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Habitats adequados e aspectos ecológicos do tubarão-baleia (*Rhincodon typus* Smith 1828) no Oceano Atlântico Sudoeste e Equatorial

Recife/2016

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“One thing I have learned in a long life: that all our science, measured against reality, is primitive and childlike - and yet it is the most precious thing we have”

“But, on the other hand, everyone who is seriously involved in the pursuit of science becomes convinced that a spirit is manifest in the laws of the Universe—a spirit vastly superior to that of man, and one in the face of which we with our modest powers must feel humble.”

— Albert Einstein

RESUMO

Compreender detalhadamente a história de vida do tubarão-baleia é fundamental para assegurar a sua conservação. No entanto, apesar da espécie possuir distribuição circumglobal e ser relativamente bem estudada entre os elasmobrânquios, ainda existe uma grande escassez de informações relacionadas a muitos dos seus aspectos ecológicos e biológicos em todo o mundo, principalmente no que diz respeito aos seus movimentos migratórios e ciclo reprodutivo. No Oceano Atlântico, particularmente, a espécie vem sendo investigada majoritariamente no Golfo do México/ Mar do Caribe, permanecendo uma grande lacuna para o restante dessa bacia oceânica. O presente estudo representa a primeira iniciativa de investigação da distribuição espacial do tubarão-baleia em escala oceânica no sudoeste do Atlântico baseada em registros de ocorrências na costa do Brasil, além de ter sido o primeiro trabalho também sobre o rastreamento de tubarões-baleia na região equatorial. Com o objetivo de complementar o conhecimento acerca da distribuição geográfica e movimentação do tubarão-baleia nas regiões sudoeste e equatorial do oceano Atlântico, foram empregadas técnicas modernas de modelagem ecológica e rastreamento via satélite, além da utilização do método tradicional de censo visual para identificação de aspectos populacionais no Arquipélago de São Pedro e São Paulo (ASPSP). Primeiramente, foram realizadas predições referentes à distribuição espacial de habitats adequados para alimentação e inferências sobre a influência de variáveis ambientais específicas para ocorrência do tubarão-baleia na costa do Brasil/ sudoeste do oceano Atlântico. Em seguida, a sazonalidade, a abundância relativa e a estrutura populacional dos tubarões-baleia que visitam o ASPSP foram investigadas, incluindo inferências acerca da importância de ecossistemas insulares oceânicos para a parcela madura da espécie. Por fim, na terceira parte da Tese, os deslocamentos horizontais e verticais de tubarões-baleia marcados com transmissores via satélite no ASPSP foram descritos e o comportamento de mergulho avaliado com relação a fatores biofísicos e ambientais específicos. Os resultados obtidos no presente estudo são relevantes não somente para a conservação do tubarão-baleia, mas para o ecossistema marinho na costa do Brasil, de uma forma geral, posto que o mapeamento de habitats ideais para alimentação da espécie também serve para identificar áreas ecologicamente importantes para outras espécies. Ademais, a identificação do ASPSP como uma área importante para a parcela adulta dos tubarões-baleia ressalta sua importância ecológica no ciclo de vida da espécie, destacando a necessidade de se envidar maiores esforços para a conservação do local.

Palavras-chave: Oceano Atlântico. Biogeografia. Alimentação. Modelagem ecológica. Ecossistema insular. Reprodução. Telemetria via satélite. Conservação.

ABSTRACT

Understanding the life history of the whale shark is fundamental to assure its conservation. However, in spite of the circumglobal distribution of the species and the fact that it is relatively well studied among elasmobranchs, there is still a serious lack of information concerning its biology in the entire world, mainly regarding its migratory movements and reproductive cycle. In the Atlantic Ocean, particularly, the whale sharks have been predominantly studied in the Gulf of Mexico/Caribbean Sea, with a big gap still remaining for the rest of this ocean basin. Aiming to help to fill this gap on geographical distribution and movement patterns of whale sharks in the Equatorial and Southwest Atlantic regions, modern techniques of ecological modelling and satellite tracking were used, in addition to the use of scientific traditional method of visual census to describe the population aspects of the species in the archipelago of São Pedro and São Paulo (ASPSP). Firstly, geographical predictions of suitable habitats for whale shark feeding and inferences of the influence of specific environmental variables on the occurrence distribution in the Brazilian coast/southwestern Atlantic Ocean were conducted to describe the potential spatial distribution of the species. Then, the seasonality of occurrence, relative abundance and population structure of the whale sharks visiting the ASPSP were investigated, including a discussion regarding the importance of the insular oceanic ecosystems to the mature portion of the species. Finally, in the third part of the thesis, the horizontal and vertical displacements of whale sharks satellite tagged off ASPSP were described and the diving behavior assessed in relation to specific biophysical and environmental factors. The present study represents the first oceanic-scale spatial distribution investigation effort in the southwest Atlantic on whale shark presence records from the Brazilian coast, besides of being the first study using satellite tracking on the species in the equatorial Atlantic as well. The results presented here are of great relevance not only for the whale shark conservation but also for the Brazilian marine ecosystem, as the mapping of suitable feeding habitats could contribute to the identification of areas of ecological importance to other marine species. Moreover, the identification of the ASPSP as an important area for the mature part of whale shark populations highlights its ecological relevance on the species life cycle, emphasizing the need of increasing the conservation efforts in this habitat.

Key-words: Atlantic Ocean; Biogeography; Feeding; Ecological modeling; Species distribution modeling; Insular ecosystem; Reproduction; Satellite telemetry; Conservation.

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LISTA DE ABREVIATURAS E SIGLAS

ANOVA – *Analysis of variance*

ASPSP – Arquipélago de São Pedro e São Paulo

AUC – *Area under the curve*

BC – *Brazil Current*

BIOCLIM - sistema de análise bioclimática e predição

BRT - árvores de regressão impulsionadas

CES – Corrente Sul Equatorial

CHL – *chlorophyll concentration*

CITES - Convenção sobre o Comércio Internacional das Espécies da Flora e Fauna Selvagens em Perigo de Extinção

COMP – *compiled dataset*

EEZ – *Economic Exclusive Zone*

ENFA- fator de análise de nicho ecológico

EUC - *Equatorial Undercurrent*

FAD - *fish aggregating device*

FO% - *relative frequency of occurrence*

GAM - modelos aditivos generalizados

GARP - algoritmo genético para a produção de conjunto de regras (

GLM - modelos lineares generalizados

GLMM - modelos lineares generalizados de efeito misto

GoM – Golfo do México

HSI – *Habitat suitability index*

ITCZ - *Intertropical Convergence Zone*

IUCN – União Internacional para a Conservação da Natureza

k490 - *Downwelling diffuse attenuation coefficient*

KFTrack – *Kalman filter state space model*

LRM - *linear rate of movement*

MARS - regressão multivariada adaptativa

MaxEnt – *Maximum entropy*/máxima entropia

MMA – Ministério do Meio Ambiente

NBC – *North Brazil Current*

PDT - *profiles of depth and temperature*

PNMA - Programa Nacional de Monitoramento de Avistagens do Tubarão-baleia

PP- *primary productivity*

PSAT – *Pop up satellite archival transmitting tag*

RF - florestas aleatórias

ROC – *Receiver operating characteristic*

S – *South*

SACW - *South Atlantic Central Water*

SAO – *Southwestern Atlantic Ocean*

SAT - *satellite-linked transmitting tag*

SBEEL - Sociedade Brasileira para o Estudo dos Elasmobrânquios

SDM – Modelos de distribuição espacial (*species distribution modeling*)

SE – *Southeast*

SEC – *South Equatorial Current*

SPUE - Sightings per Unit of Effort

SST - *sea surface temperature*

SURV – *surveyed dataset*

TAD - *time spent at depth*

TAT - *time spent at temperature*

TLD - *total linear distance*

UKFSST – *unscented kalman filter including sst*

VIF – *Variance inflation factor*

SUMÁRIO

Apresentação

O presente estudo apresenta informações coletadas ao longo de mais de uma década de estudo sobre o tubarão-baleia no Arquipélago de São Pedro e São Paulo, além da compilação de registros históricos ao longo de toda a costa brasileira. Os conhecimentos sobre o tubarão-baleia na costa do Brasil produzidos no presente estudo foram organizados de maneira a apresentar uma visão geral sobre a história de vida da espécie no oceano Atlântico, em comparação com o resto do mundo (**Introdução geral**), ressaltando-se as lacunas de conhecimento; seguida das diretrizes que guiaram o desenvolvimento do trabalho (**Objetivos e Hipóteses**). Na sequência, apresenta-se uma descrição do estado-da-arte do conhecimento sobre a história de vida do tubarão-baleia e dos métodos mais recentemente desenvolvidos e utilizados para estudar a espécie (**Revisão da literatura**). Ao término da introdução ao problema abordado, as informações geradas por este estudo foram organizadas de maneira lógica com o intuito de inicialmente se compreender os fatores que governam a distribuição da espécie na costa Brasileira. Assim, no **Capítulo 1-** Distribuição espacial de habitats adequados para o tubarão-baleia no Oceano Atlântico Equatorial e Sudoeste (*Spatial distribution of suitable habitats for whale sharks in the Equatorial and Southwestern Atlantic Ocean*), foram realizadas modelagens ecológicas para o mapeamento dos habitats mais adequados para ocorrência do tubarão-baleia, avaliando-se a influência das variáveis ambientais em sua distribuição. Em seguida, no **Capítulo 2-** Ocorrência sazonal, abundância e estrutura demográfica do tubarão-baleia no Oceano Atlântico Centro-equatorial (*Whale shark, Rhincodon typus, seasonal occurrence, abundance and demographic structure in the Mid-Equatorial Atlantic Ocean*), foram avaliados os aspectos ecológicos da subpopulação que frequenta o Arquipélago de São Pedro e São Paulo, incluindo uma avaliação da sazonalidade, da abundância e da estrutura populacional dos tubarões-baleia que visitam o ASPSP, com comentários adicionais acerca da importância do ambiente insular para a espécie. No **Capítulo 3-** Rastreamento via satélite do tubarão-baleia a partir do Arquipélago de São Pedro e São Paulo, Oceano Atlântico Centro-Equatorial (*Movements of whale sharks (Rhincodon typus) from an isolated archipelago located in mid-equatorial Atlantic Ocean*), buscou-se elucidar os padrões de movimentação a partir de um habitat insular oceânico, avaliando-se os deslocamentos horizontais e verticais (*i.e.* comportamentos de mergulho) realizados pelos tubarões-baleia marcados com transmissores monitorados por satélite. Para finalizar, todos os resultados acerca da história de vida do tubarão-baleia gerados no presente estudo foram avaliados sinergicamente e as implicações para a conservação da espécie sumarizadas na **Conclusão geral**, seguida dos direcionamentos para pesquisas complementares, sugeridas nas **Recomendações futuras**.

Introdução geral

O tubarão-baleia (*Rhincodon typus* Smith 1828) é considerado uma espécie carismática devido às suas características de vida como o grande porte, seu hábito alimentar filtrador e, principalmente, seu comportamento dócil, quando comparado a outras espécies de tubarão. Apesar de atingir grandes proporções e distribuir-se amplamente em todos os maiores oceanos, sabe-se ainda muito pouco sobre sua dinâmica populacional e bioecologia, principalmente no que diz respeito ao ciclo reprodutivo (Rowat e Brooks 2012). A descrição precisa da distribuição geográfica mundial e a elucidação de aspectos ecológicos e biológicos são fundamentais para a manutenção e conservação de qualquer espécie em um ecossistema, sobretudo para o tubarão-baleia, que devido às suas características intrínsecas de desenvolvimento, como *k*-estrategista (*i.e.* maturação tardia, longevidade alta, crescimento lento), é considerada uma espécie de baixa resiliência e, por essa razão, os impactos causados pela pesca são responsáveis por um declínio populacional e a espécie atualmente está classificada como ‘ameaçada de extinção’ (A2bd+4bd), segundo a União Internacional para Conservação da Natureza (IUCN) (Pierce e Norman 2016). Já no Brasil, o tubarão-baleia é classificado como “vulnerável”, sendo a captura, transporte, armazenamento, guarda, manejo, beneficiamento e comercialização proibidos (MMA 2004, IN nº 5 de maio de 2004). Por essa razão, existe uma elevada necessidade de se gerar conhecimento acerca da dinâmica populacional, dos ciclos biológicos e de se mapear a distribuição geográfica da ocorrência, de habitats de importância ecológica e de se avaliar os potenciais riscos para a espécie, para que seja possível subsidiar um planejamento apropriado para tomada de medidas adequadas para o manejo e conservação da espécie.

Nas últimas décadas houve um grande avanço em pesquisas sobre o tubarão-baleia globalmente. Aspectos da dinâmica e/ou estrutura populacional em áreas costeiras, onde geralmente ocorrem agregações de indivíduos jovens para alimentação (Heyman et al. 2001; Taylor et al. 1996; de la Parra-Venegas et al. 2011; Ketchum et al. 2013; Robinson et al. 2013), compreendem a maior parte do conhecimento acerca da espécie. Por outro lado, estudos em regiões oceânicas são bastante escassos, embora resultados recentes tenham demonstrado que são ambientes importantes no ciclo de vida de espécimes adultos (Ramirez-Macias et al. 2012a; Acuña-Marrero et al. 2014; Clingham et al. 2016; Macena e Hazin 2016). Ademais, além dos métodos científicos tradicionais, três ramos da ciência vêm sendo explorados mais recentemente para se ampliar o conhecimento sobre o tubarão-baleia, nomeadamente: (1) a biologia molecular (Castro et al. 2007; Schmidt et al. 2009, 2010;

Vignaud et al. 2014; Toha et al. 2016), que busca identificar o grau de conectividade e outras relações inter- e intra-populacionais em escala global; (2) a modelagem ecológica da distribuição de espécies (*species distribution modeling*, SDM) (Sequeira et al. 2011; 2013; Mckinney et al. 2012; Rohner et al. 2013a; Afonso et al. 2014; Hacohen-Domené et al. 2015), que visa a relacionar os registros de ocorrências de uma dada espécie com as variáveis ambientais para predizer áreas com maior probabilidade de ocorrência ou ambientalmente adequadas; e (3) a telemetria via satélite (Wilson et al. 2006; Graham et al. 2006; Brunnschweiler et al. 2009; Thums et al. 2013; Hueter et al. 2013; Berumen et al. 2014; Tyminski et al. 2015; Norman et al. 2016), que permite avaliar os deslocamentos verticais e horizontais dos animais marcados, possibilitando inferir, de forma remota, sobre comportamentos de mergulho e preferências termais na coluna d'água e deslocamentos para áreas de importância no ciclo de vida.

No intuito de se utilizar as ferramentas mais adequadas para estudar a ecologia do tubarão-baleia na costa do Brasil, foram selecionados equipamentos e métodos estatísticos mais recentes, de forma a permitir a realização de comparações entre diferentes regiões e análises compatíveis com o estado-da-arte da pesquisa ecológica e oceanográfica. Para tanto, no presente estudo foram aplicadas técnicas de modelagem e análise estatística robustas e atuais (Phillips et al. 2006; Elith et al. 2011; Nielsen e Siebert 2007; Nielsen et al. 2006; Lam et al. 2008, 2010; Galuardi et al. 2010), aliadas à tecnologia de última geração (Nielsen et al. 2009; Stevens et al. 2010; Block et al. 2011), amplamente difundidas mundialmente (Hammerschlag et al. 2011; Yackulic et al. 2014).

No Brasil, informações referentes à ecologia ou biologia do tubarão-baleia são ainda bastante escassas. A grande maioria do que se conhece sobre a espécie na costa brasileira é proveniente de registros de avistagem, encalhes ou capturas incidentais (Soto e Nisa-Castro-Neto 2000; Gadig e Rosa 2008; entre outros). Existem apenas alguns estudos que reportam informações além de registros pontuais de avistagem; desenvolvidos no ASPSP, os autores se embasaram em coletas sistemáticas de censos visuais para descrever as primeiras informações sobre os aspectos da ecologia e biologia do tubarão-baleia no Brasil. Estes estudos são precursores da presente tese e vem sendo objeto de estudo do autor desde a sua graduação (Macena, 2006; Hazin et al. 2008, Macena, 2010).

Atualmente, a maior parte das informações acerca da história de vida do tubarão-baleia no mundo restringe-se principalmente a estudos desenvolvidos no oceano Índico, o qual possui a maior quantidade de informações publicadas, seguido pelo oceano Pacífico e a região de transição Indo-Pacífica, entre essas duas bacias oceânicas (Colman 1997; Rowat e Brooks 2012; Sequeira et al 2013). As informações mais abrangentes sobre os aspectos bioecológicos do tubarão-baleia no oceano Atlântico são provenientes majoritariamente do Golfo do México e Mar do Caribe (Graham et al. 2006; Graham e Roberts 2007; Motta et al. 2010; de la Parra-Venegas et al. 2011; Ramírez-Macías et al. 2012b; Hueter et al. 2013; Tyminski et al. 2015), com pouquíssimas informações disponíveis sobre outras áreas, como no leste da América do Norte, oeste da Europa, Atlântico Central, costa oeste da África e costa leste da América do Sul. Entretanto, apesar de haver informações disponíveis para algumas dessas áreas (Hazin et al. 2008; Capietto et al. 2014; Afonso et al. 2014; Clingham et al. 2016), uma parte razoável da literatura é restrita apenas a registros de avistagem, encalhes ou de interações com a pesca (Soto e Nisa-Castro Neto 2000, Thurnbull e Randell 2007; Gadig e Rosa 2008; Faria et al. 2009; Weir 2010; Andrades et al. 2012; Rodrigues et al. 2012; Barbosa-Filho et al. 2016, entre outros), restando ainda uma grande lacuna a respeito dos aspectos ecológicos (*e.g.* demografia da população; rotas de migração; áreas de reprodução) e biológicos (*e.g.* ciclo reprodutivo; idade e crescimento; fisiologia), não apenas no Oceano Atlântico, mas em todo o mundo.

Embora existam excelentes revisões sobre a ecologia e biologia do tubarão-baleia (Colman 1997; Stevens 2007; Rowat e Brooks 2012), estas não retratam todos os aspectos da história de vida da espécie e, por vezes, são revisões temáticas, norteadas de acordo com a linha de pesquisa dos autores. Uma revisão verdadeiramente compreensiva seria praticamente impossível, além de ir muito além, também, do escopo desta tese. Portanto, a revisão da literatura a seguir se limitará a expor aspectos da história de vida, da distribuição geográfica, dinâmica populacional e movimentação do tubarão-baleia, ou seja, tópicos referentes aos assuntos abordados no presente trabalho.

Revisão da literatura

Classificação taxonômica

O tubarão-baleia, *Rhincodon typus* (Smith 1828), é um elasmobrânquio da ordem Orectolobiformes pertencente à família Rhincodontidae, não possuindo morfo-semelhantes e sendo, portanto, o único representante do gênero *Rhincodon* (Fig 1). Embora a grande maioria dos representantes dessa ordem possuam hábitos bentônicos, o tubarão-baleia possui hábitos pelágicos, ocupando tanto a província nerítica quanto oceânica, além de se alimentar por um mecanismo de filtração (Compagno, 2001). O primeiro exemplar de tubarão-baleia foi descrito no ano de 1828 em *Table Bay*, na África do Sul (Compagno 2001). A espécie é facilmente identificada devido ao seu padrão de manchas e listras ao longo do corpo; quilhas proeminentes nos flancos; cabeça larga e achatada, com focinho truncado; boca terminal à frente dos olhos e nadadeira caudal lunada ou semi-lunada (Figs 1 e 2).

Kingdom	Animalia
Subkingdom	Bilateria
Infrakingdom	Deuterostomia
Phylum	Chordata
Subphylum	Vertebrata
Infraphylum	Gnathostomata
Superclass	Chondrichthyes
Class	Chondrichthyes
Subclass	Elasmobranchii
Superorder	Euselachii
Order	Orectolobiformes
Family	Rhincodontidae
Genus	Rhincodon
Species	*Rhincodon typus*

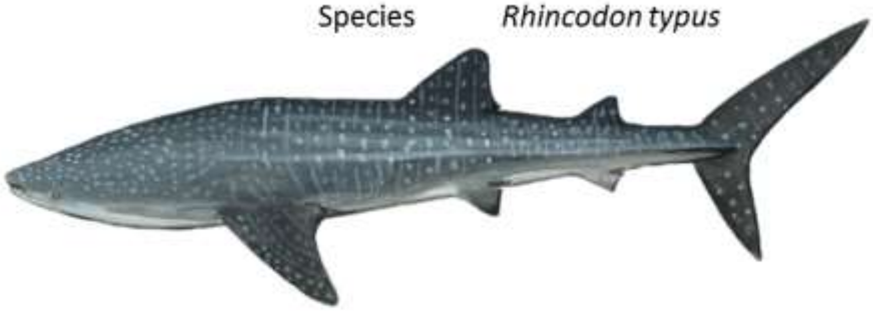

Figura 1- Apresentação do tubarão-baleia. Classificação taxonômica e ilustração do tubarão-baleia, *Rhincodon typus* (Smith 1828). Fonte: *Integrated Taxonomic Information System* (www.itis.gov); Animal Diversity (www.animaldiversity.org).

Histórico

Os primeiros estudos com o tubarão-baleia tiveram início na década de 1900 com trabalhos relatando registros de avistagens, capturas e encalhes (Bean, 1902; Gill, 1902; Smith, 1925; Herre, 1932, 1942, entre outros), embora trabalhos importantes, relacionados com a sua distribuição, comportamento, alimentação e reprodução (Gill, 1905; Bigelow e Schroeder, 1948; Baughman e Springer, 1950; Baughman, 1955; Reid, 1957; Garrick, 1964; entre outros), fundamentais para a compreensão da sua história natural e etologia, tenham sido também reportados nessa época. De particular importância é o trabalho do Dr. Gudger, que publicou 47 artigos sobre a espécie, expondo desde relatos de ocorrência até informações ecológicas e biogeográficas. Porém, grande parte dos seus trabalhos são reiterativos e se reutilizam de suas próprias ideias. Os mais relevantes, entretanto, focam em aspectos biológicos e fisiológicos da espécie, constituindo importantes referências (Gudger 1915, 1931, 1934, 1939, 1941a, 1941b, 1953). Uma extensiva revisão sobre os trabalhos realizados com o tubarão-baleia até 1980 pode ser encontrada em Wolfson e Notarbartolo di Sciara (1981). Desde sua identificação até o ano de 1985, apenas 320 registros de ocorrência de tubarão-baleia haviam sido registrados na literatura científica no mundo inteiro (Wolfson, 1986).

Figura 2- Ilustração do tubarão-baleia. *Rhincodon. typus* jovem fotografado no Arquipélago de São Pedro e São Paulo, Brasil. © Bruno Macena.

Entretanto, nas últimas décadas, os registros de tubarão-baleia tornaram-se muito mais frequentes, com a espécie sendo atualmente estudada nas três bacias oceânicas, principalmente em locais onde é possível se observar tubarões-baleia em agregações sazonais costeiras (Colman, 1997; Stevens 2007; Hammerschlag et al. 2011; Rowat e Brooks 2012). Por essa razão, e concomitantemente com a modernização das ferramentas para coleta de dados e das técnicas de análise, vários avanços nos estudos acerca dos aspectos bioecológicos da espécie se tornaram possíveis, em diversos ramos da ciência, como biotecnologia (Castro et al. 2007; Schmidt et al. 2009; Borrell et al. 2011; Dove et al. 2012; Vingnaud et al. 2014; Marcus et al. 2016), ecologia e biologia (Wintner et al. 2000; Rohner et al. 2011; McKinney et al. 2012; Hueter et al. 2013; Afonso et al. 2014; Hacohen-Domené et al. 2015; Meekan et al. 2015; Hsu et al. 2014a; Araújo et al. 2016; Norman et al. 2016; Norman e Morgan 2016), oceanografia (Wilson et al. 2001; Hsu et al. 2007; Rowat et al. 2007; Sleeman et al. 2010ab; Rohner et al. 2013a; Tyminski et al. 2015), entre outros.

Reprodução e crescimento

Pouco ainda se sabe sobre a reprodução da espécie, como a fisiologia e o ciclo reprodutivo. Embora a espécie fosse considerada ovípara, as únicas informações sobre a reprodução do tubarão-baleia eram provenientes de cápsulas embrionárias capturadas em pescarias (Southwell 1913; Breuer 1954; Baughman 1955; Reid 1957; Garrick 1964). Em meados dos anos 1980, Wolfson (1986) analisou sete neonatos capturados com rede-de-cerco no Golfo da Guiné e sugeriu, baseado na fina espessura das paredes das cápsulas embrionárias (diferente dos típicos tubarões ovíparos) e sub-desenvolvimento dos ganchos de ancoragem, que as cápsulas haviam sido provenientes de aborto e que o modo de reprodução era ovovivíparo. Entretanto, no ano de 1995 uma fêmea de 10,6 m foi capturada em Taiwan, grávida com cerca de 300 embriões em seus úteros (Joung et al. 1996), sendo essa a maior fertilidade já registrada entre os tubarões. Os embriões se apresentavam em três diferentes estágios de desenvolvimento, com comprimentos variando entre 42 e 64 cm, com a presença de saco vitelínico sendo observada apenas nos menores embriões, ainda dentro das cápsulas embrionárias. Já os embriões maiores se encontravam fora das cápsulas, com o vitelo totalmente absorvido (oviparidade retida), encontrando-se aparentemente prontos para o nascimento. Assim, o modo reprodutivo do tubarão-baleia ficou definido como ovíparo lecitotrófico, similar ao tubarão-lixa (*Gynglimostoma cirratum* Bonnaterre, 1788) (Castro 2000), pertencente à mesma ordem.

Embora haja relatos de que o tubarão-baleia possa alcançar até cerca de 20 m comprimento, os registros de espécimes deste tamanho são questionáveis devido aos métodos utilizados para aferição (Colman 1997; Compagno 2001). O comprimento assintótico considerado como válido atualmente situa-se em torno de 14.0 m, enquanto os maiores tubarões observados na natureza possuem uma média de 12.0 m (Colman 1997; Stevens 2007). Informações sobre a maturidade sexual e longevidade do tubarão-baleia ainda são escassas. Estima-se que os tubarões-baleia não atinjam a maturidade sexual até que possuam 30 anos de idade ou mais do que 9.0 m de comprimento (Taylor 1994; Colman 1997). Informações recentes sugerem um tamanho de primeira maturação (L_{50}) para machos, baseada na regressão logística entre o comprimento do clásper e o tamanho do tubarão, em torno de 9.1 m, em Moçambique (Rohner et al. 2015), 8.1 m, na Austrália (Norman e Stevens 2007), e 7.0 m, no Golfo do México (Ramírez-Macías et al. 2012b), sugerindo potenciais diferenças intra-populacionais entre diferentes regiões do mundo, como observado para outras espécies de tubarão (Simpfendorfer 1992; Bonfil *et al.* 1993; Wintner & Cliff 1995; Castro 1996; Lucifora *et al*. 2005). Diferentemente dos machos, não é possível se estimar a maturidade sexual das fêmeas através de características merísticas. Fêmeas dissecadas na África do Sul (Beckley et al. 1997) e Índia (Pai et al. 1983; Satyanarayana Rao 1986), porém, revelaram que fêmeas menores que 9.0 m estavam todas imaturas, enquanto que a menor fêmea madura observada em Formosa tinha 9.6 m (Hsu et al. 2014a). Diferenças geográficas no tamanho de maturação de outras espécies de tubarão já foram observadas (Simpfendorfer 1992; Castro 1996; Bonfil 2008) e pode ser o caso para os tubarões-baleia também, conforme as informações apresentadas.

Alimentação

O tubarão-baleia é uma das três espécies de tubarão filtradoras, juntamente com o tubarão-peregrino (*Cetorhinus maximus* Gunnerus, 1765) e o tubarão-megaboca (*Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983). Entre essas espécies, é o único que não necessita estar em constante movimento para realizar a filtração, uma vez que possui um versátil mecanismo de sucção o qual permite sugar a água para sua boca com uma velocidade maior do que a alcançada pelos outros tubarões filtradores, possibilitando, desta forma, um maior volume de captura em agregações de presas nectônicas e zooplanctônicas (Taylor et al., 1983; Motta et al. 2010). São conhecidas pelo menos três estratégias de alimentação apresentadas pela espécie, as quais são específicas para cada tipo de presa, nomeadamente: ativa (Fig 3), passiva e vertical (descrições em Taylor 2007; Nelson e Eckert 2007; Motta et al. 2010). Alimenta-se principalmente de ovos e larvas de peixes e invertebrados, pequenos crustáceos, como copédodos e eufasiáceos, pequenos peixes e lulas (Colman 1997, Rowat e Brooks 2012).

Figura 3- Comportamento de alimentação do tubarão-baleia. *Rhincodon typus*, exibindo comportamento ativo de alimentação na superfície nas imediações do Arquipélago de São Pedro e São Paulo, Brasil. © Bruno Macena.

Distribuição mundial e no Brasil

O tubarão-baleia apresenta distribuição circumglobal, podendo ser encontrado em regiões costeiras e oceânicas de águas tropicais e subtropicais nos oceanos Pacífico, Índico e Atlântico, entre as latitudes 35°N e 35°S (Fig 4; Compagno 2001). Possui comportamento altamente migratório, sendo capaz de atravessar longas distâncias e cruzar bacias oceânicas inteiras, razão pela qual o estudo de sua ecologia e biologia torna-se particularmente difícil e logisticamente complexo.Entretanto, a maior parte dos locais de agregação de tubarões-baleia se localizam próximos à costa, sendo frequentados predominantemente por indivíduos jovens, com predominância de machos (Rowat e Brooks 2012). Apesar de ser possível se observar espécime adulto nessas agregações ainda existe uma grande lacuna sobre onde os tubarões-baleia adultos se distribuem mundialmente. Estudos parecem confirmar, no entanto, que habitats oceânicos insulares são importantes para os indivíduos adultos, particularmente para o ciclo reprodutivo, pois fêmeas com abdômen anormalmente dilatado foram observadas em grande parte dos ambientes insulares como nas Ilhas Galápagos (Acuña-Marrero et al. 2014), Baixa Califórnia (Ramírez-Macías et al. 2012a), Ilha Santa Helena (Clingham et al. 2016) e ASPSP (presente estudo); além de registros de possíveis comportamentos de cortejo (presente estudo) e cópula (Clingham et al. 2016).

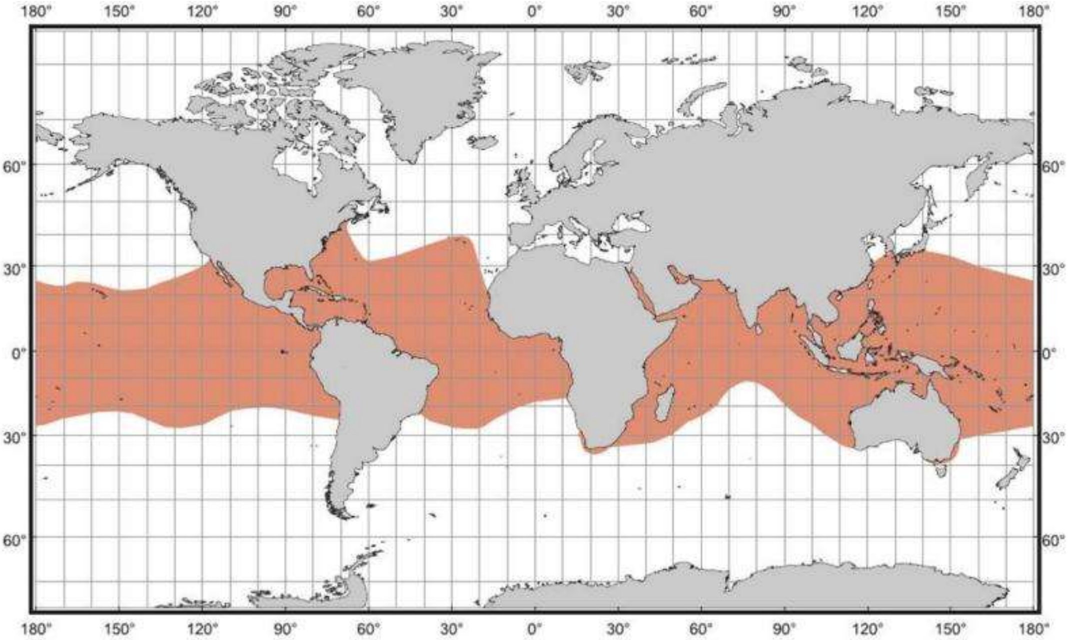

Figura 4- Distribuição global do tubarão-baleia. Distribuição geográfica mundial do *Rhincodon typus*. A faixa vermelha representa a área virtual de ocorrência. Fonte: Compagno, 2001.

No Brasil, o tubarão-baleia também é conhecido como pelos pescadores por pintadinho ou cação-estrela. e embora os registros de tubarão-baleia sejam raros, as avistagens da espécie em áreas oceânicas têm se tornado cada vez mais frequentes nas proximidades de plataformas de petróleo e próximo à costa. Presente em toda região costeira e oceânica do Brasil (Soto e Nisa-Castro-Neto 2000), o tubarão-baleia apresenta registros de ocorrência nas regiões sudeste, sul, nordeste e em ilhas oceânicas, incluindo o Atol das Rocas (Campos et al 2005), e os Arquipélagos de Trindade e Martim Vaz (Pinheiro et al 2009), Fernando de Noronha, Abrolhos (Soto e Nisa-Castro-Neto 2000) e ASPSP, sendo este último o único local do território brasileiro com previsibilidade de ocorrência da espécie (Hazin et al. 2008).

Modelos de distribuição de espécies

A correta identificação da distribuição espacial de uma espécie é de grande interesse para disciplinas como ecologia e biologia da conservação, sendo importante para o manejo, planejamento, previsões de cenários futuros (Ferrier 2002; Liu et al. 2013), e para compreender os fatores ecológicos e evolucionários que determinam os padrões espaciais da biodiversidade (Graham et al. 2006; Escalante et al. 2013). Modelos de distribuição de espécies (SDM, acrônimo em inglês) inferem sobre a relação das variáveis ambientais com

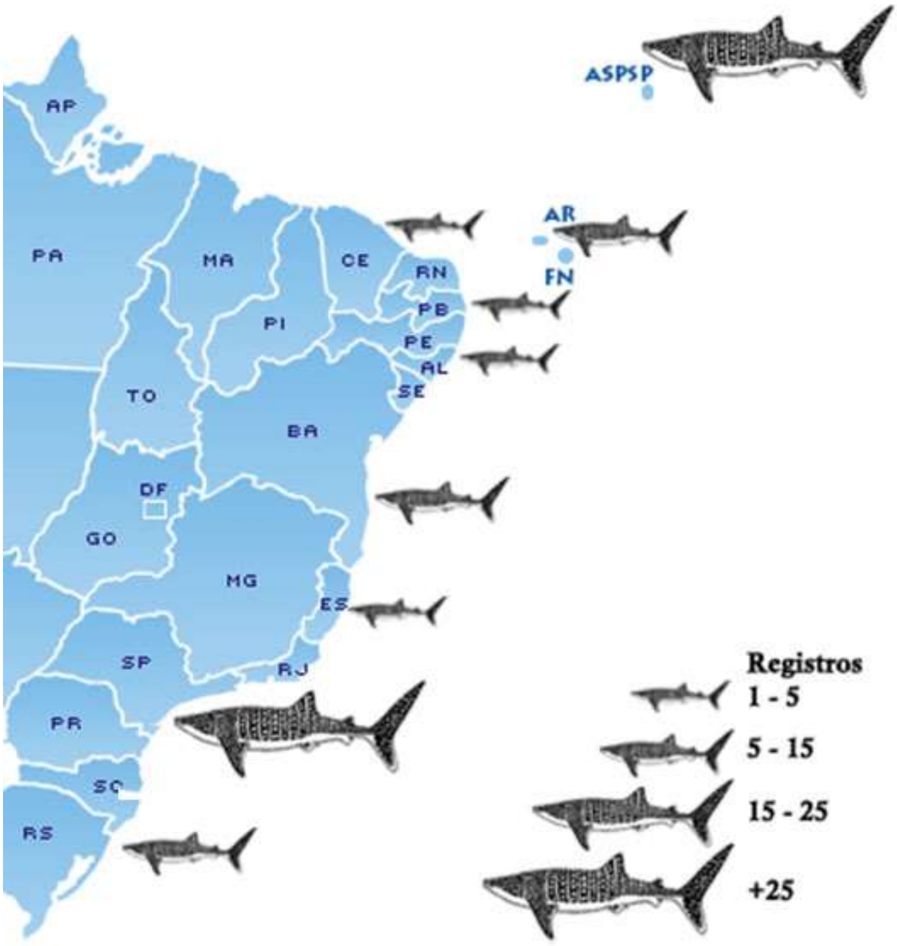

Figura 5- Distribuição do tubarão-baleia em águas brasileiras. Distribuição geográfica dos registros do *Rhincodon typus*, ao longo da costa brasileira. AR- Atol das Rocas; FN- Fernando de Noronha; ASPSP- Arquipélago de São Pedro e São Paulo. Fonte: Macena, 2010.

os registros de presenças ou abundância para estimar a probabilidade de ocorrência (ou áreas de maior adequabilidade) de uma dada espécie, assistindo na predição da potencial extensão de sua distribuição (Guisan e Thuiller 2005; Franklin 2009; Elith e Leathwick 2009). Em outras palavras, é uma avaliação dos nichos ecológicos essenciais no espaço ambiental (*i.e.* resposta da espécie às covariáveis), além de consistir em uma predição da probabilidade da distribuição espacial de uma espécie para áreas não amostradas (Guisan e Zimmermann 2000). É o *likelihood* de um envelope ambiental adequado para uma ou mais espécies, dependendo do método selecionado (Elith e Leathwick 2009; Elith et al. 2011). Os métodos SDM são aplicados em uma ampla gama de áreas de conhecimento como a biologia, ecologia, biogeografia (Peterson 2007; Elith e Leathwick 2009), e também para o planejamento de ações para conservação (Ferrier 2002; Araujo et al. 2004; Bomhard et al. 2005; Pawar et al. 2007; Liu et al. 2013).

Uma ampla variedade de métodos de SDMs estão disponíveis na literatura, como as técnicas de regressão logística [modelos lineares generalizados (GLM; McCullagh e Nelder 1989), modelos aditivos generalizados (GAM; Hastie e Tibshirani 1990), splines (suavização) de regressão multivariada adaptativa (MARS, Friedman 1991a)]; técnicas de perfilamento [fator de análise de nicho ecológico (ENFA; Hirzel et al. 2002), sistema de análise bioclimática e predição (BIOCLIM; Busby 1991), algoritmo domain (DOMAIN; Carpenter et al. 1993)]; e as técnicas de aprendizado de máquina [árvores de regressão impulsionadas (BRT; Friedman 2001b); algoritmo genético para a produção de conjunto de regras (GARP; Stockwell e Peters 1999), florestas aleatórias (RF; Breiman 2001), máxima entropia (MaxEnt; Phillips et al. 2006)], entre outros (Segurado e Araujo 2004; Elith et al. 2006; Thuiller er al 2009).

A natureza dos dados (*i.e.* registros oportunísticos, coleções de museus, dados de amostragens sistematizadas, etc.) é um fator essencial para se levar em consideração na seleção do modelo adequado. Os métodos de perfilamento consideram apenas dados de ‘presença’ de uma espécie, enquanto as regressões e as técnicas de aprendizado de máquina usam dados de ambos ‘presença’ e ‘ausência’ ou ‘pseudo-ausência/*background’*. Por conseguinte, as técnicas de SDM “diferem quanto ao tipo de dado requerido, à complexidade e natureza das funções de estimativa, e a performance preditiva” (Franklin 2009). Ademais, a escolha do método de modelagem e sua acurácia também dependem da qualidade e quantidade dos dados (Guisan e Zimmerman 2000; Stockwell e Peterson 2002; Elith e Leathwick 2009).

Apenas em anos recentes os SDMs começaram a ser utilizados para inferir sobre a influência de variáveis ambientais na ocorrência de tubarões-baleia. Estes estudos revelaram a influência de variáveis ambientais particulares na distribuição espacial em diversos locais do mundo. No entanto, a maior parte destes estudos foi conduzida no oceano Índico (Austrália, Sleeman et al. 2010ab; bacia oceânica inteira, Sequeira et al. 2011,2013; Moçambique, Rohner et al. 2013a), e no Golfo do México e Mar do Caribe (Mckinney et al. 2012; Cardenas-Palomo et al. 2014; Hacohen-Domené et al. 2015). Apenas um único estudo utilizando SDMs foi realizado estritamente para algum local no oceano Atlântico (Açores, Afonso et al. 2014), os outros dois estudos que compreendem esta bacia oceânica modelaram a distribuição de habitat adequados do tubarão-baleia em escala mundial (Sequeira et al.

