inner zone around Grand Cayman, and *N. brevirostris* only within the inner zone around Little Cayman. It can be inferred that the four-recorded species utilise different factors belonging to the range of sites, therefore exhibiting different ecologies. It is important to consider that a range of different sites must be surveyed to include all ecologies, and to therefore survey as many species as possible. A study by Tickler *et al.* (2017) examined other causes of variation in abundance and found prey availability to a more significant factor than habitat type. The authors put forward that marine protection, such as shark sanctuaries, should consider the protection of the overall ecosystem as opposed to species-specific policies to limit prey depletion.

Depth and zone proved the strongest predictors of species composition across sites and this was shown clearly on the resulting MDS plots (Fig. 2.8). *C. perezi* were more closely associated with the deeper sites in outer zones and *G. cirratum* with shallower depths and inner zones. However, interactions between the depth and zone were not significant. Habitat type, protected areas and island were not found to contribute to differences in species composition. This can be expected, as both species were found across the two islands and both within and outside of protected areas. Habitat effects could perhaps become more apparent if habitat groups were reclassified into fewer subgroups. However, each habitat type is distinctly different from each other. This investigative analysis suggests that species displayed different ecologies, based on their presence at differing sites.

Exploratory analyses into the drivers of demographic groups found that none of the factors affected the sex and maturity group composition across sites. This could be because these demographic groups do not utilise completely different factors; there may be substantial overlap between groups. However, potential study limitations must be acknowledged: a larger data set may be of benefit. Similarly, when analysing groups of species segregated by sex (maturity excluded), no factors were found to be significant. It can therefore be inferred that there is no difference in site use between males and females of these two species. However, the composition of species and maturity groups (sex excluded) were found to differ across depth (Table 2.9), specifically between shallow and deep sites (Appendix F2). This is an interesting find; this may be where the difference within species lies. It appears as if mature *C. perezi* have a strong drive to the sites with deeper depth, whereas immature *C. perezi* utilise these deep sites and mid depth sites. Contrarily, mature *G. cirratum* utilised shallow and mid depth sites and immature *G. cirratum* utilised sites irrespective of depth. Therefore, it is important to consider that individuals belonging to one species do not necessarily frequent the same sites. Mature and immature individuals utilise different depths. This is especially important with research concerning the implementation of Marine Protected Areas and is vital when endeavoring to protect all individuals within a species.

General study observations are that BRUVS were deployed during daylight hours only (Appendix D). It would be interesting to broaden this to include crepuscular periods, and even during night; to explore whether the diversity of species changes, and if more or less individuals are recorded. However, this would require an additional light source and more complex logistical considerations. Current may also affect assemblages, due to the distance and speed of the bait plume spread, but this has not been studied in great detail, despite recommendations (Taylor *et al.*, 2013). It would also be worthwhile investigating if the time of year has an effect; seasonality may be an important factor that should be considered in species composition analysis and abundance counts. In the wider Caribbean it has been reported by that the abundance of both *C. perezi* and *G. cirratum* were higher in summer than winter, whereas *N. brevirostris* were more abundant in winter (Brooks *et al.*, 2011; DeAngelis *et al.*, 2008). The deepest BRUVS was recorded at 23.9 m. Depth is limited by the fringing reef surrounding the island, as beyond this the substrate falls away deeply. To broaden the range of depth that can be sampled, an adaptation from the typical BRUVS design such as pelagic-BRUVS could be implemented near to the reef's edge (Bouchet and Meeuwig, 2015).

The main downfall with using BRUVS for photo-ID is the occurrence of unsuccessful identification due to poor visibility and the distance and angle of the shark to the camera. This issue also arose when assigning sex to individuals, as a clear view of the clasper area must be shown. Sex was established for 60% of sharks. This was partly due to environmental conditions and partly the sharks' movement and behaviour in front of the camera. Due to the method used, it is probable that fewer females were sexed correctly. Additionally, in circumstances of poor visibility, misidentification of species may occur. Whilst BRUVS are non-invasive, they have been proven to provide significantly less data on species, sex and size than longline surveys (Brooks *et al.*, 2011). The size of individuals was estimated within the constraints of mono-BRUVS. Estimates were verified by using two different methods by two annotators, and only when all estimates resulted in the same maturity assignment, did the individual receive that maturity. This method could be improved upon by upgrading equipment to stereo-BRUVS; however smaller projects, such as this, are limited by cost. An additional camera angle would also increase the chance of viewing the reproductive area of the sharks, as in stereo-BRUVS or alternatively as designed by Whitmarsh *et al.* (2018) to create a 360° view.

One observation from the study was the lack of 're-sights' of individual sharks. None of the identified sharks were recorded more than once. This meant that mark-recapture estimates could not be undertaken to estimate population size. However, this could be seen as "good news" for the local shark populations; of the 70 sharks recorded, it is highly likely that none of them were the same. This suggests that populations are healthier than if sharks were re-sighted. In order to estimate population sizes, more sampling would be required, either at a larger number of sites or replicated at the same sites, both within the season and across multiple seasons. In the Cayman Islands, the BRUVS sites are strategically located to cover a large area around both Grand Cayman and Little Cayman. However, BRUVS should be implemented around Cayman Brac to gain a fuller picture of Cayman shark populations and to allow a wider tracking of individual movements.

Conclusions

In conclusion, photo-identification via BRUVS can provide abundance estimates of sharks, without the implications of invasive sampling techniques. The identification of individuals not only allows for a more sensitive abundance estimate, but it also allows for a broader range of research questions to be answered and finer-scale analyses to be undertaken. Abundance accuracy is especially vital when tracking threatened or endangered populations temporally, and justifies the extra cost and analysis time of additional batteries. The study found merit in implementing a longer recording period beyond 60 min, which resulted in higher abundance counts and more recorded species. However, not all studies require such fine-scale analysis, so advantages and disadvantages would need to be assessed based on the research aims. Depth and zone were found to affect the relative abundance of *G. cirratum* and *C. perezi* and species composition across the sites. Photo-ID enabled the assignation of sex and maturity, which led to the discovery that the composition of species and maturity groups differed across sites: different maturity stages utilised different depths. This consideration is important when evaluating environmental and other factors for species as a whole, especially in protection planning. However, mono-BRUVS lacked the resolution to successfully identify species, sex and assign maturity to all of individuals. To develop the population demographics analysis beyond exploratory analysis and to improve the success of photo-ID, investment into stereo-BRUVS would be an important consideration. In the Cayman Islands, the current survey sites encompass a wide range of sites and therefore factors. Future research should expand to encompass different times of day, deeper depths, across seasons and years. Other environmental data could also be investigated, such as current speed and direction, as this may impact the sharks' response time and the number of individuals attracted to the bait. Studying shark populations around Cayman Brac should also be considered. Paired with photo-ID, this could present interesting findings, including the potential to track individuals between all three islands through mark-recapture techniques, and with the addition of multiple years of data, changes in relative abundance to be tracked temporally.

Acknowledgements

First and foremost, thank you to Johanna Kohler, my field supervisor, mentor and friend. It was an absolute pleasure to work alongside her at all times. Her support and guidance have been invaluable, throughout the process of data collection in the Cayman Islands and beyond. Her friendship and patience is deeply appreciated, especially as she had her own PhD thesis to contend with. Research needs more dedicated scientists like her. I wish her the very best in completing her PhD and for all that she does after.

Thank you Dr. Mauvis Gore, for accepting me as a student and for her invaluable insight into the world of research. I am grateful for the opportunity to have been in the tagging team during my stay. Thank you for working so hard to protect the sharks and rays around Cayman over the last 10 years.

I would like to thank the Cayman Islands Department of Environment; in particular Deputy Director Tim Austin for all of his help, not only with project logistics, but also with health and visa "issues" whilst in Cayman. I will be forever grateful for the unwavering support and guidance, no matter the situation.

A big thank you to Professor Dr. Karim Erzini, for agreeing to supervise me and for supporting me from afar; providing assistance whenever necessary.

A tremendous thanks to Mike and Meredith Guderian, who always made our trips to Little Cayman a pleasure. Thanks to Mike – for his patience, hard work and good humour during our long days on the boat. Meredith – for her kindness, consideration and always-jolly nature. Thanks to both for welcoming us into their home as friends. I will never forget it.

I would like to extend my appreciation to those from the DoE who volunteered their time to be our skipper each day: Bradley Johnson, Cody Panton, Nathan Dack and Paul Chin. Big appreciation to the DoE Ops staff, who always made sure our cars and boats were operational.

I was fortunate to benefit from Erasmus+ Traineeship funding for my time spent researching in the Cayman Islands. I am incredibly grateful for this programme and the opportunities it presents for students. I would also like to express my deepest gratitude to the Shark Conservation Cayman team, who covered all research costs whilst in Cayman. I could not have completed my fieldwork otherwise.

A special mention to my amazing friends in Cayman for not only supporting me in my work, but for ensuring I always took enough breaks to function. Dr. Jane Hardwick (my R guru), Ségolène "Sego like Lego" Jacob and Kati Frosin. Also to Erin and Brandon, for helping me out enormously and allowing me to spend time with their two beautiful, crazy dogs each week.

Last, but not least, I am forever grateful to my parents for their continuing support, both emotionally and financially, in everything I do. As always, their unwavering confidence and trust in my endeavours is everything to me, and I would not have been able to follow my dreams without them. They truly are the best.

References

Anderson, S., D., Goldman, K.J., 1996. Photographic evidence of white shark movements in California waters. *California Fish and Game* **82**, 182–186.