2014ab). Dados específicos do oceano Atlântico Equatorial e Sudoeste, no entanto, nunca foram avaliados até o momento.

Dinâmica populacional

Estudos pretéritos sobre a ecologia e biologia do tubarão-baleia têm sugerido uma relação entre sua movimentação e fatores ambientais, como temperatura da superfície do mar, concentração de clorofila *a*, relevo submarino e correntes oceânicas (Taylor e Pearce 1999; Eckert e Stewart 2001; Rowat e Gore 2007; Hsu et al. 2007; Sleeman et al. 2010a; Kumari e Raman 2010; Sequeira et al. 2011, 2013; Rohner et al. 2013a; Afonso et al. 2014). Usualmente, ambientes que oferecem um ótimo cenário para a ocorrência de tubarões-baleia propiciam condições adequadas para as produtividades primária e secundária, sendo o forrageamento o principal propósito das agregações mundialmente conhecidas até hoje (Heyman et al. 2001; Meekan et al. 2006; Nelson e Eckert 2007; Rowat e Brooks 2012). Locais onde ocorrem agregações previsíveis sazonais de tubarões-baleia oferecem uma excelente oportunidade para estudar a espécie em uma base regular. Informações coletadas a partir destes fenômenos tem sido de grande valia para avaliar vários aspectos da história de vida da espécie, como sazonalidade de ocorrência, aspectos da dinâmica e estrutura populacional em locais como Austrália (Meekan et al. 2006, Holmberg et al. 2008), Golfo do México (de la Parra Venegas et al. 2011), Golfo da Califórnia (Ketchum et al. 2013), Belize (Graham e Roberts 2007), Seicheles (Rowat et al. 2009) e Maldivas (Riley et al, 2010), entre outros locais (revisão em Rowat e Brooks 2012).

Estudos sobre a dinâmica populacional do tubarão-baleia estimaram o número de indivíduos em algumas das principais agregações. No oeste da Austrália (Meekan et al. 2006), modelos de população aberta (Jolly-Seber) estimaram uma super-população em Nigaloo Reef entre 319 e 436 indivíduos. Em Seicheles, os mesmos modelos estimaram que entre 469 e 557 individuos (Brooks et al. 2010) fazem uso da ilha. Já no México, a estimativa de população aberta foi de 521 a 809 indivíduos no Golfo do México (Holbox) (Ramirez-Macías et al. 2012b) e entre 19 e 64 indivíduos do Golfo da Califórnia (Ramirez-Macías et al. 2012a). Portanto, percebe-se que as algumas dessas agregações são compostas por um relativamente baixo número de indivíduos e medidas de conservação são fundamentais para a manutenção da espécie no ecossistema.

As agregações conhecidas até hoje geralmente apresentam segregações ontogenética e sexual, com predominância de indivíduos machos imaturos em agregações alimentares costeiras (Rowat e Brooks 2012). Adultos, entretanto, são raramente observados, com a maioria das avistagens tendo sido registradas em habitats oceânicos, como nas ilhas Galápagos (Acuña-Marrero et al. 2014), na Baixa Califórnia Sul (Ketchum et al. 2013, Ramirez Macias et al. 2012a), nos Açores (Afonso et al. 2014), na Ilha de Santa Helena (Clingham et al. 2016) e no ASPSP (Hazin et al. 2008). No entanto, informações mais precisas sobre a distribuição dos tubarões-baleia adultos, e das localizações das áreas de cópula e berçário, caso realmente tais áreas sejam bem definidas como em outras espécies de tubarão, continuam escassas apesar de serem cruciais para se garantir a conservação da espécie.

Telemetria via satélite

O uso de tecnologia baseada em satélites para monitoramento de animais marinhos em ambientes naturais iniciou-se na década de 1990, sendo bastante difundido nos últimos anos (Block et al 1998; Goodley et al. 2008; Sims 2010; Hammerschlag et al. 2011), e tem sido de grande importância para preencher a lacuna sobre o conhecimento de padrões de distribuição (Southall et al. 2005), uso (Afonso e Hazin 2015) e seleção (Curtis et al. 2014) de habitat, estrutura populacional espacial (Block et al. 2005), padrões de movimentação (Hazin et al. 2013) e muitos outros campos relacionados, como fisiologia (Thums et al. 2013), estratégias de forrageamento (Motta et al. 2010), comportamento de natação (Meekan et al. 2015) e até biologia da conservação (Queiroz et al. 2016). Dadas as vantagens de se utilizar técnicas de telemetria via satélite (*e.g.* monitoramento remoto, dados ambientais sinóticos), estas ferramentas têm sido aplicadas com sucesso para o rastreamento de tubarões-baleia nas três maiores bacias oceânicas (Hammerschlag et al. 2011) como, por exemplo, na Austrália (Wilson et al. 2001), Golfo do México (Hueter et al. 2013), Ilha Galápagos (Hearn et al. 2013), entre outros locais (revisão em Rowat e Brooks 2012).

Os primeiros experimentos de rastreamento via satélite com tubarão-baleia foram conduzidos no final da década de 1990 no Golfo da Califórnia, onde 17 animais monitorados apresentaram diferentes direções em suas movimentações, com um dos indivíduos tendo se deslocado cerca de 13.000 km, em 37 meses, em direção ao oeste do oceano Pacífico (Eckert e Stewart 2001); e no sudeste da Ásia, onde dois dos seis tubarões-baleia rastreados viajaram cerca de 4.500 e 8.000 km (Eckert et al. 2002). A partir da segunda metade dos anos 2000, os estudos com telemetria via satélite se expandiram e uma grande quantidade de informações sobre os movimentos horizontais e verticais dos tubarões-baleia passaram a ser gerados em diferentes partes do mundo (Graham et al. 2006; Wilson et al. 2006; Brunnschweiler et al. 2009; Berumen et al. 2014; entre outros), incluindo detalhes acerca da fisiologia (Thums et al. 2013) e comportamento dos mergulhos (Tyminski et al. 2015) e comportamentos de natação (Meekan et al. 2015). Os dados provenientes da marcação via satélite podem ainda ser utilizados em associação com métodos científicos alternativos para elucidar diferentes aspectos da história de vida da espécie, como a avaliação da ecologia do forrageamento (Motta et al. 2010) ou da relação com os fatores ambientais inferidas usando técnicas de modelagem ecológica (Sleeman et al. 2010b).

Entretanto, apesar de já haver relativamente uma boa quantidade de informação sobre rastreamento via satélite do tubarão-baleia no mundo, dados acerca do oceano Atlântico ainda são escassos e restritos à região que engloba o Golfo do México e o Mar do Caribe (Graham et al. 2006; Gifford et al. 2007; Hueter et al. 2013; Tyminski et al. 2015), enfatizando a necessidade de mais esforços de rastreamento nesta bacia oceânica. Recentemente, um tubarão-baleia fêmea, com 8 m e suspeita de gravidez, foi rastreado a partir do Golfo do México, tendo viajado mais de 7.000 km em 150 dias, com o transmissor tendo se desprendido a sudeste do ASPSP (Hueter et al. 2013). Informações como esta destacam a importância de se elucidar os padrões de movimentação dos tubarões-baleia em habitats oceânicos, onde a maior parte dos espécimes maduros é encontrada. Ademais, as informações sobre os rastreamentos da espécie disponíveis na literatura são geralmente provenientes de agregações alimentares costeiras, o que enfatiza ainda mais a relevância de se conduzir o monitoramento via satélite em ecossistemas oceânicos.

Hipóteses

Tendo em vista contribuir para o conhecimento disponível sobre a história de vida do tubarão-baleia nas regiões equatorial e sudoeste do oceano Atlântico, este estudo baseou-se nas seguintes hipóteses:

(1) A distribuição das áreas adequadas para a ocorrência do tubarão-baleia na costa brasileira apresenta diferenças latitudinais (biogeográficas/bioclimáticas), sendo a sua presença governada por fatores oceanográficos físicos químicos e biológicos;

(2) Áreas oceânicas, como ilhas e montes submarinos, são ecossistemas importantes para o ciclo de vida dos tubarões-baleia, principalmente da parcela adulta da subpopulação. No ASPSP, os tubarões-baleia estão apenas de passagem, com uma baixa abundância e maior proporção de indivíduos maduros, que usam suas imediações principalmente durante o primeiro semestre do ano, e;

(3) Ao deixarem o ASPSP, os tubarões-baleia migram em direção oeste, seguindo o fluxo da corrente Sul Equatorial..

Objetivos

Gerais

O presente estudo teve como objetivo geral descrever a distribuição espacial da ocorrência do tubarão-baleia no Oceano Atlântico Sudoeste; avaliar os aspectos da estrutura da população e os deslocamentos do tubarão-baleia a partir do ASPSP; e discutir as implicações dos resultados obtidos para a conservação da espécie no oceano Atlântico.

Específicos

Especificamente para alcançar os objetivos propostos, pretende-se:

(i) Mapear os 'habitats adequados' para a ocorrência do tubarão-baleia no Oceano Atlântico Sudoeste e inferir sobre as variáveis ambientais que influenciam na sua distribuição, com auxílio de técnicas de SDM;

(ii) Identificar e descrever a sazonalidade, estrutura populacional, abundância, uso do habitat no ASPSP, e;

(iii) Avaliar os deslocamentos horizontais (migração) e verticais (comportamentos de mergulho) a partir de um ambiente insular oceânico, o ASPSP.

Capítulo 1- Spatial distribution of suitable habitats for whale sharks in the Equatorial and Southwestern Atlantic Ocean

Abstract

The modelling of a species distribution can be done by inferring the relationship between the environmental variables and its occurrences, a knowledge crucial for a better understanding of spatial patterns of biodiversity geographical range and for conservation planning. In the present work, data on whale shark presence were collected from 1983 to 2016, through scientific literature, local news, social media and from fishermen, divers and researchers from Brazil. We used the presence-only modeling approach of maximum entropy (MaxEnt) to predict the most suitable habitats for whale shark (*Rhincodon typus*) occurrences in the Southwestern Atlantic Ocean (SAO), testing six predictors: sea surface temperature: *sst*; chorophyll *a* concentration: *chl*; primary productivity: *pp*; diffuse coefficient of attenuation: *k490*; bottom depth: *bathy*; and the degree of bathymetric slope: *slope*. All these factors are ecologically relevant and are considered as indicatives of biological productivity. The discriminative power of the models was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC). We also assessed the best threshold for data distribution by comparing the ten different methods provided by MaxEnt software. The best performed threshold had maximum test sensitivity, plus specificity, and presented a good AUC score (0.903). The selected model used only four predictors, with the most influential one being *pp* (56.9%), followed by *chl* (38.5%), *slope* (4.2%) and *sst* (0.4%). The response curves of the relationship between environmental variables and occurrences indicate adequate habitats when *sst* is around 26.3°C, mean *chl* is 0.9 $mg.m^{-3}$, the *slope* has a high declivity (75.7°) and *pp* is 1,679 $mg.C.m^{-2}.day^{-1}$. The habitat suitability index (HSI) map indicated several areas, distributed along almost the entire Brazilian shoreline, with adequate sites identified in the northernmost part of Brazil, south of northeast region and in oceanic domain, near the archipelago of São Pedro and São Paulo; and the most suitable habitats found in almost all the extension of the Southeast/South (SE/S) regions. It is likely that localized oceanographic phenomena of water enrichment and consequent enhancement of biological productivity have driven whale sharks to specific areas along the Brazilian coast, with the SE/S being identified as the most suitable for the whale sharks in the SAO. Despite the distribution of suitable habitats encompassed an extensive part of Brazilian shoreline, and also few scattered oceanic areas, no whale shark aggregation was ever recorded or even anedoctally reported. This was the first study to assess the spatial distribution of the whale shark's ecological niches and to infer the environmental predictors influencing their occurrence in SAO. We conclude commenting the implication of the results for the species conservation and recommending measures to increase the knowledge of whale shark distribution in Brazil.

Key-words: species distribution models; presence-only; MaxEnt; remote sensing; feeding habitats; Brazil; Southwestern Atlantic Ocean.

Introduction

A clear identification of the spatial distribution of a given species is an issue of great concern in ecology and conservation biology, being important for management planning, forecasting (Ferrier 2002; Liu et al. 2013), and to understand ecological and evolutionary factors determining spatial patterns of biodiversity (Graham et al. 2006; Escalante et al. 2013). Species distribution models (SDMs) infer the relationship of environmental variables with species presence records or abundance to estimate the probability of occurrence (or the most suitable areas) for a given species, assisting in the prediction of its potential geographic range (Guisan and Thuiller 2005; Franklin 2009; Elith and Leathwick 2009). In other words, it is an assessment of essential ecological niches in the environmental space (*i.e.* responses of the species to the covariates), as well as a prediction of the spatial distribution of probability of the presence of a given species for areas not surveyed (Guisan and Zimmermann 2000). It is the likelihood of an environmental envelope suitable for one or more species (Elith and Leathwick 2009; Elith et al. 2011), depending on the method chosen. SDM models were applied in wide range of areas such as biology, ecology, biogeography (Peterson 2007; Elith and Leathwick 2009) and for conservation planning (Ferrier 2002; Araujo et al. 2004; Bomhard et al. 2005; Pawar et al. 2007; Liu et al. 2013).

An ample variety of SDM methods are available from the literature, such as regression-based techniques [generalized linear models (GLM; McCullagh and Nelder 1989), generalized additive models (GAM; Hastie and Tibshirani 1990), multivariate adaptive regression splines (MARS, Friedman 1991a)]; profile techniques [ecological niche factor analysis (ENFA; Hirzel et al. 2002), bioclimate analysis and prediction system (BIOCLIM; Busby 1991), domain algorithm (DOMAIN; Carpenter et al. 1993)]; and the machine learning techniques [boosted regression trees (BRT; Friedman 2001b); genetic algorithm for rule set production (GARP; Stockwell and Peters 1999), random forests (RF; Breiman 2001), maximum entropy (MaxEnt; Phillips et al. 2006)], among others (Segurado and Araujo 2004; Elith et al. 2006; Thuiller er al 2009).

The nature of the data (*i.e.* opportunistic records, museum collections, systematic survey data, etc.) is a key issue to be taken into account when selecting the right model. The profile methods only consider ‘presence’ data, while regression and machine learning use both ‘presence’ and ‘absence’ or ‘background’ data. Therefore, SDM techniques “differ in the types of data required, complexity and nature of the estimate functions, and predictive performance” (Franklin 2009). Moreover, the choice of the modeling method and its accuracy also depend on the data quality and quantity (Guisan and Zimmerman 2000; Stockwell and Peterson 2002; Elith and Leathwick 2009).

Presence-absence data have the advantage of bringing valuable information about surveyed locations and prevalence, which allows the analysis of biases (Phillips et al. 2009). There are, however, concerns regarding species' detectability, such as the reliability of the absence if the detection of a presence record fails (*i.e.* false negative), not ensuring that the species is absent from that area/location, thus not distinguishing unsuitable from an unoccupied habitat (MacKenzie et al. 2002, 2005; Jimenez-Valverde et al. 2008). Besides, low or negative rates of species-environment relationship do not necessarily indicate areas where species is not present, but may hide imprints of biotic interactions, rates of dispersal, disturbances (*e.g.* invasions, climate change) or inaccessibility that might induce a species absence from otherwise optimal habitats (Araújo and Williams 2000; Jimenez-Valverde et al. 2008).

Presence-absence and presence-only techniques differ in the types of projections used for forecasting/novel environments; with the former type generally performing better than those using only the occurrences (Elith et al. 2006), which tend to predict greater losses of suitable habitat (Pearson et al. 2006). The regression methods are considered the most accurate to predict the optimal habitats with high probability of occurrence, and the sub-optimal habitats with lower occurrence probabilities (Hirzel et al. 2001; Brotons et al. 2004). Conversely, presence-only methods may occasionally perform equally or even better than logistic regressions in some cases, as, for example, the MaxEnt (Elith and Graham 2009; Gaston and Garcia-Viñas 2009).

The whale shark, *Rhincodon typus* (Smith 1828), is distributed in coastal and oceanic waters through tropical and warm-temperate seas around the globe (Compagno 2001). The occurrences in the Atlantic Ocean are reported from the Gulf of Mexico (GoM) and the Caribbean Sea (de la Parra-Venegas et al. 2011; Hueter et al. 2013); east and northeast USA (Compagno 2001); Archipelago of São Pedro and São Paulo (ASPSP; Hazin et al. 2008; Macena and Hazin 2016); Azores (Afonso et al. 2014); Madeira (Wirtz et al. 2007); Portugal (Rodrigues et al. 2012); Gulf of Guinea (Sequeira et al. 2014a; Capietto et al. 2014); Santa Helena Is. (Clingham et al. 2016) and Brazil (Soto and Nisa-Castro-Neto 2000). The occurrences encompass all boundaries of this ocean basin and vary from opportunistic punctual records to large coastal aggregations. Despite its wide distribution, *R. typus* is not abundant and population decline was detected since the species is very susceptible to impacts such as overfishing due their intrinsic characteristics of a *k*-selected species; hence the species is listed as “endangered” by the International Union for the Conservation of Nature (IUCN; Pierce and Norman 2016) and as “vulnerable” by the Brazilian Ministry of Environment (MMA 2004).

The whale shark is a versatile filter-feeder (Taylor 2007) which feeds on a wide variety of planktonic and nektonic organisms, such as small fishes and crustaceans, and squids (Colman 1997; Compagno 2001; Rowat and Brooks 2012). Locals where aggregations occur seasonally are food-enriched during particular periods of the year, promoting aggregation of foraging whale sharks. The main phenomena inducing these food-driven seasonal migrations are the enhancement of biological productivity, such as upwelling (Taylor and Pearce 1999; Wilson et al. 2001; Nelson and Eckert 2007; de la Parra-Venegas 2011; Hacohen-Domené et al. 2015) and the spawning of fishes or invertebrates (Taylor 1996; Colman, 1997; Heyman et al. 2001; Robinson et al. 2013). Oceanographic and atmospheric factors also influence the species occurrence and abundance (Cardenas-Palomo et al. 2010; Kumari and Raman 2010, Sleeman et al. 2010ab; Sequeira et al. 2011,2013; Mckinney et al. 2012; Rohner et al. 2013a; Afonso et al. 2014; Hacohen-Domené et al. 2015).

Only in recent years, SDMs started to be used to infer the influence of environmental variables on whale shark’s occurrence. Besides, most of the studies so far have been conducted in the Indian Ocean (Sleeman et al. 2010ab; Sequeira et al. 2011,2013; Rohner et al. 2013a), and GoM/ Caribbean Sea (Mckinney et al. 2012; Cardenas-Palomo et al. 2014; Hacohen-Domené et al. 2015). Only one SDM study was done in the Atlantic Ocean (Afonso et al. 2014), while the remaining two (Sequeira et al. 2014ab) modeled the worldwide distribution and forecasting. The equatorial and southwestern Atlantic Ocean (SAO), however, have not been assessed to date.

The lack of information on this region encouraged the assessment of whale shark's habitat suitability in SAO. For that purpose, records of whale shark occurrences in Brazilian waters in relation to selected environmental variables were analyzed, aiming to describe the areas with optimal conditions for whale shark occurrence in the SAO region and the covariates that may influence their occurrence. Our hypothesis postulates that there is latitudinal difference in the dissemination of whale shark suitable habitats in the two main biogeographic/bioclimatological regions off Brazilian coast, and that specific physical, chemical and biological oceanographic features govern their occurrences.

Material and Methods

Study area

The study area comprehended the coast of Brazil and the offshore region (Fig 1.1). The Brazilian coast has 7,367 km of latitudinal extension and an area of 3,539,919.22 km^2 of Economic Exclusive Zone (ZEE) (IBGE, 2016). Moreover, the extension of the shoreline represents a significant portion of SAO coastal zone and also covers the southern range of the whale shark distribution (Compagno 2001).

The South Atlantic Ocean current system directly influences the physical-chemical processes on Brazilian coastal waters. The South Equatorial Current (SEC) is a broad westward flowing current with boundaries on 4°N and 15-25°S, depending on the time of the year. The SEC flows towards the Brazilian shelf, splitting near 14°S with one branch heading northward, called the North Brazil Current (NBC), and the other one heading southward, called the Brazil Current (BC) (Rodrigues et al. 2007). The latitude of the bifurcation could be indicative of the amount of temperate waters carried to the Tropics and that recirculate into subtropical gyre. This variation also influences the amplitude of both branches, the NBC and BC, hence the magnitude of the interactions with the shoreline topography and of the confluence with the Malvinas current (Rodrigues et al. 2007).

Although Brazil has a tropical climate in the majority of its territory, it varies considerably from the tropical northernmost part to warm temperate below 20°S. The seasonal variation near the equator is little and the seasons are generally divided into wet (March to August) and dry (September to April). Nevertheless, the typical division of four seasons is more noticeable in the temperate zones (15% of the territory), down south. The littoral possesses a considerable number of distinct coastal environments (*e.g.* sandy and muddy beaches, rocky shore and restingas/sandbanks, coastal lagoons and estuaries, mangroves and coral reefs) and geographical features (*e.g.* reefs, bays and islands) sheltering great biodiversity and constituting a mosaic of diverse ecosystems (MMA 2002). Some of the Brazilian islands are located in oceanic environment, namely: the archipelagos of Fernando de Noronha, ASPSP, Abrolhos, Trindade and Martim Vaz, and the Rocas Atoll; all with records of whale shark occurrences (Soto et al. 2000; Campos et al. 2005; Hazin et al. 2008; Pinheiro et al. 2009). Detailed description of the Brazilian shelves and other features can be found on Miloslavic et al. (2011, p16)

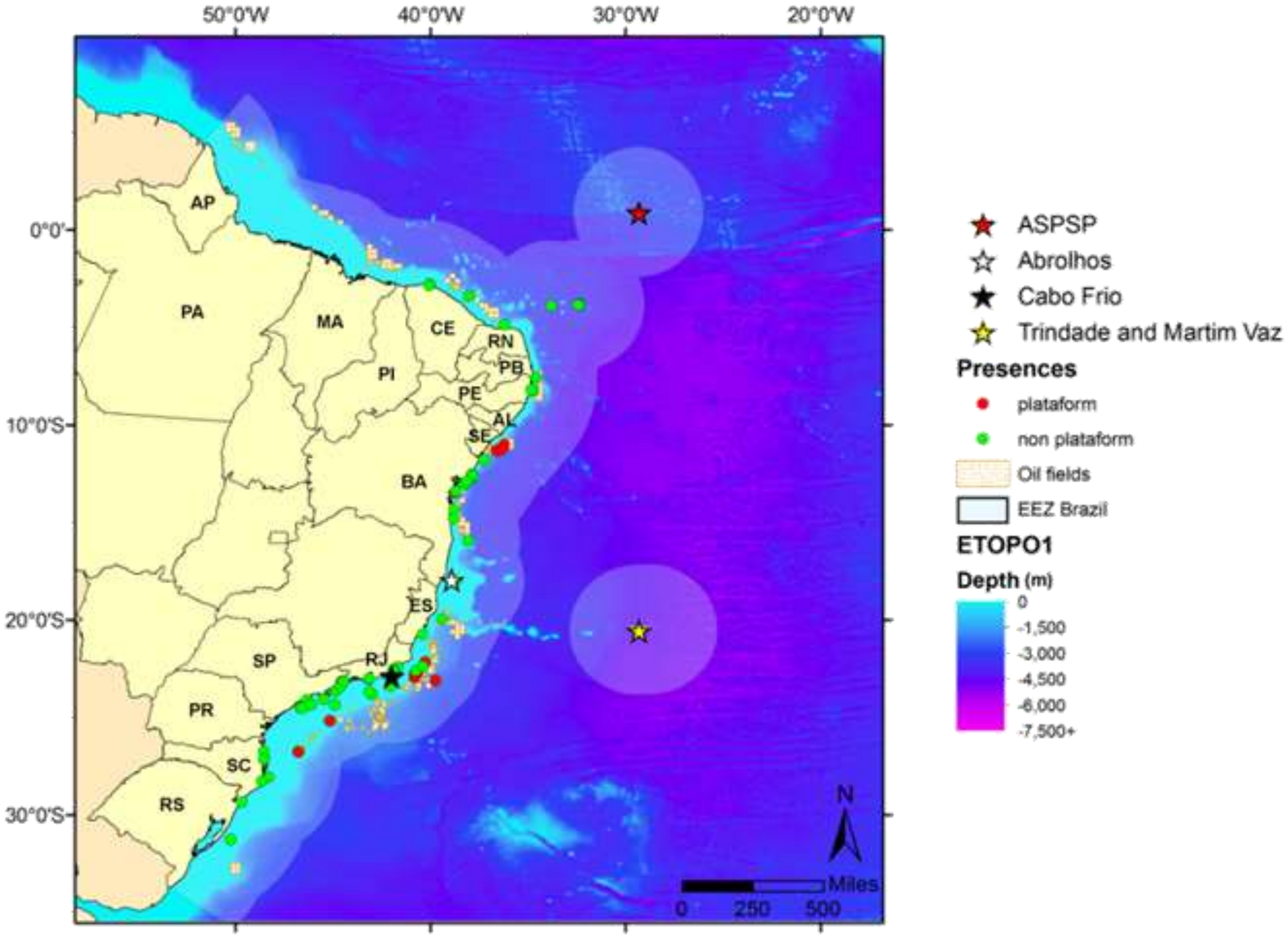

Figure 1.1- Study area. Bathymetric map of Brazil and offshore area and location of *R. typus* presences compiled (green circles), including platform records (red circles). ASPSP- Archipelago of São Pedro and São Paulo.

Data collection

Whale shark records in Brazilian waters were compiled from 1983 to 2016 through extensive searching of scientific literature, local news and social media. Information was also collected opportunely through interviews with fishermen, divers and researchers from Brazil and through the creation of a Brazilian Program for Whale Shark Sightings (facebook.com/tubaraobaleia), a social media-based web page created in 2011 aiming at gathering records of the species and helping to promote public awareness on the conservation of elasmobranchs in Brazil. The records collected, if not from literature, were always confirmed through direct contact with the observer and analysis of images (photographs or videos). Records with sighting location restricted to a place name (*e.g.* some city or beach) or from stranding were estimated to ten nautical miles away from the shoreline towards east (90°). Occurrence data from the ASPSP were excluded from the analysis to avoid bias in the models since the sightings were based on rigorous surveys and the region is already described as an important oceanic habitat for the species (Hazin et al. 2008; Macena and Hazin, 2016). The whale shark sightings dates and locations (longitude and latitude) were pooled into 0.1° grid cells, and counted according to the Brazilian geopolitical/biogeographical divisions of North/Northeast (N/NE) and South/Southeast (S/SE) regions (Fig. 1.1).

Environmental data

Six independent predictors were considered to describe the suitable habitats for whale sharks in the equatorial and southwest Atlantic Ocean based on previous ecological modeling studies (Sequeira et al. 2011, 2014a; McKinney et al. 2012; Rohner et al. 2013a; Afonso et al. 2014; Hacohen-Domené et al. 2015). Sea surface temperature (s*st*) is a variable well-known to influence the distribution of whale shark (Sleeman et al. 2007; Sequeira et al. 2011, Mckinney et al. 2012; Rohner et al. 2013a; Afonso et al. 2014). Chlorophyll *a* concentration (*chl*) is also widely used as a proxy for food availability (Kumari and Raman, 2010; Mckinney et al. 2012; Afonso et al. 2014, Hacohen-Domené et al. 2015). Downwelling diffuse attenuation coefficient at 490 nm (*k490*) (Hacohen-Domené et al. 2015) is a measure of water clarity calculated from the vertical profiles of irradiance in the water column, derived from the extent of irradiance on the surface; higher values designate lower clarity of water. Net primary productivity of Carbon (*pp*) (Hacohen-Domené et al. 2015) is a biomass measure which uses the amount of organic carbon generated by photosynthesis in planktonic organisms minus the amount of organic carbon used by these organisms in respiration, indicating thus areas with potentially high biological productivity. Bathymetric slope (*slope*) (Mckinney et al. 2012) represents the degree of topographic inclination of the seafloor and it is used to specify the location of a seamount and the continent; higher values suggest steeper seamounts or continental slopes. Bathymetry (*bathy*) (Sleeman et al. 2007; Sequeira et al. 2011; Afonso et al. 2014) indicates the bottom depth in which the presences were recorded.

The *sst*, *chl*, *pp* and *k490* were collated into a time-series dataset that span over a decade (2003 to 2016), corresponding to half of the period in which presence records were compiled. Additionally, the physical variables of bathymetry depth (*bathy*) and degree of bottom slope (*slope*) were extracted and calculated with ArcMap 10.1®. All environmental variables were obtained through remotely sensed online repositories (Table 1.1). The environmental data were compiled by monthly means and aggregated into a standardized spatial resolution of 0.1° (~9 km) pixel size and spatial extent from 7°N to 35°S of latitude and from 25°W to 55°W of longitude, yielding a 310 x 420 grid with 130,200 pixels containing data for all variables within the study area. Multicollinearity of covariates was investigated using Pearson's moment correlation and the variance inflation factor (VIF) using the function *corvif* (Zuur et al. 2010), where predictors with $| r | > 0.80$ and/or VIF > 5 were removed.

Table 1.1- Predictors selected for MaxEnt modeling. Summary of the remotely sensed environmental variables.

Predictor	Short name	Unit	Spat. resol.	Temp. resol.	Description	Source
Sea surface temperature	*sst*	°C	0.05°	Month	SST, Aqua MODIS, NPP, Daytime (11 microns)	http://oceancolor.gsfc.nasa.gov
Chlorophyll *a* concentration	*chl*	mg.m^{-3}	0.05°	Month	Chlorophyll-a, Aqua MODIS, NPP, L3SMI	http://oceancolor.gsfc.nasa.gov
Diffuse attenuation coefficient	*k490*	m^{-1}	0.05°	Month	Diffuse Attenuation K490, Aqua MODIS, NPP, L3SMI	http://oceancolor.gsfc.nasa.gov
Net primary productivity of carbon	*pp*	mg.C.m^{-2}.day^{-1}	0.1°	Month	Primary Productivity, Aqua MODIS and Pathfinder, Global	http://coastwatch.pfeg.noaa.gov/infog/PP_bfp2_las.html
Bathymetric depth	*bathy*	Meters	1 arc minute	-	Depth extracted from ETOPO1 Global Relief Model	http://www.ngdc.noaa.gov/mgg/global/global.html
Bathymetric slope	*slope*	Degrees	1 arc minute	-	Bottom slope of calculated from ETOPO1 Global Relief Model	http://www.ngdc.noaa.gov/mgg/global/global.html

Model description

The MaxEnt v3.3.3k modeling approach (www.cs.princeton.edu/~schapire/ maxent/; Phillips et al. 2006) was used to predict the spatial distribution of the probability of occurrence of whale sharks in the equatorial and southwestern Atlantic Ocean. MaxEnt fits the probability distribution of a given species following the principle of maximum entropy (*i.e.* that is most spread out, or closest to uniform) and assumes that the environmental envelope that regulates the species occurrence is included in the deterministic estimation procedure. In other words, the logistic output estimates the probability of the occurrence in relation to sites with "typical" conditions for the species and it is, therefore, considered as a habitat suitability index (HSI; Boyce et al. 2002; Elith et al. 2011). This modeling method uses covariate data from the presence points and background environmental data of the entire study area to estimate the habitats with likely occurrence of the species (Phillips et al. 2006; Elith et al. 2006, 2011).

Our data are composed by presence-only records. The MaxEnt was selected because: (1) is a general-purpose method for making predictions or inferences from incomplete information, applied frequently to presence-only species distribution, from sparse or limited data (Phillips et al. 2006); (2) in most cases outperformed other presence-only methods (Elith et al. 2006; Rebelo and Jones 2010); (3) it is particularly useful for rare/endangered species (Hernandez et al. 2006; Wisz et al. 2007); and (4) it is widely used (Yackulic et al. 2013), facilitating comparisons and cross-reference.

Model construction

MaxEnt assumes that sampling of presence locations is unbiased (Phillips et al. 2006), although the assumption of lack of bias in the present data was violated since the collection effort was biased towards more easily accessed areas (Phillips et al. 2009), than from opportunistic encounters (*e.g.* mainly above the continental shelf). To account for spatial bias in presence records, we conducted a latitudinal correction by removing the spatially auto-correlated occurrence points to reduce the multiple occurrence records to a single record within the specified grid (presences were rarefied at $10km^2$ spatial resolution), and then we created the bias files by background selection using the python-based set of functions SDMtoolbox (Brown 2014). This procedure controls the background points selection and the density of background sampling, up-weighting the occurrence points by reducing the geographic landscape to constrained areas; thus avoiding habitat greatly outside of a species' known occurrence or accounting for both regional sampling biases and latitudinal biases associated with coordinate data (Brown 2014).

We compared 10 replicates of each of the four different methods creating the bias files to assess the best technique, all with 100 km of buffer distance, and sampled by: (i) Gaussian kernel density of localities (GAU); (ii) buffered local adaptive convex-hull (ACH); (iii) buffered maximum convex polygon (MCP); and (iv) distance from observation points (DOP).

The response variable (*presences*) and six environmental predictors were used. The presence points were sampled by the subsample method with a random seed to 30 different random training/testing partitions with 70% of presence records used for training (calibration) and 30% used for testing (evaluating) the models. All runs (model replicates) were set with the MaxEnt software default convergence threshold of $1.0\ E^{-5}$ with 500 iterations maximum, regularization parameter of 1 and 10,000 background points. The sample size (<79) only allowed using linear (L), quadratic (Q) and hinge (H) feature types for model parametrization (Phillips et al. 2006).

Model performance evaluation

The discriminative power of the models was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Hanley and McNeil 1982). AUC is a discrimination index which denotes that the likelihood of a 'presence' will have higher predicted value than of an 'absence' (Hosmer & Lemeshow, 2000). It is important to note that AUC scores for presence-only models are a measure of presence *vs.* background points, which may or may not be true absences (Phillips et al. 2006). However, "if the analyses are based on haphazardly collected data and/or if detection probability varies with the covariates that determine relative occupancy levels, then AUC is actually addressing the problem of classifying species detections (which are themselves a product of true presence, variation in sampling intensity and detection probability) *vs.* background" (Yackulic et al. 2013). The AUC index provides a logistic rank spanning from 0 to 1, where an AUC value of > 0.5 indicates that the fitted model performed better than random. Although there are no rules for classification, an AUC of less than 0.80 is considered a poor model, between 0.80-0.90 a fair model, between 0.90 and 0.95 a good one, and > 0.95 an excellent model (Beaumont et al. 2009). The final AUC score was obtained from the statistical average of 30 model replicates. In order to assist the model validation, interpretation and to check for robustness of results, the ten MaxEnt thresholds outputs were assessed to select the model with best performance for the input data (Liu et al. 2005; Jimenez-Valverde & Lobo 2007; Warren and Seifert 2011; Norris 2014). At last, the selected model was compared with 30 replicates of a model with identical parametrization, but without the bias grid, to assess the influence of bias on the distributional prediction. All AUC scores derived from each of 30 model replicates per threshold were compared using ANOVA one factor (threshold) with *post hoc* Tukey HSD test if differences were found.

Results

Distribution of presences and habitat suitability

Whale shark presence data accounted for 78 occurrences (Table S1.1) unevenly distributed throughout almost the entire Brazilian coast (Fig 1.1). About three fourths of the sightings (75.9%) were distributed between 12°S and 30°S (Fig 1.1). The highest number of presences was observed in the south of NE region, specifically off Bahia (17); and in the SE and S regions, mainly off Rio de Janeiro (19), São Paulo (14) and Santa Catarina (10), with an increase of presence records in recent years (Table S1.1).

Prior MaxEnt modeling, the presences were filtered and 16 (20.5%) sighting records from oil and seismic platforms were excluded to avoid bias from the permanent observers on these structures. The remaining 62 presences were counted for N/NE (n= 31; 39.8%) and S/SE (n= 47; 60.2%) regions. Despite the regional balance of presence distribution, the data were further corrected using, and additional nine records were excluded by rarefying multiple points to one point per cell function (in SDMtools). By the end of processing, 53 geographically balanced presences (unbiased) were used for modeling.

The predicted distribution of habitat suitability for *R. typus* was not homogeneous in the study area. Visual analysis suggests the entire Brazilian coast has numerous suitable habitats (*i.e.* HSI > 0.80; Fig 1.2). Appropriate areas were found in N/NE region: off Sergipe and Bahia, in the southern part; and from Rio Grande do Norte to Amapá, in the northern part. Suitable habitats were also observed in the oceanic domain, especially in the ASPSP surroundings (Fig 1.3). The largest suitable areas were observed in the S/SE regions, namely in coastal waters from Espírito Santo to Rio Grande do Sul (Fig 1.4).

Model performance and environmental influences

The inference of habitats considered good (HSI > 0.80) encompassed only 273 (0.2%) of the grid cells, representing a total area of suitable habitats of *ca.* 27,000 km^2, although most of the HSI scores were < 0.20 (Fig 1.5). Despite the distribution of suitable habitats encompassed an extensive part of Brazilian shoreline, and also few scattered oceanic areas, no whale shark aggregation was ever recorded or even anedoctally observed.

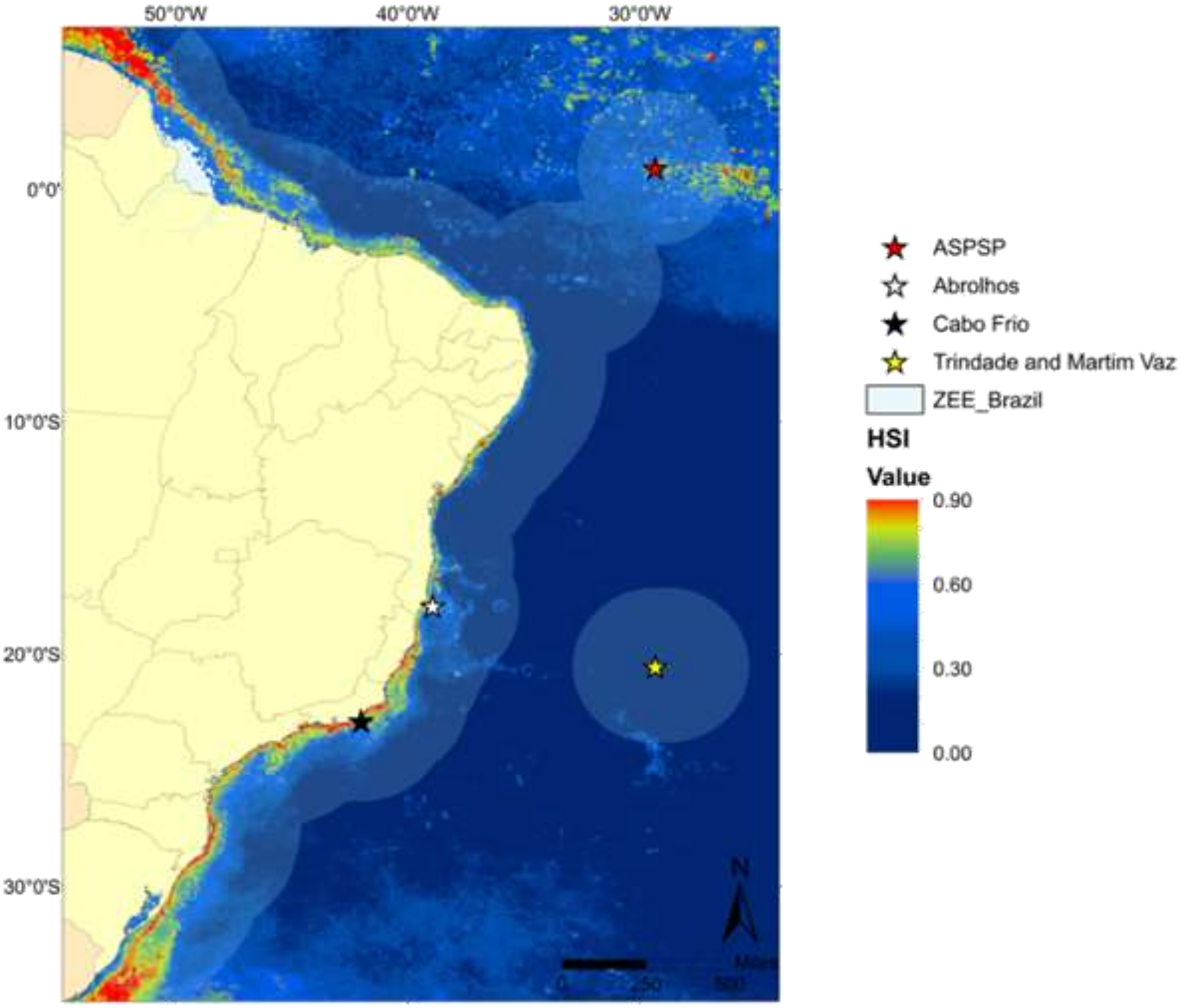

Figure 1.2- Suitable habitats for whale sharks in Equatorial and Southwestern Atlantic Ocean. Habitat suitability map for *R. typus* in the Equatorial and SAO inferred with MaxEnt algorithm. Habitat Suitability Index (HSI) value > 0.80 was considered good and are indicated by yellow and red colors. ASPSP- Archipelago of Sao Pedro and São Paulo. Blank pixels indicate no data.