Araujo, G., Lucey, A., Labaja, J., Lee So, C., Snow, S., Ponzo, A., 2014. Population structure and residency patterns of whale sharks, Rhincodon typus, at a provisioning site in Cebu, Philippines. *PeerJ* **2**, e543. https://doi.org/10.7717/peerj.543

Asher, J., 2017. A Deeper Look at Hawaiian Coral Reef Fish Assemblages: A Comparison of Survey Approaches and Assessments of Shallow to Mesophotic Communities (PhD). *Curtin University, Australia.*

Bascompte, J., Melian, C.J., Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* **102**, 5443–5447. https://doi.org/10.1073/pnas.0501562102

Bassett, D.K., Montgomery, J.C., 2011. Investigating nocturnal fish populations in situ using baited underwater video: With special reference to their olfactory capabilities. *Journal of Experimental Marine Biology and Ecology* **409**, 194–199. https://doi.org/10.1016/j.jembe.2011.08.019

Baum, J.K., Myers, R.M., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and Conservation of Shark Populations in the Northwest Atlantic. *Science* **299**, 389–392. https://doi.org/10.1126/science.1079777

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society: *Series B (Methodological)* **57**, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bernard, A., Götz, A., 2012. Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. *Marine Ecology Progress Series* **471**, 235–252. https://doi.org/10.3354/meps10039

Bonfil, R., 1997. Status of shark resources in the southern Gulf of Mexico and Caribbean: implications for management. *Fisheries Research* **29**, 101–117. https://doi.org/10.1016/S0165-7836(96)00536-X

Bouchet, P.J., Meeuwig, J.J., 2015. Drifting baited stereo-videography: a novel sampling tool for surveying pelagic wildlife in offshore marine reserves. *Ecosphere* **6**, art137. https://doi.org/10.1890/ES14-00380.1

Brooks, E., Sloman, K., Sims, D., Danylchuk, A., 2011. Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endangered Species Research* **13**, 231–243. https://doi.org/10.3354/esr00331

Campbell, M.D., Pollack, A.G., Gledhill, C.T., Switzer, T.S., DeVries, D.A., 2015. Comparison of relative abundance indices calculated from two methods of generating video count data. *Fisheries Research* **170**, 125–133. https://doi.org/10.1016/j.fishres.2015.05.011

Cappo, M., 2010. Development of a baited video technique and spatial models to explain patterns of fish biodiversity in inter-reef waters (phd). *James Cook University, Australia.*

Cappo, M., Harvey, E., Malcolm, H., Speare, P., 2003. Potential of video techniques to monitor diversity, abundance and size of fish in studies of Marine Protected Areas, in: Beumer, J.P., Grant, A., Smith, D.C. (Eds.), *Aquatic Protected Areas. What Works Best and How Do We Know?* Presented at the World

Congress on Aquatic Protected Areas proceedings, Queensland: University of Queensland, Cairns, Australia, 2002, pp. 455–464.

Cappo, M., Harvey, E., Shortis, M., 2006. Counting and measuring fish with baited video techniques-an overview, in: Lyle, J.M., Furlani, D.M., Buxton, C.D. (Eds.), *Cutting-Edge Technologies in Fish and Fisheries Science*. Presented at the ASFB Workshop Proceedings, Hobart, Tasmania, August 2006, pp. 101–114.

Cappo, M., Stowar, M., Syms, C., Johansson, C., Cooper, T., 2011. Fish-habitat associations in the region offshore from James Price Point – a rapid assessment using Baited Remote Underwater Video Stations (BRUVS). *Journal of the Royal Society of Western Australia* **94**, 303–321.

Castro, A.L.F., Rosa, R.S., 2005. Use of natural marks on population estimates of the nurse shark,Ginglymostoma cirratum, at Atol das Rocas Biological Reserve, Brazil. *Environmental Biology of Fishes* **72**, 213–221. https://doi.org/10.1007/s10641-004-1479-7

Castro, J.I., 2000. The Biology of the Nurse Shark, Ginglymostoma cirratum, Off the Florida East Coast and the Bahama Islands. *Environmental Biology of Fishes* 1–22.

Cayman Islands Government, 2019. Marine Parks : Grand Cayman Department of Environment. *Department of Environment*. URL http://doe.ky/marine/marine-parks/ (accessed 8.29.19).

Clarke, C., Lea, J., Ormond, R., 2012. Comparative abundance of reef sharks in the Western Indian Ocean, in: *Proceedings of the 12th International Coral Reef Symposium*. Presented at the Reef sharks and coral reefs, Cairns, Australia, 9-13 July 2012, p. 5.

Compagno, L., J.V., 1984. Sharks of the world: An annotated and illustrated catalogue of shark species known to date, *FAO Species Catalogue*.

DeAngelis, B., McCandless, C., Kohler, N., Recksiek, C., Skomal, G., 2008. First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. *Marine Ecological Progress Series*. **358**, 257–271. https://doi.org/10.3354/meps07308

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. https://doi.org/10.1007/s00227-006-0380-7

Espinoza, M., Cappo, M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2014. Quantifying Shark Distribution Patterns and Species-Habitat Associations: Implications of Marine Park Zoning. *PLOS ONE* **9**, e106885. https://doi.org/10.1371/journal.pone.0106885

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

Field, I.C., Meekan, M.G., Buckworth, R.C., Bradshaw, C.J.A., 2009. Chapter 4 Susceptibility of Sharks, Rays and Chimaeras to Global Extinction, in: *Advances in Marine Biology*. Elsevier, pp. 275–363. https://doi.org/10.1016/S0065-2881(09)56004-X

Gallagher, A.J., Hammerschlag, N., 2011. Global shark currency: the distribution, frequency, and economic value of shark ecotourism. *Current Issues in Tourism* **14**, 797–812. https://doi.org/10.1080/13683500.2011.585227

Garla, R.C., Chapman, D.D., Shivji, M.S., Wetherbee, B.M., Amorim, A.F., 2006. Habitat of juvenile Caribbean reef sharks, Carcharhinus perezi, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. *Fisheries Research* **81**, 236–241. https://doi.org/10.1016/j.fishres.2006.07.003

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**, e0150160. https://doi.org/10.1371/journal.pone.0150160

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J., White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* **90**, 1215–1247. https://doi.org/10.1111/brv.12155

Harasti, D., Lee, K.A., Laird, R., Bradford, R., Bruce, B., 2016. Use of stereo baited remote underwater video systems to estimate the presence and size of white sharks (Carcharodon carcharias). *Marine and Freshwater Research* **68**, 1391. https://doi.org/10.1071/MF16184

Hervé, M., 2019. RVAideMemoire: Testing and Plotting Procedures for Biostatistics. R package version 0.9-73. URL https://CRAN.R-project.org/package=RVAideMemoire (accessed 9.23.19).

Jaiteh, V.F., Lindfield, S.J., Mangubhai, S., Warren, C., Fitzpatrick, B., Loneragan, N.R., 2016. Higher Abundance of Marine Predators and Changes in Fishers' Behavior Following Spatial Protection within the World's Biggest Shark Fishery. *Frontiers in Marine Science* **3**, e0200960. https://doi.org/10.3389/fmars.2016.00043

Kilfoil, J., J. Wirsing, A., Campbell, M., Kiszka, J., Gastrich, K., Heithaus, M., Zhang, Y., Bond, M., 2017. Baited Remote Underwater Video surveys undercount sharks at high densities: insights from full-spherical camera technologies. *Marine Ecology Progress Series* **585**, 113–121.

McConville, A., Grachev, I., Keane, A., Coulson, T., Bekenov, A., Milner-Gulland, E., 2009. Reconstructing the observation process to correct for changing detection probability of a critically endangered species. *Endangered Species Research* **6**, 231–237. https://doi.org/10.3354/esr00166

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283. https://doi.org/10.1038/nature01610

Oksanen, J., Blanchet, F., G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., R., O'Hara, R., B., Simpson, G., L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.4-6. URL https://CRAN.R-project.org/package=vegan (accessed 9.23.19)

Ormond, R., Gore, M., Bladon, A., Dubock, O., Kohler, J., Millar, C., 2017. Protecting Cayman Island Sharks: *Monitoring, Movement and Motive* **15**.

Pauli, J.N., Whiteman, J.P., Riley, M.D., Middleton, A.D., 2010. Defining Noninvasive Approaches for Sampling of Vertebrates. *Conservation Biology* **24**, 349–352. https://doi.org/10.1111/j.1523-1739.2009.01298.x

Perneger, T.V., 1998. What's wrong with Bonferroni adjustments. *BMJ* **316**, 1236–1238. https://doi.org/10.1136/bmj.316.7139.1236

Pikitch, E., Chapman, D., Babcock, E., Shivji, M., 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Marine Ecology Progress Series* **302**, 187–197. https://doi.org/10.3354/meps302187

Pollock, K.H., Solomon, D.L., Robson, D.S., 1974. Tests for Mortality and Recruitment in a K-Sample Tag-Recapture Experiment. *Biometrics* **30**, 77. https://doi.org/10.2307/2529619

R Core Team, 2017. R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. URL https://www.r-project.org/ (accessed 9.23.19).

Rohner, C.A., Richardson, A.J., Prebble, C.E.M., Marshall, A.D., Bennett, M.B., Weeks, S.J., Cliff, G., Wintner, S.P., Pierce, S.J., 2015. Laser photogrammetry improves size and demographic estimates for whale sharks. *PeerJ* **3**, e886. https://doi.org/10.7717/peerj.886

Sherman, C.S., Chin, A., Heupel, M.R., Simpfendorfer, C.A., 2018. Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? *Journal of Experimental Marine Biology and Ecology* **503**, 80–85. https://doi.org/10.1016/j.jembe.2018.03.002

Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.D., Babcock, R.C., Pillans, R.D., Bradshaw, C.J.A., 2016. Reef shark movements relative to a coastal marine protected area. *Regional Studies in Marine Science* **3**, 58–66. https://doi.org/10.1016/j.rsma.2015.05.002

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. https://doi.org/10.1006/jmsc.2000.0724

Stevick, P.T., Palsbell, P.J., Smith, T.D., Bravington, M.V., Hammond, P.S., 2001. Errors in identification using natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1861–1870. https://doi.org/10.4135/9781412974615.n24

Stobart, B., Díaz, D., Álvarez, F., Alonso, C., Mallol, S., Goñi, R., 2015. Performance of Baited Underwater Video: Does It Underestimate Abundance at High Population Densities? *PLOS ONE* **10**, e0127559. https://doi.org/10.1371/journal.pone.0127559

Taylor, M.D., Baker, J., Suthers, I.M., 2013. Tidal currents, sampling effort and baited remote underwater video (BRUV) surveys: Are we drawing the right conclusions? *Fisheries Research* **140**, 96–104. https://doi.org/10.1016/j.fishres.2012.12.013

Tickler, D.M., Letessier, T.B., Koldewey, H.J., Meeuwig, J.J., 2017a. Drivers of abundance and spatial distribution of reef-associated sharks in an isolated atoll reef system. *PLOS ONE* **12**, e0177374. https://doi.org/10.1371/journal.pone.0177374

Ward-Paige, C.A., Mora, C., Lotze, H.K., Pattengill-Semmens, C., McClenachan, L., Arias-Castro, E., Myers, R.A., 2010. Large-Scale Absence of Sharks on Reefs in the Greater-Caribbean: A Footprint of Human Pressures. *PLOS ONE* **5**, e11968. https://doi.org/10.1371/journal.pone.0011968

White, J., Simpfendorfer, C.A., Tobin, A.J., 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. https://doi.org/10.1016/j.jembe.2013.08.004

Whitmarsh, S.K., Fairweather, P.G., Huveneers, C., 2017. What is Big BRUVver up to? Methods and uses of baited underwater video. *Reviews in Fish Biology and Fisheries* **27**, 53–73. https://doi.org/10.1007/s11160-016-9450-1

Whitmarsh, S.K., Huveneers, C., Fairweather, P.G., 2018. What are we missing? Advantages of more than one viewpoint to estimate fish assemblages using baited video. *Royal Society Open Science* **5**, 171993. https://doi.org/10.1098/rsos.171993

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. *Springer, Verlag New York*.

Willis, T., Millar, R., Babcock, R., 2000. Detection of spatial variability in relative density of fishes:comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**, 249–260. https://doi.org/10.3354/meps198249

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy* **40**, 194–204. https://doi.org/10.1016/j.marpol.2012.12.034

Appendix A.

Photo-ID methodology

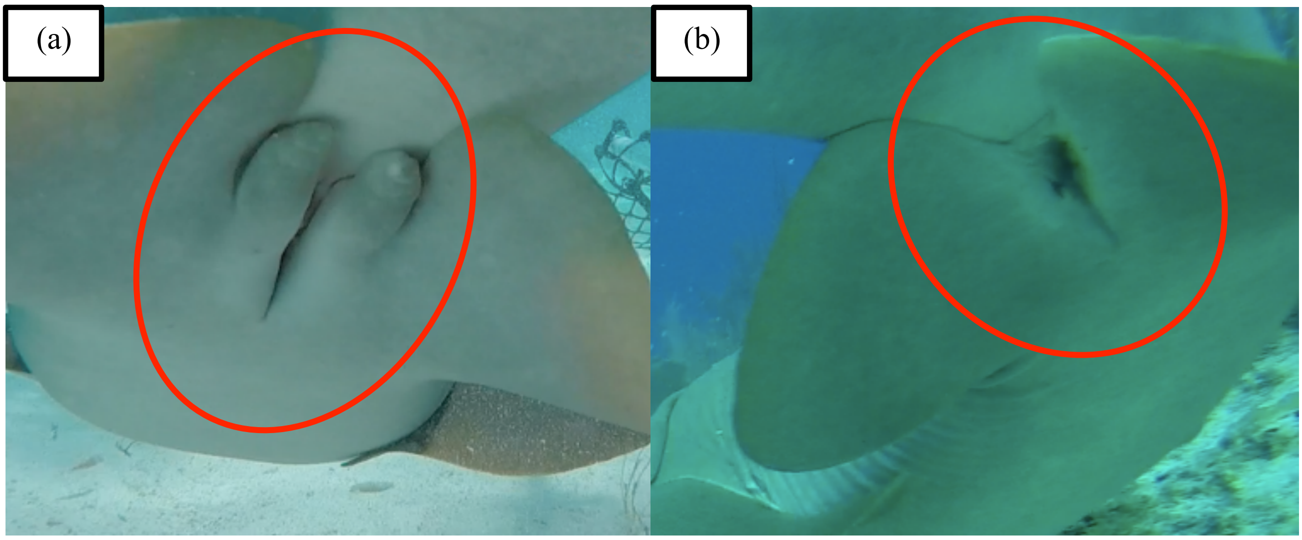


Figure A1. Examples of sexing an individual based on the presence or absence of claspers: (a) male, (b) female

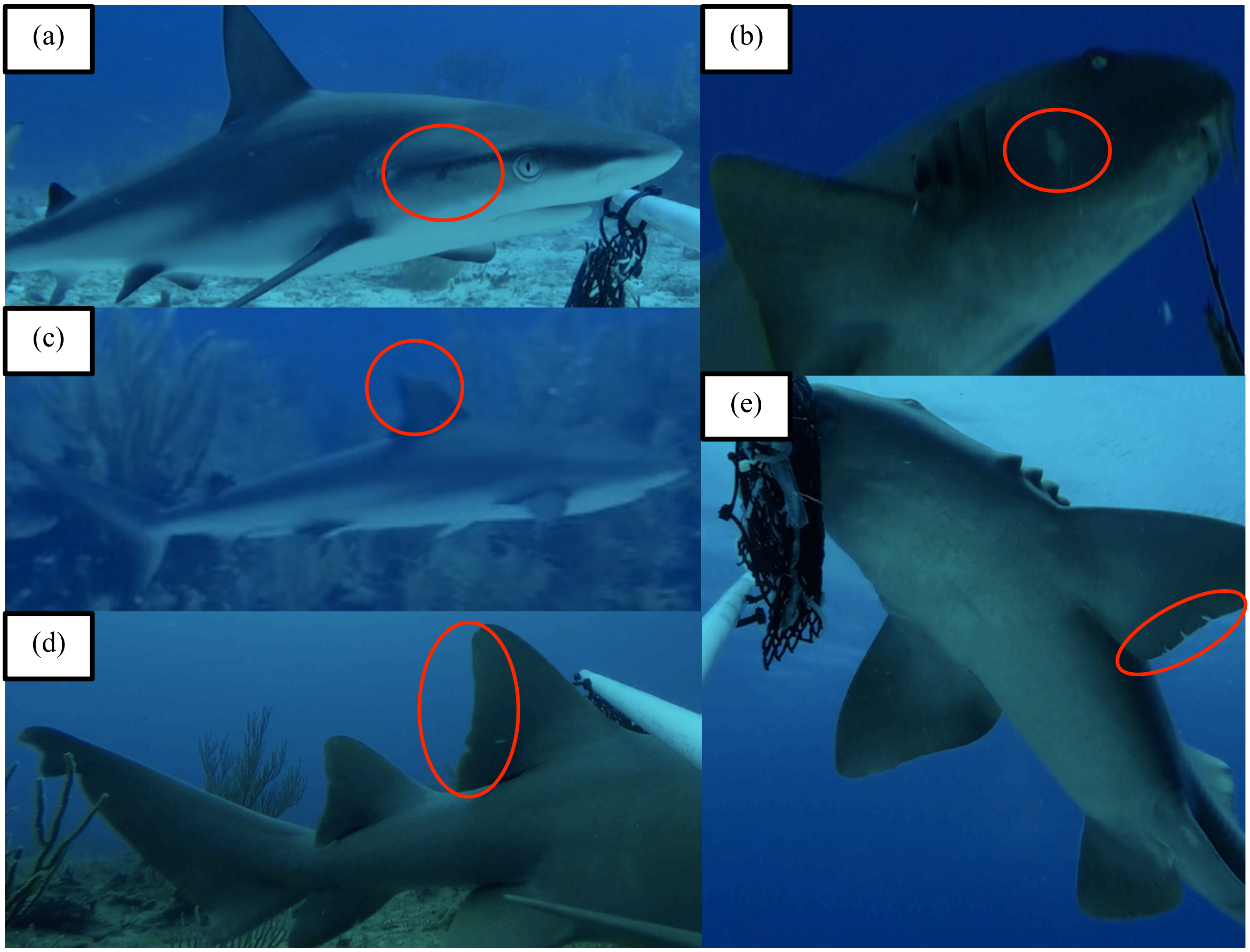


Figure A2. Examples of variation (circled) between individuals of *C. perezi* and *G. cirratum* used for photo identification: (a) & (b) face discolouration, (c) cut dorsal fin, (d) dorsal fin notches and (e) pectoral fin cuts

Appendix B.

Nind to MaxN ratios

Table B. The ratios of Nind to MaxN for *C. perezi* and *G. cirratum* species for the 120 min deployment period

Species	n	Ratio (Nind/MaxN)
C. perezi	20	1.13
G. cirratum	24	1.11

Appendix C.