Multicollinearity analysis indicated high correlation between *chl* and *k490* (Table S1.2), thus the latter predictor was excluded from the modeling. The model that includes all remaining variables had the best AUC score (mean of 0.917), although the variable contribution/permutation importance of *bathy* (87.8/91.0%) highly surpassed all other variable contribution (the sum was only 12.2/9.0%) possibly masking the relative importance of the other variables. This high contribution of *bathy* was considered as a bias from the observer, since almost all presence records were made in continental shelf, and consequently this variable was also excluded.

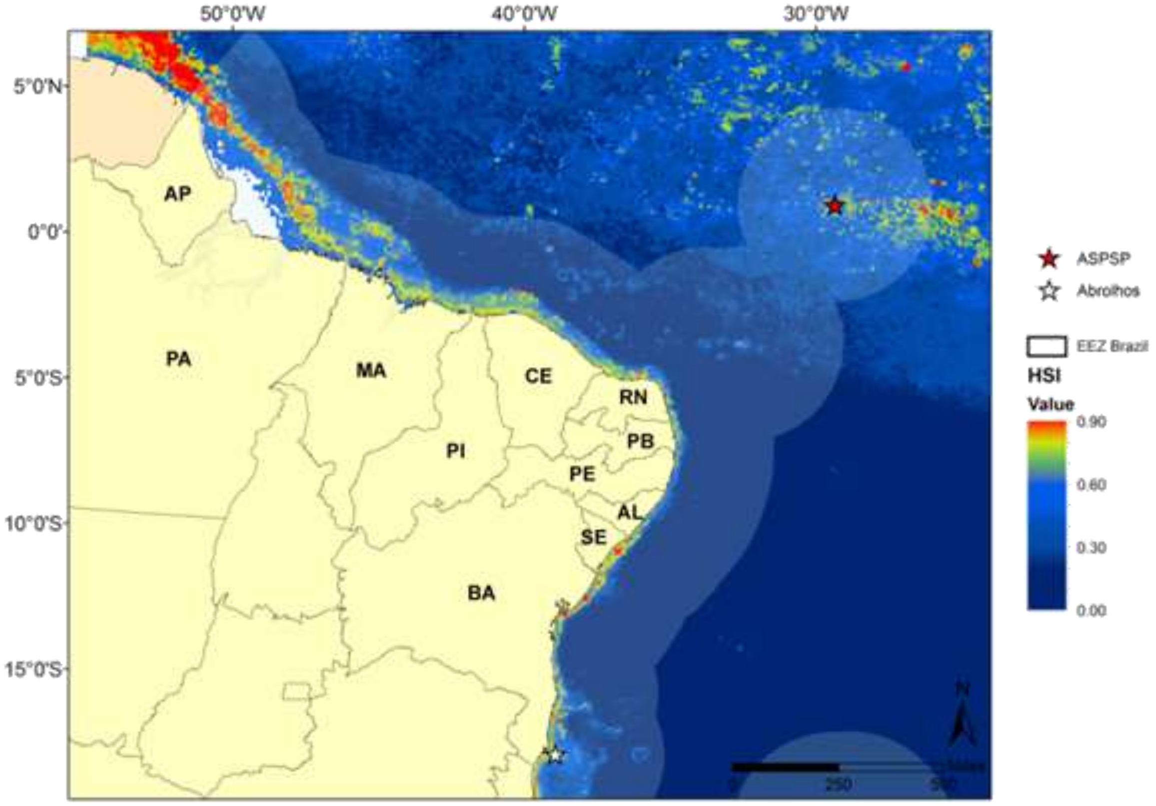

Figure 1.3- Suitable habitats for whale sharks in the N/NE region of Brazil. Habitat suitability map *R. typus* of the Brazilian N/NE region. Habitat Suitability Index (HSI) value > 0.80 was considered good and are indicated by yellow and red colors. BA- Bahia; SE- Sergipe; RN- Rio Grande do Norte; AP- Amapá; ASPSP- Archipelago of Saint Peter and Saint Paul. Blank pixels indicate no data.

The MaxEnt models with the remaining predictors (*i.e. chl, sst, slope, pp*) resulting from the 30 replicates of each of the ten different thresholds performed better than random and produced AUC scores spanning from 0.885 to 0.903 with the latter value, from “maximum test sensitivity plus specificity” threshold, selected as the one that better matched the data (Table 1.2). Additionally, the selected model also performed better than the same model without the bias file (AUC = 0.878), without training data (AUC = 0.897) and changing *chl* for *k490* (Table S1.3).

The most influential predictor used to identify the suitable habitats for whale shark occurrence was *pp* (56.9%), followed by *chl* (38.5%), *slope* (4.2%) and *sst* (0.4%), respectively (Fig S1.1). The response curves of whale shark presences to environmental variables suggested adequate habitats when *sst* is around 26.3 °C, *chl* around 0.9 mg.m^{-3}, *slope* with high declivity (75.7°) and *pp* of 1,679 mg.C.m^{-2}.day^{-1} (Fig 1.6; Table 1.3).

Discussion

Performance and model validation

Regression techniques are robust for SDMs and give high importance to absence data in the prediction. Since whale shark absence data were not available, one alternative to infer the probabilistic distribution was the creation of pseudo-absences, but when using data of a widespread species or with scarce presences (both our cases) the results may be biased (Boyce et al. 2002; Brotons 2004). The MaxEnt modeling seemed adequate to infer the spatial distribution of ecological niches for whale shark occurrence in SAO based on presence-only data. It has been suggested that rarer species may be niche-specialists and the predictable patterns of occurrence relative to environmental gradients more sensitive, potentially increasing the model accuracy (Segurado and Araújo 2004), independently of sample prevalence (Franklin 2009). Moreover, considering that it is likely preferable to overestimate rather than underestimate areas for rare or endangered species conservation, then presence-only methods may be advantageous (Zaniewski et al. 2012).

The bias correction (*i.e.* refined background point selection) of presences is particularly important when studying wide areas in order to avoid the selection of background points within a never colonized, but environmentally suitable habitat. This could increase the commission errors (false positives), leading to model over-fitting due the use of less informative points and failing to predict un-colonized environmentally adequate habitats for the species (Barbet-Massin et al. 2012; Brown 2014). Our analysis indicates that the method creating the bias file influences the model performance and should be carefully selected by comparing different techniques before modeling. Splitting the study area by climatological regions (*e.g.* Tropical for N/NE and Subtropical for S/SE) and modeling the whale shark occurrence by these specific regions separately could enhance the ecological niche prediction along the Brazilian coast, due the reduction of the study area (McPherson et al. 2004) and climatological differences between these regions; although such possibility was only noticed after modeling therefore not assessed in the present study.

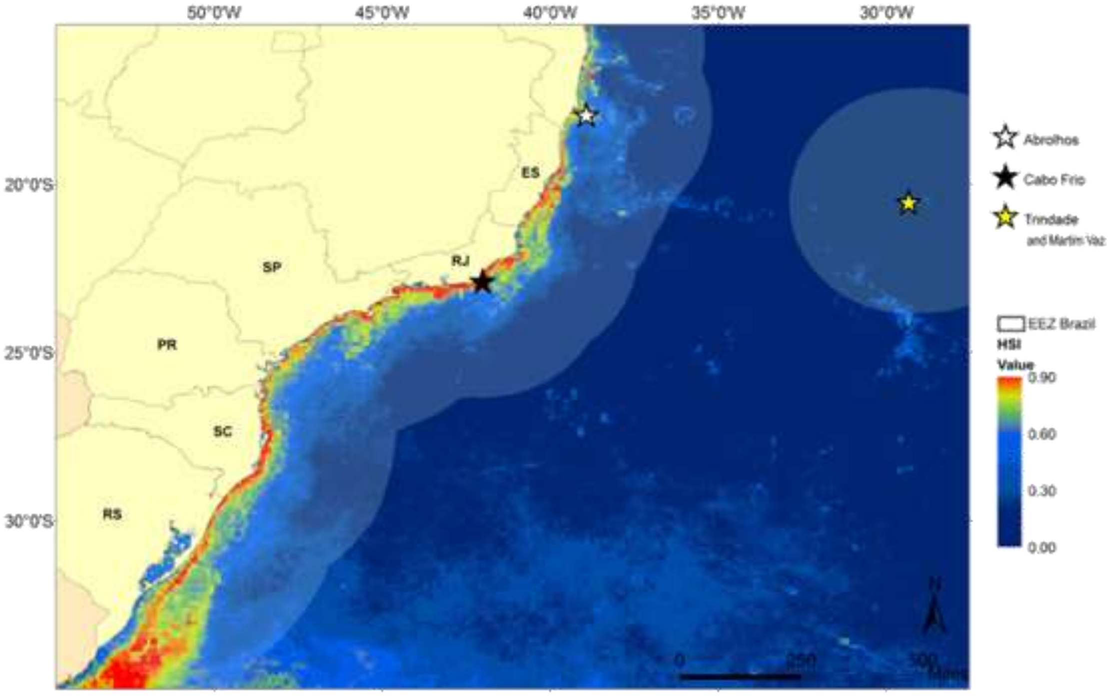

Figure 1.4- Suitable habitats for whale sharks in the S/SE region of Brazil. Habitat suitability map *R. typus* of the Brazilian S/SE region. Habitat Suitability Index (HSI) value > 0.80 was considered good and are indicated by yellow and red colors. ES- Espírito Santo; RJ- Rio de Janeiro; SP- São Paulo; PR- Paraná; SC- Santa Catarina; RS- Rio Grande do Sul.

Comparison with other MaxEnt models on whale sharks

Our models yielded fair to good AUC scores according Beaumont et al (2009), positively indicating potentially important habitats for whale shark occurrences. These results are consistent with earlier observations using the same modeling method to predict the habitat suitability for the whale sharks globally (Sequeira et al. 2011; Mckinney et al. 2012; Hacohen-Domené et al. 2015). The MaxEnt algorithms were successfully applied in the Caribbean Sea and the GoM to identify key environmental factors that influence the feeding aggregations of whale sharks and to assess the seasonal patterns in the suitability of habitats (Mckinney et al. 2012; Hacohen-Domené et al. 2015).

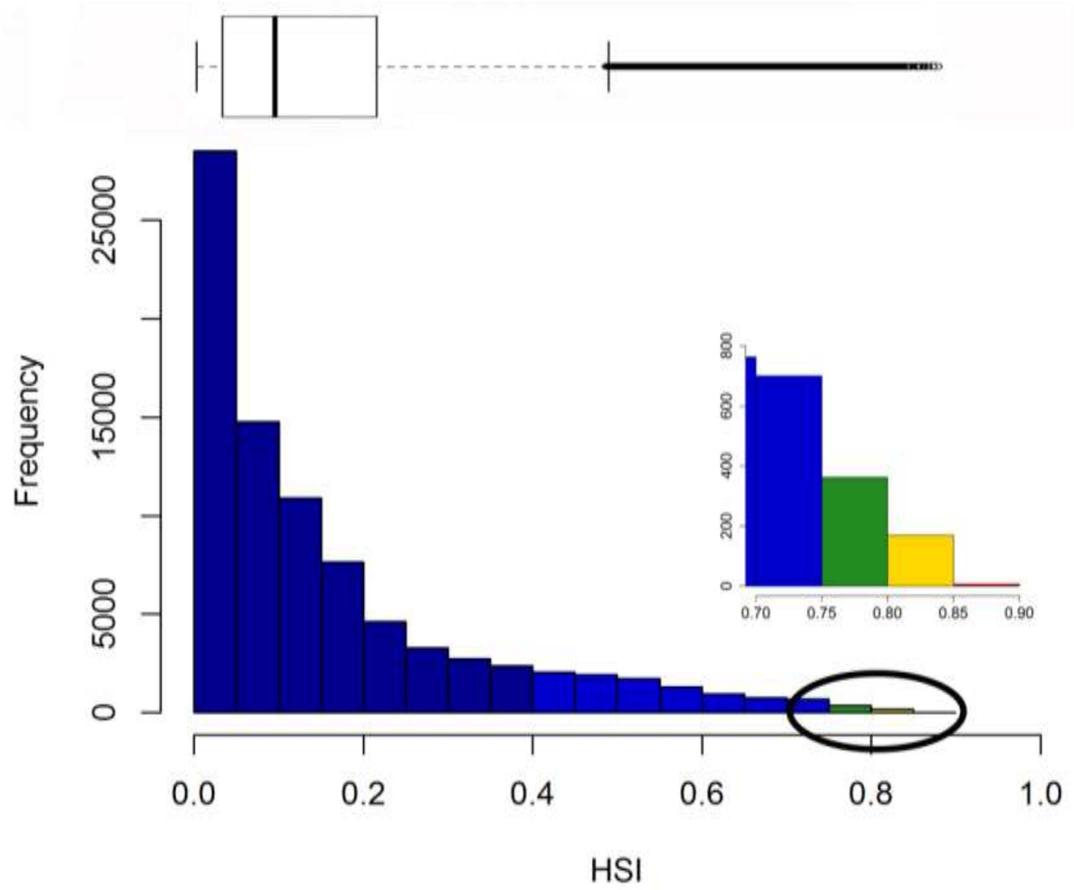

Figure 1.5- Distribution of the Habitat Suitability Index (HSI) values. Empirical (top) and frequency (bottom) distributions of the HSI within the prediction area for the Equatorial and SAO. Habitat Suitability Index (HSI) scores > 0.80 were considered good and are indicated by yellow and red colors. The inset histogram details the ellipse-marked bars. Bold vertical black line represents the median and the blank circles indicate outliers (top).

MaxEnt was also compared with GLM/GLMM to infer the distribution patterns of whale sharks for the entire Indian Ocean, relating the presence locations with selected environmental variables to infer the spatiotemporal patterns in habitat suitability (Sequeira et al. 2011). In a global-scale basis, Sequeira et al. (2014) used environmental covariates to predict the spatial distribution of whale sharks suitable habitats across the three ocean basins. The information regarding the Atlantic Ocean predicted a large suitable area in the SAO, however, the results were rather generalist with coarse resolution for the coastal areas and also it did not include data of whale shark presences from the equatorial and southwestern region. The present study was the first to assess environmental influences on the whale shark occurrences and to identify potentially suitable habitats for the species in this region of the world.

Table 1.2- Summary of MaxEnt threshold model selection. Performance comparison of the ten different MaxEnt thresholds used to fit the models with feature type = LQH. Model performances are indicated by mean ± standard deviation AUC of 30 replicates of each threshold. Bold indicates the best performance threshold.

Model threshold	**AUC**	**s.d.**
Fixed cumulative- 1	0.885	0.040
Fixed cumulative- 5	0.898	0.035
Fixed cumulative- 10	0.898	0.042
Minimum training presence	0.886	0.030
10 percentile training presence	0.895	0.036
Equal training sensitivity and specificity	0.895	0.032
Maximum training sensitivity plus specificity	0.886	0.033
Equal test sensitivity and specificity	0.892	0.036
Maximum test sensitivity plus specificity	**0.903**	**0.027**
Equate entropy of thresholded and original distributions	0.900	0.035

Table 1.3- Environmental variable preferences. Summary of remotely sensed environmental factors associated with *R. typus* presences.

Variable	**Min.**	**Max.**	**Mean**	**Sd**
Chl	0.04	10.60	0.92	1.72
Sst	23.58	28.20	26.35	1.21
slope	27.94	89.87	75.77	16.88
depth	-6.00	-2,633.00	-256.10	706.91
Pp	314.30	6,765.00	1,679.00	1,280.52

Variable contribution

The interrelationships of covariates (*i.e.* collinearity) lead to parameter redundancies, thus invalidating the model interpretation (Wheeler and Tiefelsdorf 2005; Veloz 2009). The predictor *k490* presented strong correlation with *chl*, and thus the former was excluded from the final model, since the latter is more commonly used (Kumari and Raman, 2010; Mckinney et al. 2012; Afonso et al. 2014, Hacohen-Domené et al. 2015) and described better whale shark presences (Table S1.3). *Bathy* yielded the highest variable contribution in the final model and HSI scores presented on the map were strongly constrained by the depth, with the most suitable habitats being similar to the bathymetric contour of the continental shelf (Figure S1.2). Given the sampling geographical bias to shallow depths, this variable was excluded since may be a source of inaccuracy in the final model and could lead to incorrect predictions (Leitão et al. 2011; Bystriakova et al. 2012). The combination of all remaining variables is supposed to designate potential areas with relevant biological production along the Brazilian coast, hence considered here as potentially suitable habitats for whale shark feeding.

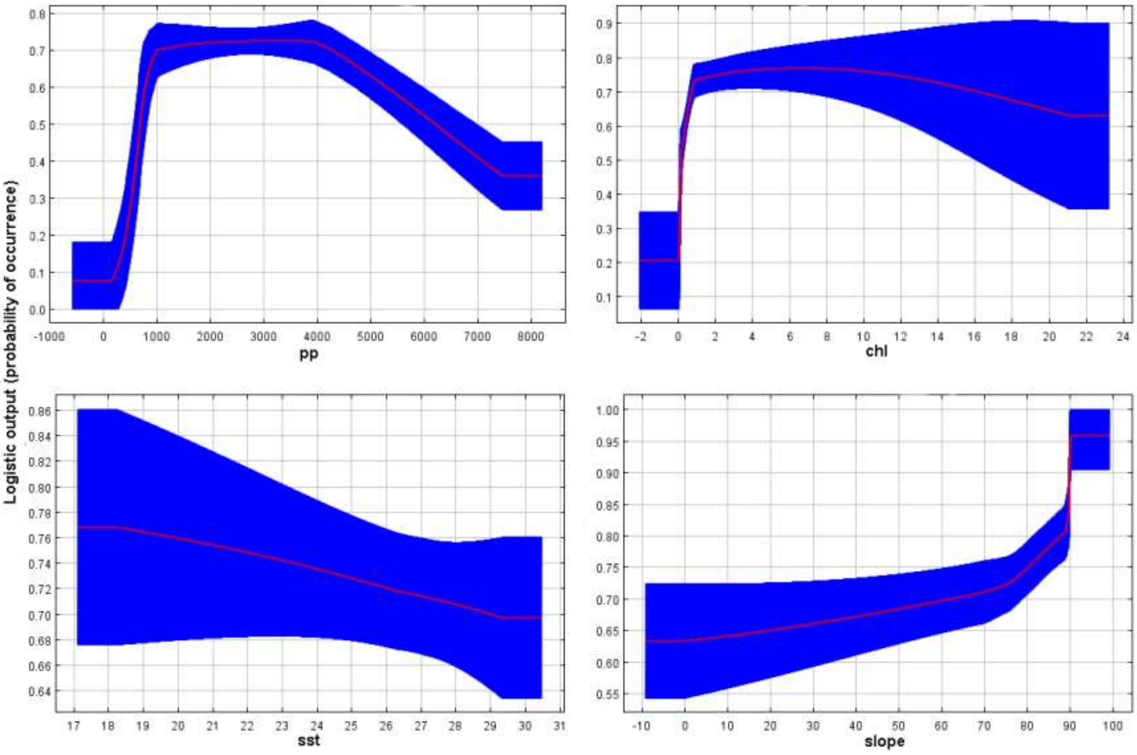

Figure 1.6- Presence response curves to environmental variables. Marginal response curves of the predictors on the habitat suitability for *R. typus* occurrence in Equatorial and SAO using MaxEnt algorithm. The blue area represents the 95% of confidence interval.

Suitable habitats from N/NE Brazil

Suitable areas were predicted in two geographically and environmentally different regions of N/NE Brazil. In the northernmost portion of N/NE there are suitable habitats on almost the entire coast. The HSI values presented a slight increase from the northern coast off Rio Grande do Norte to Amapá. This enhancement of habitat suitability towards the Caribbean is probably influenced by the Amazon plume, which is nutrients-rich and highly productive (Smith 1996; Conroy et al. 2016); and, thus, the most influential variables in the model were likely derived from ocean productivity. Indeed, towards northwest in the Caribbean direction, whale sharks are known to occur off Suriname (De Boer et al. 2015), Venezuela (Romero et al. 2000), Dutch Caribbean (Debrot et al. 2013) and in great part of the Caribbean Sea and GoM (Hueter et al. 2013). The eastern part of NE had the poorest habitats among all the regions. This area is considered highly oligotrophic (Marone et al. 2010) and whale sharks might be only passing through; consequently, fewer occurrences are expected in this area.

Conversely, in the southernmost area of the NE region, suitable habitats were observed off Sergipe and north of Bahia, and in the south of Bahia. The latter region has complex bathymetry due the location of two shallow banks, Royal Charlotte and Abrolhos, respectively. The continental shelf in this region varies with latitude narrowing and widening along the coast, with seamounts found near the lower slope. The archipelago of Abrolhos was the first National Marine Park of Brazil and is the largest and richest reef of the South Atlantic, sheltering a great biodiversity of marine fauna (Dutra et al. 2005). High diversity and abundance of teleost and coral reef in Abrolhos surroundings could drive whale sharks in search for food derived from spawning or high larvae concentration of these organisms (Nonaka et al. 2000), in this area. Feeding behaviors of whale shark off Bahia were recorded before. On one occasion, the shark was described to forage on small fish and shrimp (Barbosa-Filho et al. 2016); and on another one, an individual was recorded feeding on a cloud of a Geryonid crab larvae (BCLM, *unp. data*). Additionally, 76% (n = 56) of the fishermen interviewed by Barbosa-Filho et al. (2016) reported solitary whale shark sightings in this area.

An alternative explanation for the identification of suitable areas in both extremes of the N/NE region could be the interactions between SEC, namely NBC and BC, with the continental shelf physiography and topography that could cause localized upwellings (*i.e.* the changes in shoreline orientation and/or seafloor topography modifies the geostrophic gradient leading to a bottom-up flow by Ekman spiral or by the abrupt shelf-break). Near surface waters in the northern N/NE, for example, showed enhanced nutrient content generated by the retroflection of the NBC (Oudot et. al., 1998). In the southern part of NE, the SEC runs into the continental shelf and bifurcates in latitudes located almost in the middle of Bahia. This ocean-continent dynamic and the tidal-topography interaction could generate localized small-scale water enrichment (Campos et al. 2000; VargasYáñez et al. 2002; Pereira et al. 2005), thus attracting whale sharks to these areas.

Suitable habitats from SE/S Brazil

Upwelling appears to be the cause for the suitable areas in SE region, specifically off Rio de Janeiro state, where the Cabo Frio upwelling system is found (23°S, 42°W). This phenomenon is controlled by the synergy of east-northeast wind with the change in coastal physiography (from north-south to east-west) and the proximity of the 100 m isobaths; attaining the highest intensity during austral spring/ summer (Valentin et al. 1987a; Coelho-Souza et al. 2012). This region had the highest number of occurrences in the present study and the association of whale sharks with this upwelling system was mentioned before (Alecrim-Santos et al. 1988; Barbosa-Filho et al. 2016). The area is enriched with planktonic organisms, such as copepods (91 different species), and small nektonic organisms, like squids (*Loligo* spp.) and sardine (*Sardinella brasiliensis*) (Valentin et al. 1987b), and hosts large fishing grounds (*e.g.* sardine and skipjack tuna *Katswonus pelamis*) and some of the largest oil deposits/ platforms of Brazil (Fig 1.1) (Matsuura 1996; Castro et al. 2008).

Also, platforms appears to attract whale sharks (Soto and Nisa-Castro-Neto 2000; Hoffmayer et al. 2005; Weir et al. 2010; Mckinney et al. 2012; Robinson et al. 2013, present study) as they act like a fish aggregating device (FAD), creating heterogeneity on the environment, enhancing the biological productivity, and consequently congregating reef and pelagic fauna (Franks, 2000; Friedlander et al. 2014). Sixteen occurrences of whale sharks from oil and from seismic platforms were compiled. The great number of occurrences on platforms could be also related to the permanent onboard observers (increasing the sighting probability), however, we did not evaluate the specific influence of platforms on whale shark ocurrence in our study.

The South Atlantic Central Water (SACW) regulates the upwelling event in Cabo Frio and the productivity enhancement farther south in the SE/S region. As a result of the bifurcation of SEC in Brazilian continental shelf, the cold and nutrient-rich SACW emerges from below the thermocline (at 400-500 m depth) in the latitudes of 20-24°S (Stramma and England 1999). The confluence of the Malvinas with the BC occurs in the Subtropical Convergence region (33-38°S) consolidating the SACW (Stramma and Peterson, 1990), and causing a strong thermohaline frontal region (Boebel et al. 1999). This current dynamics is responsible for the enhancement of productivity in the S/SE region (from São Paulo to Rio Grande do Sul coasts), presented down south in the HSI map (Fig 1.4). Records of other filter-feeding elasmobranchs such as devil rays (*Mobula tarapacana M. japanica* and *M. thurstoni*; Gadig and Sampaio 2002; Gadig et al. 2003; Casas et al. 2006) and basking shark (*Cetorhinus maximus*; Soto 2000 were already reported in this region. Additionally, this area was indicated as the richest in terms of the number of species in the Brazilian shelf (Miloslavic et al. 2011)

Oceanic islands and seamounts

The majority of suitable areas were found in the coastal zone due the water enrichment from continental runoff, almost contouring the Brazilian continental shelf. However, one large area was identified near the equator in the oceanic domain, in ologitrophic waters. The equatorial upwelling may be responsible for this environmentally adequate oceanic area, at least in part. This type of upwelling occurs mainly due to the divergence of the SEC, which intensity is governed by the season and the longitude (Oudot 1986). Nevertheless, at 30°W vertical mixing was considered more important than the upward transport in the process of nutrient enrichment of the equatorial layer because it lasts longer (Kaiser and Postel 1979; Oudot 1986). Another important process of enrichment, further north (around 3°N), is the convergence between the SEC and the North Equatorial Counter Current causing consequent aggregation of prey organisms.

Coincidently, in spite of the exclusion of the archipelago's presences from MaxEnt model, the only oceanic suitable area found encompasses the ASPSP where whale sharks are predicted to occur from February to June (Hazin et al. 2008; Macena and Hazin 2016). The oceanographic conditions during this period, *i.e.* reproductive period of various fish and invertebrate species, coupled with weaker oceanic currents and, consequently, high larval retention rates and abundance of planktonic organisms, provide optimal conditions for foraging (Macena and Hazin 2016). The demographic structure of whale sharks visiting ASPSP showed an absence of ontogenetic segregation, although juveniles and adults may be using the area for different purposes. Additionally, the vicinity seems to be an important habitat for the species' reproductive cycle, since records of females with the abdomen suggestive of pregnancy and evidences of courtship/ mating were also observed (Macena and Hazin 2016).

Implications for conservation

Despite the increase of presence records of whale sharks in recent years, this may not reflect any trend in the abundance of the species, being more likely due to the spreading of information access, social media, and also due to the raise of public awareness, which accessed our whale shark sighting program to report presence records.

The limited knowledge of elasmobranch's biodiversity, ecology and biology in Brazilian coast is a reflection of the low priority given by the government and echoes a relatively reduced number of publications on this class of vertebrates for the region (MMA 2002).

Conversely, other marine vertebrates such as cetaceans, manatees and sea turtles receive good support and have specific government agencies exclusively dedicated to study and protect them. Since teleost fishes and elasmobranchs do not have this kind of government support, the conservation of these groups is very challenging in Brazil. The main threats for marine animals are basically: fishery, loss of habitats and pollution. These three factors impact, alone or in synergy, a wide range of marine organisms from the bottom to the top of the food chain, or in other words, from microscopic plankton to the huge whales.

The Brazilian Ministry of Environment (MMA), by the way of an assessment and identification of priority actions and areas for the conservation of biodiversity and biomes (MMA 2002), suggested measures for public policies, research and monitoring and the creation of conservation areas, but the goals proposed are yet far to be completed (MMA 2008; updated maps available in IBGE 2011). Among the recommendations, the ones related to our study were: i) generation of quality data on ecology, biology and spatial distribution of elasmobranchs; ii) implementation of a fishery observer program; iii) the creation of protection areas in the Brazilian North Seamount Chain, ASPSP and Trindade and Martim Vaz archipelagos, and in the Cabo Frio region; and iv) increase of the efforts on environmental education to raise public awareness.

Following the above recommendations of MMA, we: i) generated relevant information of suitable habitats distribution for the whale shark, which could be used as an umbrella (Roberge and Agelstram 2004) to protect sympatric species; ii) proposed to expand and adapt the observer programs to obligate the fishery and the oil and seismic platforms observers to include records of whale sharks (and other large elasmobranchs like mobulid rays) in the logbooks; and iii) recommend the implementation of marine protected areas in the sites referred above which had been proved to be important for the life cycle of several marine species, including whale sharks.

Conclusion

Despite few records of whale shark from Uruguayan and Argentinian waters (Compagno 2001), the assessment of whale shark suitable habitats was restricted to Brazilian records due to the lack of detailed sighting records below 33°S (from literature, surveyed or anecdotal). Moreover, the virtual distribution range proposed (Pierce and Norman 2016) do not exceed the extension of Brazilian shoreline and our study encompassed almost the entire coastal zone of the western SAO thus considered enough to extrapolate to the entire region.

Moreover, the range distribution of the species in the western SAO should be revised in order to include the Southestern and South regions of Brazil in the worldwide virtual distribution maps of the whale shark.

The present study was the first to spatially quantify the suitable habitats of whale sharks and to describe the potential environmental variables associated with the distribution of the species in SAO. The south of NE and SE/S regions presented the majority of presence records. This zone is highly productive due the influence of localized topographic upwellings and the confluence of different water masses, being thus considered as the most suitable habitat for the whale shark in Brazilian coast. The results presented show how the collection of casual observations can provide insights into species' biogeography and may encourage further and more extensive studies on both the species and the suitable habitats.

Mapping suitable habitats for endangered species such as the whale shark could aid the elucidation of the species distribution dynamics in the Atlantic Ocean. It may also serve as a baseline for the development of conservation measures, based on the geographical distribution of the occurrences of the species, as well as on the identification of areas where the species might be present but not sighted with the same frequency. Additionally, some groups of marine species have limited distribution data or even lack dedicated researches to study them, making their conservation much more challenging. For this reason, the use of a charismatic species as an umbrella to achieve a bigger goal such as the protection of a marine area which is important for the life cycle of several species becomes very relevant.

Supporting information

Table S1.1– Summary of compiled records of whale shark presences in the Brazilian coast

Month	Year	Longitude	Latitude	Region	State	Location	Type	Authorithy
5	1922	-38.6856	-17.9714	NE	BA	Farol de Abrolhos	sighting	Gudger 1922
2	1983	-40.4178	-22.3706	SE	RJ	Plataforma Garoupa/Bacia de Campos	sighting	Soto and Nisa-Castro-Neto 1995
3	1984	-42.0076	-22.9304	SE	RJ	Arraial do Cabo, Cabo Frio	capture	Alecrim-Santos et al. 1988
3	1984	-42.0200	-22.9678	SE	RJ	Praia Grande, Arraial do Cabo, Cabo Frio	stranding	Alecrim-Santos et al. 1988
12	1985	-44.9333	-24.3333	SE	SP	29 milhas da costa de São Sebastião	capture	Sadowsky et al. 1986
1	1986	-44.8767	-23.6410	SE	SP	Ao largo de Ubatuba	capture	Gadig 1991
7	1989	-38.0108	-12.8114	NE	BA	Vila Arembepe, Camaçari	sighting	Bertoncini and Sampaio 2002
1	1990	-38.8126	-14.3263	NE	BA	Itacaré	sighting	Bertoncini and Sampaio 2002
3	1990	-38.7379	-13.391	NE	BA	Morro de São Paulo	sighting	Bertoncini and Sampaio 2002
2	1990	-48.3167	-28.0667	S	SC	14 milhas da costa de Garopaba	capture	Soto and Nisa-Castro-Neto 2000
3	1990	-45.5000	-24.0500	SE	SP	10 milhas a NE do Arq. de Alcatrazes	capture	Gadig 1991
5	1990	-46.3688	-24.1068	SE	SP	Sul de Santos	sighting	Soto and Nisa-Castro-Neto 2000
11	1991	-40.0889	-2.8265	NE	CE	Acaraú	stranding	Soto and Nisa-Castro-Neto 2000
1	1991	-50.2667	-31.2667	S	RS	25 milhas do farol a Solião, Mostardas	sighting	Soto and Nisa-Castro-Neto 1995
11	1991	-41.7153	-22.4156	SE	RJ	Costão do Ilhote , sul do arq. de Santana, Macaé	sighting	Soto and Nisa-Castro-Neto 1995
11	1991	-46.5833	-24.5333	SE	SP	Ilha Queimada Grande	sighting	Soto and Nisa-Castro-Neto 2000
8	1992	-37.2683	-11.7876	NE	BA	Vila Serimbinha, Conde	sighting	Bertoncini and Sampaio 2002
2	1992	-40.2889	-22.1725	SE	SP	Plataforma Petrolífera Vermelho/ Bacia de Santos	platform	Soto and Nisa-Castro-Neto 2000
4	1992	-45.1689	-25.1761	SE	SP	Plataforma Petrolífera Merluza/ Bacia de Santos	platform	Soto and Nisa-Castro-Neto 2000
5	1993	-43.1969	-23.0496	SE	RJ	Ilhas Redonda e Comprida	sighting	Present study
5	1993	-42.0251	-22.9867	SE	RJ	Arraial do Cabo, Cabo Frio	Sighting	Soto and Nisa-Castro-Neto 2000
4	1993	-40.8362	-22.9424	SE	SP	Plataforma Petrolífera Badejo/ Bacia de Santos	Platform	Soto and Nisa-Castro-Neto 2000
4	1993	-45.1685	-25.1761	SE	SP	Plataforma Petrolífera Merluza/ Bacia de Santos	Platform	Soto and Nisa-Castro-Neto 2000
7	1993	-45.1687	-25.1762	SE	SP	Plataforma Petrolífera Merluza/ Bacia de Santos	platform	Soto and Nisa-Castro-Neto 2000
3	1994	-38.2974	-13.0192	NE	BA	Amaralina, Salvador	sighting	Bertoncini and Sampaio 2002

6	1994	-40.6900	-22.7039	SE	RJ	Plataforma Petrolífera Enchova	platform	Soto and Nisa-Castro-Neto 2000
11	1994	-40.8300	-22.7311	SE	RJ	Plataforma Petrolífera P17	platform	Soto and Nisa-Castro-Neto 2000
8	1995	-46.7839	-26.7728	S	SC	Plataforma Petrolífera P14	platform	Soto and Nisa-Castro-Neto 2000
6	1995	-42.0214	-22.9901	S	SC	Praia Grande, Arraial do Cabo, Cabo Frio	sighting	Gomes et al. 1997
6	1996	-46.7837	-26.7729	S	SC	Plataforma Petrolífera P14	platform	Soto and Nisa-Castro-Neto 2000
6	1996	-46.7837	-26.7727	S	SC	Plataforma Petrolífera P14	platform	Soto and Nisa-Castro-Neto 2000
11	1997	-33.8164	-3.8802	NE	RN	Atol das Rocas	sighting	Campos et al. 2005
7	1998	-32.3778	-3.8500	NE	FEN	Pedras Secas	sighting	Soto and Nisa-Castro-Neto 2000
2	1999	-46.7837	-26.7731	S	SC	Plataforma Petrolífera P14	platform	Soto and Nisa-Castro-Neto 2000
8	2000	-38.2944	-13.0487	NE	BA	Rio Vermelho, Salvador	sighting	Bertoncini and Sampaio 2002
9	2000	-34.6237	-7.5530	NE	PE	Plataforma continental em frente a Itamaracá	sighting	Present study
2	2001	-38.2944	-13.0487	NE	BA	Rio Vermelho, Salvador	sighting	Bertoncini and Sampaio 2002
2	2001	-38.2944	-13.0487	NE	BA	Rio Vermelho, Salvador	sighting	Bertoncini and Sampaio 2002
8	2002	-38.8407	-14.7988	NE	BA	Ilhéus	sighting	Bertoncini and Sampaio 2002
4	2002	-46.6833	-24.4833	SE	SP	Ilha ao largo de São Sebastião	capture	Ferreira e Amorim 2002
7	2007	-32.4470	-3.8339	NE	FEN	Laje Dois Irmãos	sighting	Machado and Aguiar 2008
5	2008	-38.7733	-13.4644	NE	BA	Próximo à plataforma petróleo	platform	Present study
1	2009	-38.0611	-3.3766	NE	CE	Mucuripe - 40km off coast	capture	Faria et al. 2009
7	2009	-43.0042	-23.8236	SE	RJ	58 milhas RJ rumo 170°	sighting	Present study
7	2009	-46.1708	-24.3188	SE	SP	Laje de Santos - Ponta da Boca da Baleia	sighting	Present study
1	2010	-38.0819	-15.9340	NE	BA	Porto Seguro/ Royal Charlote Bank	sighting	Present study
1	2010	-32.3924	-3.8059	NE	FEN	Ponta da Macaxeira	sighting	Present study
12	2010	-34.8724	-8.1975	NE	PE	Próximo ao tanque-rede dos beijupirás	sighting	Present study
7	2010	-36.2450	-11.0183	NE	SE	Navio de sísmica	platform	Present study
2	2011	-34.7533	-8.2366	NE	PE	Naufrágio Taurus	sighting	Present study
5	2011	-39.4314	-19.9417	SE	ES	Costa do Espírito Santo	sighting	Andrades et al. 2012
11	2011	-40.7716	-22.5947	SE	RJ	Bacia de Campos / 65 km de Macaé	sighting	Present study
12	2011	-43.1567	-23.6892	SE	RJ	49 milhas a 180° da costa do RJ	sighting	Present study
8	2012	-37.9686	-12.8004°	NE	BA	Praia do Forte	sighting	Present study
9	2012	-37.8946	-12.5262	NE	BA	Aprox. 04 milhas em frente à Imbassaí	sighting	Present study

6	2012	-36.3695	-11.2722	NE	SE	Plataforma de perfuração	platform	Present study
6	2012	-36.6225	-11.3092	NE	SE	Navio de sísmica	platform	Present study
2	2012	-44.6617	-23.4210	SE	RJ	Paraty / próximo à costa	sighting	Present study
4	2012	-46.1708	-24.3188	SE	SP	Laje de Santos	sighting	Present study
10	2013	-38.1796	-12.8958	NE	BA	Praia de Busca Vida	stranding	Present study
4	2013	-48.6633	-28.2671	S	SC	Praia da Vila Nova, Imbituba	stranding	Present study
6	2013	-48.5708	-27.1321	S	SC	Praia de Perequê, Porto Belo	stranding	Present study
8	2014	-36.2230	-4.8604	NE	RN	Praia de Galinhos	stranding	Present study
3	2014	-39.7564	-23.1033	SE	RJ	Bacia de Campos	platform	Present study
3	2014	-41.9410	-22.5388	SE	RJ	Rio das Ostras (Laje Trinta Reis)	sighting	Present study
2	2015	-37.9203	-12.6298	NE	BA	Praia do Forte	sighting	Present study
11	2015	-37.9000	-12.600	NE	BA	Praia do Forte	sighting	Present study
2	2015	-42.0800	-23.3900	SE	RJ	Rio de Janeiro (60 milhas da costa)	sighting	Present study
5	2015	-41.8422	-22.7267	SE	RJ	Búzios	sighting	Present study
5	2015	-41.8944	-22.6548	SE	RJ	Praia de Unamar, Cabo Frio	sighting	Present study
1	2016	-49.7021	-29.3444	S	RS	Ilha dos Lobos	sighting	Present study
4	2016	-48.5453	-27.1247	S	SC	Porto Belo	sighting	Present study
4	2016	-48.5580	-26.7438	S	SC	Praia da Penha – Itajaí	sighting	Present study
3	2016	-40.4271	-20.7118	SE	ES	Guarapari	sighting	Present study
5	2016	-44.4574	-23.1432	SE	RJ	Angra dos Reis	sighting	Present study
6	2016	-43.1751	-22.9970	SE	RJ	Copacabana	sighting	Present study
4	2016	-46.1458	-24.3348	SE	SP	Laje de Santos - Oeste dos Calhaus	sighting	Present study

Table S1.2- Summary of the multicollinearity analysis. Pearson's correlation matrix plus the variance inflation factor (VIF) before and after excluding the collinear predictor. Bold indicate values above constraints of| r | > 0.80 or VIF > 5.