Comparing time of arrival and time of Nind between species

Table C. The results of the 2-sample t-tests comparing the time of arrival and the time of Nind between *C. perezi* and *G. cirratum* species (df - degrees of freedom; *p* - statistical significance)

	Species	Mean	S.D.	t	df	*p*
Time of Arrival	*C. perezi*	63.25	32.23	0.061	51	0.95
	G. cirratum	62.63	40.65			
Time of Nind	*C. perezi*	63.16	32.93	0.027	40	0.98
	G. cirratum	62.84	40.99			

Appendix D.

Raw BRUVS data

Table D. Raw data – BRUVS samples, environmental data and shark species abundance

BRUVS No.	Date recorded	Island	Location	Site	Camera	Latitude (DD)	Longitude (DD)	Cloud cover (/8)	Wind strength (kph)	Wind direction	Water depth (m)	Sea state	Swell (m)	Wave height (m)	Current speed (s/m)	Current direction (degree)	Habitat
1	10/10/18	LC	NE	Outer	A	19.70466	-80.02345	6	17	180	15.9	1	0.1	0.1	6	130	Hard Bottom + Reef
2	10/10/18	LC	NE	Outer	B	19.70731	-80.01504	6	20.9	150	18.1	1	0.1	0.15	5	260	Hard Bottom + Reef
3	10/10/18	LC	NE	Outer	C	19.70976	-80.00645	6	14.07	76	17.4	1	0.1	0.15	6	350	Hard Bottom
4	10/10/18	LC	NE	Outer	D	19.71177	-79.99809	7	12.2	145	16.4	1	0.1	0.15	7	270	Hard Bottom
5	11/10/18	LC	S	Outer	A	19.67874	-80.02734	6	2.2	55	13.5	1	0.4	0.1	8	80	Reef + Sediment
6	11/10/18	LC	S	Outer	B	19.68005	-80.02312	6	2.8	100	13.3	1	0.5	0.1	5	90	Hard Bottom
7	11/10/18	LC	S	Outer	C	19.68185	-80.01875	6	5.9	75	16.8	1	0.5	0.1	6	95	Hard Bottom
8	11/10/18	LC	S	Outer	D	19.68329	-80.01376	6	5	50	22.5	1	0.5	0.1	4	100	Hard Bottom
9	12/10/18	LC	E	Outer	A	19.69579	-79.95760	7.5	18.5	320	17.5	1	0.3	0.1	4	240	Hard Bottom
10	12/10/18	LC	E	Outer	B	19.70595	-79.95441	7.5	18.5	280	9.8	2	0.4	0.2	5	240	Hard Bottom
11	12/10/18	LC	E	Outer	C	19.71398	-79.95919	7.5	23.2	290	10.5	2	0.4	0.2	6	280	Hard Bottom + Reef
12	12/10/18	LC	E	Outer	D	19.72007	-79.96625	7.5	12.4	300	18	2	0.5	0.3	13	300	Hard Bottom + Reef
13	12/10/18	LC	N	Outer	A	19.68194	-80.08611	6.5	none	none	5.9	1	0.2	0.01	15	25	Hard Bottom + Reef
14	12/10/18	LC	N	Outer	B	19.68479	-80.07889	6.5	4.6	315	6.8	1	0.3	0.01	none	none	Reef
15	12/10/18	LC	N	Outer	C	19.68885	-80.07178	6.5	3.7	340	17.2	1	0.3	0.01	none	none	Hard Bottom
16	12/10/18	LC	N	Outer	D	19.69618	-80.06828	6	65	315	6.5	1	0.3	0.01	8	310	Hard Bottom
17	13/10/18	LC	W	Outer	A	19.66691	-80.10914	4	11.1	135	16.8	1	0.1	0.05	8	120	Hard Bottom + Reef
18	13/10/18	LC	W	Outer	B	19.66338	-80.11244	4	18.5	120	16.1	1.5	0.3	0.01	none	none	Hard Bottom
19	13/10/18	LC	W	Outer	C	19.65924	-80.11389	2	13.9	135	20.7	1	0.3	0.01	3	160	Hard Bottom
20	13/10/18	LC	W	Outer	D	19.65469	-80.11277	2	12.9	120	15.1	1	0.3	0.01	2	220	Hard Bottom
21	13/10/18	LC	SW	Outer	A	19.65513	-80.08559	4	9.3	120	16.3	1	0.4	0.1	7	80	Hard Bottom
22	13/10/18	LC	SW	Outer	B	19.65627	-80.08989	3	5.6	160	16.9	2	0.5	0.1	5	110	Hard Bottom
23	13/10/18	LC	SW	Outer	C	19.65624	-80.09523	4	12	110	15.5	2	0.4	0.1	5	140	Hard Bottom
24	13/10/18	LC	SW	Outer	D	19.65559	-80.10002	3	17.6	110	17.4	1.5	0.3	0.1	6	130	Reef
25	17/10/18	LC	SSE	Inner	A	19.66821	-80.06068	4	24.1	130	1.2	1.5	0	0.25	10	110	Sediment
26	17/10/18	LC	SSE	Inner	B	19.67306	-80.06303	4	14.8	100	0.7	1.5	0	0.2	5	100	Seagrass
27	17/10/18	LC	SSE	Inner	C	19.67299	-80.05314	3	24.1	100	1.5	2	0	0.25	6	60	Sediment
28	17/10/18	LC	SSE	Inner	D	19.67675	-80.05347	2	11.1	70	0.8	1	0.1	0.01	20	160	Seagrass
29	17/10/18	LC	SSW	Inner	A	19.65798	-80.08321	1	20.4	80	1.6	1	0.5	0.1	5	90	Reef
30	17/10/18	LC	SSW	Inner	B	19.65799	-80.07811	2	16.7	70	2.5	2	0.3	0.1	4	60	Sediment
31	17/10/18	LC	SSW	Inner	C	19.65886	-80.07343	1.5	19.5	100	2.3	1	0.2	0.05	3	10	Sediment
32	17/10/18	LC	SSW	Inner	D	19.66112	-80.06920	1	22.2	80	1.5	2	0.3	0.05	4	60	Sediment
33	05/11/18	GC	NS	Outer	A	19.38907	-81.34275	3	4	10	17	2	0.4	0.1	7	40	Hard Bottom
34	05/11/18	GC	NS	Outer	B	19.38480	-81.33443	3	4	80	18.8	3	0.4	0.1	8	90	Hard Bottom
35	05/11/18	GC	NS	Outer	C	19.38357	-81.32489	3	7	100	19.8	2	0.4	0.1	7	90	Hard Bottom + Reef

BRUVS No.	Seabed arrival real time	Total time on seabed	Departure seabed/tape end	Current on bottom	Exposure to current	Visibility	BRUVS placement	*C. perezi*		*C. limbatus*		Unidentified *Carcharhinus*		*G. cirratum*		*N. brevirostris*	
								Nind	MaxN	Nind	MaxN	Nind	MaxN	Nind	MaxN	Nind	MaxN
1	12:18:37	02:15:25	14:34:02	none	medium	good	medium	1	1	0	0	0	0	0	0	0	0
2	12:10:46	02:14:30	14:25:16	weak	medium	medium	good	0	0	0	0	0	0	1	1	0	0
3	12:03:49	02:13:17	14:17:06	weak	good	medium	bad	1	1	0	0	0	0	1	1	0	0
4	11:49:51	02:29:00	14:18:51	weak	good	medium	good	2	1	0	0	0	0	0	0	0	0
5	09:17:17	01:57:15	11:14:32	none	medium	medium	medium	1	1	0	0	0	0	1	1	0	0
6	09:10:27	01:58:22	11:08:49	weak	good	medium	good	2	2	0	0	0	0	1	1	0	0
7	09:02:04	02:03:08	11:05:12	weak	good	good	good	0	0	0	0	0	0	0	0	0	0
8	08:55:14	02:06:31	11:01:45	medium	good	medium	good	3	2	0	0	0	0	1	1	0	0
9	09:31:09	02:19:16	11:50:25	medium	good	medium	bad	1	1	0	0	0	0	4	3	0	0
10	09:39:50	02:15:12	11:55:02	medium	good	medium	good	1	1	0	0	0	0	1	1	0	0
11	09:53:13	02:09:05	12:02:18	weak	medium	medium	medium	1	1	0	0	0	0	0	0	0	0
12	10:05:09	02:02:45	12:07:54	weak	good	medium	good	0	0	0	0	0	0	1	1	0	0
13	13:32:12	01:17:21	14:49:33	weak	good	good	medium	0	0	0	0	0	0	2	1	0	0
14	13:39:25	01:22:55	15:02:20	weak	medium	medium	medium	0	0	0	0	0	0	1	1	0	0
15	13:48:49	01:44:53	15:33:42	weak	good	bad	good	1	1	0	0	0	0	0	0	0	0
16	13:53:37	01:32:59	15:26:36	none	medium	medium	medium	0	0	0	0	0	0	0	0	0	0
17	09:07:21	02:03:59	11:11:20	weak	good	medium	good	1	1	0	0	0	0	1	1	0	0
18	09:13:27	02:06:10	11:19:37	strong	good	medium	bad	0	0	0	0	0	0	0	0	0	0
19	09:19:34	02:08:13	11:27:47	weak	good	medium	good	2	2	0	0	0	0	0	0	0	0
20	09:27:42	02:09:26	11:37:08	weak	good	good	good	0	0	0	0	0	0	0	0	0	0
21	13:56:30	01:58:27	15:54:57	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
22	13:50:28	01:32:11	15:22:39	medium	good	good	good	0	0	0	0	0	0	0	0	0	0
23	13:44:28	01:37:14	15:21:42	weak	good	good	good	0	0	0	0	0	0	0	0	0	0
24	13:35:55	01:17:30	14:53:25	weak	medium	good	medium	1	1	0	0	0	0	0	0	0	0
25	10:12:27	02:04:55	12:17:22	medium	good	medium	good	0	0	0	0	0	0	0	0	2	2
26	10:03:02	02:09:10	12:12:12	weak	good	bad	good	0	0	0	0	0	0	0	0	0	0
27	09:53:34	02:13:49	12:07:23	weak	good	bad	good	0	0	0	0	0	0	0	0	0	0
28	09:44:05	02:19:20	12:03:25	none	medium	bad	good	0	0	0	0	0	0	0	0	0	0
29	13:00:56	01:18:04	14:19:00	very strong	good	bad	bad	0	0	0	0	0	0	1	1	0	0
30	12:49:29	01:30:42	14:20:11	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
31	12:42:13	01:45:31	14:27:44	strong	good	good	good	0	0	0	0	0	0	0	0	0	0
32	12:33:15	01:34:52	14:08:07	medium	good	good	good	0	0	0	0	0	0	0	0	0	0
33	11:09:49	02:01:36	13:11:25	weak	good	medium	good	0	0	0	0	1	1	1	1	0	0
34	11:22:29	02:15:47	13:38:16	weak	good	medium	good	1	1	0	0	0	0	1	1	0	0
35	11:37:54	02:15:17	13:53:11	medium	good	medium	good	1	1	0	0	0	0	0	0	0	0