Predictor	Chl	Sst	depth	Slope	k490	Pp	VIF initial	VIF final
chl	1						15.485	1.308
sst	-0.040	1					3.457	3.359
bathy	0.390	-0.059	1				2.115	1.957
slope	-0.355	-0.002	-0.377	1			1.335	1.272
k490	**0.965**	-0.060	0.417	-0.364	1		**15.873**	
pp	0.778	-0.080	0.569	-0.460	0.786	1	3.572	3.352

Table S1.3- Summary of additional MaxEnt model comparison. Performance comparison of alternative parametrizations of MaxEnt models using feature type = LQH. Model performances are indicated by mean ± standard deviation of area under the curve (AUC). All models included the bias file, except when explicit.

Model threshold	AUC	s.d.
Maximum test sensitivity plus specificity (without bias file)	0.878	0.058
Maximum test sensitivity plus specificity (without training)	0.897	0.096
Maximum test sensitivity plus specificity (including depth)	0.917	0.014
Maximum test sensitivity plus specificity (changing chl to k490)	0.891	0.037

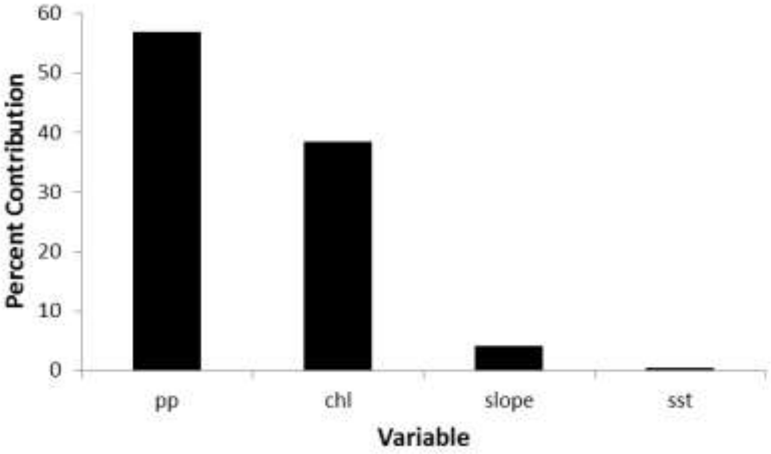

Figure S1.1– Relative contribution of the environmental variables. Estimate of relative contributions of the environmental variables influencing *R. typus* suitable habitats inferred with MaxEnt algorithm.

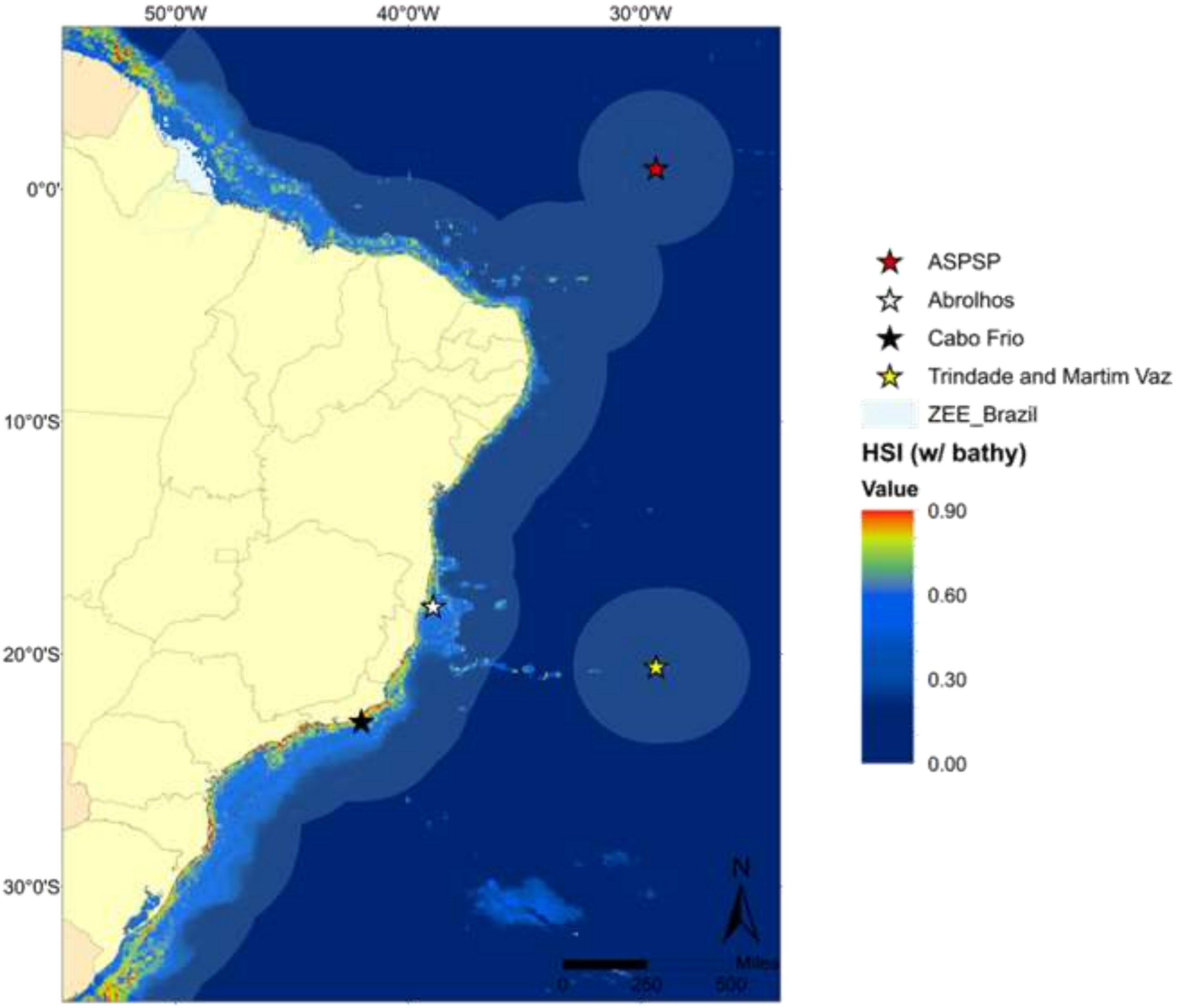

Figure S1. 2- Suitable habitats for whale sharks in Equatorial and SAO including the predictor *bathy*. Habitat suitability map for *R. typus* in the Equatorial and Southwestern Atlantic Ocean inferred with MaxEnt algorithm including the predictor *bathy*. Habitat Suitability Index (HSI) value >0.80 was considered good and are indicated by yellow and red colors. ASPSP – Archipelago of Sao Pedro and São Paulo. Blank pixels indicate no data.

Capítulo 2- Whale shark (*Rhincodon typus*) seasonal occurrence, abundance and demographic structure in the Mid-Equatorial Atlantic Ocean [1]

Abstract

Whale sharks are generally associated with environmental factors that drive their movements to specific locations where food availability is high. Consequently, foraging is believed to be the main reason for the formation of whale shark aggregations. Feeding aggregations occur mainly in nearshore areas and are composed primarily of immature individuals. Conversely, aggregations of mature adults are rarely observed, and their occurrence is correlated with oceanic environments. Despite an increase in the number of whale shark studies, information on mating and parturition grounds is still lacking. In the present work, we assessed the ecological and behavioural aspects of the whale sharks that visit the archipelago of São Pedro and São Paulo (ASPSP), located ~1,000 km off the coast of Brazil in the equatorial Atlantic Ocean. Forty-nine whale sharks were recorded from February 2005 to May 2014. The estimated mean ± SD size was 8.27 ± 2.52 m (range: 2.5-14.0 m) with no significant differences in size across the year. The maturational stages were classified by size as immature (<8.0 m; 32.56%) and mature (>9.0 m; 46.51%); with almost half of the observed animals being mature specimens. The majority of sightings occurred between February and June. During this period, the ocean current weakens and the waters are enriched by eggs and larvae of fishes and invertebrates that attract marine life to forage. At the same time, evidence of reproductive activity in adult females (*i.e.* swollen abdomen and bite marks on the pectoral fins), and the potential mating behaviour exhibited by one male, suggest that the ASPSP area might also have a role in whale shark reproduction. Irrespective of its use for feeding or reproduction, this insular habitat serves as a meeting point for both juvenile and adult whale sharks, and may play an important ecological role for the species.

Key-words: opportunistic foraging; mating; parturition; migration; oceanic island; pelagic environment; habitat use; Saint Peter and Saint Paul archipelago; Mid-Atlantic Ridge.

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[1] Artigo científico aceito pelo Jornal PLoS ONE (doi:10.1371/journal.pone.0164440) em Outubro de 2016.

Introduction

The whale shark *Rhincodon typus* (Smith 1828) is a pelagic and highly migratory filter-feeding species distributed around the globe in tropical and subtropical waters (Compagno 2001; Rowat and Brooks 2012). Past studies on the ecology and biology of whale sharks have suggested a relationship between their movements and environmental features, including sea surface temperature, chlorophyll *a* concentrations, bottom relief and ocean currents (Taylor and Pearce 1999; Eckert and Stewart 2001; Rowat and Gore 2007; Hsu et al. 2007; Sleeman et al. 2010ab; Kumari and Raman 2010; Sequeira et al. 2011, 2013a; Rohner et al. 2013a; Afonso et al. 2014). Commonly, environments with an optimal scenario for whale shark occurrence provide suitable conditions for primary and secondary productivity, as the main known purpose for whale shark aggregation is foraging (Heyman et al. 2001; Meekan et al. 2006; Nelson and Eckert 2007; Rowat and Brooks 2012). Sites with predicted seasonal foraging aggregations of whale sharks offer the best opportunity to study the species on a regular basis. Information gathered from these phenomena, for instance, has been valuable to assess the seasonality of occurrence, aspects of population structure and dynamics of whale sharks in coastal waters of Australia (Meekan et al. 2006, Holmberg et al. 2008); the Gulf of Mexico (de la Parra Venegas et al. 2011); the Gulf of California (Ketchum et al. 2013); Belize (Graham e Roberts 2007); the Seychelles (Rowat et al. 2009); and the Maldives (Riley et al, 2010).

In Brazil, the whale shark occurs in coastal waters from Ceará to Rio Grande do Sul States and at oceanic islands, like the archipelagos of Fernando de Noronha, São Pedro and São Paulo (Soto e Nisa-Castro-Neto 2000) and Trindade (Pinheiro et al. 2009). However, the knowledge of whale shark life history in Brazilian waters is still largely limited to the description of anecdotal sighting records, strandings and incidental catches (Soto e Nisa-Castro-Neto 2000; Gadig and Rosa 2008). The only exception is in the archipelago of São Pedro and São Paulo (ASPSP) where data from sighting records have been systematically collected, and suggest a much higher frequency of occurrence from January to June, probably due to biological factors (*i.e.* food availability) (Hazin et al. 2008).

ASPSP is a small and isolated oceanic archipelago located in the equatorial mid-Atlantic Ridge. Considered a hotspot for pelagic biodiversity (Morato et al. 2010) due to its strategic location in the middle of the Atlantic Ocean, the archipelago provides shelter for marine life and may serve as a stopover during large-scale migrations of pelagic species

(Fréon and Dagorn 2000). The archipelago is also an important feeding ground for commercially important pelagic fishes such as yellowfin tuna (*Thunnus albacares*), bigeye tuna (*T. obesus*), wahoo (*Acanthocybium solandri*), rainbow runner (*Elagatis bipinnulata*) and many species of sharks (Vaske et al. 2003; Vaske et al. 2006a). Most of these species gather at the archipelago between January and June, which coincides with the reproduction and high abundance period of flying fish species (Exocetidae) (Lessa et al. 1999), and when the environmental conditions are suitable for reproduction and recruitment of fish larvae and invertebrates (Macedo-Soares et al. 2012). Consequently, Brazilian fishing boats have been operating in ASPSP since the 1980s (Oliveira et al. 1997; Viana et al. 2015). Whale sharks, however, were never targeted by the fishery in the area, with no record of any specimen being ever caught. Classified as “endangered” by the International Union for Conservation of Nature (IUCN) (Pierce and Norman 2016), the whale shark is also protected by Brazilian law as “vulnerable” species (MMA 2004).

Whale shark aggregations known to date are generally size and sex segregated, with a predominance of immature individuals in coastal feeding aggregations (Rowat and Brooks 2012). Adult whale sharks are infrequently observed, and the majority of sightings have been recorded at oceanic locations, such as the Galapagos Islands (Acuña-Marrero et al. 2014), Baja California Sur (Ketchum et al. 2013, Ramirez Macias et al. 2012a), the Azores (Afonso et al. 2014), St. Helena Island (Clingham et al. 2016) and ASPSP (Hazin et al. 2008; present study). However, complete information on the distribution of mature whale sharks, and on the location of mating and nursery grounds, if any, remains lacking, despite being crucial for the conservation of the species.

To help fill the gap of information on oceanic life history of whale sharks, trends of long-term sighting records in ASPSP were assessed to identify the seasonality of occurrence, relative abundance and population structure, with additional observations on habitat use and behaviour. The information provided here reinforces the hypothesis that oceanic habitats are crucial to whale shark life history, independent of age, and must be better understood to ensure the adoption of adequate conservation measures for both the sharks and this unique habitat.

Material and Methods

The data used in this research was obtained with full approval of the Instituto Chico Mendes de Conservação da Biodiversidade of the Brazilian Ministry of the Environment (permit no. 14124-6).

Study area

The ASPSP is a remote group of small rocky islets, located in the mid-Atlantic Ridge, almost in the middle of the equatorial Atlantic Ocean (00°55'03"N; 029°20'45"W), approximately 100 km north of the equator and nearly midway between South America (1,100 km from Brazil) and Africa (1,600 km from Guinea Bissau) (Fig 2.1). The archipelago is part of an E-W seamount chain, located at the Saint Paul Transform Fault, rising from abyssal depths near 5,000 m, and presenting a rough bottom relief close to the islets (Hekinian et al. 2000).

The ASPSP region is directly influenced by the trade winds and by the Equatorial Current System, namely the South Equatorial Current (SEC) and the Equatorial Undercurrent (EUC), which control the dynamics of physicochemical and biological parameters around the archipelago. The intensification of the NE trade winds, between December and May, pushes the Intertropical Convergence Zone (ITCZ) southward, towards the archipelago (Molinari et al. 1986), resulting in the wet season. During this period, the SE trade winds weaken, reducing the intensity of the westward flowing SEC in the area (Stramma and Schott 1999; Lumpkin and Garzoli 2005). Conversely, during the dry season, from June to November, the ITCZ moves farther north of the archipelago due to the intensification of the SE trade winds (Molinari et al. 1986), which strengthens the SEC (Stramma and Schott 1999; Lumpkin and Garzoli 2005). The EUC, a very strong eastward subsurface current flowing at 50-100 m depth (Schott et al, 1998), is also directly influenced by the SE trade winds, becoming shallower and weaker between December and May and deeper and stronger from June to September (Stramma and Schott 1999; Lumpkin and Garzoli 2005).

Data collection

Frequency of occurrence and abundance

The presence of whale sharks in the ASPSP was recorded by visual surveys (SURV) through direct observation by on board or free diving observers, which were carried out during 37 scientific expeditions of 15 days each, from February 2005 to May 2014. Additionally, anecdotal sighting records were compiled (COMP) through interviews with local fishermen and other researchers, and collated with sightings from the literature (Hazin et al. 2008) from February 2000 to May 2014. Sightings data included: date, time, location, number of individuals, estimated size and photographs, if available.

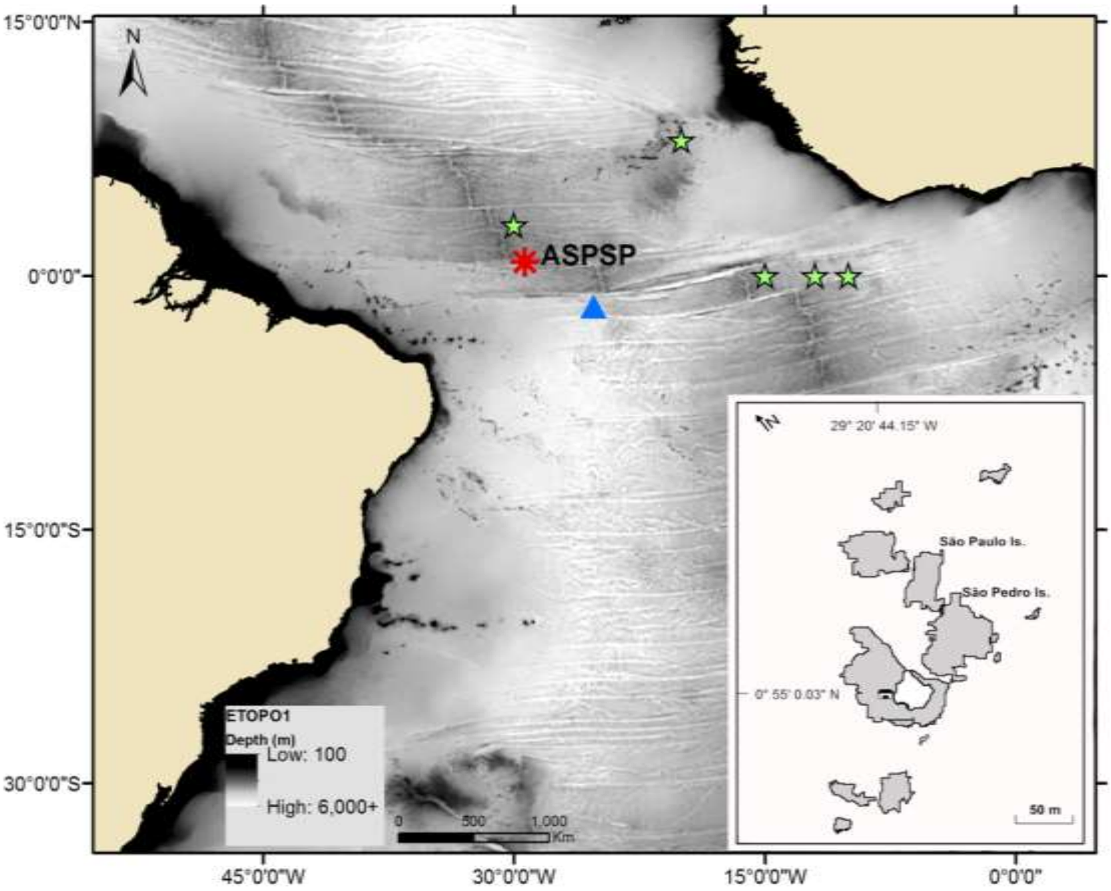


Figure 2.1- Study area. Geographical location and details (inset) of the Archipelago of São Pedro and São Paulo (ASPSP; red asterisk). The blue triangle indicates the satellite-tag pop up location from a female whale shark tagged in Caribbean Mexico (Hueter et al. 2013). The green stars indicate the location of recorded neonates (Wolfson 1983; Kukuyev 1996).

Oceanographic conditions

In order to characterize the oceanographic conditions in ASPSP surroundings, sea surface temperature (SST) (°C) remote sensing monthly image composites were obtained from the Advanced Very High Resolution Radiometer (AVHRR) aboard the NOAA Polar Operational Environmental Satellites (POES) (http://coastwatch.pfeg.noaa.gov/infog/AG_ssta_las.html). Chlorophyll-*a* concentration (CHL) (mg.m^{-3}) remote sensing monthly image composites were obtained from the Moderate Resolution Imaging Spectroradiometer-MODIS-Aqua (http://oceancolor. gsfc.nasa.gov/). Remote sensing data were collected from January, 1, 2005, to December, 31, 2014.

Demographic structure

Whale shark total lengths (L_T) (*i.e.* from the tip of snout to the end of the tail) were estimated to the nearest 0.5 m by comparing the size of the whale shark with known marks on a fishing vessel, after placing the boat in parallel with the shark, or with a diver of known size. Sex was determined in water by the presence or absence of claspers.

To assess the maturity of whale sharks visiting the ASPSP, shark sizes were compared to estimates available in the literature for other Atlantic Ocean sites. For males, information from the Mexican Caribbean (Ramirez Macias et al. 2012b) showed that 95% of males in that region were mature at 8.1 m. These authors, however, did not assess free-swimming female maturity, and no other information is available on female size at maturity in the Atlantic Ocean. Information from other ocean basins, suggests a size at maturity of 9.0+ m (Rowat and Brooks 2012; Colman 1997). We thus chose, conservatively, to consider animals <8.0 m as juveniles, those >9.0 m as adults, and we did not classify animals within the potentially ambiguous 8.0-9.0 m size class.

Photo-identification

The area behind the fifth gill slit and in front of the first dorsal fin of the ASPSP whale sharks was photographed for individual identification and further population dynamic analysis (Speed et al. 2007; van Thienhoven et al. 2007). Both left and right sides were photographed whenever possible. Additionally, information on other marks, scars, size and sex were also used to assist in identification. If available, images from collaborators (*i.e.* other researchers and fishermen) were also collected during the interviews and used for analysis if the quality was suitable.

Data analysis

Comparison of frequency of occurrence between datasets

The relative frequency of occurrence (FO%) per month of whale sharks in the ASPSP was calculated by dividing the number of whale sharks sighted in each month by the total of whale sharks observed and multiplying by 100. A linear regression between the FO% per month was calculated using SURV and COMP data, and the similarity between estimations was assessed using the Welch *t*-test with the null hypothesis of no difference (H_0 = true slope = 1) between datasets. The motivation for performing this analysis was to verify the reliability of the FO% of SURV when compared to the COMP for the period in which fewer scientific surveys were conducted.

Relative abundance index

Before the calculation of Sightings per Unit of Effort (SPUE), the data were filtered in order to minimize the potential duplicate sightings within each surveyed month. Since it was not possible to photo-identify all individuals to remove duplicates, the "short-term resightings" (*i.e.* recorded individuals with similar size and sex within a four day interval between sightings) were discarded. Although this does not entirely eliminate the possibility of inclusion of duplicates, it is expected to remove the majority of the multiple records (details in discussion). Relative abundance indices were calculated using only the SURV SPUE, expressed as the number of individuals sighted per day of expedition (sig.day^{-1}), and grouped by median per month. The differences of SPUE between months and years were verified using Analysis of Variance (ANOVA) of one factor (month or year) with *post hoc* TukeyHSD, if differences were detected.

Oceanographic conditions

SST and CHL data with 0.1° and 0.05° of spatial resolution, respectively, were averaged in squares of 1° x 1° to characterize the general oceanographic conditions per month within a 100 km^2 area around the ASPSP. The differences of monthly means of each variable were compared using ANOVA of one factor (*month*) with *post hoc* Tukey HSD test, if differences were detected.

Demographic structure

Size estimates of whale sharks using surface or underwater visual references tend to have an error of ± 0.5 m (Meekan et al. 2006, Graham and Roberts 2007, Homberg et al. 2009). Since in the present work L_Ts were collected by both methods, the error of visual estimates was calculated based on the creation of a virtual random bias, standardized with fixed upper and lower constraints, and compared with the observed estimates in order to validate the SURV L_T for demographic analysis.

The error estimate of the SURV L_Ts based on the intervals of ±0.5 and ±1.0 m was generated, and considered as the bias in our visual estimations. A new dataset was then created, which randomly included three bias values (-0.5, 0.0, 0.5 or -1.0, 0.0, 1.0) to the SURV L_T to add the bias variance in the estimates. The mean was then calculated and a paired Student t-test was run to compare the mean of the new dataset with the SURV L_T mean. The process was looped 10,000 times to assure the use of all possible combinations of the three bias values; for each new random dataset generated, the mean and the p-value result from the t-tests were saved for further validation. Finally, we calculated the relative frequency of the number of t-test p-values which were smaller than 0.05 to assess if the bias assumed could be accepted. The validation was conditioned to the analysis of the quantity of p-value <0.05 which lies within the 95% confidence interval from all replicates. In other words, we generated 10,000 different datasets with standardized random bias, statistically compared each mean with the SURV L_T mean and verified the proportion of the t-test p-values <0.05 within the 95% of confidence interval to validate the SURV L_T visual size estimation.

The SURV and COMP L_T's were compared using Welch *t*-test and the mean size differences per month were compared using ANOVA of one factor (*month*) with *post hoc* Tukey HSD test, if necessary. The number of whale sharks in each maturity stage was compared to test the hypothesis of predominance of adults using Pearson's chi square test. All statistical analysis were performed using the R programming environment v.3.2.2 (R Core Development Team 2015).

Photo-identification

Photo-identification images were classified by their quality, processed following Speed et al. (Speed et al. 2007), and analyzed using the I^3S software (van Thienhoven et al. 2007). The photo-ID dataset was composed of photographs from SURV and COMP. It should be noted that images from distinct occasions could represent the same individual if only one side were photographed (Meekan et al. 2006).

The left side was chosen for analysis since there were more left side images, and because this is the standard established for the online whale shark global database "Wildbook for Whale Sharks" at www.whaleshark.org. Some whale sharks had both sides photographed and we were able to compare these with the sharks which had only the right side. All photo-identified individuals were compared within our own database and also submitted to the "Wildbook for Whale Sharks" to compare with images of other individuals identified around the world. When only one of the flanks was recorded, to assist the visual confirmation of identification analysis and to avoid duplicity in the photo-identification, more than one character (*i.e.* scars and stripe patterns) were used in parallel with individual intrinsic characteristics such as size and sex.

Results

Frequency of occurrence and relative abundance index

Forty-nine whale sharks were sighted between March 2005 and May 2014 over 555 expedition days (SURV), whereas 92 sightings were compiled from February 2000 to May 2014 (COMP), resulting in 141 combined sightings. Eighteen whale sharks, 5 from SURV and 13 from COMP, were excluded from the analysis by the filtering procedure.

FO% trends of the independent datasets, SURV and COMP, were similar, presenting a related sighting distribution, with peaks in the same months (March and June), but with an intriguing decrease in May (Fig 2.2). The comparison of COMP with SURV FO% revealed positive correlation between datasets ($r^2 = 0.611$; $p = 0.002$), with the linear model slope ($\beta_1 =$ 0.93) very close to the null hypothesis ($H_0 =$ true slope = 1) and no statistical difference detected (Welch: $t = 0.019$, $df = 21.388$, $p = 0.984$). It was considered therefore, that the COMP fulfilled its purpose, which was to supplement the SURV with information on sightings records during the months when the research team was not in the ASPSP, particularly during the last six months of the year (Fig 1.2).

The SPUE dataset had 43 sample units (*i.e.* months). The months with highest median SPUE were June (0.1034) and March (0.1031), followed by May (0.0566) and April (0.0556; Fig 2.2). No expedition was conducted in August. Differences were not detected among the months SPUE (ANOVA: $F = 0.433$, $df = 11$, $p = 0.929$). The independent FO% of COMP was also consistent with the SPUE and presented trends of increasing abundance between February and June with peaks in March and June and decrease in the last six months (Fig 2.2).

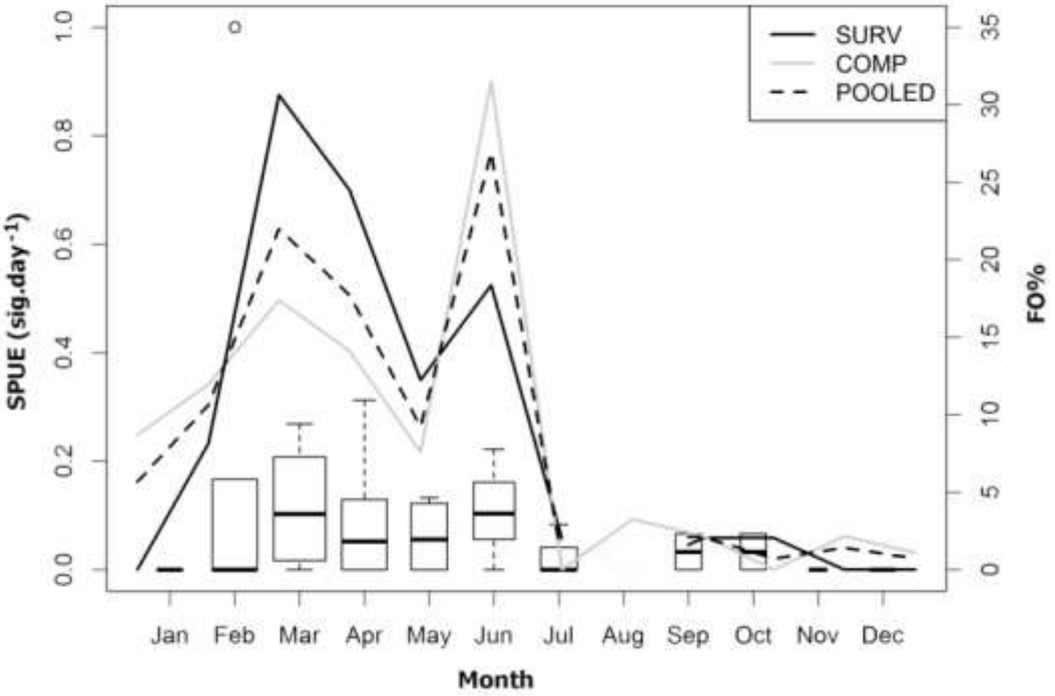


Figure 2.2- Distribution of whale shark sightings per month. Relative frequency of occurrence (FO%) per month of the SURV (n = 49; solid black), COMP (n = 92; solid grey) and POOLED (n = 141; dashed black) datasets; and SURV Sightings per Unit of Effort (SPUE; sig.day^{-1}) per month of *R. typus* in the ASPSP. The width of the boxes is proportional to the square-roots of the number of observations in the groups, the horizontal bar is the median and the open circle indicates a single outlier

The median SPUE per year spanned from nearly 0 in 2005, 2012, 2013 and 2014 to 0.625 in 2006 (Fig. 2.3). No expedition was conducted in 2007. Statistically significant differences were only found between 2006 and all other years (ANOVA: F = 5.082, df = 9; p = 0.000248; TukeyHSD: p < 0.001). The high SPUE observed in 2006 was due to an expedition undertaken between February and March of 2006, when three whale sharks were sighted in the three days of the expedition that fell during February, thus generating an SPUE = 1 (Fig 2.2 and 2.3).

Oceanographic conditions

The SST increased gradually from August until a peak in May, subsequently decreasing from June to August (Fig 2.4, red line). Significant differences in SST were found (ANOVA: F = 2785, df = 11, p = <0.001) among almost all the months (TukeyHSD: p < 0.05; Table S2.1). The CHL concentration was lower in October, slightly increasing from

November to February, further decreasing between March and May, and finally increasing from June to July (Fig 2.4, green line). Differences in CHL were found (ANOVA: F = 403, df = 11, p = <0.001) among almost all the months (TukeyHSD: $p < 0.05$; Table S2.1). The whale shark SPUE in relation to the oceanographic variables showed SST and CHL preferences ranging from 27 to 29 °C and 0.10 to 0.16 $mg.m^{-3}$, respectively (Fig 2.4).

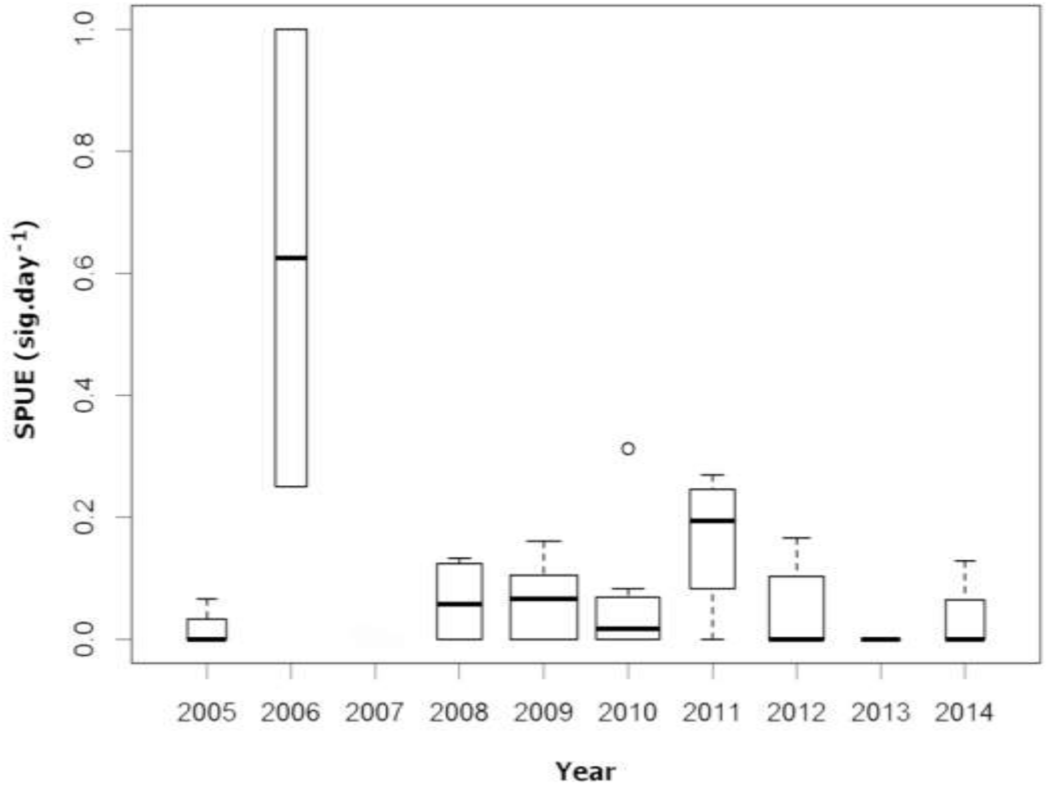


Figure 2.3- Distribution of whale shark sightings per year. SURV Sightings per Unit of Effort (SPUE; $sig.day^{-1}$) per year of *R. typus* in the ASPSP. The width of the boxes is proportional to the square-roots of the number of observations in the groups, the horizontal bar is the median and the open circle indicates a single outlier.

Demographic size structure

The mean ± SD size of whale sharks recorded in SURV was 8.27 ± 2.52 m (range: 2.5 to 14.0 m; n = 43) and was statistically different (Welch: t = 2.167; df = 83.28; p= 0.033) from COMP (7.24 ± 2.44 m; range: 1.8 to 14.0 m; n = 79) (Fig 2.5A). Despite the overall mean difference of 1.03 m, the changes in SURV and COMP sizes throughout the year was quite similar (Fig 2.5B,C). Given the difference between the size estimates, we decided to perform demographic analysis only with the SURV dataset. The first author made 86.4% of the SURV size estimates, while the remaining SURV observations were done by one other biologist.

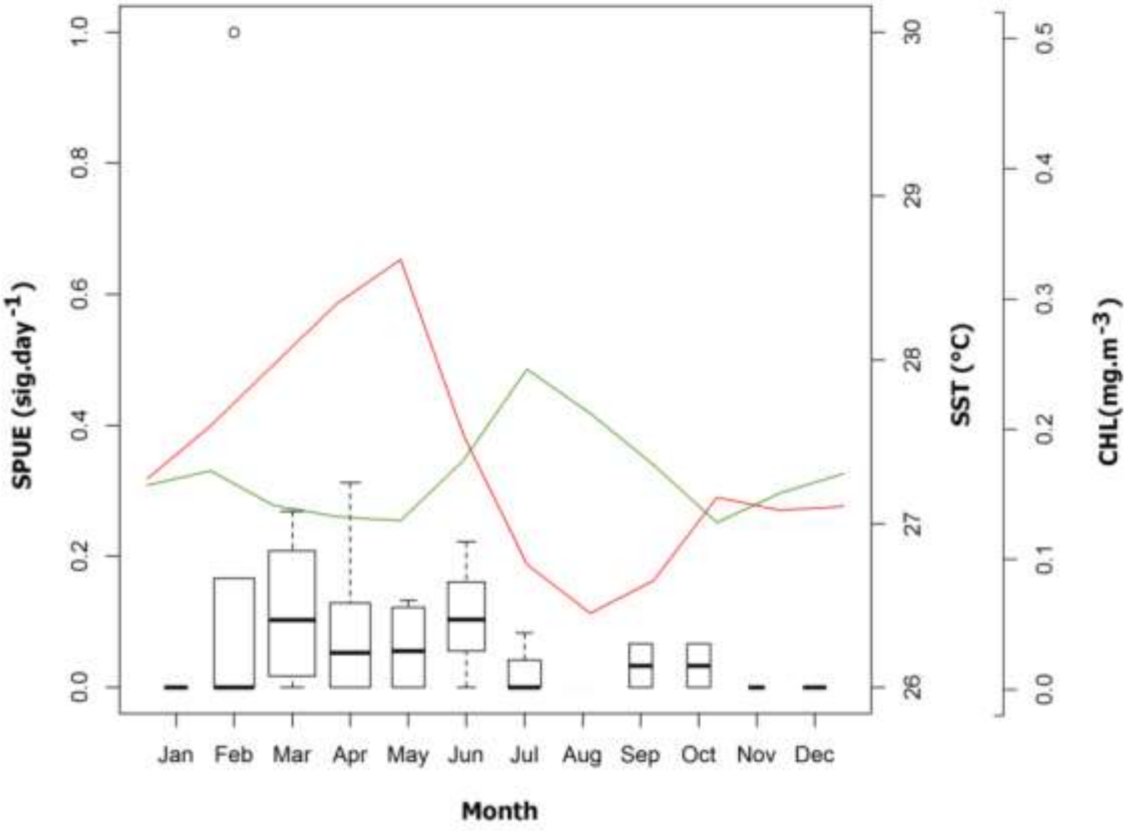


Figure 2.4- Primary productivity and sea surface temperature of ASPSP surroundings. Sighting per Unit of Effort (SPUE) in relation to sea surface temperature (SST; red line) and chlorophyll *a* concentration (CHL; green line) satellite image composites, from January 2005 to December 2014 for a ~100 km^2 area around the ASPSP. The width of the boxes is proportional to the square-roots of the number of observations in the groups, the horizontal bar is the median and the open circle indicates a single outlier.

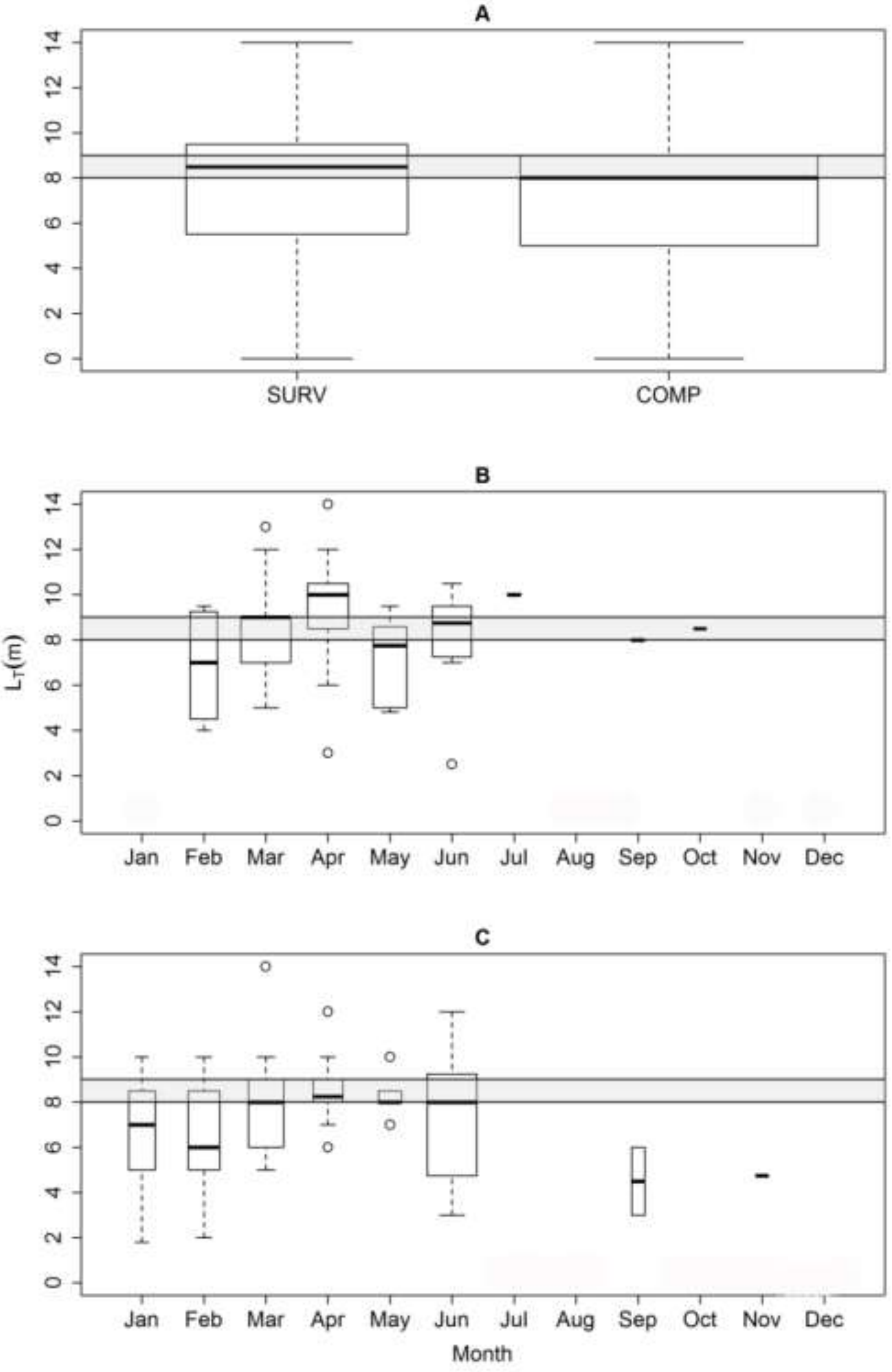


Figure 2.5- Distribution of whale shark lengths. (A) Comparison of *R. typus* sizes between SURV and COMP; and (B,C) size distribution per month for (B) SURV (n= 43) and (C) COMP (n= 79) in the ASPSP. Immature (below) and mature (above) animals are separated by a shaded area indicating the transitional 8.0-9.0 m size class. The width of the boxes is proportional to the square-roots of the number of observations in the groups, the horizontal bar is the median and the open circles indicate outliers.

Demographic analysis of whale shark sizes was conditioned to the calculation of the error in the size bias to validate the visual estimates. The L_Ts from the resampled analysis (bootstrapped) resulted in 10,000 dataset replications producing an equivalent number of means and p-values from the t-tests performed in each run. The mean of the resampled dataset for ±0.5 bias was 8.26 m, spanning from 7.94 to 8.59 m. The proportion of resampled dataset means which had significant differences (*i.e.* $p<0.05$) was 4.41%, within the confidence interval of 95% indicating no difference between the SURV L_T and the resampled means. Thus the bias in visual estimate was considered acceptable and used for further demographic analysis. Comparable results were obtained using a bias of ±1.0 m, where only 4.99% of the replicates had significant differences with an overall mean of 8.27 m spanning 7.87 to 8.68 m. Despite the slight increase in whale shark mean L_T observed from February to April (Fig 2.5B), these differences were not statistically significant (ANOVA: F = 0.547, df = 7, p = 0.793).

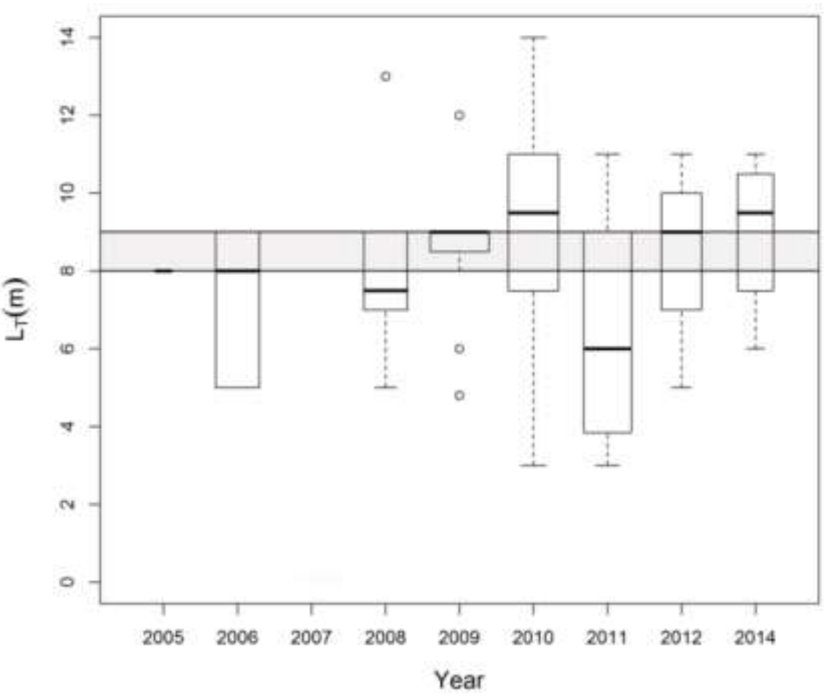


Figure 2.6- Annual distribution of whale shark lengths. Size distribution per year (SURV; n= 43) in the ASPSP. Immature (below) and mature (above) animals are separated by the shaded area indicating the transitional 8.0-9.0 m size class. The width of the boxes is proportional to the square-roots of the number of observations in the groups, the horizontal bar is the median and the open circles indicate outliers.

In almost all years the mean L_T was equal or above 8.0 m; the two exceptions, 2006 and 2011, had means of 7.3 and 6.5 m, respectively (Fig 2.6). The years with largest and smallest means were 2010 (9.1 m) and 2011 (6.5 m) but no difference in sizes were found between the years (ANOVA: F = 0.75, df = 7, p = 0.632).

The size frequency distribution exhibited a continuous distribution from 8.0 to 10.0 m with a minor peak at 10.0-11.0 m (Fig 2.7). The mean ± SD of immature and mature sharks were 5.37 ± 1.53 m and 10.25 ± 1.46 m, respectively. Based on the estimated size, 32.6% (14) of sharks were immature, and 46.5% (20) were mature. The remaining 20.9% (9) belonged to the 8.0 to 9.0 m class, not included in the demographic analysis. No differences in number of individuals were found between the two maturity classes (Pearson's χ^2 = 1.058, df = 1, p-value = 0.303). The sex was identified in 14 records (28.6%; n = 49), of which 11 were females (78.6%) and 3 were males (21.4%), a sex ratio of 3.7:1.0, with mean L_T ± SD of 9.5 ± 1.3 m (range: 6.0 to 12.0 m) and 9.4 ± 4.6 m (4.7 to 14.0 m), respectively.

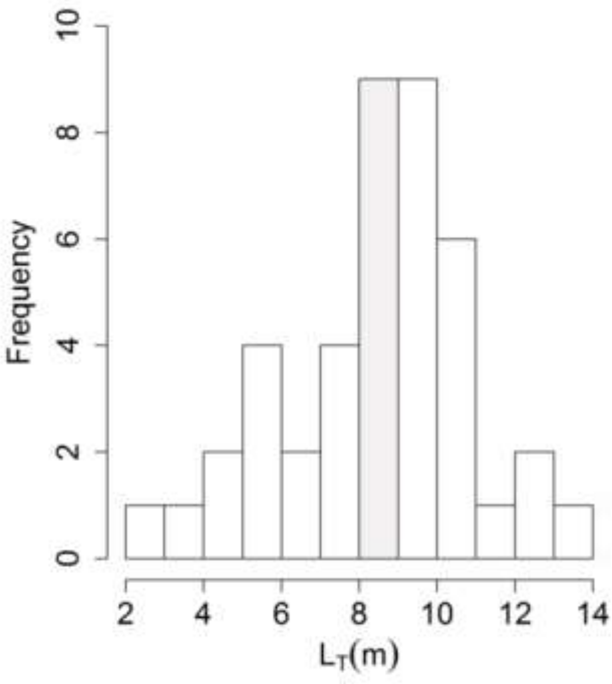


Figure 2.7- Length frequency of whale sharks. Absolute frequency of *R. typus* L_T (m) in the ASPSP. Immature (left) and mature (right) are separated by the shaded area of transitional size animals.

Of 768 photos and 133 videos (118.58 min), 27 whale sharks were recorded in the identification area, although after quality inspection only 16 had images considered adequate for photo-identification. I^3S software was used to analyze the spot patterns from these 16 animals, nine sharks with photos from the left or both sides and seven animals with photos only from the right side, which were compared only with sharks that had images from both sides. One whale shark was identified only by a remarkable scar (absence of first dorsal fin). Only two re-sights were found among the 16 (36.4%; n = 49) whale sharks photo-identified in the ASPSP. These two identifications (12.5%, n = 16) were a 10.0 m female and a 5.5 m male re-sighted one and three days after the first encounter, respectively. No match for any of the ASPSP sharks was found in the "Wildbook for Whale Sharks" global database.

Generally the whale sharks seen in the ASPSP exhibited solitary behavior. Only seven conspecific associations were recorded, with three individuals observed in the same moment on two different occasions. All other associations were composed of two sharks. An adult male with an apparent abrasion of the claspers displayed an atypical behaviour of repeatedly rolling the body longitudinally alongside and below the fishing vessel (Fig 2.8), diving and returning near the boat three times within a 10 min interval. Furthermore, some females presented a distinctly swollen pelvic region and one female had scars on both pectoral fins (Fig 2.9). Both of these findings may be suggestive of reproductive behavior.

Only on five occasions were whale sharks observed feeding by the research team; three times during the day and twice at night. Fishermen also reported several night foraging events near the boats. Surface vertical and ram-filter feeding behaviours were observed during feeding activities during both day and night. In several instances, other marine organisms were seen alongside whale sharks. The most commonly observed were remoras (*Remora brachyptera*, *R. osteochir*, *R. remora*, *Remorina albescens*), which were attached to the sharks in large numbers (up to 23 on one individual), and Chilean devil rays (*Mobula tarapacana*). Other species recorded were rainbow runner (*Elagatis bipinnulata*), almaco jack (*Seriola rivoliana*), blackjack (*Caranx lugubris*), ocean sun-fish (*Mola mola*), pilot fish (*Naucrates ductor*), yellowfin tuna (*Thunnus albacares*), blackfin tuna (*T. atlanticus*), silky shark (*Carcharhinus falciformis*), scalloped hammerhead shark (*Sphyrna lewini*), bentfin devil ray (*M. thurstoni*), and bottlenose dolphin (*Tursiops truncatus*).

Figure 2.8- Male potential courtship behaviour. Multiple rolling behaviour by a large male *R. typus* displayed with the fishing vessel and close up of its clasper abrasion recorded in the ASPSP. Credit: Sibele Mendonça©.

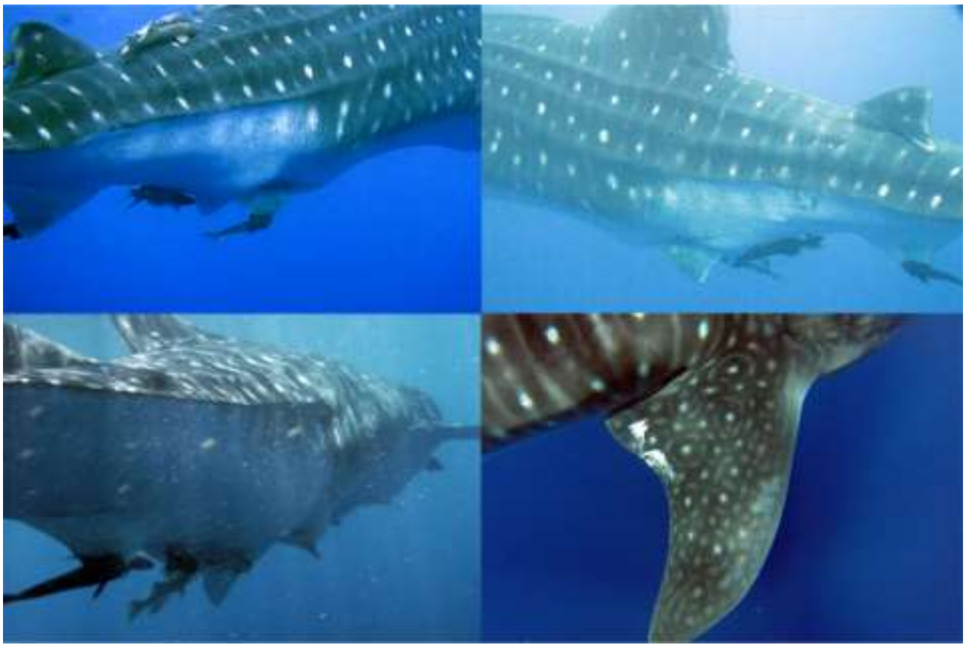


Figure 2.9- Females showing indications of reproductive activity. *R. typus* females showing swollen pelvic region and bite scar on the pectoral fins, suggestive of mating, recorded in the ASPSP. Credit: Bruno Macena©.

Discussion

Frequency of occurrence and relative abundance

Information collected through collaborators (*i.e.* diving operators, fishers, citizens), and compiled in datasets analogous to direct science-based surveys, have been used in scientific research to increase the capacity of data acquisition or to promote data collection in areas which require complex logistics (Ward-Paige and Lotze 2011; Davies et al. 2012; Vianna et al. 2014). Although traditional approaches used in scientific studies involve rigorous standardized techniques based on tested and approved methods (MacNeil et al. 2008), such parallel databases have intrinsic limitations (*i.e.* biases) that prevent their use for direct inferences for abundance, biomass and density of shark populations (MacNeil et al. 2008, Ward-Paige et al. 2010). Scientific survey data combined with citizen-science data, however, have been successfully used to identify seasonal frequency of occurrence and population structure and dynamics of whale sharks in Australia (Meekan et al. 2006; Holmberg et al. 2008; Norman and Stevens 2007; Davies et al. 2012). Nevertheless, in order to use an analogous dataset in a reliable manner, an independent *in situ* validation is necessary (Vianna et al. 2014). In the present case, the reliability of the COMP FO% from the collation of the SURV dataset was successfully verified.

Logistic difficulties can affect the development of research programs at remote and inhospitable islands such as ASPSP. Since previous research (Hazin et al. 2008) and records from fishermen had already indicated that whale shark FO% in the area was much higher during the first six months of the year, from 2009 on the major part of the research effort was carried out during this period to facilitate the deployment of satellite tags and the collection of tissue samples.

Seasonality

Whale sharks are widely distributed in the Atlantic Ocean, occurring in Central America (Caribbean Sea and Gulf of Mexico (GoM) (Hueter et al. 2013), Northwest Atlantic (Thurnbull and Randell 2006); Northeast Atlantic (Afonso et al. 2014), Equatorial Atlantic (Hazin et al. 2008), Southeast Atlantic (Sequeira et al. 2014) and Southwest Atlantic (Soto e Nisa-Castro-Neto 2000; BCLM, unpub. data). In all these locations, the whale sharks appear to show distinct spatio-temporal distributions. Strategically located in the middle of the Atlantic Ocean, the ASPSP may play an important role in the transoceanic cycle of the whale shark in the Atlantic, as suggested by a satellite-tagged female that moved from the GoM towards the mid-Atlantic Ridge, with the tag popping-off near ASPSP (Hueter et al. 2013) (Fig. 2.1). However, other evidence of connectivity between Atlantic Ocean locations, from satellite tracking or photo-identification, have so far only been found in Central America (Hueter et al. 2013).

In the Galapagos, of 82 individual whale sharks photo-identified, only 12 sharks were re-sighted within a 7-day period, and only one shark was re-sighted between years (Acuña-Marrero et al. 2014). The same authors found no matches when searching for intra and inter-annual re-sightings in the "Wildbook for Whale Sharks". These results are quite dissimilar from the coastal aggregations where the re-sighting rates are high, with intra and inter-annual matches detected and residence time varying from 11 to 180 days (Homberg et al. 2009; Ramirez Macias et al. 2012a; Hueter et al. 2013; Fox et al. 2013).

Our photo-identification analysis detected only two re-sightings with a short period of time between the encounters. Given the lack of re-sightings it was not possible to apply demographic models, thus preventing any inference regarding population size, residency time or fidelity. The absence of long-term re-sightings in the area may be explained by (1) the reduced photo-ID sample size, if the whale sharks do return to the archipelago but were not re-sighted or (2) absence of return on a long term basis. The short residence time (~2 days), strong intra-seasonal abundance and high turnover rate of Galapagos whale sharks (Acuña-Marrero et al. 2014) helped to define the assumptions of the SPUE filtering technique used here to avoid duplicates, considering the similarities between the Galapagos and ASPSP habitats. To explain the trends of occurrence of whale sharks, it is necessary to understand the dynamics of oceanographic, atmospheric and biological phenomena in the area.

Araújo and Cintra (2010) used hypothetical models of particle dispersion to predict larval plankton retention/recruitment, and ocean circulation to identify potential increases in primary productivity in the ASPSP. The authors estimated a higher probability of larval retention/recruitment in February (SEC with lowest zonal speed), whereas in June (SEC with highest zonal speed), the inverse was observed. The ocean circulation models indicated small areas of potential submerged topographic upwelling at the east side of the ASPSP, between 100-150 m depth. The latter conclusion is probably a consequence of the strengthening of the EUC, as a result of the interaction between this subsurface current and the rough bottom relief of the ASPSP area (Hekinian, 1982; Hekinian et al. 2000). Nevertheless, no large-scale upwellings have yet been described in the ASPSP area (Travassos et al. 1999; von Bröckel e Meyerhöfer 1999). A small scale, seasonal sea-water enrichment, however, is observed during the rainy season (February to May); when the increased precipitation caused by the ITCZ results in a runoff of nutrients from excretion of the abundant marine birds that congregate at the ASPSP (BCLM, *pers. obs.*).

Opportunistic feeding ground hypothesis

The whale shark swims independently of the ocean currents (Sleeman et al. 2010b); but ocean currents may provide clues on potential feeding opportunities, therefore influencing the movement of fishes (Carey and Scharold 1990; Gunn et al. 1999; Rowat and Gore 2007; Hsu et al. 2007). The filter-feeding whale shark feeds mainly on invertebrate and/or fish spawn and larvae, squid and schooling fishes (reviewed in Rowat and Brooks 2012). They aggregate to feed in specific seasons and locales where oceanographic (*i.e.* upwelling) or biological (*i.e.* fish or invertebrate spawning) phenomena occur (Heyman et al. 2001; Wilson et al. 2001; Nelson and Eckert 2007; de la Parra Venegas et al. 2011). In the Coral Sea, during the lantern fish spawning period, whale sharks associate with tuna to forage (Gunn et al. 1992). The association of whale sharks with tuna is observed elsewhere (Matsunaga et al. 2003; Sequeira et al. 2011; Ramirez Macias et al. 2012b; Afonso et al, 2014), and they may commonly forage on the same prey.

Yellowfin tuna and wahoo (the two main species fished in the ASPSP) were also the most abundant species caught during the first six months of the year (Viana et al. 2015). Both species, as well as other fishes and sharks, prey on flying fish (Vaske et al. 2003; Vaske et al. 2006a), the third most important fishery resource in the ASPSP (Viana et al. 2015). In ASPSP, records of whale shark feeding behaviours (description in Nelson and Eckert 2007; Taylor 2007; Ketchum et al. 2013) are rare, but observed on some occasions. Fishermen from ASPSP reported several foraging events in which whale sharks preyed on flying fish during the night (or their eggs and larvae), but no large feeding aggregation was observed. Therefore, despite the lack of large foraging events recorded in ASPSP, the largest concentration of planktonic organisms observed in the first six months of the year coincides with the highest abundance of whale sharks. Whale sharks may therefore use of the ASPSP area as a feeding station during their oceanic migration.

The timing of whale shark sightings in ASPSP coincides with the period of lowest current speed, highest SST and lowest CHL values. The later may suggest a potential lagged response between CHL and whale shark presence, as observed in the Azores (Afonso et al. 2014) and India (Kumari and Raman 2010), since they actively prey on zooplankton and small planktivorous fishes. Although the strengthened oceanic currents from June to August probably increase the levels of CHL due to higher nutrient contents in the water resulting from submerged upwellings in response to the rough topography, they would also tend to carry zooplankton organisms away from the archipelago. On the other hand, the CHL increase from November to February may be responsible for the biological enrichment of the waters around ASPSP from February to May, as the ocean currents are weakening and the larval retention/ recruitment is higher during this period.

The ASPSP offers optimal conditions for reproduction, spawning, larval development and feeding of invertebrates and fishes (Macedo-Soares et al. 2012). Water temperature is known to induce fish reproduction/spawning events (Sims et al. 2004; Genner et al. 2010; Pankhurst et al. 2011). Fish reproduction studies conducted in ASPSP have indicated spawning periods of several species mainly between January and June (Lessa et al. 1999; Pinheiro et al. 2011; Viana et al. 2013; Bezerra et al. 2013; Lira dos Santos et al. 2014). The abundant sally lightfoot crab (*Grapsus grapsus*) reproduces in ASPSP during the whole year, but largest abundances of ovigerous females were observed from December to May (Freire et al. 2011). The zooplankton near ASPSP was dominated by copepods followed by brachyuran crab larvae (zoea), with higher density during the night and in warmer months (Macedo-Soares et al. 2009; Brandão et al. 2013). Additionally, the most abundant fish larvae in ASPSP were the flying fishes (Exocetidae), halfbeaks (Hemiramphidae) and lantern fishes (Myctophidae) with the highest abundances increasing with distance from the archipelago (Lessa et al. 1999; Macedo-Soares et al. 2012). This could explain why whale shark foraging events were not seen with greater frequency during the day and closer to the ASPSP, where the majority of the surveys were carried out.

Demographic structure

Sexual and ontogenetic segregation is common in shark species (Springer 1967; Mucientes et al. 2009), including whale sharks (Rowat and Brooks 2012). Most coastal whale shark aggregations are composed predominantly of immature males, at sites such as Western Australia (Meekan et al. 2006; Norman and Stevens 2007), Djibouti (Rowat et al. 2007), Seychelles (Rowat and Gore 2007), Philippines (Araujo et al. 2014), Maldives (Riley et al. 2010), Belize (Graham and Roberts, 2007), Honduras (Fox et al. 2013) and Mexico (de la

Parra Venegas et al, 2011; Ramirez Macias et al. 2012a; Ramirez Macias et al. 2012b). While both large (>9 m), and female, whale sharks are seen less frequently in these aggregations, they are commonly observed at oceanic sites such as in in the Azores (Afonso et al. 2014), at Saint Helena (Clingham et al. 2016), at Baja California Sur (Ramirez Macias et al. 2012a; Ketchum et al. 2013), at the Galapagos Islands (Acuña-Marrero et al. 2014), and as we show here at the ASPSP. In Baja California and the Galapagos, a great number of adult females were observed, including potentially gravid ones, as inferred by their distended pelvic region. Nevertheless, the only confirmed pregnant female recorded to date was caught in Taiwan (Joung et al. 1996). The size of ASPSP whale sharks ranged from 2.5 m to 14.0 m (mean = 8.27 m) with roughly equal numbers of immature and mature animals, indicating an absence of ontogenetic segregation. This type of structure is uncommon worldwide, as most other sites show primarily immature or mature animals, but not both. Similar size distributions have been observed in Taiwan and India, with whale sharks spanning from 1.0 to 13.0 m (mean = 4.6 m) (Hsu et al. 2012) and from 3.1 m to 14.5 m (mean = ~7.0 m) (Pravin 2000), respectively, but in both locations the number of immature animals was considerably greater than that seen at ASPSP.

In the Galapagos, the whale sharks have been found to span from 4.0 to 13.1 m with large females dominating (91.5%), and the mean size of immature (5.33 m) and mature (11.35 m) (Acuña-Marrero et al. 2014), close to that observed at ASPSP. Similarities between the Galapagos and ASPSP are significant, as both are isolated oceanic environments located in the equatorial region. Given the similarity of the habitat, it is perhaps not surprising they have a similar population structure composed of transient adult females with a high incidence of pregnancy. In St. Helena, preliminary results show an equal mix of mature male and females with sizes varying from 8.5 to 11.0 m in length. Additionally, the authors suggest evidence of mating behaviour in the area based on two anecdotal records (Clingham et al. 2016). Given the information on demographic structure of whale sharks in pelagic environments, oceanic habitats appear to have important roles in the reproductive cycle of whale sharks.

The age at sexual maturity of a given species is a critical factor in evaluating the dynamics of its population, particularly for endangered or vulnerable species, and for those with slow maturation rates (Pierce and Norman 2016, Bradshaw et al. 2007). In Western Australia, Norman and Stevens (2007), indicated that ~10% of male whale sharks less than 8.0 m were mature, based on clasper morphology, while 50% and 95% were adult at 8.1 m and 9.1 m, respectively. About 50% of male whale sharks from South Africa and Mozambique (also Indian Ocean sites) were mature at 9.1 m (Rohner et al. 2015). In the Mexican Caribbean (Atlantic Ocean), 50% and 95% of the males were mature at 7.0 m and 8.1 m, respectively, based on clasper morphology (Ramirez Macias et al. 2012b). Female sharks commonly reach maturity at larger sizes than males. Whale shark females smaller than 9.0 m dissected in India (Pai et al. 1983; Satyanarayana Rao 1986)) and South Africa (Beckley et al. 1997) were all immature, while the smallest mature female observed in Taiwan was 9.6 m (Hsu et al. 2014a). Geographic differences in size at maturity have been observed in other shark species (Simpfendorfer 1992; Castro 1996; Bonfil 2008) and may also occur for whale sharks given the information above.

Size estimates of whale sharks, using surface reference or underwater visual observation, tend to have an error of ± 0.5 m (Meekan et al. 2006; Graham and Roberts 2007; Homberg et al. 2009), particularly if the sharks are >8.0 m (Acuña-Marrero et al. 2014; Sequeira et al. 2016). Visual measurements of whale sharks compared with laser photogrammetry resulted in calculated errors of *c.* ± 0.70 m and less than one meter, in Mozambique (Rohner et al. 2011) and Galapagos (Acuña-Marrero et al. 2014), respectively, of visual estimations. In Western Australia, the visual estimate error was calculated between 0.75 and 1.49 m compared with stereo-video camera (Sequeira et al. 2016). The studies compared above had a tendency to underestimate the visual measurements of the sharks compared to the more reliable measurements techniques. Considering these errors of visual estimation, the bias of ±0.5 and ±1.0 m used to validate our visual measurements seemed reasonable, thus the SURV L_T data was used to perform demographic analysis. Given the differing estimates of whale shark size at maturity noted in the literature, and the potential for 0.5 to 1.0 m error in size estimation, we chose to exclude the 8.0-9.0 m transitional size category from the demographic analysis.

Reproductive ground hypothesis

Despite the absence of a statistically significant difference in monthly mean sizes of whale sharks at the ASPSP, a slight increase between February and April is noticeable and may suggest that the largest specimens are arriving in the area during the peak period of abundance. Movement of satellite-tracked whale sharks from the Gulf of Mexico revealed that a 7.5 m female, with external evidence of possible pregnancy, traveled from Holbox, Mexico, through the mid-Atlantic Ocean (Hueter et al. 2013). The tracking started in August and stopped after the tag detached in January, at a position 543 km southeast from the ASPSP (Fig. 2.1). The location and timing of tag detachment coincides with the beginning of the warmest period in the equatorial region. There is evidence for reproductive behavior at the ASPSP in other elasmobranch species as well. In devil rays (*M. thustoni* and *M. tarapacana*) in the ASPSP, reproductive behaviour (following, close swim, and grouping) and anatomical evidence of mating (bite scars in females and abraded claspers in males) have been seen in captured animals and by underwater recordings between March and June in ASPSP (BCLM, *pers. obs.*). Additionally, one early pregnant *M. thurstoni* (Mendonça et al. 2012) and a mid-term pregnant scalloped hammerhead shark (BCLM, *pers. obs.*) were captured in March and April, respectively, indicating the use of ASPSP as part of the reproductive cycle for some elasmobranch species in the first six months of the year. Whale sharks of 8.0 to 9.0 m, that are completing their maturation and moving into their reproductive lifespan, may be making use of the warmer waters of the equatorial Atlantic and of the higher food abundance in the ASPSP, compared to the oligotrophic open ocean surrounding it.

The mean sizes of both male and female whale sharks seen at the ASPSP were close to that of mature animals. In April 2010, a solitary male was seen performing what appeared to be a mating behavior, swimming very close to the boat, rolling longitudinally and curving the body ventrally three times within a 10 min interval. This male showed abrasion of the claspers (Fig. 2.8) indicating mating activity may have occurred recently (Norman and Stevens 2007). In Seychelles, a 9.5 m whale shark was videoed performing exactly the same behaviour in relation to the research boat (D. Rowat, *pers. comm.*) Martin (2007) noted putative courtship behaviours of following and parallel swimming performed by whale sharks in Western Australia. Many reproductive behaviours of elasmobranchs have been already described (Pratt and Carrier 2001) but the longitudinal rolling observed in ASPSP and Seychelles appears to be a new behavior.

The lack of neonates and/or large females in coastal aggregations suggests that mating/pupping areas of whale sharks are likely to be located far from the coastal environment. Conversely, the presence of gravid females in oceanic regions, such as Baja California Sur (Ketchum et al. 2013; Ramirez Macias et al. 2012a) and Galapagos Islands (Acuña-Marrero et al. 2014), St Helena (Clingham et al. 2016) and now the ASPSP, and the concurrent occurrence of small juveniles in areas from major ocean basins such as Indian [Djibouti (Rowat et al. 2007); India, Pakistan, Bangladesh and Seychelles (Rowat et al.

2008)]; Indo-Pacific [Philippines (Aca and Smith 2011); Taiwan (Hsu et al. 2014b)]; Pacific [open ocean (Kukuyev 1996)] and Atlantic [equatorial open ocean (Wolfson 1983; Kukuyev 1996); ASPSP (Hazin et al, 2008; present study)], provides clues to where reproductive activity may occur worldwide.

These data seem to support the hypothesis that whale shark mating and/or parturition might occur in the deep ocean (Speed et al. 2007; Rowat et al. 2007; Martin 2007; Hueter et al. 2013), and oceanic features (*i.e.* seamounts and islands) like ASPSP may offer suitable conditions for the development of part of the reproductive cycle of this species. Despite the lack of additional indicators of reproductive activity of whale sharks in ASPSP, due to the difficulty of direct *in situ* observation, the evidence from the animals presented here raises the possibility that whale sharks use the ASPSP for reproductive purposes. The suspected gravid females plus the young whale sharks observed in ASPSP, combined with recorded neonates in the equatorial Atlantic Ocean (Wolfson 1983; Kukuyev 1996; Fig 2.1), suggest that the surrounding areas of ASPSP could be also used as pupping ground. Additional evidence and/or the development of new techniques that allow the identification of sexual maturity of free swimming sharks are needed to better understand the reproductive ecology of whale sharks and the role of this remote archipelago. The use of satellite tags at ASPSP may help to elucidate the migration patterns of young sharks and potential pregnant females in the Atlantic Ocean.

Conclusions

The majority of the studies on whale sharks have been carried out on coastal feeding aggregations, with few studies developed so far in deep-water oceanic regions. Information on where whale sharks reproduce (*i.e.* mating and pupping areas) is crucial to the development of appropriate conservation measures at regional and international levels. The present study provides information on the ecology and biology of whale sharks visiting an isolated oceanic habitat located in the middle of the equatorial Atlantic Ocean, the ASPSP. The seasonality of occurrence is likely related to the oceanographic and biological features of the area, suggesting that whale sharks could be using the ASPSP to opportunistically feed during their transoceanic migration. The demographic structure of the ASPSP aggregation is quite different from most other aggregations, with a lack of size segregation resulting in individuals ranging from small juveniles to large adults. Juvenile and adult whale sharks may be using the archipelago with different purposes. Reproductive indicators suggest that the archipelago could serve as a mating and/or pupping ground, although more information is needed to test these hypotheses. Regardless of its role, the ASPSP insular habitat is important from an ecological point of view and represents a unique opportunity to gather relevant information on this iconic species.

Supporting information

Table S2 1-Summary of TukeyHSD test results from the comparisons environmental variables per month.

	SST				CHL			
Month	**diff**	**Lwr**	**Upr**	**P**	**diff**	**lwr**	**upr**	**p**
2-1	0.3233	0.2353	0.4112	0.0000	0.0107	-0.0008	0.0222	**0.0958**
3-1	0.6993	0.6115	0.7872	0.0000	-0.0156	-0.0256	-0.0055	0.0000
4-1	1.0731	0.9852	1.1610	0.0000	-0.0243	-0.0341	-0.0144	0.0000
5-1	1.3379	1.2500	1.4257	0.0000	-0.0271	-0.0368	-0.0175	0.0000
6-1	0.2586	0.1707	0.3464	0.0000	0.0193	0.0097	0.0288	0.0000
7-1	-0.5228	-0.6107	-0.4350	0.0000	0.0883	0.0788	0.0979	0.0000
8-1	-0.8207	-0.9086	-0.7328	0.0000	0.0546	0.0450	0.0643	0.0000
9-1	-0.6197	-0.7075	-0.5318	0.0000	0.0154	0.0057	0.0252	0.0000
10-1	-0.1134	-0.2012	-0.0255	0.0015	-0.0285	-0.0382	-0.0187	0.0000
11-1	-0.1918	-0.2796	-0.1039	0.0000	-0.0059	-0.0157	0.0038	**0.7023**
12-1	-0.1675	-0.2554	-0.0797	0.0000	0.0088	-0.0014	0.0190	**0.1770**
3-2	0.3761	0.2881	0.4640	0.0000	-0.0263	-0.0368	-0.0158	0.0000
4-2	0.7498	0.6619	0.8378	0.0000	-0.0350	-0.0453	-0.0246	0.0000
5-2	1.0146	0.9267	1.1026	0.0000	-0.0378	-0.0479	-0.0277	0.0000
6-2	-0.0647	-0.1526	0.0233	**0.4035**	0.0086	-0.0015	0.0186	**0.1841**
7-2	-0.8461	-0.9340	-0.7581	0.0000	0.0776	0.0676	0.0877	0.0000
8-2	-1.1440	-1.2319	-1.0560	0.0000	0.0440	0.0338	0.0541	0.0000
9-2	-0.9429	-1.0309	-0.8550	0.0000	0.0047	-0.0055	0.0150	**0.9384**
10-2	-0.4366	-0.5246	-0.3487	0.0000	-0.0392	-0.0494	-0.0289	0.0000
11-2	-0.5150	-0.6030	-0.4271	0.0000	-0.0166	-0.0269	-0.0064	0.0000
12-2	-0.4908	-0.5787	-0.4028	0.0000	-0.0019	-0.0126	0.0088	**1.0000**
4-3	0.3738	0.2859	0.4616	0.0000	-0.0087	-0.0174	0.0000	0.0510
5-3	0.6385	0.5507	0.7264	0.0000	-0.0115	-0.0200	-0.0031	0.0005
6-3	-0.4408	-0.5286	-0.3529	0.0000	0.0348	0.0265	0.0432	0.0000
7-3	-1.2222	-1.3100	-1.1343	0.0000	0.1039	0.0955	0.1122	0.0000
8-3	-1.5200	-1.6079	-1.4322	0.0000	0.0702	0.0618	0.0787	0.0000
9-3	-1.3190	-1.4068	-1.2311	0.0000	0.0310	0.0224	0.0396	0.0000

10-3	-0.8127	-0.9006	-0.7249	0.0000	-0.0129	-0.0215	-0.0043	0.0001
11-3	-0.8911	-0.9789	-0.8032	0.0000	0.0096	0.0010	0.0183	0.0139
12-3	-0.8669	-0.9547	-0.7790	0.0000	0.0244	0.0152	0.0335	0.0000
5-4	0.2648	0.1769	0.3526	0.0000	-0.0028	-0.0111	0.0054	**0.9935**
6-4	-0.8145	-0.9024	-0.7267	0.0000	0.0435	0.0354	0.0516	0.0000
7-4	-1.5959	-1.6838	-1.5081	0.0000	0.1126	0.1045	0.1207	0.0000
8-4	-1.8938	-1.9817	-1.8059	0.0000	0.0789	0.0707	0.0872	0.0000
9-4	-1.6928	-1.7806	-1.6049	0.0000	0.0397	0.0313	0.0481	0.0000
10-4	-1.1865	-1.2743	-1.0986	0.0000	-0.0042	-0.0126	0.0042	**0.8941**
11-4	-1.2649	-1.3527	-1.1770	0.0000	0.0183	0.0099	0.0267	0.0000
12-4	-1.2406	-1.3285	-1.1528	0.0000	0.0331	0.0241	0.0420	0.0000
6-5	-1.0793	-1.1671	-0.9914	0.0000	0.0464	0.0385	0.0542	0.0000
7-5	-1.8607	-1.9486	-1.7728	0.0000	0.1154	0.1076	0.1233	0.0000
8-5	-2.1586	-2.2464	-2.0707	0.0000	0.0818	0.0738	0.0898	0.0000
9-5	-1.9575	-2.0454	-1.8697	0.0000	0.0425	0.0344	0.0507	0.0000
10-5	-1.4512	-1.5391	-1.3634	0.0000	-0.0013	-0.0095	0.0068	**1.0000**
11-5	-1.5296	-1.6175	-1.4418	0.0000	0.0212	0.0130	0.0293	0.0000
12-5	-1.5054	-1.5932	-1.4175	0.0000	0.0359	0.0272	0.0446	0.0000
7-6	-0.7814	-0.8693	-0.6936	0.0000	0.0691	0.0613	0.0768	0.0000
8-6	-1.0793	-1.1671	-0.9914	0.0000	0.0354	0.0275	0.0433	0.0000
9-6	-0.8782	-0.9661	-0.7904	0.0000	-0.0038	-0.0119	0.0042	**0.9239**
10-6	-0.3720	-0.4598	-0.2841	0.0000	-0.0477	-0.0557	-0.0397	0.0000
11-6	-0.4503	-0.5382	-0.3625	0.0000	-0.0252	-0.0332	-0.0172	0.0000
12-6	-0.4261	-0.5140	-0.3382	0.0000	-0.0105	-0.0191	-0.0019	0.0041
8-7	-0.2979	-0.3857	-0.2100	0.0000	-0.0337	-0.0416	-0.0258	0.0000
9-7	-0.0968	-0.1847	-0.0090	0.0166	-0.0729	-0.0809	-0.0649	0.0000
10-7	0.4095	0.3216	0.4973	0.0000	-0.1168	-0.1248	-0.1088	0.0000
11-7	0.3311	0.2432	0.4189	0.0000	-0.0943	-0.1023	-0.0862	0.0000
12-7	0.3553	0.2675	0.4432	0.0000	-0.0795	-0.0881	-0.0709	0.0000
9-8	0.2010	0.1132	0.2889	0.0000	-0.0392	-0.0474	-0.0311	0.0000
10-8	0.7073	0.6195	0.7952	0.0000	-0.0831	-0.0912	-0.0750	0.0000

11-8	0.6289	0.5411	0.7168	0.0000	-0.0606	-0.0688	-0.0524	0.0000
12-8	0.6532	0.5653	0.7410	0.0000	-0.0458	-0.0546	-0.0371	0.0000
10-9	0.5063	0.4184	0.5941	0.0000	-0.0439	-0.0522	-0.0356	0.0000
11-9	0.4279	0.3400	0.5158	0.0000	-0.0214	-0.0297	-0.0131	0.0000
12-9	0.4521	0.3643	0.5400	0.0000	-0.0066	-0.0155	0.0022	**0.3763**
11-10	-0.0784	-0.1662	0.0095	**0.1351**	0.0225	0.0142	0.0308	0.0000
12-10	-0.0541	-0.1420	0.0337	**0.6836**	0.0373	0.0284	0.0461	0.0000
12-11	0.0242	-0.0636	0.1121	**0.9991**	0.0147	0.0059	0.0236	0.0000

Output from TukeyHSD test of monthly comparison of sea surface temperature (SST) and chlorophyll a concentration (CHL). Bold values indicate no significant difference ($p > 0.05$).

Capítulo 3- Movements of whale sharks (*Rhincodon typus*) from an isolated archipelago located in the mid-equatorial Atlantic Ocean

Abstract

Satellite-based technology has been of great relevance to unravel many aspects of marine life ecology, ultimately aiding in the conservation of various species. Whale shark satellite tagging studies in recent years has gathered important information on spatial ecology and diving behavior of the species in all ocean basins. Most of whale shark aggregation sites worldwide are formed predominantly by immature specimes, close to the continental margin. Conversely, the observation of mature sharks in few oceanic environments suggests that these habitats are important for the adult portion of the species. The only information on whale shark long-distance oceanic movement in the Atlantic Ocean derives from a single female tagged in the Gulf of Mexico that moved towards central equatorial Atlantic. In the present study, whale sharks were satellite tagged aiming at describing their horizontal displacements and infering on the influence of biophysical and environmental factors in the diving behavior of the species from an oceanic remote archipelago located at the Mid-Atlantic Ridge in the equatorial Atlantic Ocean. Horizontal movements of the tagged sharks were assessed using the KFtrack state-space model and the behavioral diving patterns in relation to environment predicted using generalized linear mixed-effect models (GLMM) and generalized linear models (GLM). Whale shark horizontal movements in the present study corroborates previous studies in the region, which suggested a short-residency time for the species and distinct movement patterns for juveniles and adults. Moreover, the diving behavior of the species (*i.e.* time spent at great depths and deep divings) seems to be influenced by local and seasonal environmental conditions. The satellite tagging results presented here are consistent with the hypotheses of ASPSP being a "meeting point" in the transatlantic migration route of whale sharks with different objectives for different age groups. The immature specimes seem to use it for foraging purposes, while the mature ones may also be utilizing it for reproduction. To better understand the movement patterns of whale sharks, particularly of mature specimes, is of extreme relevance in order to ensure the conservation of the species.