BRUVS No.	Date recorded	Island	Location	Site	Camera	Latitude (DD)	Longitude (DD)	Cloud cover (/8)	Wind strength (kph)	Wind direction	Water depth (m)	Sea state	Swell (m)	Wave height (m)	Current speed (s/m)	Current direction (degree)	Habitat
36	05/11/18	GC	NS	Outer	D	19.38434	-81.31462	3	12	80	20.7	2	0.4	0.1	4	70	Hard Bottom
37	06/11/18	GC	FS	Outer	A	19.29029	-81.17502	5	18.9	90	12	2.5	0.5	0.1	4	120	Sediment
38	06/11/18	GC	FS	Outer	B	19.29050	-81.17001	5	20	100	14	2.5	0.5	0.1	5	310	Reef + Sediment
39	06/11/18	GC	FS	Outer	C	19.28970	-81.16494	6	19.3	90	17.1	2.5	0.5	0.1	4	110	Reef
40	06/11/18	GC	FS	Outer	D	19.28983	-81.16035	6	16.7	100	18.1	2.5	0.5	0.1	5	110	Hard Bottom
41	07/11/18	GC	SS	Outer	A	19.26542	-81.35509	5	12.6	90	18.3	1	0.4	0.1	7	130	Hard Bottom + Reef
42	07/11/18	GC	SS	Outer	B	19.26656	-81.35007	5	8.5	70	17.4	1	0.4	0.1	13	140	Hard Bottom
43	07/11/18	GC	SS	Outer	C	19.26778	-81.34538	5	16.7	80	18.5	1	0.4	0.1	5	140	Reef
44	07/11/18	GC	SS	Outer	D	19.26890	-81.34068	5	15.7	60	16.7	1	0.4	0.1	6	270	Hard Bottom
45	08/11/18	GC	NE	Outer	A	19.35782	-81.11057	1	7.4	60	19.8	1	0.2	0.05	6	120	Reef
46	08/11/18	GC	NE	Outer	B	19.35830	-81.11491	1	9.3	80	18.3	1	0.2	0.05	8	100	Hard Bottom
47	08/11/18	GC	NE	Outer	C	19.35859	-81.12021	1	4.6	110	17	1	0.2	0.05	none	none	Hard Bottom
48	08/11/18	GC	NE	Outer	D	19.35892	-81.12515	1	10.2	100	19.6	1	0.2	0.05	5	110	Hard Bottom
49	09/11/18	GC	EE	Outer	A	19.30807	-81.07074	3	6.3	60	13.6	1	0.3	0.05	5	110	Reef
50	09/11/18	GC	EE	Outer	B	19.30360	-81.07236	3	10.2	50	13.7	1	0.3	0.05	4	110	Hard Bottom
51	09/11/18	GC	EE	Outer	C	19.30039	-81.07600	3	10.2	90	13.1	1	0.3	0.05	none	none	Hard Bottom + Reef
52	09/11/18	GC	EE	Outer	D	19.29728	-81.07967	3	6.3	60	14.6	1	0.3	0.05	9	90	Reef
53	13/11/18	GC	WB	Outer	A	19.34184	-81.39182	6	12	65	17.6	1	0.3	0.05	5	30	Sediment
54	13/11/18	GC	WB	Outer	B	19.34895	-81.39330	6	18.5	70	17.3	1	0.2	0.05	5	80	Hard Bottom
55	13/11/18	GC	WB	Outer	C	19.35618	-81.39510	6	14.8	70	13.2	1	0.1	0.05	7	180	Hard Bottom
56	13/11/18	GC	WB	Outer	D	19.36082	-81.40047	6	15.7	60	17	1	0.1	0.05	6	90	Sediment + Hard Bottom
57	14/11/18	GC	N	Outer	A	19.35293	-81.22832	1	9.3	30	13.5	1	0.4	0.05	5	90	Hard Bottom + Reef
58	14/11/18	GC	N	Outer	B	19.35327	-81.23292	1	11.1	5	14.4	1	0.3	0.05	4	80	Hard Bottom
59	14/11/18	GC	N	Outer	C	19.35494	-81.23817	1	10.2	30	15.3	1	0.4	0.05	5	90	Hard Bottom + Reef
60	14/11/18	GC	N	Outer	D	19.35643	-81.24265	1	11.1	35	14.1	1	0.3	0.05	4	40	Hard Bottom
61	15/11/18	GC	NS	Inner	A	19.37388	-81.34782	2	10.7	40	2.8	1	0.1	0.05	8	45	Seagrass
62	15/11/18	GC	NS	Inner	B	19.37260	-81.33823	3	8.3	10	2.9	1	0.1	0.05	6	10	Sediment
63	15/11/18	GC	NS	Inner	C	19.37113	-81.32768	3	8.3	15	3.4	1	0.1	0.05	8	120	Seagrass
64	15/11/18	GC	NS	Inner	D	19.36979	-81.31835	3	3.7	60	3.3	1	0.1	0.05	5	80	Seagrass
65	19/11/18	GC	SS	Inner	A	19.26886	-81.36706	6	25	30	2.1	1	0.1	0.02	3	60	Hard Bottom
66	19/11/18	GC	SS	Inner	B	19.27048	-81.36221	6	14	40	2.5	1	0.1	0.02	4	100	Hard Bottom
67	19/11/18	GC	SS	Inner	C	19.27158	-81.35811	6	11.7	20	2.1	1	0.1	0.02	5	110	Seagrass
68	19/11/18	GC	SS	Inner	D	19.27312	-81.35343	6	13.9	60	1.7	1	0.1	0.02	5	100	Hard Bottom
69	20/11/18	GC	NS	Inner	A	19.34215	-81.28246	5	21.3	60	3.5	1	0.1	0.2	5	100	Seagrass
70	20/11/18	GC	NS	Inner	B	19.33754	-81.27587	4	5.6	130	2.8	1	0.1	0.1	5	80	Seagrass

BRUVS No.	Seabed arrival real time	Total time on seabed	Departure seabed/tape end	Current on bottom	Exposure to current	Visibility	BRUVS placement	*C. perezi*		*C. limbatus*		Unidentified *Carcharhinus*		*G. cirratum*		*N. brevirostris*	
								Nind	MaxN	Nind	MaxN	Nind	MaxN	Nind	MaxN	Nind	MaxN
36	11:48:36	02:23:16	14:11:52	weak	good	medium	good	1	1	0	0	0	0	0	0	0	0
37	11:11:21	02:31:00	13:42:21	medium	good	good	good	0	0	0	0	0	0	1	1	0	0
38	11:19:29	02:16:13	13:35:42	weak	medium	good	medium	0	0	0	0	0	0	0	0	0	0
39	11:27:59	02:07:56	13:35:55	weak	good	good	good	0	0	0	0	0	0	1	1	0	0
40	11:35:14	01:56:05	13:31:19	none	good	good	good	0	0	0	0	0	0	0	0	0	0
41	09:47:32	02:40:31	12:28:03	weak	good	medium	good	1	1	0	0	0	0	1	1	0	0
42	09:56:36	02:15:09	12:11:45	weak	good	medium	medium	0	0	0	0	0	0	0	0	0	0
43	10:03:59	02:15:29	12:19:28	medium	good	medium	medium	2	1	0	0	0	0	1	1	0	0
44	10:09:35	02:05:28	12:15:03	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
45	11:04:42	01:59:57	13:04:39	weak	good	medium	good	1	1	0	0	0	0	0	0	0	0
46	10:56:37	02:12:15	13:08:52	weak	good	good	good	0	0	0	0	0	0	0	0	0	0
47	10:48:29	02:16:05	13:04:34	weak	good	medium	good	0	0	0	0	0	0	1	1	0	0
48	10:41:30	02:32:53	13:14:23	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
49	10:38:21	02:12:46	12:51:07	medium	good	medium	good	2	1	0	0	0	0	0	0	0	0
50	10:47:25	02:08:33	12:55:58	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
51	10:52:34	02:07:31	13:00:05	weak	good	medium	good	0	0	0	0	0	0	1	1	0	0
52	10:58:43	02:05:58	13:04:41	medium	good	medium	good	0	0	0	0	0	0	1	1	0	0
53	11:01:58	02:41:08	13:43:06	none	good	medium	good	0	0	0	0	0	0	1	1	0	0
54	11:09:28	02:16:15	13:25:43	none	good	medium	good	0	0	0	0	0	0	0	0	0	0
55	11:15:23	02:15:48	13:31:11	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
56	11:24:30	02:05:51	13:30:21	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
57	11:06:27	02:18:22	13:24:49	weak	good	medium	good	1	1	0	0	0	0	0	0	0	0
58	11:14:23	02:14:29	13:28:52	weak	good	medium	good	1	1	0	0	0	0	0	0	0	0
59	11:21:41	02:10:33	13:32:14	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
60	11:27:36	02:08:21	13:35:57	weak	medium	medium	medium	0	0	0	0	0	0	0	0	0	0
61	09:51:11	02:28:50	12:20:01	medium	good	medium	good	0	0	1	1	0	0	0	0	0	0
62	09:59:09	02:16:26	12:15:35	weak	good	bad	good	0	0	0	0	0	0	0	0	0	0
63	10:06:08	02:16:29	12:22:37	weak	good	medium	good	0	0	1	1	0	0	0	0	0	0
64	10:14:09	02:19:05	12:33:14	weak	good	bad	good	0	0	0	0	1	1	0	0	0	0
65	10:11:06	02:04:00	12:15:06	medium	good	bad	good	0	0	0	0	0	0	1	1	0	0
66	10:05:11	02:02:50	12:08:01	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
67	09:59:08	02:03:38	12:02:46	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
68	09:53:07	02:04:32	11:57:39	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
69	09:50:12	02:17:22	12:07:34	weak	good	bad	good	0	0	0	0	0	0	0	0	0	0
70	09:59:10	02:15:27	12:14:37	weak	good	bad	good	0	0	1	1	0	0	0	0	0	0

BRUVS No.	Date recorded	Island	Location	Site	Camera	Latitude (DD)	Longitude (DD)	Cloud cover (/8)	Wind strength (kph)	Wind direction	Water depth (m)	Sea state	Swell (m)	Wave height (m)	Current speed (s/m)	Current direction (degree)	Habitat
71	20/11/18	GC	NS	Inner	C	19.33241	-81.27037	3	8	120	2.7	1	0.1	0.1	5	90	Seagrass
72	20/11/18	GC	NS	Inner	D	19.32769	-81.26504	3	12.2	120	2.5	1	0.1	0.1	7	80	Seagrass
73	21/11/18	GC	WB	Inner	A	19.35962	-81.39164	5	11.1	65	3.4	1	0.01	0.02	10	100	-
74	21/11/18	GC	WB	Inner	B	19.35542	-81.38953	6	14.8	70	3.2	1	0.01	0.02	5	100	Hard Bottom
75	21/11/18	GC	WB	Inner	C	19.35186	-81.38712	6	15.7	50	3.5	1	0.01	0.02	4	45	Hard Bottom
76	21/11/18	GC	WB	Inner	D	19.34665	-81.38465	6	9.3	30	2.8	1	0.01	0.02	10	110	Sediment + Hard Bottom
77	22/11/18	GC	EE	Inner	A	19.32472	-81.08160	5	15.9	30	3.5	2	0.2	0.05	3	20	Seagrass
78	22/11/18	GC	EE	Inner	B	19.31587	-81.08002	5	16.3	90	4.7	2	0.2	0.05	3	60	Seagrass
79	22/11/18	GC	EE	Inner	C	19.30659	-81.08106	5	20.4	85	5.6	2	0.2	0.05	6	90	Seagrass
80	22/11/18	GC	EE	Inner	D	19.30041	-81.08952	5	21.9	13.5	4.8	2	0.2	0.05	4	50	Seagrass
81	23/11/18	GC	FS	Inner	A	19.29457	-81.16090	4	125	18.5	1.8	1	0.2	0.05	7	50	Sediment
82	23/11/18	GC	FS	Inner	B	19.29405	-81.17123	5	140	19.5	2.1	1	0.1	0.05	5	100	Hard Bottom
83	23/11/18	GC	FS	Inner	C	19.29402	-81.18076	5	130	20.7	2	1	0.1	0.05	4	125	Sediment + Hard Bottom
84	23/11/18	GC	FS	Inner	D	19.29347	-81.19042	4	120	16.9	2.4	1	0.1	0.05	9	80	Hard Bottom

BRUVS No.	Seabed arrival real time	Total time on seabed	Departure seabed/tape end	Current on bottom	Exposure to current	Visibility	BRUVS placement	*C. perezi*		*C. limbatus*		Unidentified *Carcharhinus*		*G. cirratum*		*N. brevirostris*	
								Nind	MaxN	Nind	MaxN	Nind	MaxN	Nind	MaxN	Nind	MaxN
71	10:08:08	02:13:46	12:21:54	weak	good	bad	good	0	0	0	0	0	0	0	0	0	0
72	10:17:11	02:10:44	12:27:55	weak	good	bad	good	0	0	0	0	0	0	0	0	0	0
73	10:38:00	00:00:00	10:38:00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
74	10:23:15	02:13:07	12:36:22	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
75	10:17:10	02:16:34	12:33:44	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
76	10:10:07	02:32:37	12:42:44	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
77	10:20:08	02:09:07	12:29:15	weak	good	medium	good	0	0	0	0	0	0	2	1	0	0
78	10:27:10	02:05:42	12:32:52	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
79	10:35:12	02:02:24	12:37:36	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
80	10:41:11	01:54:29	12:35:40	weak	good	medium	good	0	0	0	0	0	0	1	1	0	0
81	10:59:10	02:36:51	13:36:01	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
82	11:08:10	02:16:38	13:24:48	medium	good	medium	good	0	0	0	0	0	0	0	0	0	0
83	11:22:25	01:44:32	13:06:57	weak	good	medium	good	0	0	0	0	0	0	0	0	0	0
84	11:31:08	01:54:24	13:25:32	weak	good	medium	good	0	0	0	0	0	0	1	1	0	0

Appendix E.

Statistical outputs: Dunn's post-hoc test

Table E. Statistical output of Dunn's post-hoc test for Table 2.5 on the factor depth using FDR p-value adjustment method (*p* – statistical significance)

Factor	Pairwise comparison	*p*
Depth	Shallow *vs*. Mid	0.059
	Shallow *vs*. Deep	0.0034*
	Mid *vs*. Deep	0.40

Appendix F.

Statistical outputs: PERMANOVA pairwise comparisons

Table F1. Statistical output of PERMANOVA pairwise comparisons for Table 2.6 on the factor depth, using FDR *p*-value adjustment method (*p* - p-values based on 999 permutations)

Factor	Pairwise comparison	*p*
Depth	Shallow *vs*. Mid	0.009*
	Shallow *vs*. Deep	0.006*
	Mid *vs*. Deep	0.77

Table F2. Statistical output of PERMANOVA pairwise comparisons for Table 2.8 on the factor depth, using FDR *p*-value adjustment method (*p* - p-values based on 999 permutations)

Factor	Pairwise comparison	*p*
Depth	Shallow *vs*. Mid	0.24
	Shallow *vs*. Deep	0.009*
	Mid *vs*. Deep	0.31

Appendix G.