Key-words: spatial ecology; vertical migration; deep diving behavior; feeding; reproduction

Introduction

The satellite-based technology to monitor marine animals in their natural environment has been widely used and it is a great tool to improve the knowledge on the bioecology of various species (Block et al 1998, Goodley et al. 2008; Sims 2010; Hammerschlag et al. 2011). Nevertheless, it has already been instrumental to advance the knowledge on the distribution (Southall et al. 2005), habitat use (Afonso and Hazin 2015) and selection (Curtis et al. 2014), spatial population structure (Block et al. 2005), movement patterns (Hazin et al. 2013) and many other related fields of several species, such as physiology (Thums et al. 2012), foraging strategies (Motta et al. 2010), swimming behavior (Meekan et al. 2015) and conservation biology (Queiroz et al. 2016).

The whale shark (*Rhincodon typus* Smith 1828) is the largest species among the elasmobranchs, being widely distributed in tropical and subtropical regions of all oceans (Colman 1997; Compagno et al. 2001; Rowat and Brooks 2012). Generally found in coastal feeding aggregations (Heyman et al. 2001; Meekan et al. 2006; de la Parra Venegas et al. 2011), it can be also observed in oceanic environments (Hazin et al. 2008; Ketchum et al. 2012; Hearn et al. 2013; Afonso et al. 2014). It is an epipelagic species most of the time (Wilson et al. 2006; Tyminski et al. 2015), but it is also capable to make use of the meso- and bathypelagic zones (Brunnschweiler et al. 2009; Tyminski et al. 2015; present study). Recently, it has been shown that insular deep-ocean environments are ecologically and biologically important for the species because the mature part of their sub-populations may use these regions for reproductive purposes (Ketchum et al. 2012; Ramírez-Macías et al. 2012; Acunã-Marrero et al. 2015). This is the case of the present study area- the archipelago of São Pedro and São Paulo (ASPSP), Brazil (Macena and Hazin 2016).

Given the advantages of using satellite telemetry (*e.g.* remote monitoring, synoptic environmental data), these tools were successfully used to track whale sharks in Australia (Wilson et al. 2001), Gulf of Mexico (GoM) (Hueter et al. 2013), Galapagos Island (Hearn et al. 2013), among other locations (see Rowat and Brooks 2012, for review). The gentle behavior of whale sharks makes them particularly accessible to tagging experiments due to their size, slow surface swimming and predictable areas of seasonal occurrence. Besides, the species is greatly susceptible to impacts due to their *k*-selection life history, being thus listed as ‘endangered’ by the International Union for the Conservation of Nature (IUCN; Pierce and Norman 2016) and also by the Brazilian Ministry of Environment (MMA, 2004), increasing the importance of studies on the species.

The first two satellite tracking experiments on *R. typus* were conducted in late 1990's. The first took place in the Gulf of California (Eckert and Stewart 2001), where 17 animals were tracked and showed different movements. Two sharks travelled great distances, one of them presenting a controversial tracking (Hearn et al. 2013; Sequeira et al. 2013) of 13,000 km over 37 months towards western Pacific Ocean and the other swimming *c.* 7,700 km over almost 22 months westward. The second experiment was carried out in South-east Asia, where two of the six tracked sharks travelled 4,567 and 8,025 km (Eckert et al. 2002). From the second half of the 2000's, whale shark satellite tracking studies expanded significantly, with satellite taggings being carried out in the three major ocean basins (Hammerschlag et al. 2011). These experiments resulted in a great deal of information on horizontal and vertical movements from different parts of the world (Graham et al. 2006; Wilson et al. 2006; Brunnschweiler et al. 2009; Berumen et al. 2014; among others), including details on diving physiology (Thums et al. 2012) and behavior (Tyminski et al. 2015). Satellite tagging data were also used in association with alternative scientific methods to elucidate different aspects of the species' life history, such as the assessment of foraging ecology (Motta et al. 2010) and the relationship with environmental factors inferred by ecological modeling techniques (Sleeman et al. 2010b).

Despite a relatively good amount of information on satellite tracking of whale sharks, data from the Atlantic Ocean are still scarce and mostly restricted to the GoM and the Caribbean (Graham et al. 2006; Gifford et al. 2007; Hueter et al. 2013; Tyminski et al. 2015), underlining the need for more satellite tagging efforts in this ocean basin. Recently, an 8 m female, possibly pregnant, was satellite tagged in the GoM and travelled over 7,000 km in 150 days, with the tag being released southeast of ASPSP (Hueter et al. 2013). Information like this emphasizes the importance of elucidating the movement patterns of whale sharks in oceanic habitats, where most of the mature specimens are found. Moreover, the tracking data available from literature are generally from coastal feeding aggregations, underlining the relevance of conducting satellite tagging in oceanic ecosystems.

The ASPSP is a very small and isolated oceanic archipelago geographically located in the equatorial mid-Atlantic Ridge. It is an important multi-use oceanic habitat for *R. typus*, providing food resources in the middle of the ocean and possibly being also used for reproductive purposes (Macena and Hazin 2016). Beyond the ecological importance of the species, the strategic location of ASPSP, in the center of the Atlantic Ocean, makes it biogeographically relevant. Firstly, it acts like a hotspot of pelagic biodiversity (Morato et al.

2010), which, in association with particular environmental factors and meso-scale oceanographic features (*i.e.* upwellings, eddies or fronts) (Wingfield et al. 2011), enhances the biological productivity of the oligotrophic oceanic environment (Palacios et al. 2011) surrounding it. Besides, it plays an important role in the migratory route of a wide range of marine species (Worm et al. 2003, 2005), including the whale shark (Hazin et al. 2008).

Understanding the movement patterns of whale sharks in oceanic habitats are critical to elucidate their migration routes and to identify the importance of insular ecosystems for the species, especially for its mature portion, ultimately supporting adequate conservation measures to protect both the species and the marine habitat. In the present study, whale sharks were satellite tagged to assess their horizontal displacements and diving behavior in relation to biophysical and environmental variables, from an insular deep-ocean environment in the middle of the Atlantic Ocean.

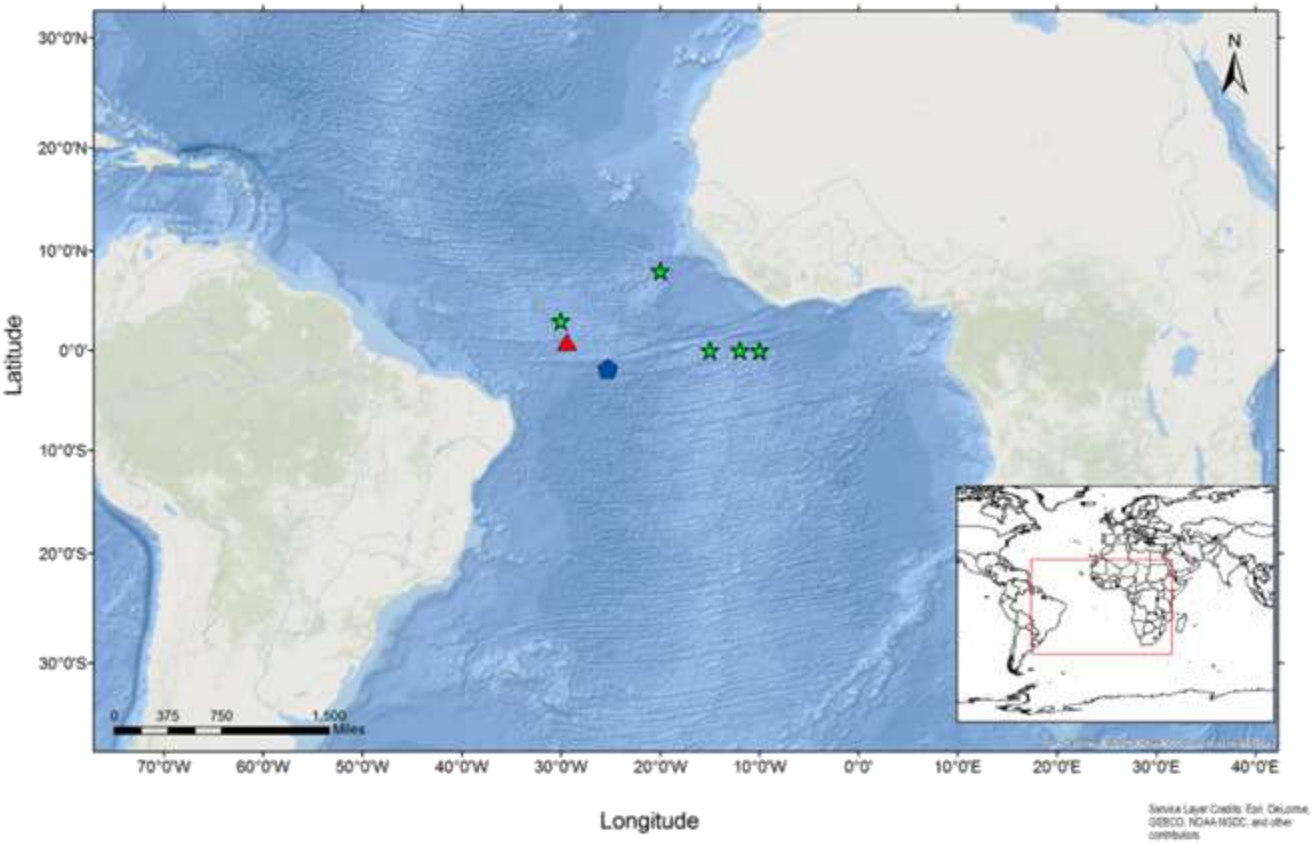
Material and Methods

Study Area

The ASPSP is a remote group of small rocky islets, located in the mid-Atlantic Ridge, almost in the midst of the equatorial Atlantic Ocean (00°55’03’’N; 029°20’45’’W), approximately 100 km north from the equator, between both north and south hemispheres; and almost at midway between South America (1,100 km from Brazil) and Africa (1,600 km from Guinea Bissau) (Fig 3.1). A detailed description of the ASPSP region can be found in Macena and Hazin (2016).

Satellite tags

Pop-up satellite archival transmitting tag (PSAT) and two types of satellite-linked transmitting tag (SAT) from Wildlife Computers, USA, were used. The PSAT tag, model Mk-10, archives light intensity (converted in geo-location), pressure (converted in depth) and water temperature readings during deployment. The Mk-10 self-releases from the whale shark after a user-programmed period to send summaries of the archived data to the ARGOS satellite system. The SAT tag, model SPLASH, collects pressure, water temperature and the geo-location, calculated by the position from the received signal when the tag reaches the surface and successfully transmit at least four messages to the ARGOS satellite system containing all collected data. The SAT tag model SPOT is similar to SPLASH but do not have pressure sensor. The precision of geo-location estimates for both SAT tags used is classified according to location scores where the best locations varies from 1,500 m to 250 m respective from the values of 0 to 3 (Argos, 2016). The estimated position is finer when more than three messages are received by the Argos satellite. When three or less messages are received, the estimate is classified as A or B (>1500 km), respectively, while the class Z is considered an invalid location.



Service Layer Credits: Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

Figure 3.1- Study area. Geographic location of the archipelago of São Pedro and São Paulo, Brazil (red triangle). Blue pentagon indicates pop-up location of a potentially pregnant whale shark tagged in the Gulf of Mexico (Hueter et al. 2013). Green triangles indicate neonate (<1m) observations (Wolfson 1983; Kukuyev 1996).

Mk-10 tags were arranged with 2.0 mm polyamide monofilament coated with high-resistance spectra braid and dark heat shrinking tubing according procedures conducted in Hazin et al. (2013). The SAT tags were rigged with 1.8 mm stainless steel multifilament coated with polyamide tube. Tags were fixed to the whale sharks with a 2,000 mm aluminum pole with a spike of 150 mm and custom-made stainless steel dart of 55 mm.

Satellite tag programming

The PSAT and SAT tags (SPLASH and SPOT) were programmed to record depth (±0.5 m) and water temperature (± 0.05°C) every 10 seconds, and summarize the data into temporal bins of 3 to 6 hours. The PSATs were programmed to pop off after 90 to 180 days, and the depth and temperature data binned into 14 user-defined strata. The SAT data were binned in 12 strata (manufacturer's maximum number of strata allowed). Despite of slight variations in deployment, the depth bins were classed as < 1; 1−5; 5−10; 10–20; 20–40; 40–60; 60–80; 80–100; 100–300; 300–450; 450–750; 750–900; > 900 m, whereas temperature strata were arranged as < 4; 4–8; 8–12; 12–14; 14–18; 18–20; 20–22; 22–24; 24–26; 26–28; 28–29; > 29°C.

Satellite tag deployment

Six whale sharks, three males and three females, spanning from 4.8 to 9.5 m, were tagged with satellite transmitters in ASPSP (Table 3.1). One shark was double tagged with Mk-10 and SPOT (WS-03), however, the SAT lasted only for four days of tracking. Other shark (WS-04) was tagged twice; the first tag deployed (SPOT) was lost after 4 days of tracking. On the occasion, the shark was swimming around an illegal fishing vessel in the ASPSP surroundings when one of the fishermen jumped into the water and took the tag off the shark. Luckily, the whale shark returned to ASPSP after seven days of the first encounter making it possible to tag the animal again with an Mk-10 tag (Table 1). Both WS-02 and WS-03 sharks presented enlarged abdomen, suggestive of pregnancy. The time between the deployment and pop-up of all tags varied from 3 to 19 days (n = 55 d) with a mean of 9.8 d. Two tags never reported the collected data. All Mk-10 which successfully transmitted attained the maximum depth supported by the tag (~1,800 m) and were premature released. Only the whale sharks with more than 10 days at liberty were used in the study of horizontal and vertical movements, resulting in 47 d of tracking (mean of 15.6 d).

Data processing

The data transmitted by the tags were downloaded from the CLS Argos System and decoded using tag manufacturer's software WC-DAP® (Wildlife Computers, USA). After decoding, only for PSAT, the raw light data were separately processed in WC-GPE® for light attenuation correction and visual inspection of geo-location estimates (*i.e.* exclusion of the light curves grossly distinct from nearby locations).

Table 3.1- Summary of whale shark tagging. Description of whale shark satellite tagging conducted in the ASPSP *Double tagging; **Same shark re-tagged; DaL- days at liberty; TLD- total linear distance; LRM- linear rate of movement.

						Release					
ID tag	**ID**	**Size**	**Sex**	**Type**	**Deployment date**	**Date**	**Lat**	**Lon**	**DaL**	**TLD (km)**	**LRM (km.day-1)**
78014	WS-01	4.8	M	SPLASH	05/23/09	05/25/09	1.305	-29.823	3	68.19	22.73
73059	WS-02	9.0	F	MK10	06/19/09	07/01/09	1.482	-34.429	12	568.34	47.36
95269	WS-03.1*	9.0	F	SPOT	03/27/10	04/01/10	2.452	-28.978	4	-	-
90814	WS-03.2*	9.0	F	MK10	03/27/10	04/14/10	3.43	-32.475	18	445.86	24.77
95270	WS-04.1**	6.0	M	SPOT	02/27/11	03/03/11	0.919	-29.342	5	-	-
90817	WS-04.2**	6.0	M	MK10	03/06/11	03/19/11	1.0067	-22.294	13	784.32	60.33
52664	WS-05	5.5	M	MK10	03/15/11	-	-	-	-	-	-
129565	WS-06	9.5	F	MK10	05/30/15	-	-	-	-	-	-

Data analysis

The geo-location estimates were refined using the state space model Kalman Filter with the function KFtrack (Sibert and Nielsen 2007). Two additional corrections for the geolocation estimates were separately applied, one for the sea surface temperature (UKFSST; Lam et al. 2008) and other for bathymetry (analyzepsat; Galuardi et al. 2012). The total linear distance (TLD) is the straight-line distance (in km) between tag deployment and pop-up locations. Linear rate of movement (LRM) is the straight-line distance between tag deployment and pop-up locations divided by the deployment duration (km.day^{-1}).

Vertical movements were assessed using the profiles of depth and temperature (PDT) and relative time spent at temperature (TAT) and depth (TAD) data, based on the approach used in Afonso and Hazin (2015). For PDT analysis, the maximum/minimum depths (*maxdepth*; *mindepth*) and temperatures (*maxtemp*; *mintemp*) and the differences between these variables (*depthrange*; *temprange*) were used as response to infer the influence of the predictors *diel* cycle (2-level factor comprising of 6:00-17:59h as day and 18:00-5:59h as night; GMT-2) and *moon* phase (4-level factor) (fixed effects) on individual (*ID*) whale sharks (random effect) diving behavior. A generalized linear mixed-effect models (GLMM) with Gaussian probability of distribution and 'identity' link function was used for this purpose. The predictions of the influence of these same covariates, plus the *ID*, were assessed using generalized linear models (GLM) with binomial probability distribution and 'logit' link function to infer time expended at both temperature and depth intervals. To ensure a more comprehensive vertical analysis of the PDT, the influence of selected environmental factors on the diving behavior were estimated using logistic regressions. The bins of TAD and TAT were pooled into water column layers of oceanographic interest to be used as response variables as following: surface (*D.10m*); mixed layer (*ML*), thermocline (*TC*) and deep water (*DW*); the model name prefix D and T means depth or temperature, respectively. TAD bins were grouped into oceanographic layers of interest (*D.10m*; *D.ML*; *D.TC*; *D.DW*) to assess the influence of the diel cycle and moon phase on the time spent on each depth stratum per whale shark. Temperature and depth ranges of thermocline, subsequently from the mixed layer and deep water, were estimated using the PDT data by individual shark and per month. Surface was defined as the first 10 m of water column. The GLMM and GLM were conducted using {lme4} and {MASS} libraries, respectively. All data analysis was performed using R programing language (R Development Core v3.2.2, 2015).

Results

Horizontal movements

The light-based geolocation correction performed for sea surface temperature with UKFSST did not converge. The bathymetric correction did not show any difference in the most probable tracks compared to the KFtrack models, thus only the latter was used to estimate the most probable track of the whale sharks.

The horizontal displacements indicated that the large females moved towards the western Atlantic Ocean, remaining mostly in the equatorial region; while the immature male WS04.2 moved east, towards the African continent (Fig 3.2).The whale shark WS02 presented an enlarged abdomen suggestive of pregnancy (Fig 2.9 bottom left in Macena and Hazin, 2016) and moved over a potential area of interest as suggested by the last days of tracking when the shark appeared to be circling on a particular region, when it dove to 1,972 m, culminating with the premature release of the tag (Figs 3.2, 3.3). The WS03.2 was also likely pregnant and the premature pop-up of the tag (far *c.* 300 km northeast of the WS02 pop-up) being a consequence of a deep dive as well. The WS04.2 was the only shark which moved towards east swimming on the counter-flow of the south equatorial current (SEC). The total linear distance (TLD) travelled by the sharks WS01, WS02, WS03.2 and WS04.2 were

68.19, 568.34, 445.86 and 784.32 km (Table 3.2), resulting in a linear rate of movement (LRM) of 22.73, 43.72, 24.77, 60.33 km.day^{-1}, respectively.

Vertical movements

Depth and temperature ranges of thermocline were estimated between 50 and 100 m and 26 and 14°C, respectively, for the months of March, April, June and July in the equatorial Atlantic Ocean. The mixed layer spanned from 0 to 50 m indicated by the little thermal variation (Figure S3.1). Depths greater than 300 m were considered as deep water.

Overall, the whale sharks experienced a wide range of depth and temperature gradients along the monitoring period in the equatorial Atlantic Ocean (Fig 3.3; Table 3.2). During the tracking period, the adult females utilized bathyal depths more frequently than the juvenile one (Fig 3.3). Both WS02 and WS03.2 made five deep dives each to meso- and bathypelagic zones with the former performing the deepest dives observed (Table 3.2), probably surpassing the bathyal zone and reaching abyssal realm. Conversely, the WS04.2 made only one deep dive at the end of the tracking, making use of the epipelagic layer more often (Fig 3.3).

The prediction of the influence of the diel cycle and moon phases on the maximum depth attained by individual whale shark revealed deep diving preference in the new moon period ($GLMM_{maxdepth}$: β_4 = 202.9, p-value = <0.001), during the day ($GLMM_{maxdepth}$: β_7 = -297, p-value = <0.001), and with the greatest influence on the WS03.2 diving behavior (Fig 3.4; Table S3.2; Figure S3.2). The range of temperature experienced by the whale sharks was negatively influenced during the night ($GLMM_{temprange}$: β_1= -3.81; p-value = <0.01) and positively during the full moon ($GLMM_{temprange}$: β_2= 2.27; p-value = <0.01), with the WS02 presenting more variation of temperatures experienced during dives (Fig 3.5; Table S3.2; Figure S3.2).

During the monitoring period, all three whale sharks demonstrated slightly distinct vertical distribution in TAD (Fig 3.6). Most of the time, the individual sharks stayed in surface waters (0-10 m), except WS-04.2 which spent more time between 10-60 m (Fig 3.6). Nevertheless, the overall time spent for pooled data was quite similar between 0-10 m and 10-60 m (Fig. 3.6). All whale sharks made deep dives (>300 m), but remained predominantly at the first 60 m of c water column (mixed layer), comprising 68.9% and 82.3% of the time during the day a nd night, respectively. In general, the time spent in both periods, day and night, per depth bin was quite balanced for all sharks, except for the depths below 100 m that were predominantly visited during the day for all sharks, remarkably within the 100-300 m bin (Fig 3.6).

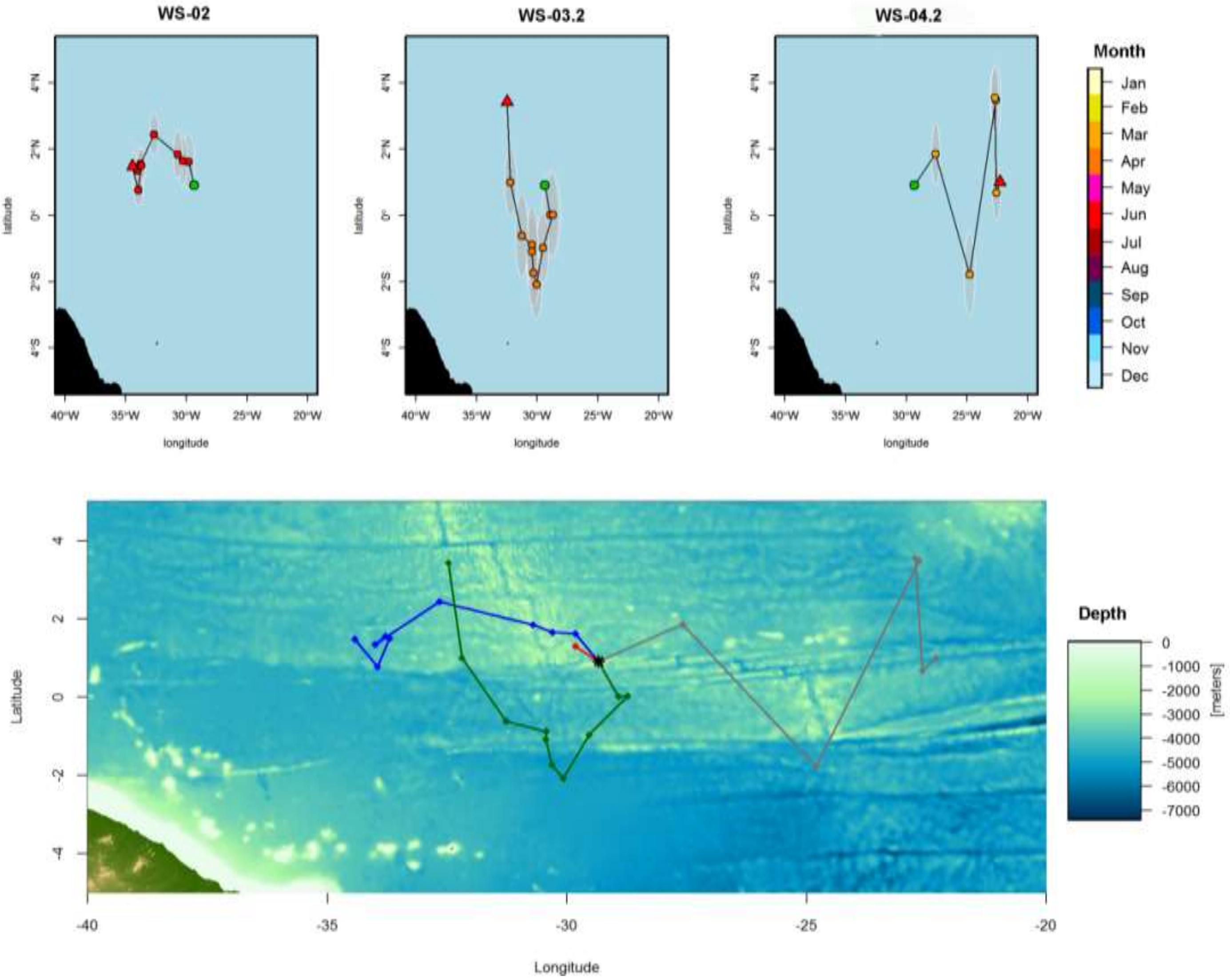


Figure 3.2- Horizontal movements of the whale sharks. Most probable track of whale sharks WS01 (red),WS-02 (blue), WS-03.2 (green) and WS04.2 (grey) satellite tagged in the ASPSP (black asterisk). Green circles indicate deployment site and red triangles indicate popup locations. Shaded ellipses indicate confidence interval.

The time spent on the surface layer was significantly influenced by the new moon ($GLM_{D.10m}$: $\beta_3 = 1.309$; p-value = <0.001), with diel cycle not showing influence on the layer use (Fig 3.7a; S3.4 Table). The use of the mixed layer was influenced negatively by the full moon ($GLM_{D.ML}$: $\beta_1 = -0.903$; p-value = 0.011) and positively by the night period ($GLM_{D.ML}$: $\beta_4 = 0.649$; p-value = 0.021) (Fig. 3.7b; Table S3.4). Despite the difference in the median of the predictor's effect from first quarter and new moon in relation to last quarter and full moon (Fig 3.7b), their influence were not significant (Table S3.4). The preference for the thermocline layer was not influenced by the diel cycle, as observed by the balance of both day

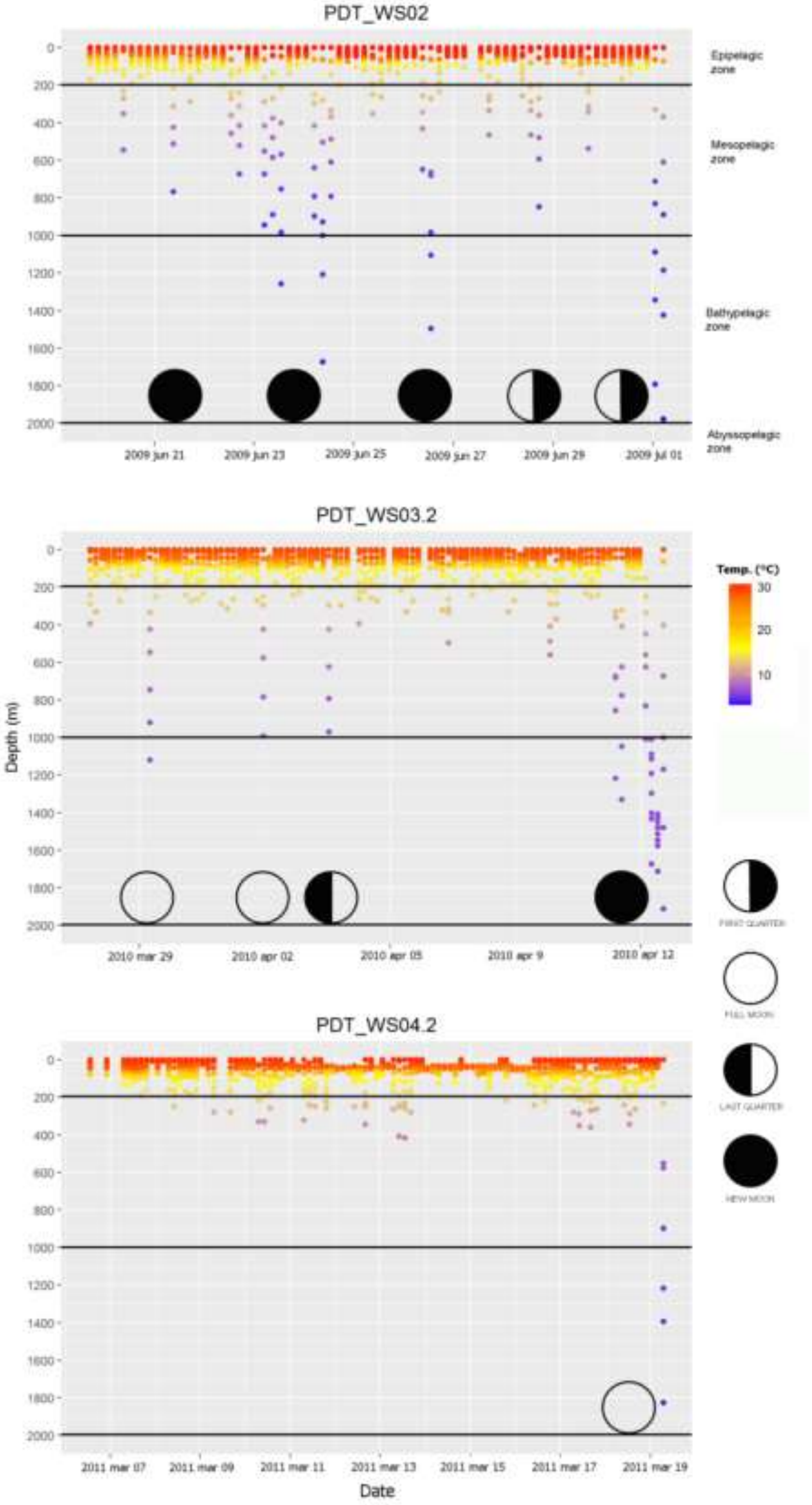


Figure 3.3- Diving profiles of the whale sharks. Profiles of depth and temperature (PDT) during tracking period by the whale sharks WS02, WS03.2 and WS04.2 satellite tagged in the ASPSP.

and night periods (Fig 3.7c). Consequently, this predictor was discarded during model selection and the layer was assessed only in relation to the moon phase. The time spent by the whale shark at the thermocline layer was negatively influenced by the full moon ($GLM_{D.TC}$: $\beta_1 = -0.877$; p-value = 0.012) (Fig 3.7c).

All whale sharks spent more time at warm waters, within the bins 26-28°C (day: 27.5%; night: 33.8%) and >28°C (d: 28.0 %; n: 36.1%), during both day and night. When summed these periods comprise more than half of the entire monitoring time (d: 55.5%; n: 69.9%). The sharks experienced colder temperatures (< 20°C) mostly during the day (Fig 3.8). Slight visual differences between the overall distributions of TAT by each shark were observed (Fig 3.8).

The influence of the environmental effects was assessed to identify the significance and magnitude of the predictors on the time spent in specific thermic layers (TAT). The use of temperatures in the mixed layer had negative effects for the full moon ($GLM_{T.ML}$: $\beta_1 = -1.22$; p-value = 0.002) and last quarter ($GLM_{T.ML}$: $\beta_2 = -1.16$; p-value = 0.006), and positive influence during the night ($GLM_{T.ML}$: $\beta_4 = 0.877$; p-value = 0.004) (Fig 3.9; S4 Table). The thermocline use was not significantly influenced by diel cycle, despite the difference observed in the median (Fig 3.9), and it was thus removed from the model selection. The use of thermocline was influenced by the full moon ($GLM_{T.TC}$: $\beta_2 = 1.281$; p-value = 0.002) and last quarter ($GLM_{T.TC}$: $\beta_3 = 1.053$; p-value = 0.019).

Table 3.2- Depth and temperature ranges of whale sharks. Summary of depth and temperature gradients experienced by the whale sharks satellite tagged in ASPSP.

	Depth (m)			Temperature (°C)		
ID	**Min**	**Max**	**Moon**	**Min**	**Max**	**Range**
WS02	0	1,976	First qt.	3.8	28.6	24.8
WS03.2	0	1,912	New	3.8	29.8	26.0
WS04.2	0	1,824	Full	3.8	29.4	25.6

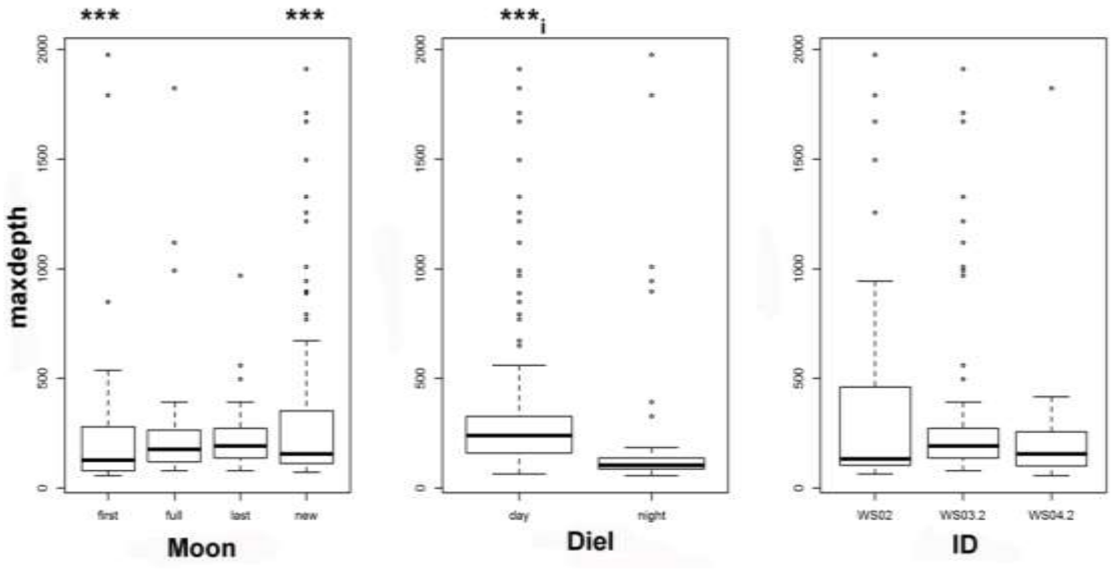


Figure 3.4- Environmental effects on maximum depth of the whale sharks. Effects of moon phase, diel cycle and whale shark ID on the maximum depth (*maxdepth* model) reached by three whale sharks (WS02; WS03.2 and WS04.2) satellite tagged in the ASPSP.1 Black and red asterisks indicate positive and negative influence, respectively. i- refers to the model Intercept (β_0). Significance codes: '***' 0.001, '**' 0.01, '*' 0.05.

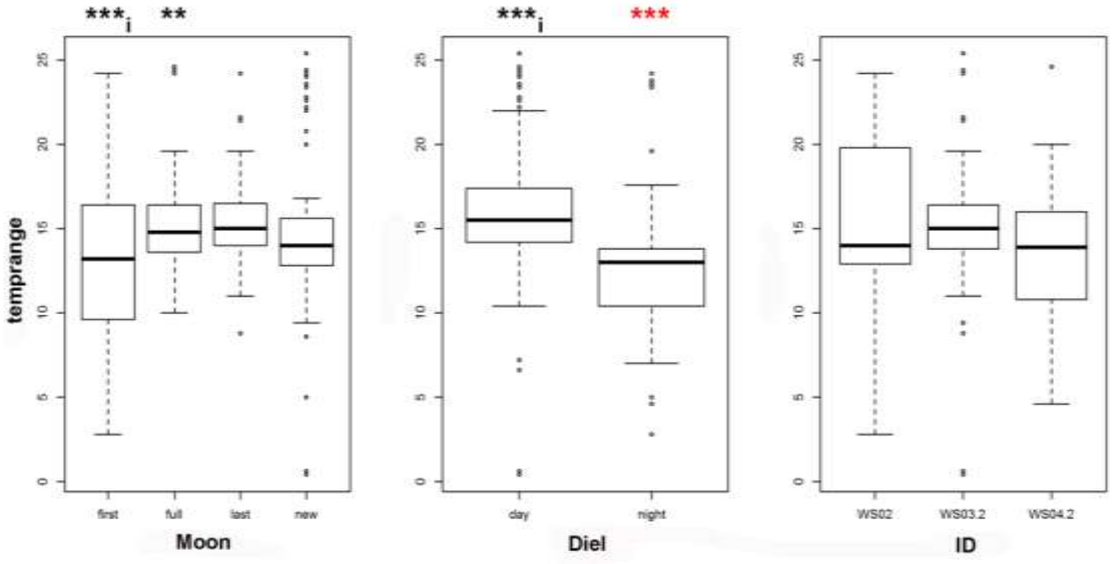


Figure 3.5- Environmental effects on temperature range experienced by the whale sharks. Effects of moon phase, diel cycle and whale shark ID on the temperature range (*temprange* model) experienced by three whale sharks (WS02; WS03.2 and WS04.2) satellite tagged in the ASPSP. Black and red asterisks indicate positive and negative influence, respectively. i- refers to the model Intercept (β_0). Significance codes: '***' 0.001, '**' 0.01, '*' 0.05.

Discussion

Horizontal movements

The attempts to use geolocation refinements for the KFtracks was not possible for our tracks. The sea surface temperature values have little variation in equatorial region, thus may prevent the UKFSST model to proper refine the geolocation positions. Similar situation was observed for the bathymetric correction, where the depths recorded by the tags were always shallower than the bottom. The results obtained from KFtrack was satisfactory given the consistency with the daily rate of movement observed for the species elsewhere of *c*. 30 km.day^{-1} (range of 9 to 61 km.day^{-1}; Eckert and Stewart 2001; Wilson et al. 2006; Brunnschweiler et al. 2009; Hueter et al. 2013).

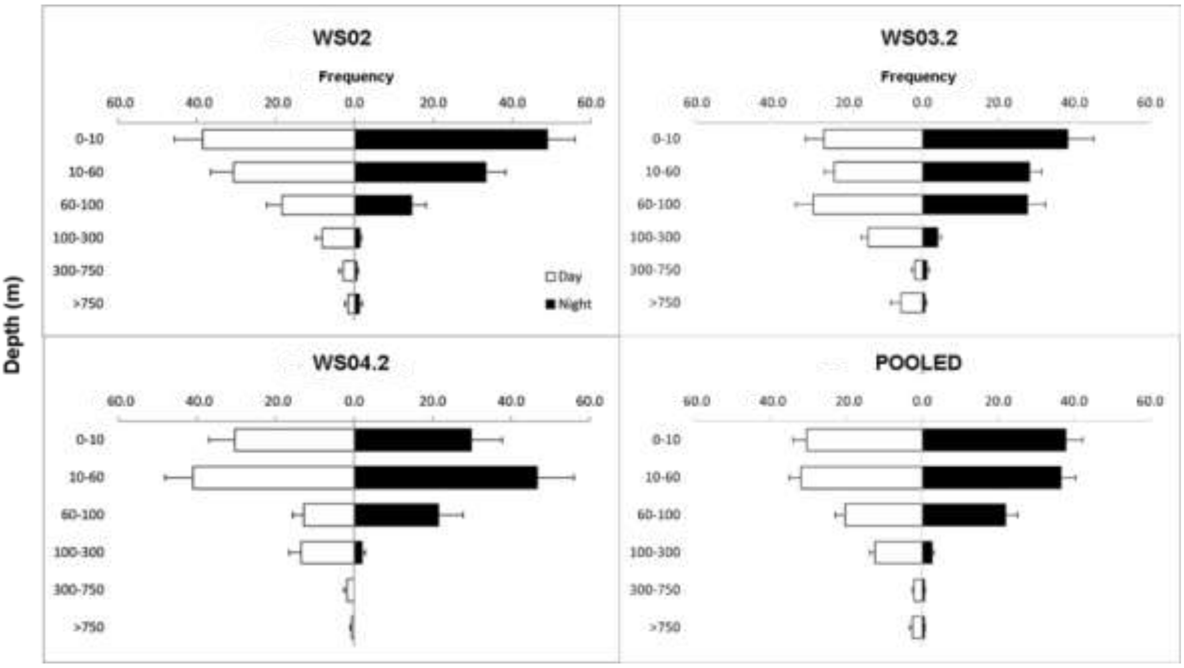


Figure 3.6- Depth bin preferences of the whale sharks. Time spent at depth (TAD) by the whale sharks WS-02, WS-03.2 and WS-04.2 satellite tagged in the ASPSP. Blank and black bars indicate day and night periods, respectively.