MDS ordinations of insignificant PERMANOVA models

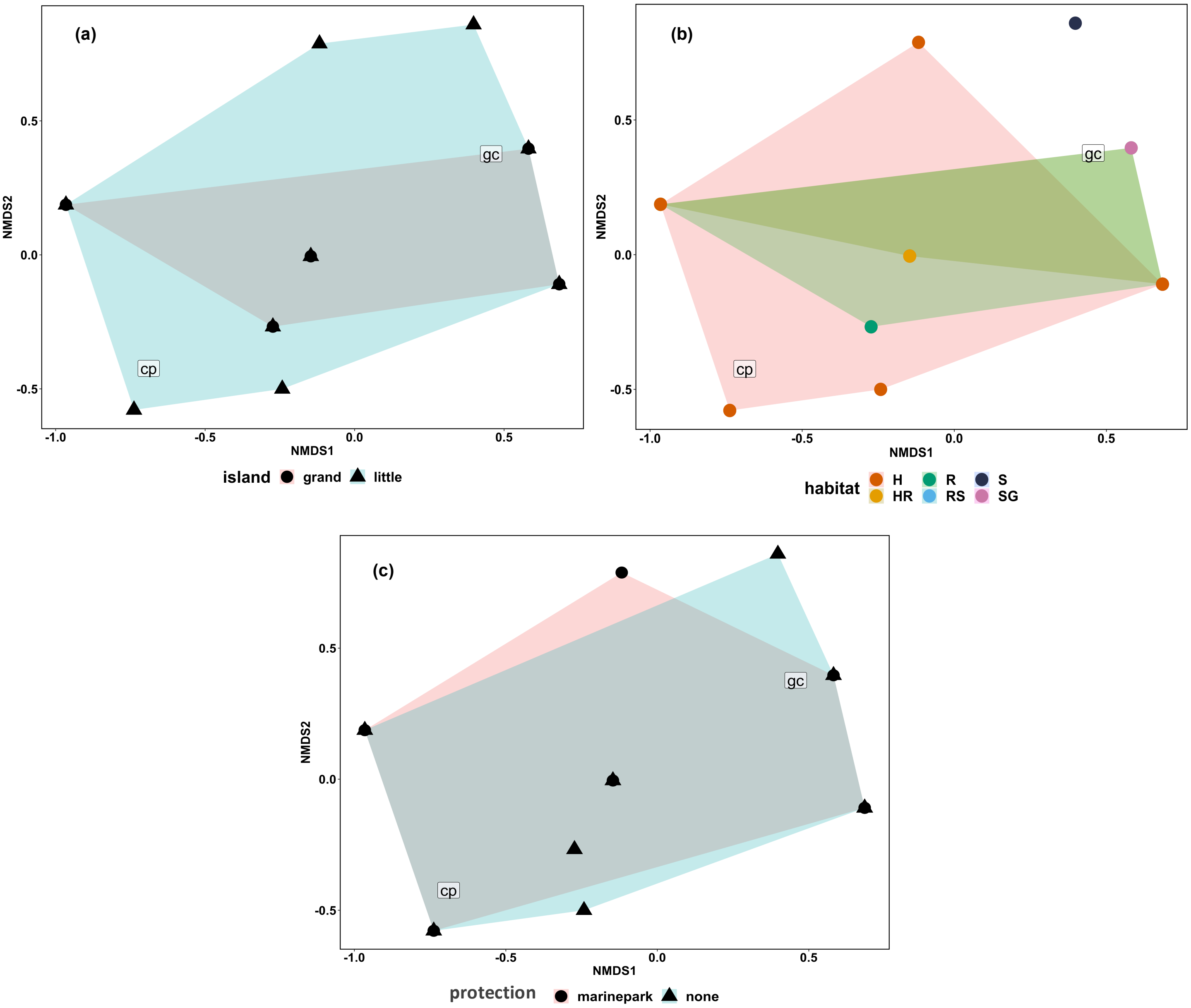
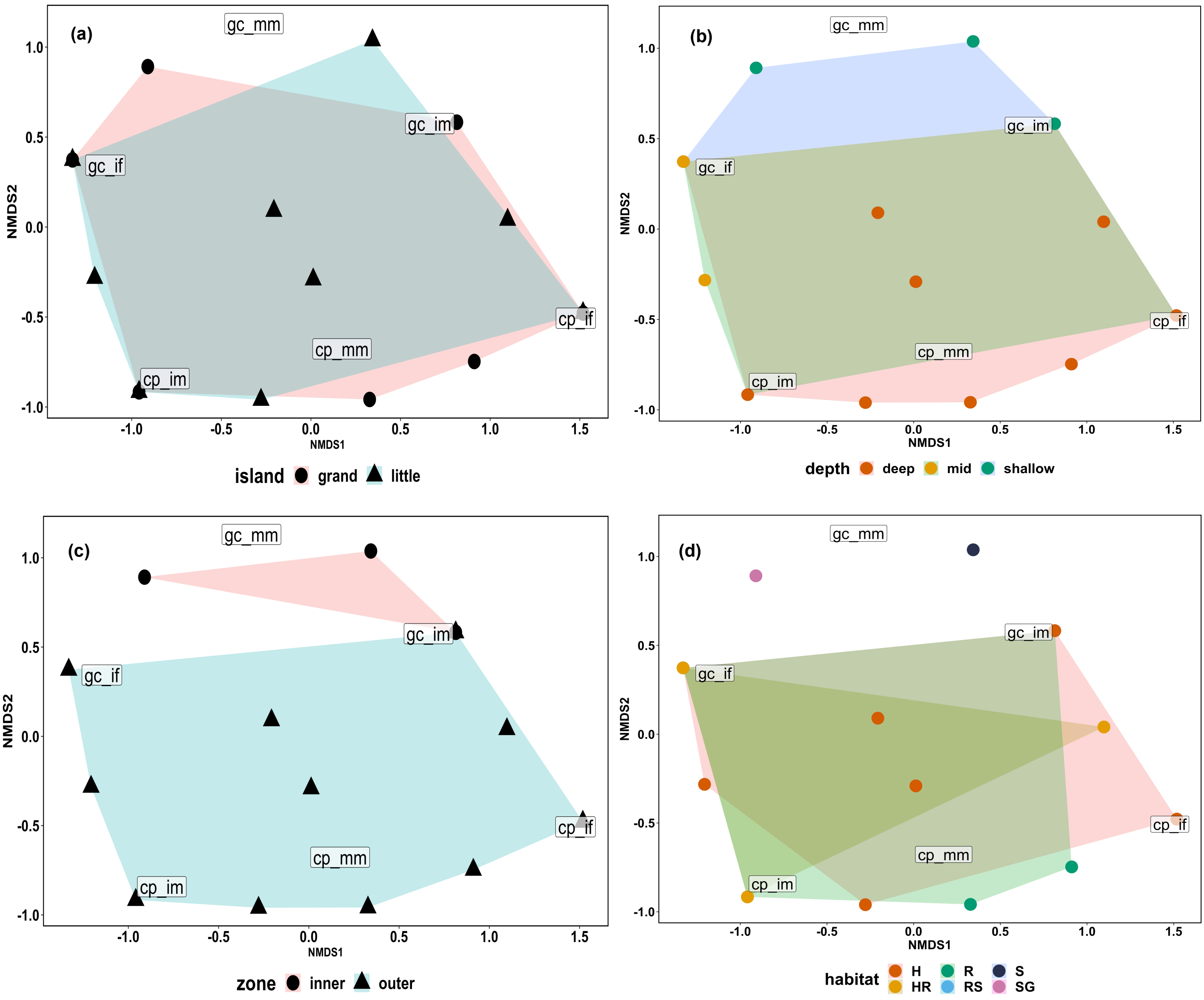


Figure G1. MDS ordinations (2D stress = 0.01235) of insignificant PERMANOVA factors from Table 2.6 affecting species composition across BRUVS sites: (a) island, (b) habitat, (c) protection. Points and shaded convex polygons are that of the factor. Labels: "cp" = *C. perezi*, "gc" = *G. cirratum*



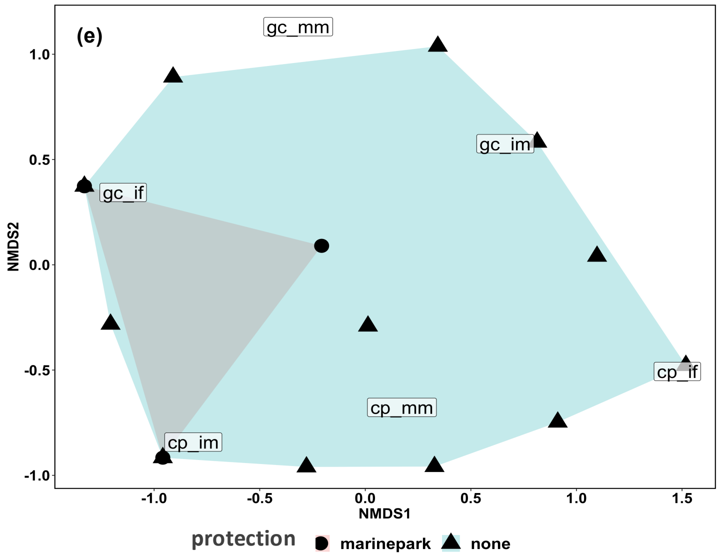
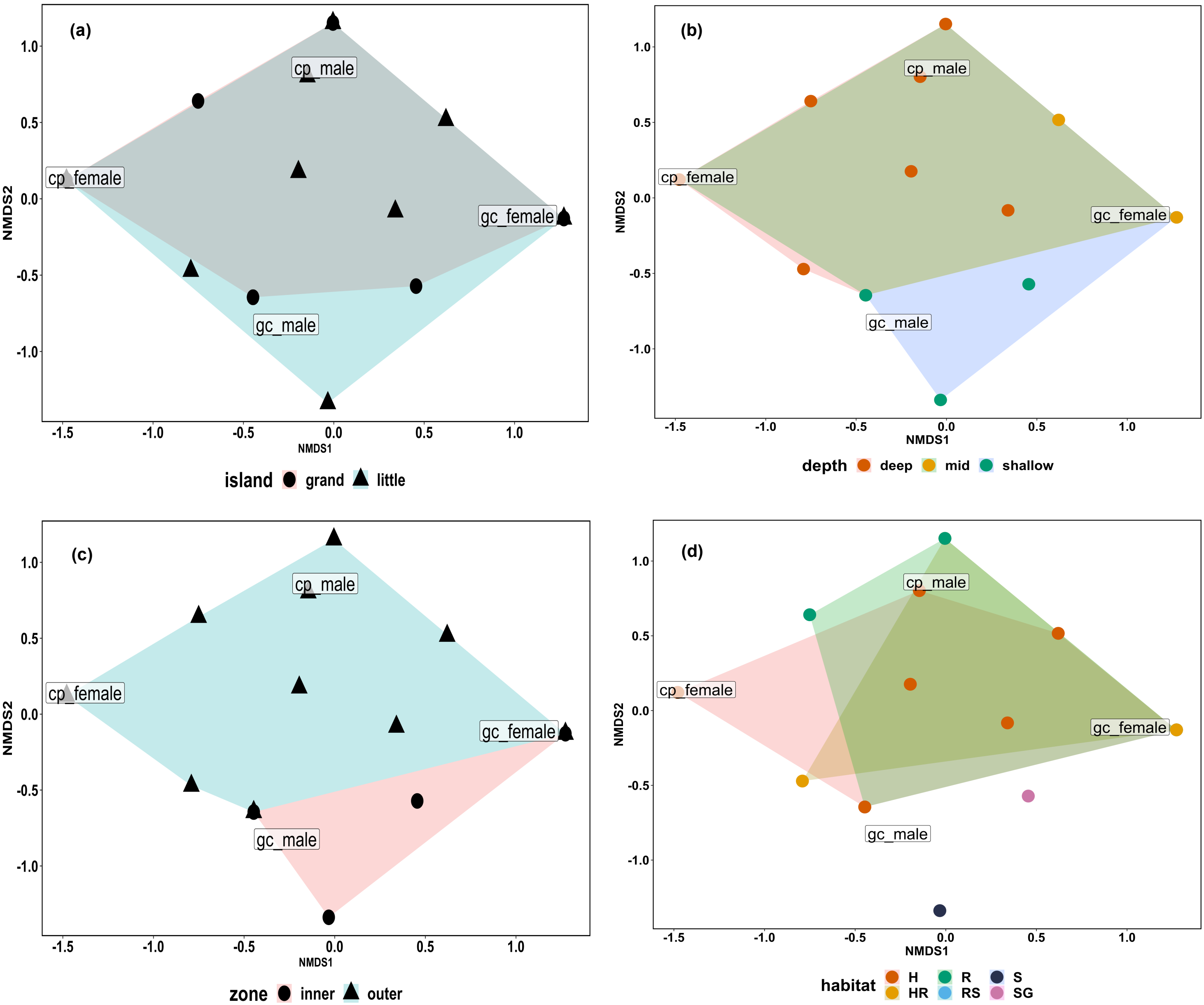


Figure G2. MDS ordinations (2D stress = 0.01467452) of insignificant PERMANOVA factors from Appendix H1 affecting species and demographic group composition (sex and maturity) across BRUVS sites:
(a) island, (b) depth, (c) zone, (d) habitat, (e) protection. Points and shaded convex polygons are that of the factor.
Labels:
“cp_mm” = *C. perezi* mature male, “cp_imm” = *C. perezi* immature male, “cp_if” = *C. perezi* immature female, “gc_mm” = *G. cirratum* mature male, “gc_im”= *G. cirratum* immature male, “gc_if”= *G. cirratum* immature female



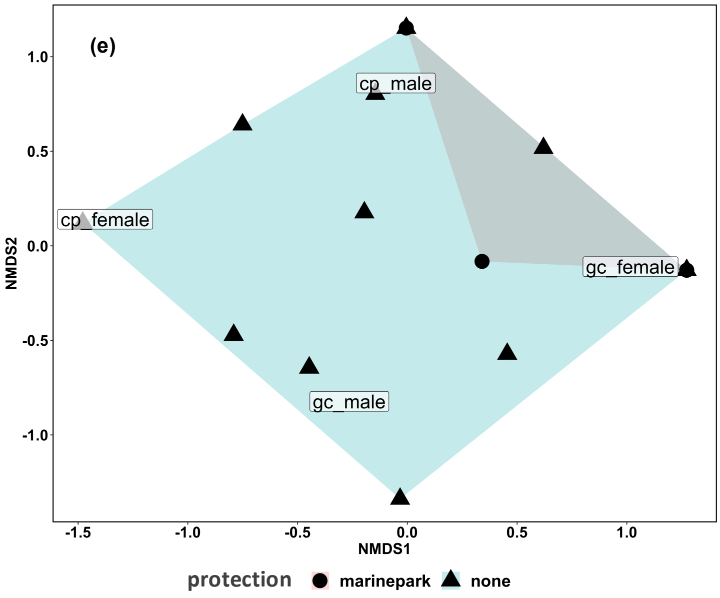


Figure G3. MDS ordinations (2D stress = 0.03419495) of insignificant PERMANOVA factors from Appendix H2 affecting species and sex composition across BRUVS sites:
(a) island, (b) depth, (c) zone, (d) habitat, (e) protection. Points and shaded convex polygons are that of the factor.
Labels: “cp_male” = *C. perezi* male, “cp_female” = *C. perezi* female, “gc_male” = *G. cirratum* male, “gc_female” = *G. cirratum* female

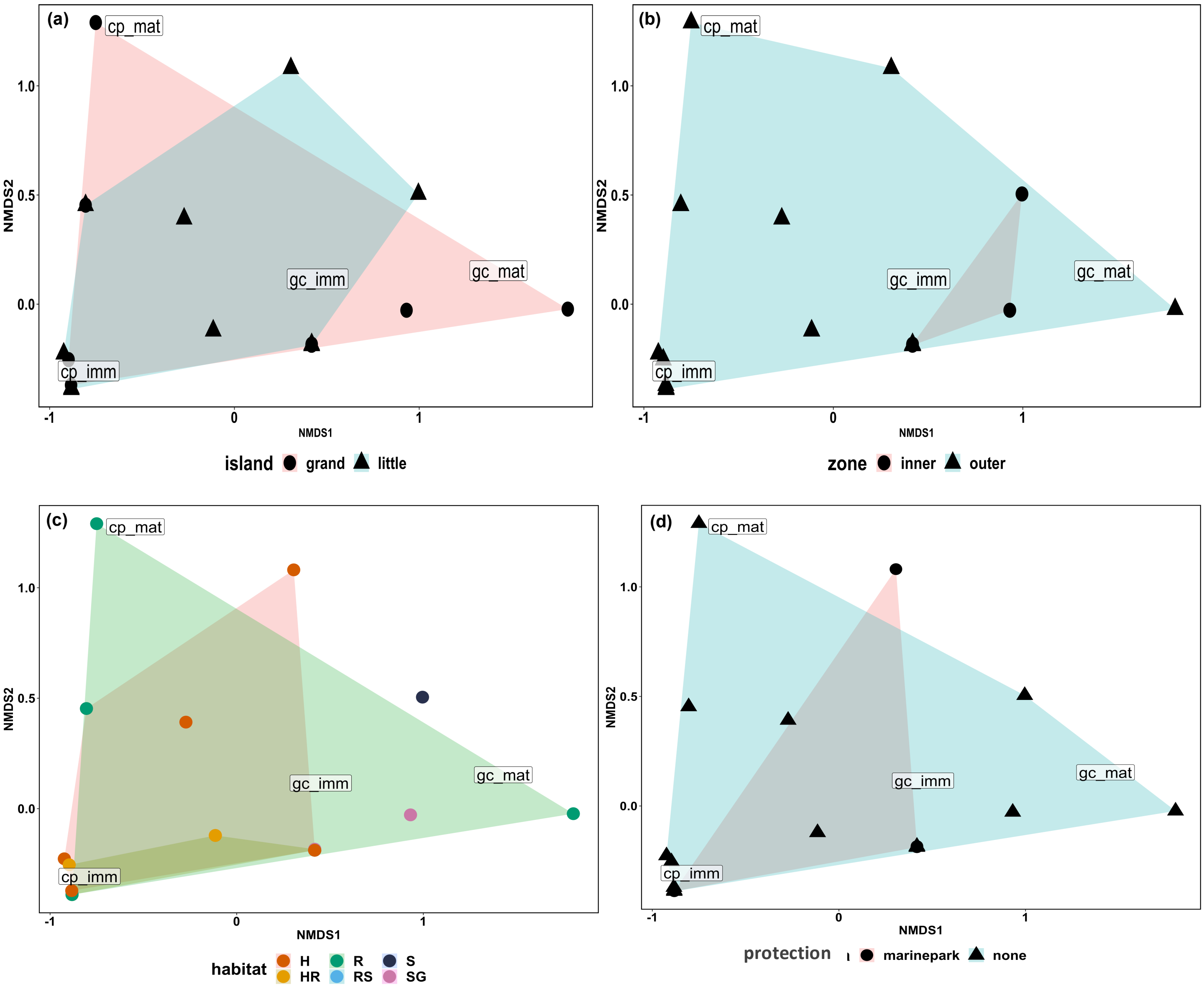


Figure G4. MDS ordinations (2D stress = 0. 0001142628) of insignificant PERMANOVA factors from Table 2.8 affecting species and maturity composition across BRUVS sites: BRUVS sites: (a) island, (b) zone, (c) habitat, (d) protection. Points and shaded convex polygons are that of the factor. Labels: “cp_mat” = mature *C. perezi*, “cp_imm” = immature *C. perezi*, *“gc_mat”= mature G. cirratum*, *“gc_imm”*= immature *G. cirratum*

Appendix H.

Statistical outputs: Insignificant PERMANOVA models

Table H1. Results of one-way PERMANOVA models on species and demographic group composition (sex and maturity), testing the effect of island, zone, depth, habitat and protection (df - degrees of freedom; SS – sum of squares; Pseudo-F – F value by permutation; *p* - p-values based on 999 permutations)

Factors	df	SS	Pseudo-F	R^2	*p*
Protection	1	0.8420	2.4557	0.09282	0.052
Zone	1	0.7205	2.0708	0.07943	0.11
Depth	2	1.1029	1.5917	0.12158	0.17
Island	1	0.3893	1.0761	0.04292	0.39
Habitat	5	1.5588	0.82994	0.17183	0.67

Table H2. Results of one-way PERMANOVA models on species and sex composition testing the effect of island, zone, depth, habitat and protection (df - degrees of freedom; SS – sum of squares; Pseudo-F – F value by permutation; *p* - p-values based on 999 permutations)

Factors	df	SS	Pseudo-F	R^2	*p*
Protection	1	0.8033	2.488	0.09051	0.057
Zone	1	0.7702	2.3755	0.08678	0.083
Depth	2	1.2624	1.9899	0.14224	0.095
Island	1	0.4988	1.4886	0.0562	0.24
Habitat	5	1.7968	1.0662	0.20246	0.41