The bulk of information comes from coastal environments, where the sharks usually spend most of the tracking period near the deployment site (Eckert et al. 2002; Wilson et al. 2006; Gifford et al. 2007; Hueter et al. 2013; Berumen et al. 2014), in spite of limited deep oceanic movements also observed (Eckert and Stewart 2001; Wilson et al. 2007; Rowat and Gore

2007; Hsu et al. 2007; Brunnschweiller et al. 2009; Sleeman et al. 2010b; Hueter et al. 2013). Moreover, the sharks tracked in these studies were predominantly juveniles. Tracking mature whale sharks are rarely accomplished due to their limited distribution, mainly restricted to oceanic habitats (Ketchum et al. 2013; Ramírez-Macías et al. 2012a; Acunã-Marrero et al. 2015; Macena and Hazin 2016). Besides ASPSP and Galapagos, efforts for tagging adult whale sharks have been conducted in the Azores (P. Afonso et al, unp. data) and in St. Helena, where pregnant females have been recorded (Clingham et al. 2016). Recently, females, likely pregnant, tagged in the Galapagos Island (Hearn et al. 2013) and monitored from 31 to 167 d, moved away from the islands in random directions after being tagged. The tracking of one large female provided information on the first homing migration for the species after traveling 1,650 km west, returning to Galapagos 4 months later, covering *c.* 6,800 km of displacement.

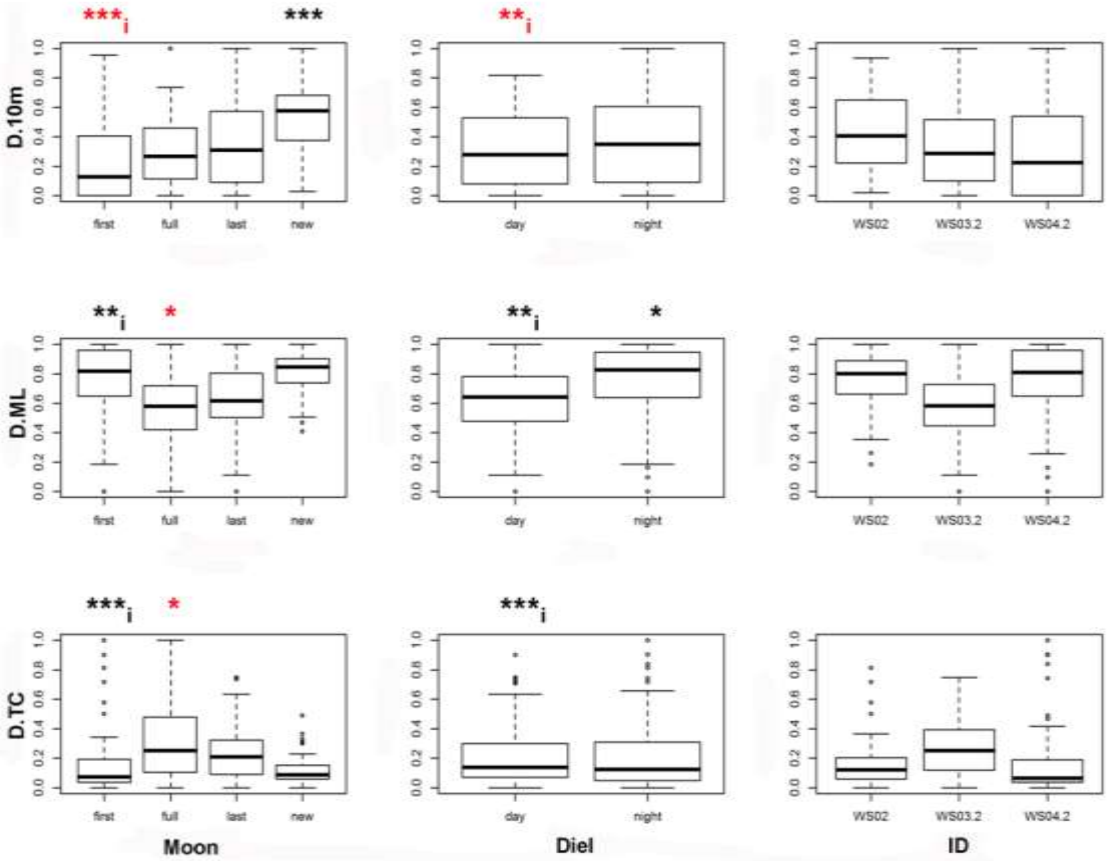


Figure 3.7- Environmental effects on time spent at depth layers by the whale sharks. Effects of moon phase, diel cycle and whale shark ID on the use of the (a) surface (D.10m), (b) mixed layer (D.ML) and (c) thermocline (D.TC) on three whale sharks (WS02; WS03.2 and WS04.2) satellite tagged in the ASPSP. Black and red asterisks indicate positive and negative influence, respectively. i- refers to the model Intercept (β_0). Significance codes: '***' 0.001, '**' 0.01, '*' 0.05.

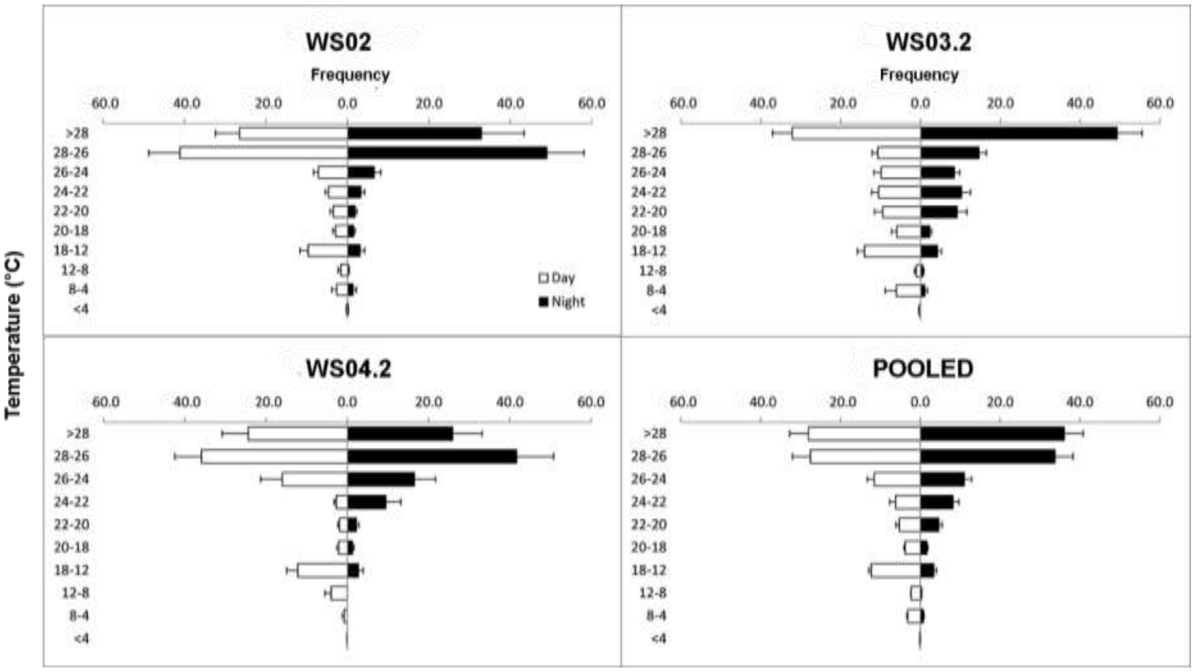


Figure 3.8- Temperature bin preferences of the whale sharks. Time spent at temperature (TAT) by the whale sharks WS-02, WS-03.2 and WS-04.2 satellite tagged in the ASPSP. Blank and black bars indicate day and night periods, respectively.

Similarly as observed in Galapagos (Hearn et al. 2013), all whale sharks tagged in the present study, including those with few days at liberty, moved away from ASPSP just after being tagged, except for the WS04 which remained in the archipelago's surroundings for at least 4 days when it was then tagged for a second time. This non-permanency behavior was expected since the whale sharks visiting ASPSP appear to spend small amount of time in the surrounding area as observed through long-term sighting surveys (Macena and Hazin 2016). Whale sharks visit this area mainly from February to June, ranging from small juveniles to massive adults, in equal numbers, with the latter class probably using the area for reproductive purposes. The two adult females tagged in the present study were suspected to be pregnant and both moved towards west in different months, opposite direction found by Hueter et al. (2013) between December and January (deep water tracking). The tags were both premature released due to deep divings (~2,000 m) with the pop-up of the tags occurring far from each other (*c.* 300 km) and after almost 15 days of tracking. Considering these coincidences, despite the lack of more data, it is reasonable to think that something drove the whale sharks to perform such deep dives in the pop-up locations in the surroundings.

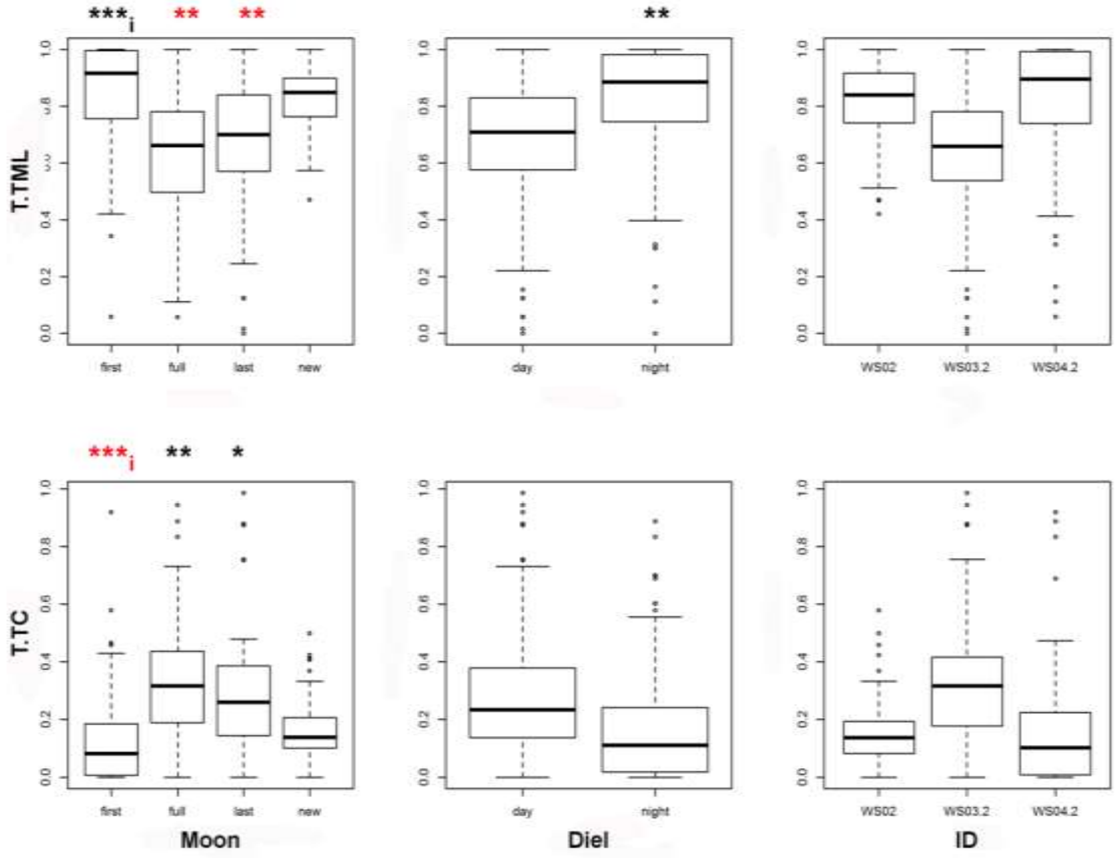


Figure 3.9- Environmental effects on time spent at temperature layers by the whale sharks. Effects of moon phase, diel cycle and whale shark ID on the use of the (a) mixed layer (T.ML) and (b) thermocline (T.TC) on three whale sharks (WS02; WS03.2 and WS04.2) satellite tagged in the ASPSP. Black and red asterisks indicate positive and negative influence, respectively. i- refers to the model Intercept (β_0). Significance codes: '***' 0.001, '**' 0.01, '*' 0.05.

The presence of small whale sharks (2.5 m) in ASPSP, associated with the capture of neonates in the surrounding area (Kukuyev 1996) and the oceanic migration of the Gulf of Mexico's whale shark towards the mid-Atlantic Ridge is suggestive of a suitable reproductive area for the species in this region. Nevertheless, the hypothesis of the use of deep water habitats in part of the reproductive cycle of whale sharks (Colman 1997; Rowat et al. 2007; Martin 2007; Hueter et al. 2013; Macena and Hazin 2016) was not possible to test in the present study due the lack of tracking data.

The immature shark swam eastward and might be performing an active searching for food, given the amount of time spent at mixed layer and the latitudinal variation of the estimated track. This surface patrolling-like swimming pattern is related to the searching for clues to locate preys, as observed for blue sharks (*Prionace glauca* Linneaus 1758) (Carey and Scharold 1990) and also for whale sharks (Gunn et al. 1999). The WS-04 travelled against the SEC flow, in opposite direction to the Gulf of Guinea's equatorial upwelling, probably taking advantage of biological productive waters (Grodsky et al. 2008; S3 Figure). Similar movement patterns have been observed in St. Helena where whale sharks are apparently moving to feed in coastal areas off western Africa and travelling to oceanic regions to fulfill stages of their reproductive cycle (Clingham et al. 2016).

Vertical movements

The estimates of thermocline using the PDT data are consistent with the profiles reported to the region (Travassos et al. 1999). It is also noteworthy that the thermocline in the ASPSP region coincides with the depth of the equatorial undercurrent (EUC), a fast and strong current that flows eastward between the latitudes 2°S and 2°N at 50-100 m, transporting oxygen-rich and high-saline water (Schott et al. 1998; Kolodziejczyk et al. 2009; Brandt et al. 2011a). The EUC likely plays an important role in larval dispersal in the Atlantic basin (Scheltema 1972; Edwards and Lubbock 1983; Muss et al. 2001).

The usage of different layers of oceanographic importance is generally influenced by biophysical and environmental factors. The whale sharks presented a reverse pattern in the time spent using the mixed layer and the thermocline, with the former positively influenced by new moon and night period, and the latter influenced positively by the last quarter and full moon. The effects of moonlight in the maximum depths attained are consistent with the results obtained from the time spent in the surface layer (<10 m), with a negative influence of new moon, which means that the sharks do not perform deep dives during this particular lunar phase. The moonlight intensity was also suggested to affect diel pattern diving behavior of the reef manta (*Manta alfredi* Krefft, 1868) in offshore waters in Red Sea, where deep dives were observed when the moon progresses to full (Braun et al. 2014). The range of temperature experienced during the track was consistent with the use of thermocline layer with significantly positive effects by the full moon and negative effects of the night period, confirming that the greatest thermal variation is related to the deep diving behavior.

In the present study, all sharks spent most of the time at the surface layer, particularly during night time, and performed deep dives mostly during the day, a pattern consistent with the one found in Belize (Graham et al. 2006) and Western Australia (Wilson et al. 2006). Conversely, a reverse pattern was observed with the sharks spending more time in the surface layer during the day and reduced time over night in the Gulf of Mexico (Motta et al. 2010), South Africa (Brunnschweiler and Sims 2011) and also in the Western Australia (Meekan et al. 2015). Nevertheless, the deepest dives recorded in these studies were all observed during daytime and show consistence with the pattern observed for other filter-feeding Chilean devil rays (*Mobula tarapacana* Phillipi 1892) off Azores (Thorrold et al. 2014).

Independently of the diel period, satellite tagged mobulid rays also showed clear preference for the surface layer (Canese et al. 2011; Graham et al. 2012; Braun et al. 2014). Sims et al. (2005) suggested that the diel pattern on the use of different layers in the water column of the basking shark (*Cetorhinus maximus* Gunnerus 1765) may be influenced by the geographic location (*i.e.* habitat), associated with seasonal (*e.g.* upwelling) and biological processes (*e.g.* deep scattering layer diel vertical migration). Seasonal differences in diving behavior (*i.e.* proportion of time spent at surface or in deep waters) was found for oceanic manta (*Manta birostris* Walbaum, 1792) (Stewart et al. 2016a). Moreover, the time Chilean devil rays spent basking at surface during daytime was related to the duration of deep dives (>800 m) (Thorrold et al. 2014). Indeed, these same behaviors may apply to the whale sharks given the reverse diel pattern observed may be result of local environmental factors that drives the use of different oceanographic layers, and whale sharks ability to dive as deep as these devil rays.

All whale sharks made very deep dives into the bathypelagic realm but the WS02 dive of 1,972 m was the deepest dive ever recorded for any fish or elasmobranch to date, surpassing those observed by Tyminski et al. (2015) and Thorrold et al. (2014). These deep dives are generally considered suggestive of prey searching. Given the maximum depth attained by the whale sharks in the present study, it is possible that they are also using the abyssopelagic zone to forage of for other unknown reason, when no depth constraints exist.

The light intensity of the moon had a significant effect on the whale shark deep water incursions. The moonlight influences the diel vertical migration of zooplanktonic organisms (Last et al. 2016), usually found at depth during the day and near the surface at night (Hays 2003; Yahel et al. 2005). As a consequence, the plankton feeders, such as the mobulid rays (Dewar et al. 2008; Jaine et al. 2012; Rohner et al. 2013a), the basking shark (Sims et al. 2005), the megamouth shark, *Megachasma pelagios* (Nelson et al.1997) and whale sharks (Graham et al. 2006; present study) tend to follow the diel movement of their prey, thus being indirectly influenced by the moon.

The diving behavior of filter-feeding species [basking shark (Sims et al. 2005), mobulid rays (Canese et al. 2011; Braun et al., 2014; Thorrold et al. 2014; Stewart et al. 2016b) and whales (Watwood et al. 2006; Schorr et al. 2014)]; and invertebrate-feeding species [leatherback turtle (Hays et al. 2004)], were related to active searching of food resources in deep water. The reasons driven the whale shark's deep diving behavior are quite difficult to guess and remain under discussion, but are frequently related to biological features (*i.e.* diel vertical migration of the deep scattering layer)/foraging (; Graham et al. 2006; Brunnschweiler and Sims 2011; Rohner et al. 2013b) and to physiological processes (Thums et al. 2013) or both (Meekan et al. 2015).

Satellite tracking studies often suggest the use of surface layer by the whale sharks to foraging purposes, but these studies were conducted mostly on immature sharks and mature sharks may very well display distinct patterns of movements, as our data suggested. Unfortunately, the present trackings were rather reduced, preventing a thorough assessment of large-scale movement patterns of adult individuals. Further studies are, thus, necessary in order to elucidate the migration routes of whale sharks in the Atlantic Ocean and the function of deep divings for mature specimens.

Conclusion

All whale shark trackings presented here were prematurely interrupted due to limitations concerning maximum depth supported by the tag, thus preventing us to gather more information on oceanic migration and diving behavior of the species in the Atlantic Ocean. The horizontal movements corroborate with the hypothesis of the ASPSP as an oceanic "stop over" (or "way point") for the whale sharks (Macena and Hazin 2016), since they moved away from the archipelago just after tagging. The diving behavior was influenced by the diel cycle and lunar phases, which affects directly the movements of their prey. Differences in the patterns of diel diving behavior of whale sharks from distinct locations may be related to specific local oceanographic conditions in response to prey availability. Moreover, in a bathymetric unconstrained region the whale shark seems to make use of the major part of the water column range. Unfortunately, the tag depth-limitation of ~2,000 m prevented us to collect more information on oceanic movement behavior. Other similar studies had the same depth constraint problem (Graham et al. 2006; Brunschweiller et al. 2009; Hueter e al 2013) and the manufacturers should develop instruments capable of resisting greater depths to allow researchers to collect data in a novel habitat, not sampled before, and get new perspectives on the behavioral ecology of movement of marine animals.

The horizontal and vertical movements performed by the tracked specimens revealed distinct directions and a slight different use of the water column by the immature and mature sharks, suggesting that ontogenetic differences in movement patterns may occur due to distinct necessities for each maturity class (Macena and Hazin 2016). Despite the rather great number of individuals tracked over a wide geographic extension, little information is available on large-scale migration patterns of whale sharks worldwide (Rowat and Brooks 2012; Sequeira et al. 2013). Most of the horizontal movement information from satellite tracking studies indicates that whale sharks penetrates different geopolitical jurisdictions (Sequeira et al. 2013), making multi-regional management necessary for the worldwide conservation of the species. The identification of migration routes and the elucidation of the deep diving behavior in adults are of extreme importance for the conservation of whale sharks since mating/parturition areas are not yet known.

Supporting information

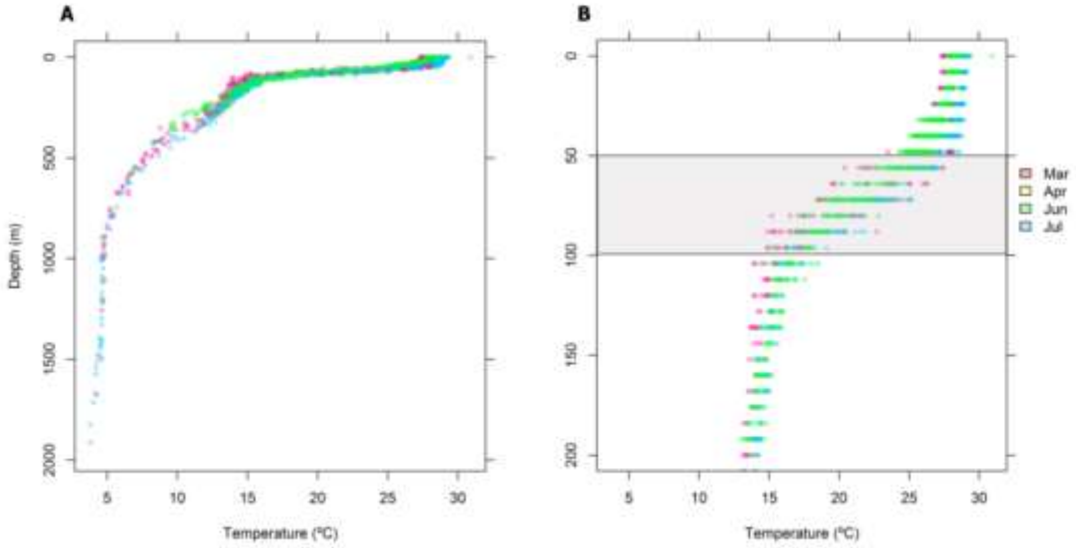


Figure S3.1- Themocline profile of ASPSP surroundings. (A) Thermocline estimate depth in the vicinity of ASPSP calculated from profiles of depth and temperature (PDT) of satellite tagged whale sharks WS-02, WS-03.2 and WS-04.2. (B) Close view of the thermocline between 0-200 m of depth.

Table S3.1- Summary of multicollinearity analysis for PDT data. Pearson's correlation matrix of the PDT data and Variance Inflation Factor (VIF) score. The number after the VIF indicates the round in which the score was calculated.

Variable	maxdepth	mintemp	mindepth	maxtemp	Depthrange	temprange	VIF-1
Maxdepth	1						2.98858
mintemp§	**-0.82**	1.00					2.263402
mindepth§	0.37	-0.22	1.00				
Maxtemp	-0.38	0.24	**-0.91**	1.00			
depthrange§	**0.95**	**-0.81**	0.05	-0.09	1.00		
Temprange	0.57	**-0.82**	-0.32	0.36	0.72	1.00	2.882911

§ response variable excluded from vertical analyses.

Table S3.2– Selected model outputs for PDT data. Summary of the regression coefficients of GLMM. Bold values indicate significance.

		Random effects		Fixed effects			Scaled residuals				
Model	**Preditor**	**Vari-ance**	**SE**	**Betas**	**SE**	**p-value**	**Min**	**Max**	**df**	**AIC**	**Devi-ance**
*maxdepth ~ diel * moon + (1 | ID)*							-1.26	5.05	10	3399.3	3379.3
	ID	7048	83.95								
	Residual	110962	333.1								
	Intercept			298.9	76.4	**<0.001*****					
	Dielnight			-30.4	91.6	0.740					
	Moonfull			10.3	83.3	0.902					
	Moonlast			-82.9	100	0.407					
	Moonnew			**202.9**	77.8	**<0.001*****					
	dielnight:moonfull			-161.6	126.3	0.201					
	dielnight:moonlast			-100.3	149.8	0.503					
	dielnight:moonnew			**-297.4**	120	**<0.001*****					
temprange~ diel + moon + (1 | ID)							-4.12	3.15	7	1298.6	1284.6
	ID	1.117	1.057								
	Residual	13.825	3.718								
	Intercept			14.95	0.833	**<0.001*****					
	Dielnight			-3.81	0.514	**<0.001*****					
	Moonfull			2.27	0.787	**0.004****					
	Moonlast			1.82	0.991	0.067					
	Moonnew			1.05	0.686	0.125					

Significance codes: '***' 0.001, '**' 0.01, '*' 0.05.

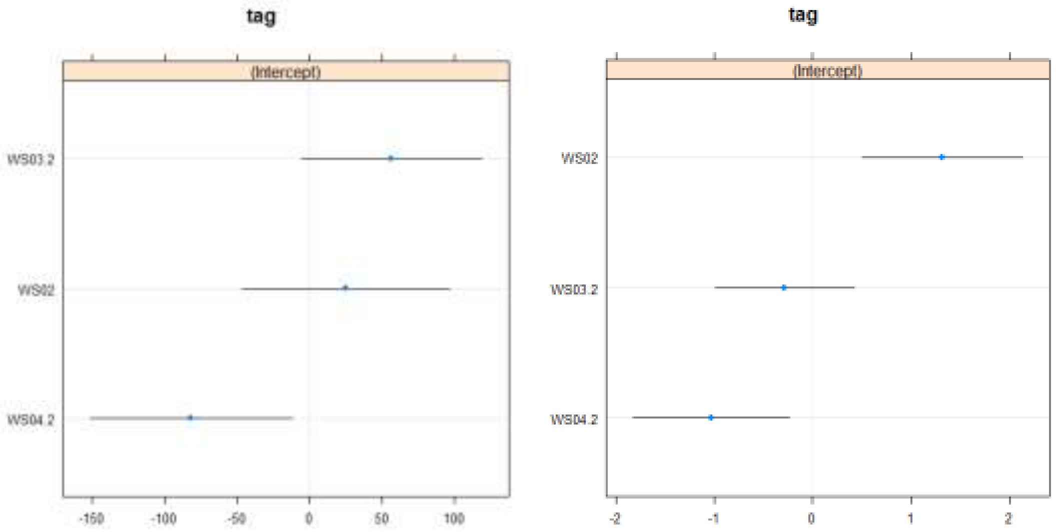


Figure S3.2 - Random effects for individual whale shark. Intercept of the influence of individual whale shark (tag ID) from GLMM for *maxdepth* (left) and *maxtemp* (right) output.

Table S3.3- Summary of multicollinearity analysis for PDT data. Pearson's correlation matrix of TAD and TAT data and Variance Inflation Factor (VIF) score. The number after the VIF indicates the round in which the score was calculated.

Variable	**T.ML**	**T.TC**	**T.DW**	**D.10m**	**D.ML**	**D.TC**	**D.DW**	**VIF-1**	**VIF-2**	**VIF-3**
Temperature of mixed layer (T.ML)§	1.00							57240.0		
Temperature of thermocline (T.TC)	**-0.86**	1.00						45742.9	2.52	1.57
Temperature of deep water (T.DW)§	-0.45	-0.06	1.00					14792.5		
Depth of surface layer (D.10m)	0.38	-0.35	-0.13	1.00				1.39	1.38	1.37
Depth of mixed layer (D.ML)	0.79	-0.67	-0.36	0.51	1.00			14.71	10.64	
Depth of thermocline (D.TC)	-0.44	0.60	-0.18	-0.47	-0.78	1.00		9.29	6.54	1.86
Depth below 300 m (D.DW)§	-0.43	-0.07	**0.98**	-0.12	-0.35	-0.16	1.00	26.23	3.48	1.08

§ response variable excluded from vertical analyses. The code after VIF indicates the VIF analysis run number.

Table S3.4- Selected model outputs for TAT and TAD data. Summary of the regression coefficients of GLM. Bold values indicate significance.

							Deviance Residuals					
Model	**Preditor**	**Betas**	**SE**	**z**	**Pr(>|z|)**		**Min**	**Max**	**df**	**AIC**	**AICc**	**deviance**
T.ML ~ moon + diel							-1.65	0.86	253	209.48	209.71	55.121
	Intercept	1.364	0.326	4.185	0.000	***						
	Moonfull	-1.228	0.398	-3.083	**0.002**	**						
	Moonlast	-1.166	0.426	-2.734	**0.006**	**						
	Moonnew	-0.171	0.487	-0.352	0.725							
	Dielnight	0.877	0.307	2.860	**0.004**	**						
T.TC ~ moon							-0.9	1.82	254	177.1	177.25	53.055
	Intercept	-1.970	0.329	-5.987	0.000	***						
	Moonfull	1.281	0.414	3.093	**0.002**	**						
	Moonlast	1.053	0.450	2.341	**0.019**	*						
	Moonnew	0.339	0.507	0.669	0.504							
D.10m ~moon + diel							-1.06	1.45	253	313.86	314.09	90.35
	Intercept	-1.316	0.293	-4.491	0.000	***						
	Moonfull	0.279	0.360	0.776	0.438							
	Moonlast	0.529	0.384	1.377	0.169							
	Moonnew	1.309	0.383	3.417	**0.001**	***						
	Dielnight	0.400	0.272	1.472	0.141							
D.ML ~ moon + diel							-1.85	0.93	253	262.25	262.48	63.43
	Intercept	0.866	0.283	3.065	**0.002**	**						
	Moonfull	-0.903	0.354	-2.553	**0.011**	*						
	Moonlast	-0.733	0.385	-1.902	0.057	.						
	Moonnew	0.284	0.444	0.639	0.523							
	Dielnight	0.649	0.281	2.311	**0.021**	*						
D.TC ~ moon												
	Intercept	-1.666	0.295	-5.65	<0.001	***						
	Moonfull	0.857	0.391	2.191	0.028	*						
	Moonlast	0.480	0.440	1.089	0.276	.						
	Moonnew	0.329	0.530	0.622	0.534							

Significance codes: '***' 0.001, '**' 0.01, '*' 0.05.

Conclusão geral

O presente estudo compreende a primeira iniciativa de estudo em longo prazo acerca da ecologia e biologia do tubarão-baleia no oceano Atlântico Sudoeste e Equatorial. Este trabalho foi fruto de mais de dez anos de esforço de pesquisa (ou o equivalente a 33 expedições científicas) realizadas ao Arquipélago de São Pedro e São Paulo (Macena, 2006; Hazin et al 2008, Macena, 2010), incluindo vários anos compilando registros de ocorrência em toda a costa do Brasil, e culminou em um documento que contém informações de relevância sobre a ecologia, biologia e biogeografia do tubarão-baleia no oceano Atlântico.

Integração e síntese dos assuntos abordados

Apesar do proeminente avanço no conhecimento acerca dos aspectos ecológicos e biológicos do tubarão-baleia no mundo inteiro, com vários novos locais de agregação sendo descritos nos últimos anos, a maior parte das informações produzidas se concentra no oceano Índico (revisão em Rowat e Brooks 2012 e Sequeira et al 2013). No oceano Atlântico, as informações sobre a espécie são predominantemente provenientes da América Central (Golfo do México e Mar do Caribe), com poucos estudos sobre aspectos ecológicos para o restante dessa bacia oceânica. Visando a colaborar com o suprimento dessa carência de conhecimento sobre o tubarão-baleia no oceano Atlântico e no mundo, e também atendendo às necessidades nacionais abordadas no "Plano de Ação para Conservação e o Manejo dos Estoques de Peixes Elasmobrânquios no Brasil" produzido pela Sociedade Brasileira para o Estudo dos Elasmobrânquios (SBEEL; http://sbeel.org.br/wp-content/uploads/2016/04/Plano-de-A%C3%A7%C3%A3o-Nacional_2005.pdf) e pelos documentos que identificam as "Áreas prioritárias para a conservação, uso sustentável e repartição de benefícios da Biodiversidade Brasileira" (MMA 2002, 2008; IBGE 2010); e internacionais, apontadas no estudo de definição de políticas e pesquisas do tubarão-baleia (Fowler 2000), aspectos importantes da história de vida, como a distribuição, estrutura da população e os movimentos migratórios, foram investigados nas regiões equatorial e sudoeste do oceano Atlântico. Adicionalmente, por meio da criação de uma página de internet proveniente do presente estudo (Projeto Tubarão-baleia[2]; www.facebook.com/ tubaraobaleia), foram envidados esforços para (i) conscientização ambiental, divulgando informações sobre elasmobrânquios e o meio ambiente

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[2] Até o dia 02/11/2016 a página possuía um total de 3.079 seguidores de vários locais do mundo.

e da importância em se conservá-los; e (ii) inclusão social, buscando aproximar a pesquisa científica com o público geral solicitando sua colaboração na coleta de registros de ocorrência do tubarão-baleia na costa do Brasil.

O entendimento (**a**) dos padrões de uso do habitat, (**b**) dos aspectos bioecológicos e (**c**) dos movimentos migratórios de espécies raras, vulneráveis e de grande mobilidade é crucial para a implementação de medidas de manejo espaciais explicitamente efetivas, como a criação de reservas marinhas ou fechamento temporário de áreas de pesca. Isto se aplica especialmente para elasmobrânquios filtradores que dependem de sua habilidade em encontrar suas presas minutas e difusas num vasto ambiente oceânico dinâmico e em constante transformação, particularmente em um contexto de mudanças climáticas. Neste sentido, as informações geradas no presente estudo servem de subsídio para a o manejo e conservação do tubarão-baleia em águas brasileiras.

No primeiro capítulo, foram apresentados os resultados de (**a**) inferências sobre os fatores ambientais que governam a distribuição espacial do tubarão-baleia na costa brasileira. Baseado em dados de avistagens pontuais e oportunas coletadas ao longo da costa, modelos de distribuição de espécies (*species distribution modeling*- SDM) foram aplicados com sucesso. Potenciais áreas de importância alimentar em diferentes partes da costa foram identificadas, sendo a região Sudeste (particularmente nas imediações de Cabo Frio/RJ) o local que apresentou a maior importância ecológica devido a características atmosféricas e oceanográficas particulares que proporcionam uma alta produtividade biológica; justificando, assim, a maior quantidade de registros coletados para esta área. Em um estudo realizado por Sequeira et al (2014a), que usou modelos ecológicos para predizer áreas adequadas para ocorrência do tubarão-baleia nas três bacias oceânicas, a adequabilidade da região Sudoeste do Atlântico foi observada; porém com menor resolução e sem a inclusão de presenças locais. Apesar dos registros de presença no Arquipélago de São Pedro e São Paulo (ASPSP) não terem sido incluídos nos modelos utilizados no presente estudo, áreas adequadas para sua ocorrência foram indicadas nas circunvizinhanças do arquipélago, aumentando ainda mais sua relevância ecológica, já previamente sugerida (Hazin et al 2008).

No Brasil, o ASPSP é o único local onde a avistagem de tubarões-baleia é previsível, aspecto que, portanto, possibilitou a realização de um estudo que buscou (**b**) compreender detalhadamente os aspectos da estrutura da população de tubarões-baleia que frequentam o ASPSP. O período sazonal de ocorrência observado foi entre janeiro e junho, com maiores abundâncias relativas em Março e Abril e um misto equivalente entre jovens e adultos. O

ASPSP se mostrou um importante local para o ciclo de vida de ambas as classes, sendo que as evidências indicam que os tubarões imaturos tendem a usar o local para alimentação, enquanto que os maduros o utilizam para reprodução. De fato, as informações disponíveis na literatura (Wolsfon 1983; Kukuyev, 1996; Hueter et al 2013) corroboram algumas das observações realizadas no presente estudo e sugerem que existe uma área importante para o ciclo reprodutivo da espécie nas imediações do ASPSP. Entretanto, mais estudos ainda são necessários para se entender melhor a importância ecológica da região e revelar mais aspectos acerca de sua reprodução.

Atualmente, existe uma grande escassez de informações sobre os deslocamentos do tubarão-baleia, especialmente em áreas oceânicas (Sequeira et al 2013). Em complemento à descrição dos aspectos populacionais da espécie no ASPSP, (**c**) os movimentos horizontais e verticais da espécie foram investigados a fim de elucidar os padrões de movimentação e os comportamentos de mergulho, em um ambiente isolado no meio do oceano Atlântico, considerado rota de migração para a espécie (Hueter et al 2013; Sequeira et al 2013). Os resultados do monitoramento via satélite coincidem com resultados sobre o uso do ASPSP com diferentes propósitos para jovens e adultos obtidos no capítulo anterior, devido aos diferentes padrões de movimentação horizontal e vertical apresentados por ambas as classes. Complementarmente, estudos preliminares indicam que padrões similares vêm sendo observados na ilha de Santa Helena (Clingham et al 2016). Ademais, uma fêmea com suspeita de gravidez apresentou movimentação diferente de todos os outros tubarões-baleia marcados no Golfo do México, viajando para áreas de grandes profundidades (Hueter et al 2013) e realizando mergulhos profundos regulares (Tyminski et al 2015). Entretanto, mais estudos são necessários para reforçar essa hipótese. Os comportamentos de mergulho (*i.e.* o tempo gasto em diferentes camadas da coluna d'água e os mergulhos profundos) foram influenciados por fatores biofísicos e ambientais. A observação de padrões tanto similares quanto distintos de outros locais do mundo sugere que os comportamentos de mergulho são governados por variações nas condições ambientais regionais, biológicas e sazonais, como observado para outras espécies de elasmobrânquios filtradores que direcionam e sincronizam suas migrações de acordo com eventos de aumento expressivo de produtividade biológica em locais específicos (Sims et al 2005; Jaine et al 2012; Baun et al 2014). Por último, mas não menos importante, os resultados preliminares das análises moleculares obtidos até o momento, apresentado no Apêndice A, permitirão ampliar a percepção sobre a dinâmica da estrutura genética populacional em nível mundial.

Implicações teóricas e políticas

Políticas internacionais de conservação e proteção do tubarão-baleia incluem a listagem no Apêndice II da Convenção sobre o Comércio Internacional das Espécies da Flora e Fauna Selvagens em Perigo de Extinção (CITES, em inglês) e a classificação como "ameaçada de extinção" na lista vermelha da União Internacional para a Conservação da Natureza (IUCN, em inglês), entre outras (revisão em Fowler et al 2000). No Brasil, a espécie é protegida por lei pela Instrução Normativa nº5, de maio de 2004, sendo a captura, comercialização e transporte proibidos em todo território nacional e águas jurisdicionais. Portanto, toda e qualquer medida de manejo direcionada a esta espécie torna-se crucial para sua conservação.

A compilação de registros pontuais de ocorrência do tubarão-baleia se mostrou uma importante forma de se gerar conhecimento sobre a distribuição da espécie na costa brasileira e pode ser utilizada como um importante subsídio para a sua conservação. A criação de ferramentas ou meios que permitam a coleta de um maior número de registros do tubarão-baleia (ou outras espécies de interesse) em maior escala, como, por exemplo, a elaboração de um Programa Nacional de Monitoramento de Avistagens do Tubarão-baleia (PNMA; www.facebook.com/tubaraobaleia), criado no âmbito da presente tese; ou tornando obrigatória a inclusão dos registros da espécie nos mapas de bordo de observadores de plataformas de sísmica, petróleo e de navios pesqueiros da frota industrial e também para os pescadores artesanais, permitirá a obtenção de inferências mais robustas e maior detalhamento do uso e importância dos habitats no oceano Atlântico Sudoeste, para a espécie. Levantamentos realizados pelo IBAMA para identificação de áreas prioritárias para conservação (MMA 2002, 2008; IBGE 2010) enfatizam a escassez de informações sobre os elasmobrânquios no país e também destacam a importância da região Sudeste para uma variedade de espécies, além de mostrar que existe uma elevada necessidade de se concentrar esforços para a adoção de medidas que resultem na proteção legal da área que, em última análise, englobará a conservação várias espécies assegurando a sua manutenção no ecossistema.

Levando-se em consideração a importância da região de Cabo Frio/RJ para várias espécies além do tubarão-baleia, e da mesma forma, tendo em vista a importância ecológica do ASPSP para diversas espécies de animais marinhos (Viana et al 2009), ações imediatas são necessárias para assegurar a preservação desses dois habitats e suas respectivas biotas. Para permitir uma melhor gestão ambiental e alcançar um maior nível de conservação é sugerido que sejam implementadas medidas mais radicais para proteção do local como, por exemplo, o fechamento temporário de áreas para a pesca durante o período de reprodução dos peixes em ambos os locais, Cabo Frio e ASPSP; e a retirada do ASPSP da Área de Proteção Ambiental de Fernando de Noronha para a criação de um comitê específico exclusivo para gestão desse ecossistema. Dessa forma, os esforços envidados para a conservação poderiam ser garantidos por lei, sendo assim mais bem direcionados e potencialmente mais efetivos.

Limitações do estudo

Apesar do sucesso na geração de informações relevantes sobre o tubarão-baleia, várias limitações foram encontradas durante o desenvolvimento do presente estudo e serão descritas cronologicamente de acordo com cada capítulo. No primeiro capítulo, uma das maiores dificuldades encontradas foi com relação ao baixo número de presenças registradas em águas brasileiras, o que reflete, além da reduzida abundância da espécie no Brasil, o baixo interesse, a falta de informação do público geral sobre a vulnerabilidade da espécie e, o pior, o desconhecimento do pertencimento da espécie à fauna nativa nacional. Ações como as descritas acima sobre a criação de ferramentas que possibilitem uma maior quantidade de registros de avistagem com a ajuda da sociedade (*i.e.* expandir o conceito e a inclusão do cidadão-cientista ou ciência cidadã[3] nas pesquisas) na coleta de dados, a exemplo do que ocorre no Parque Estadual Marinho da Laje de Santos/SP com as raias manta oceânica (Luiz Jr et al 2009), no Brasil, e também outros locais do mundo (Davies et al 2012; Wildbook for Whale shark: www.whaleshark.org), são de grande valia para a ciência e devem ser incentivadas ao máximo. Nos capítulos 2 e 3 os maiores problemas foram de ordem logística e operacional. A inospitalidade do ASPSP e a dinâmica oceanográfica do local impuseram dificuldades alheias à nossa vontade e que tiveram que ser superadas para alcançarmos os resultados pretendidos. Problemas como a quebra do motor de popa do bote inflável usado para auxiliar no censo visual ou do navio de apoio limitaram o esforço de amostragem durante algumas expedições. Outra dificuldade foi a necessidade de adequação do método para marcação via satélite. Como o estudo foi pioneiro na utilização desta técnica no Brasil, foi

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[3] *"A ciência cidadã é um tipo de ciência baseada na participação informada, consciente e voluntária, de milhares de cidadãos que geram e analisam grandes quantidades de dados, partilham o seu conhecimento e discutem e apresentam os resultados. Qualquer pessoa pode dedicar a sua inteligência ou os seus recursos tecnológicos e disponibilidade de tempo para encontrar resultados de utilidade social. Para tal, não é necessário ter conhecimentos nem dispositivos, e tal pode ser feito em qualquer lugar e em qualquer momento. A ciência cidadã é compatível com a ciência tradicional feita por cientistas profissionais, complementando-a e colocando-lhe novos problemas e desafios. A ciência cidadã é assim a investigação científica feita por um conjunto de colaboradores que na sua totalidade ou em parte não sejam cientistas profissionais."* Fonte: Wikipédia (https://pt.wikipedia.org/wiki/Ci%C3% AAncia_cidad%C3%A3).

necessário adequar o modo de marcação progressivamente após cada tentativa com ou sem sucesso. Além disso, a baixa abundância da espécie tornou esse processo mais lento devido ao reduzido número de oportunidades. Uma dificuldade adicional diz respeito particularmente aos transmissores, cujos valores elevados, associados ao alto índice de falhas eletrônicas (*i.e.* não transmissão dos dados) e à limitação de profundidade máxima suportada, contribuíram para uma menor quantidade de dados de monitoramento por satélite e, consequentemente, menos informações sobre o comportamentos dos tubarões marcados.

Alcance das metas e objetivos propostos

Os objetivos gerais de descrever a distribuição espacial da ocorrência potencial do tubarão-baleia no Oceano Atlântico Sudoeste e de avaliar os aspectos da estrutura da população e os deslocamentos no ASPSP, propostos no presente estudo, foram alcançados com êxito. Portanto, a maior parte das hipóteses levantadas, como a de distribuição dos habitats mais adequados para a região Sudeste do Brasil, da importância do ASPSP para a parcela adulta dos tubarões-baleia e de que fatores ambientais influenciam no seu comportamento de mergulho foram corroboradas. Por outro lado, algumas outras hipóteses não puderam ser verificadas por falta de dados ou pelas outras limitações apresentadas acima. Os resultados obtidos também conduziram à formulação de novos questionamentos como o da avaliação da distribuição de habitats adequados independentes para as diferentes regiões bioclimáticas (tropical no N/NE e subtropical no S/SE) na costa do Brasil; sobre a identificação de uma potencial área de cópula e nascimento nas proximidades do ASPSP; sobre a avaliação de diferenças comportamentais no padrão de movimentação entre indivíduos jovens e adultos; e, ainda, sobre a estrutura genética das diferentes populações da espécie no mundo. Em última análise, o presente estudo destacou a importância e os benefícios de se envidar maiores esforços para coleta de dados sobre o tubarão-baleia.

Recomendações futuras

No mundo inteiro o tubarão-baleia se tornou uma espécie chave na conservação, não apenas devido as suas características intrínsecas, como ser um dos maiores vertebrados marinhos e vulnerável à explotação, mas principalmente pelo carisma que possui com o público. Dessa forma, esses gigantes gentis se tornam uma espécie guarda-chuva ou porta-bandeira (Roberge e Angelstam 2004; Norman e Catlin 2007) servido de propósito para além de sua própria conservação, permitindo que espécies menores e/ou menos estudadas também sejam beneficiadas com as medidas de manejo espacial para o tubarão-baleia. Parte das recomendações apresentadas abaixo foi inspirada em informações presentes nos documentos produzidos pelo Ministério do Meio Ambiente (MMA 2004,2008), por órgãos internacionais de conservação (Fowler 2000) e de pesquisa científica (Hueter e Tyminski 2012).

Levando em consideração este papel protagonista para a conservação, devem ser criadas áreas de proteção marinha de importância para o ciclo de vida do tubarão-baleia. Conforme já sugerido pelo MMA, a região de Cabo Frio/RJ é uma importante área de alta produtividade primária, essencial para várias espécies marinhas e que exige uma prioridade extremamente alta para a criação de Unidade de Conservação (MMA 2004, 2008). Nestes documentos, a mesma recomendação também foi feita para a região do ASPSP, com a adição da inclusão da realização de inventários para se conhecer mais detalhadamente a biota local. Resultados obtidos no presente estudo são consistentes com as necessidades apontadas pelo MMA e reforçam a necessidade da implementação de medidas manejo espaciais para conservação dessas áreas.

No capítulo 1, potenciais habitats de importância alimentar para ocorrência do tubarão-baleia foram descritos. Adicionalmente, recomenda-se a realização de levantamentos de informações etnobiológicas por meio de aplicação de questionários padronizados em pontos estratégicos em que uma maior adequabilidade foi observada pelos modelos ecológicos. Este tipo de esforço de pesquisa é importante para se conhecer mais detalhadamente sobre a distribuição do uso de habitat (Johanson e Harding 2007; Barbosa-Filho et al 2016) e, como consequência, permitir o planejamento de esforços para descrever aspectos ecológicos e biológicos e fazer marcação via satélite dos tubarões-baleia que frequentam a costa do Brasil. Ademais, as interações com a pesca (Capietto et al 2014; Barbosa-Filho et al 2016) e com as plataformas de petróleo (McKinney et al 2012; presente estudo) são potenciais meios de coleta de registros de tubarão-baleia e, portanto, devem ser exploradas utilizando políticas que obriguem os observadores de bordo e pescadores artesanais a informarem em seus livros de registro as informações sobre tais encontros.

Parte dos dados coletados no presente estudo foi proveniente de encalhes ou captura incidental, mas infelizmente uma grande parcela dos dados derivados destes eventos foi subaproveitada por falta de experiência do amostrador. Dada a raridade em se obter dados sobre a biologia do tubarão-baleia (*i.e.* investigação dos aparelhos reprodutor e digestivo e da idade e crescimento, além de outros aspectos), é extremamente importante obter total vantagem dessas oportunidades de coleta de dados. Um meio de se alcançar esse objetivo é a produção de um documento ilustrado e amplamente difundido (pela internet, por exemplo) que descreva métodos adequados para coleta de dados biológicos oriundos de carcaças de tubarão-baleia para que pesquisadores inexperientes nesse campo de pesquisa tenham possibilidade de aproveitar ao máximo essas oportunidades inesperadas para dissecação e outras observações.

Por fim, conforme as informações abordadas anteriormente recomendam-se a continuidade e intensificação de estudos sobre o tubarão-baleia e a designação de áreas de proteção para a espécie na costa brasileira.

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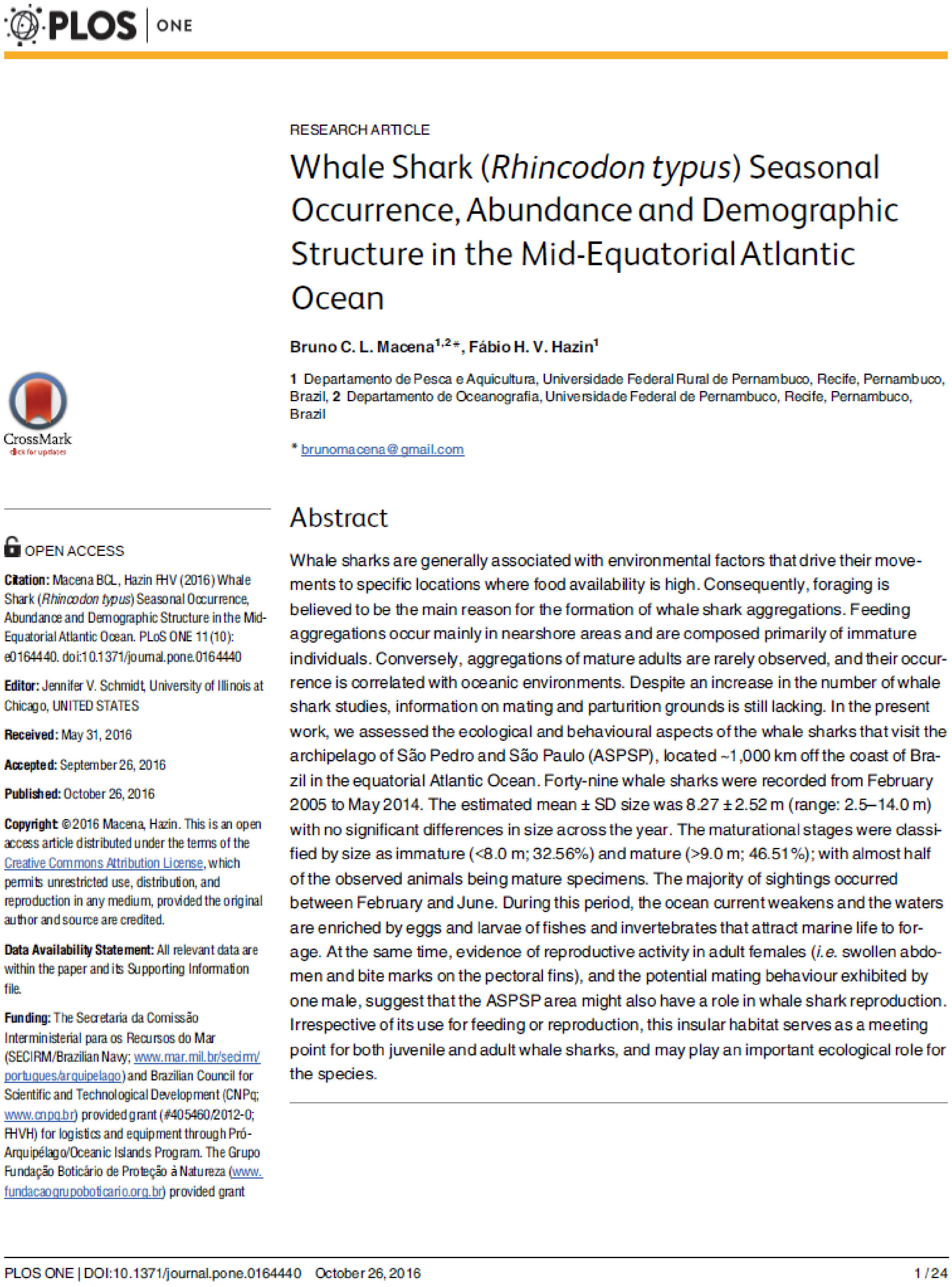
APÊNDICE A- Artigo científico publicado no jornal PLoS ONE (apenas apresentada a primeira página)



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RESEARCH ARTICLE

Whale Shark (*Rhincodon typus*) Seasonal Occurrence, Abundance and Demographic Structure in the Mid-Equatorial Atlantic Ocean

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Abstract

Whale sharks are generally associated with environmental factors that drive their movements to specific locations where food availability is high. Consequently, foraging is believed to be the main reason for the formation of whale shark aggregations. Feeding aggregations occur mainly in nearshore areas and are composed primarily of immature individuals. Conversely, aggregations of mature adults are rarely observed, and their occurrence is correlated with oceanic environments. Despite an increase in the number of whale shark studies, information on mating and parturition grounds is still lacking. In the present work, we assessed the ecological and behavioural aspects of the whale sharks that visit the archipelago of São Pedro and São Paulo (ASPSP), located ~1,000 km off the coast of Brazil in the equatorial Atlantic Ocean. Forty-nine whale sharks were recorded from February 2005 to May 2014. The estimated mean ± SD size was 8.27 ± 2.52 m (range: 2.5–14.0 m) with no significant differences in size across the year. The maturational stages were classified by size as immature (<8.0 m; 32.56%) and mature (>9.0 m; 46.51%); with almost half of the observed animals being mature specimens. The majority of sightings occurred between February and June. During this period, the ocean current weakens and the waters are enriched by eggs and larvae of fishes and invertebrates that attract marine life to forage. At the same time, evidence of reproductive activity in adult females (*i.e.* swollen abdomen and bite marks on the pectoral fins), and the potential mating behaviour exhibited by one male, suggest that the ASPSP area might also have a role in whale shark reproduction. Irrespective of its use for feeding or reproduction, this insular habitat serves as a meeting point for both juvenile and adult whale sharks, and may play an important ecological role for the species.

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APÊNDICE B- Resultados preliminares das análises da genética populacional do tubarão-baleia no Oceano Atlântico.

Phylogeography of the Atlantic Ocean whale shark population

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Introduction

Understanding the level of connection between populations that compose a species is important for the elaboration of a conservation and management plan. For instance, in the case of the whale sharks, different management strategies may be adopted depending on the level of connection between populations considered. However, determining if whales sharks travel across the oceans to breed is a difficult task. Traditional techniques based on tagging and photo-identification has failed so far in answering this question. This is due to difficulties associated to the study of such elusive and oceanic species. In order to help fill in this gap, molecular markers have been applied to this problem in the past ten years.

The first population genetics study for this species was based on the mitochondrial DNA control region and showed significant population structure between the Atlantic and the Indo-Pacific ocean basins (Castro *et al.* 2007). However, the finding of haplotype sharing between these ocean basins supported an alternative hypothesis of possible present day connection between these ocean basins or a potential for global migration (Castro et al. 2007). This view of little genetic differentiation between Atlantic and Indo-Pacific was subsequently reinforced by a subsequent study based on microsatellite data (Schmidt et al. 2009). These authors considered a history of gene flow between whale sharks in the Atlantic and Indo-Pacific that would support migration and interbreed albeit just sufficient to genetically normalize populations. Both studies stated that further genetic studies on larger sample sizes and based on specimens sampled in areas other than aggregation sites (Castro et al. 2007, Schmidt et al. 2009). A subsequent study on paternity analysis in a litter of whale shark embryos further reinforced this view of low population differentiation (Schmidt et al. 2010).

These pioneering genetic studies received different interpretations by the scientific community. Castro et al. (2007) and Schmidt et al. (2009) were thought: (1) to ‘tentatively conclude’ whale sharks to compose two distinct populations (Atlantic and Indo-Pacific) (Hueter & Tyminski 2012; Norman et al. 2016); (2) to ‘lean towards a worldwide panmictic *R. typus* population’ (Rowat & Brooks 2012); (3) to support evidence for a panmictic whale shark population, connected globally (Sequeira et al. 2013, 2014a, 2014b). Therefore, the interpretations varied from two distinct populations to a single global one.

This ambiguous situation is gradually being resolved towards the Atlantic and Indo-Pacific populations’ hypothesis. This hypothesis has been explicitly proposed based on sample sizes that were considerably larger than previous studies (Vignaud et al. 2014). In addition, it was based on both mitochondrial and microsatellite data. Currently, most studies now accept the concept of a strong separation between Atlantic and Indo-Pacific (Chabot 2015, Rohner et al. 2015, Spaet et al. 2015, Bernard et al. 2016, Bowen et al. 2016), even tough some authors still consider that worldwide gene flow still possible (Hearn et al. 2016, Sequeira *et al.* 2016). Nevertheless, recent new genetic evidence further reinforces this interpretation of two populations (Sigsgaard et al. 2016).

The issue on the level of connection between whale shark populations in the Atlantic and the Indo-Pacific is a spatial question. Having a regular spacing between sampling points is essential for population structure studies (Epperson 2003). However, due to logistic difficulties, this condition has not been met for whale shark studies so far. In all of the genetic studies conducted so far (Castro *et al.* 2007, Schmidt *et al.* 2009, Vignaud *et al.* 2014, Sigsgaard et al. 2016), all these samples came from one same region of the Atlantic: the Gulf of Mexico/ Caribbean. It is in this context that the present study as the goal to fill in this gap of knowledge by providing the constructing the first phylogeography for the Atlantic Ocean whale shark population.

Material and Methods

Sampling

A total of 10 tissue samples from Atlantic Ocean whale shark specimens obtained from 2009 and 2014. Four were directly sampled in the Archipelago of São Pedro e São Paulo (ASPSP). Three were directly sampled in the Azores, Portugal. These samples are '*fin clip*'. They were obtained during tagging studies. The remaining three samples were obtained from animals were caught or stranded in the Brazilian coast (Table 1).

Table 1: These samples from Atlantic Ocean whale shark specimens obtained between 2009 and 2014 and sequenced for the mitochondrial DNA control region.

Code	Locality	Collector	Sample/Observation
FAR 99	Ceará	T. Venâncio	Muscular tissue / specimen described in Faria *et al.* (2009)
FAR 100	ASPSP	B. Macena	*Fin clip*
FAR 101	ASPSP	B. Macena	*Fin clip*
FAR 102	ASPSP	B. Macena	*Fin clip*
FAR 103	ASPSP	B. Macena	*Fin clip*
FAR 105	Santa Catarina	J. Soto	Muscular tissue /Specimen deposited at MOVI/Univali
FAR 106	Azores (Portugal)		*Fin clip*
FAR 107	Azores (Portugal)		*Fin clip*
FAR 108	Azores (Portugal)		*Fin clip*
FAR 868	Bahia	C. Sampaio	Muscular tissue

ASPSP: Archipelago of São Pedro and São Paulo.

Laboratory Procedures

The samples were DNA extracted using a Quiagen DNeasy kit, following manufacturer instructions. The extracted DNA was submitted to Polymerase Chain Reaction (PCR) for amplification of the mitochondrial DNA control region using primers and methods described in Castro *et al.* (2007). PCR was purified using ExoSAP-IT, following manufacturer instructions (USB). Purified PCR products were submitted to DNA sequencing at Macrogen, South Korea (EZ-Seq service; http://www.macrogen.com/).

Data analysis

DNA sequences were subjected to a median-joining network analysis, in order to describe the relationships among Atlantic whale shark mtDNA haplotypes (Bandelt et al. 1999). These analyses were run in a global context after inclusion of 590 publicly available whale shark control region DNA sequences.

Further analysis included an analysis of molecular variance to assess whale shark population genetic structure (Fst) between Atlantic, Indian, and Pacific Oceans. For this analysis, a dataset was composed of sequences publicly available and were run under a Tamura and Nei + Gamma model.

Results

Network analysis: (1) our analysis revealed a third common haplotype for the Atlantic Ocean (two other common haplotypes were already known for the Gulf of Mexico); (2) this third common haplotype was already detected for the Gulf of Mexico but it was rare in that region; (3) only after a further sampling of the Atlantic it was possible to assess the importance of this referred third common haplotype; (4) None of the new haplotypes obtained was grouped with the two common haplotypes previously detected for the Gulf of Mexico – they clustered around this third common haplotype; (5) Some of the haplotypes previously found in the Gulf of Mexico are typically Indo-Pacific haplotypes; this same pattern was found in the present study: two out of the ten sequences were typical of the Indo-Pacific (6) Two of the three most representative haplotypes from the Atlantic are almost exclusive for this ocean basin (Fig. 1 and 2).

Population structure: Fst values between Atlantic and other Indo-Pacific localities varied from 0.184 to 0.403.

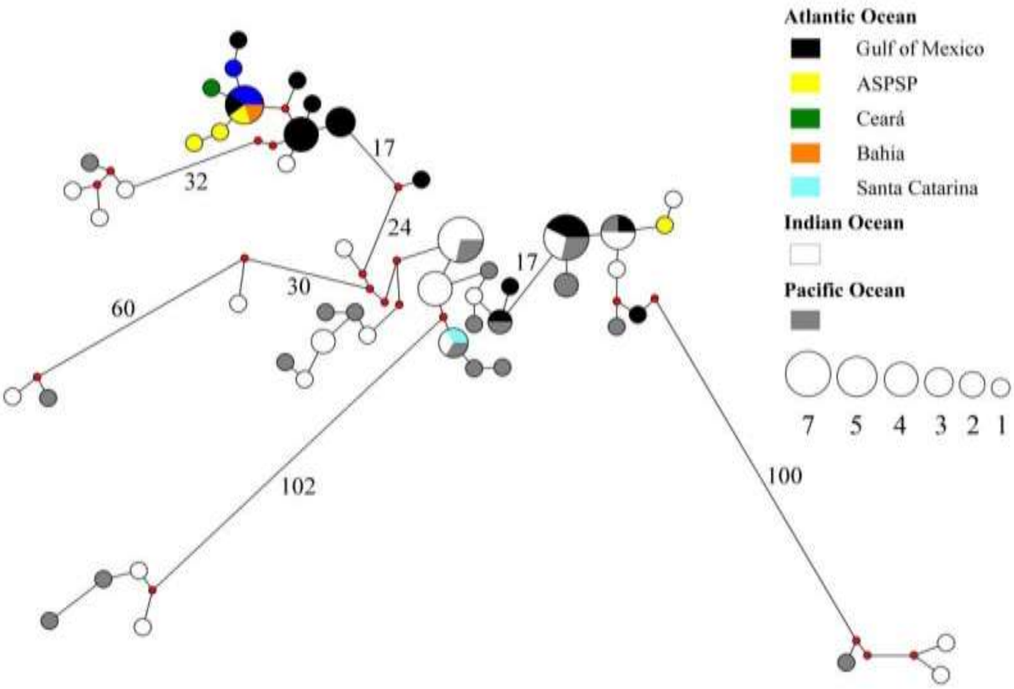

Figure A.1 - Median-Joining network based on full mitochondrial DNA control region sequences (1,381bp) obtained from 83 whale shark specimens.

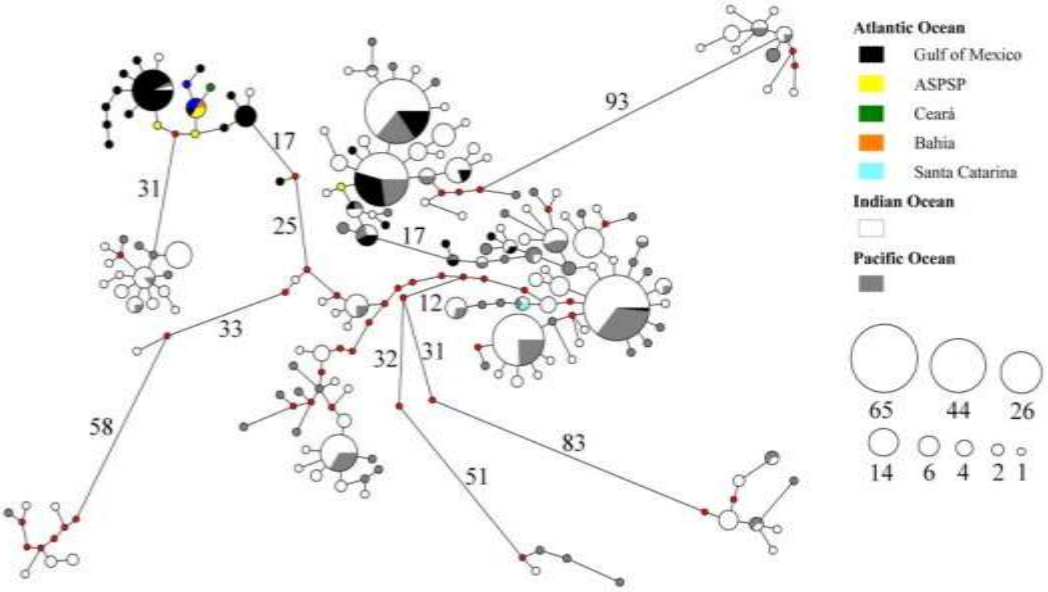

Figure A 2- Median-Joining network based on partial mitochondrial DNA control region sequences (760 bp) obtained from 590 whale shark specimens.

Discussion

This is the first population genetic structure study for whale sharks to include data from Atlantic individuals sampled outside feeding aggregation areas in the Gulf of Mexico and the Caribbean. By assessing the genetic information from regions including the southwestern, central, and northeastern Atlantic we now reach a much more complete picture of how whale sharks are structured within this ocean basin. This within Atlantic broader picture is much anticipated. Satellite tracking and occurrence studies have so far provided the first clues on how much individuals of this Atlantic population are able to travel (Sequeira et al. 2013, Macena & Hazin, 2016). But due to limitations inherent to the study of such elusive animal, data from most of the area are still lacking. The genetic results presented here help fill in this gap of knowledge.

Whale sharks compose a single population within the Atlantic. This is based on the fact that the most common haplotype was found in Azores (northeast Atlantic), ASPSP (mid-equatorial Atlantic), northeastern Brazilian coast (southwestern Atlantic) and Gulf of Mexico (northwestern Atlantic). This result reflects historical connections between these areas. Unfortunately, gene flow estimation among Atlantic sites was precluded due to sample size limitations. Nevertheless, the new genetic evidence is concordant with a hypothesis of large-scale connection within this ocean basin. In the Atlantic, whale sharks are connected through Mexico, Belize and Honduras, based on tagging evidence (Graham & Roberts, 2007). Tagging efforts also provided crucial empirical evidence of movement between Mexico to the Central Atlantic, south of the Archipelago of São Pedro e São Paulo (ASPSP). This tagging event along with the timing of whale shark distribution records suggests that ASPSP may work as a transatlantic Ocean thoroughfare (Sequeira *et al.* 2013). These authors also suggest that whale sharks could move from the Gulf of Mexico to Azores and, from there, to Portugal, West Africa and ASPSP. In fact, ASPSP has been shown to be a hotpot for whale sharks in the Central Atlantic, possibly working as a feeding station during oceanic migration (Macena & Hazin, 2016). Furthermore, whale sharks are capable of travelling long distances (Hueter *et al.* 2013, Norman *et al.* 2016) and able to actively swim for feeding, not being restricted to using currents for its migration (Hsu et al. 2007, Rowat & Gore 2007, Sleeman 2010). Finally, mitochondrial and nuclear DNA markers suggest that whales sharks are not structured within the entire Indo-Pacific (Castro et al, 2009, Schmidt et al. 2009, 2010, Vignaud et al. 2014, Sigsgaard et al. 2016). Therefore, it can be inferred that whale shark individuals within the Atlantic Ocean are not restricted to any area suitable to their presence.

Whale sharks have a breeding population in the Atlantic. Whale sharks are known to pup in the Atlantic based on the records of neonates in Central Atlantic and also egg capsules found in the Gulf of Mexico (Martin 2007, Sequeira *et al.* 2013). There is also evidence of recent reproduction for individuals sighted at ASPSP (i.e., potential mating behavior, bite marks, clasper abrasion; Macena & Hazin 2016) and Saint Helena (i.e. pregnant female; Clingham *et al.* 2016), in the South Central Atlantic. The question of where does whale sharks reproduce globally has been long unanswered and the evidence of neonates, pregnant females and mating behavior and bite scars are suggestive of a full Atlantic reproduction cycle. The finding of new exclusive central Atlantic haplotype reinforces reproduction in the Atlantic, made by Atlantic individuals.

Atlantic and Indo-Pacific whale shark populations lack any present-day connection. In the field of population genetics, the term ‘population’ most commonly refers to individuals that live in a sufficiently restricted area, in which they may interbreed and produce their offspring over generations. Here we support the hypothesis that whale sharks are composed of two populations: one in the Atlantic Ocean and another one in the Indo-Pacific. This implies no present-day gene flow between whale sharks from these two ocean-basins. Estimation of gene flow based on control region sequences in previous studies indicated isolation between Atlantic and Indo-Pacific. The following Fst values were obtained in comparisons between these two ocean basins: 0.163 to 0.215 (Castro et al. 2007), 0.194 to 0.351 (Vignaud et al. 2014), 0.30 (Sigsgaard *et al.* 2016), and 0.184 to 0.403 (present study). According to Helfman *et al.* (2009), a value of about 0.10 already indicates strong population structure and distinct manage unit. Therefore, all mitochondrial DNA based Fst values obtained so far already indicates the distinction between Atlantic and Indo-Pacific populations. This same pattern was revealed by analysis based on microsatellites (Schmidt *et al.* 2009, Vignaud *et al.* 2014).

The sharing of haplotypes between Atlantic and Indo-Pacific populations are compactible with a scenario of recent (in a geological scale) separation of populations. Castro et al. (2007) were the first to describe the haplotype sharing between Atlantic and in the Indo-Pacific. Here we further support this same pattern based on our network analysis that included the new Atlantic DNA sequences as well as additional Indo-Pacific sequences obtained by Vignaud *et al.* (2014). We here propose that, along with the Fst results discussed above, this haplotype pattern should be interpreted as evidence of recent separation of populations. This is in accordance with the seminal work of Avise et al. (1987) that developed categories of level of genetic and geographic separation of lineages. Tropical and subtropical marine species from Atlantic and Indo-Paficic have been isolated through the emergence the Isthmus of Panama and the rise of cold waters from the Benguela current. There have been periods in which the Benguela current barrier became temporarily transposable to such organisms. But these events have occurred in a geological scale of time (See discussion on this topic in Castro et al. 2007, Floeter et al. 2008, Vignaud et al. 2014, Bowen et al. 2016). The sharing of haplotypes between Atlantic and Indo-Pacific may be the product from these short historical periods in which these ocean basins were able to exchange migrants. This has permitted the cohesion of the species (these two populations most securely constitute one same species). But for practical present-day conservation issues, Atlantic and Indo-Pacific whale sharks should be viewed as two separate management units. As a consequence, if one of these populations becomes depleted, there would be no migrants from the other to help replenish it.

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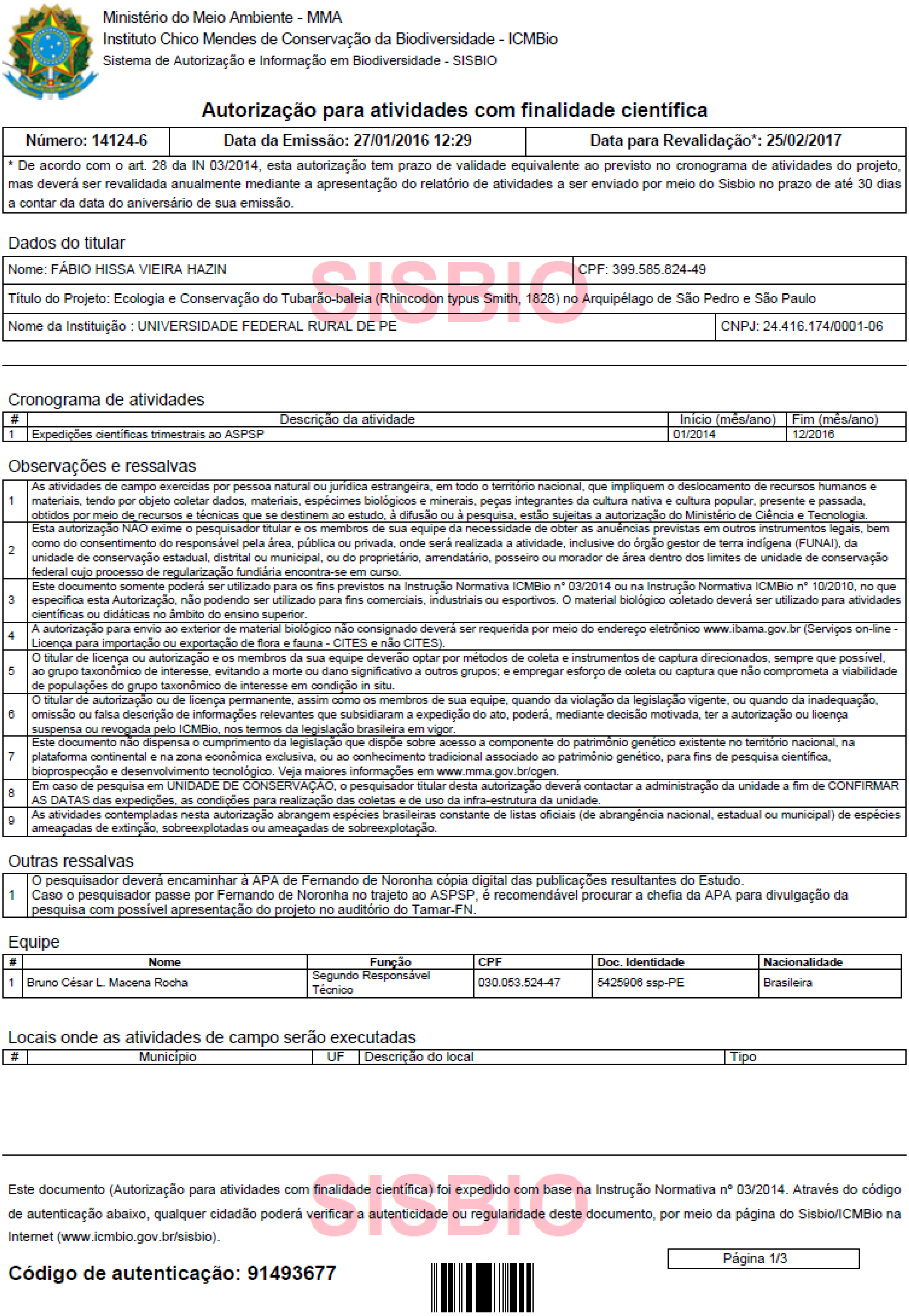
ANEXO A – Autorização para atividades com finalidade científica – SISBIO.



Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 14124-6	Data da Emissão: 27/01/2016 12:29	Data para Revalidação*: 25/02/2017
* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.		

Dados do titular

Nome: FÁBIO HISSA VIEIRA HAZIN	CPF: 399.585.824-49
Título do Projeto: Ecologia e Conservação do Tubarão-baleia (Rhincodon typus Smith, 1828) no Arquipélago de São Pedro e São Paulo	
Nome da Instituição : UNIVERSIDADE FEDERAL RURAL DE PE	CNPJ: 24.416.174/0001-06

SISBIO

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
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8	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.
9	As atividades contempladas nesta autorização abrangem espécies brasileiras constante de listas oficiais (de abrangência nacional, estadual ou municipal) de espécies ameaçadas de extinção, sobreexplotadas ou ameaçadas de sobreexplotação.

Outras ressalvas

1	O pesquisador deverá encaminhar à APA de Fernando de Noronha cópia digital das publicações resultantes do Estudo. Caso o pesquisador passe por Fernando de Noronha no trajeto ao ASPSP, é recomendável procurar a chefia da APA para divulgação da pesquisa com possível apresentação do projeto no auditório do Tamar-FN.

Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Bruno César L. Macena Rocha	Segundo Responsável Técnico	030.053.524-47	5425906 ssp-PE	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo

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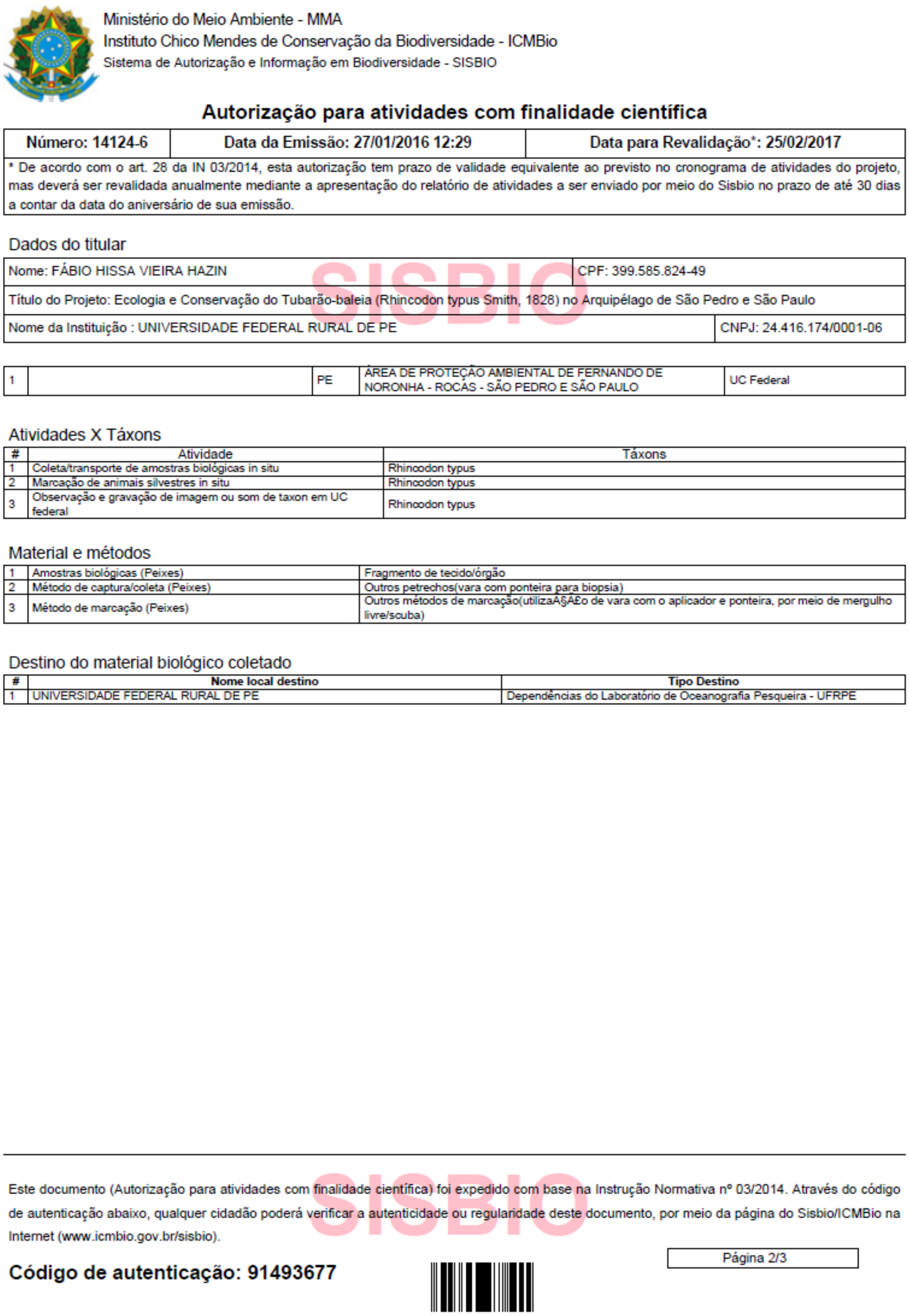

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 14124-6	Data da Emissão: 27/01/2016 12:29	Data para Revalidação*: 25/02/2017

* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

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Nome: FÁBIO HISSA VIEIRA HAZIN	CPF: 399.585.824-49
Título do Projeto: Ecologia e Conservação do Tubarão-baleia (Rhincodon typus Smith, 1828) no Arquipélago de São Pedro e São Paulo	
Nome da Instituição : UNIVERSIDADE FEDERAL RURAL DE PE	CNPJ: 24.416.174/0001-06

1		PE	ÁREA DE PROTEÇÃO AMBIENTAL DE FERNANDO DE NORONHA - ROCAS - SÃO PEDRO E SÃO PAULO	UC Federal

Atividades X Táxons

#	Atividade	Táxons
1	Coleta/transporte de amostras biológicas in situ	Rhincodon typus
2	Marcação de animais silvestres in situ	Rhincodon typus
3	Observação e gravação de imagem ou som de taxon em UC federal	Rhincodon typus

Material e métodos

1	Amostras biológicas (Peixes)	Fragmento de tecido/órgão
2	Método de captura/coleta (Peixes)	Outros petrechos(vara com ponteira para biopsia)
3	Método de marcação (Peixes)	Outros métodos de marcação(utilizaÃ§Ã£o de vara com o aplicador e ponteira, por meio de mergulho livre/scuba)

Destino do material biológico coletado

#	Nome local destino	Tipo Destino
1	UNIVERSIDADE FEDERAL RURAL DE PE	Dependências do Laboratório de Oceanografia Pesqueira - UFRPE

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Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº 03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

Táxon*	Qtde.	Tipo de amostra	Qtde.	Data

* Identificar o espécime no nível taxonômico possível.

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