UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE TECNOLOGIA E GEOCIÊNCIAS

DEPARTAMENTO DE OCEANOGRAFIA

PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

Utilização de habitat e movimentos migratórios do Agulhão Negro (*Makaira nigricans*) no oceano Atlântico Sul

Osman Crespo Neto

Recife, 2016

Universidade Federal de Pernambuco
Centro de Tecnologia e Geociências
Departamento de Oceanografia
Programa de Pós-Graduação em Oceanografia

Utilização de habitat e movimentos migratórios do Agulhão Negro (*Makaira nigricans*) no oceano Atlântico Sul

Osman Crespo Neto

Dissertação apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco (PPGO-UFPE), como requisito para obtenção do título de Mestre em Oceanografia.

Orientador: Prof. Dr. Fábio Hissa Vieira Hazin
Co-Orientador: Dr. Felipe Carvalho

Recife, 2016

Catalogação na fonte
Bibliotecária Valdicéa Alves, CRB-4 / 1260

C921u Crespo Neto, Osman.
Utilização de habitat e movimentos migratórios do Agulhão Negro (Makaira nigricans) no oceano Atlântico Sul. / Osman Crespo Neto - 2016.
60 folhas. Il., e Tab.

Orientador: Profº. Dr. Fábio Hissa Vieira Hazin.
Coorientador: Profº. Dr. Felipe Carvalho.

Dissertação (Mestrado) – Universidade Federal de Pernambuco. CTG. Programa de Pós-Graduação em Oceanografia, 2016.
Inclui Referências e Anexo.
Nota: Texto Bilíngue.

1. Oceanografia. 2. PSATs. 3. Espinhel. 4. Marcação. 5. Sobre pesca 6. Agulhões. I. Hazin, Fábio Hissa Vieira (Orientador). II. Carvalho, Felipe. III. Título.

UFPE

551.46 CDD (22. ed.) BCTG/2016 - 275

Utilização de habitat e movimentos migratórios do Agulhão Negro (*Makaira nigricans*) no oceano Atlântico Sul

Osman Crespo Neto

Dissertação defendida e aprovada pela banca examinadora. 27/06/2016

Prof. Dr. Fábio H.V. Hazin (Orientador) –
Universidade Federal de Pernambuco

Profa. Dra. Maria Elisabeth de Araújo –
Universidade Federal de Pernambuco

Dr. Dráusio Pinheiro Véras –
Universidade Federal Rural de Pernambuco

Dr. Paulo G. V. de Oliveira–
Universidade Federal Rural de Pernambuco

Agradecimentos

Agradeço a Deus, por uma vida iluminada e por me acompanhar com amor, se mostrando sempre presente nos mais diversos momentos.

Agradeço à Universidade Federal de Pernambuco (UFPE) e o departamento de Oceanografia, onde tive a oportunidade de ter um curso de grande nível que me proporcionou um importante espaço acadêmico e grande aprendizado através de seus profissionais de todas as áreas.

Agradeço ao apoio da CAPES pela provisão da bolsa de Mestrado e também à Fundação Guy Harvey e NOAA, órgãos parceiros que financiaram o projeto de pesquisa juntamente com o Programa Ciência Sem Fronteiras – Jovens Talentos.

Agradeço imensamente ao professor Fábio Hazin, que me apoiou desde o início nesse processo incrível da pós-graduação. Obrigado por acreditar no meu trabalho e por ter sido este grande tutor nas conversas e revisões de trabalho.

Sou muito grato a meu co-orientador Felipe Carvalho, principalmente por sua presença e ensinamentos nos processos estatísticos. Participação inestimável nesse processo de aprendizado. Sou grato pela sua amizade, por ter acreditado no meu potencial e me apoiado desde muito cedo em 2011.

Agradeço a todos os meus companheiros da UFRPE e UFPE, que foram grandes amigos desde a graduação e aos que nos conhecemos no mestrado, a amizade sempre fortalece o dia a dia.

Agradeço carinhosamente a minha esposa Thaynã Mota, parceira de todas as horas onde encontro sempre um carinho e amor inabaláveis que me faz sentir especial. Obrigado por ser minha companheira e me encorajar nas minhas escolhas.

Agradeço infinitamente à toda a minha família, pessoas que sempre me apoiaram durante minha formação e sempre torceram por meu sucesso. Em especial, gostaria de agradecer àqueles que estão comigo desde meus primeiros dias de vida, minha mãe Lu, meu irmão Gabriel e meu pai Osman (*In memorian)* que sempre estiveram comigo e foram suporte no aprendizado da vida.

“ Há um tal prazer nos bosques inexplorados;
Há uma tal beleza na solitária praia;
Há uma sociedade que ninguém invade;
Lá no fundo do mar, e da música no seu rugido;
Não que ame menos o ser humano, mas amo mais a natureza. ”

- Lord Byron -

Resumo

O agulhão negro (*Makaira nigricans*) é uma espécie dentre os grandes peixes pelágicos que compõe o topo da teia trófica marinha, sendo sua preservação importante para a manutenção da dinâmica populacional desses ecossistemas. Esta espécie é uma das mais procuradas pela pesca esportiva no mundo, sendo, porém, alvo de sobrepesca devido sua captura frequente como fauna acompanhante na pesca de espinhel pelágico no oceano Atlântico. O objetivo do presente trabalho de pesquisa foi compreender os movimentos migratórios, a influência de fatores ambientais em padrões de movimento e utilização de habitat pelos agulhões-negro no oceano Atlântico Sul e como essa espécie interage com o aparelho de pesca. Para o levantamento de dados sobre a utilização de habitat foram utilizadas marcas PSATs (*pop-up satellite archival tags*) para monitorar o comportamento do animal registrando um fluxo quase contínuo de parâmetros ambientais especificados (temperatura, pressão [profundidade] e luminosidade), onde os dados são arquivados e transmitem a informação via satélite após se desconectarem do animal. Além disso, foram também analisadas as profundidades de atuação dos anzóis do espinhel na pesca comercial de atuns e afins no Atlântico Sul, para melhor compreender quanto o esforço de pesca atualmente empregado se sobrepõe ao habitat utilizado pelos agulhões. O deslocamento horizontal durante o período de marcação variou de 374 a 1.838 km. Os resultados mostraram que os indivíduos maiores (>195 cm), considerados adultos, apresentaram deslocamentos direcionais segundo a estatística circular aplicada, enquanto que indivíduos juvenis ou menores (<195 cm) apresentaram deslocamentos considerados *loopings* ou sem direcionamento definido. Os dados de tempo em profundidade nos mostraram que a os indivíduos passam a maior porcentagem do tempo em águas superficiais acima dos 20m durante os períodos noturno e diurno. Os agulhões negros permaneceram a maioria do tempo dentro de uma curta faixa de temperatura, com uma média de 57% do tempo em temperaturas entre 26º e 28ºC. Os resultados quanto a sobreposição de habitat à espinhéis pelágicos nos mostrou uma relação de 59% da área rastreada sobreposta às armadilhas de pesca. A média de profundidade dos anzóis registrada foi de 49 m, sendo 90% da distribuição de profundidade dos anzóis entre 32-71m. Essa distribuição vertical quando sobreposta ao padrão de utilização vertical do habitat pelos agulhões, revelou uma sobreposição que varia entre 11% e 35% durante o período diurno e 21% e 34% durante a noite. Os resultados obtidos na presente pesquisa são relevantes para uma melhor compreensão da biologia e ecologia dos agulhões negros no oceano Atlântico Sul, compondo um importante conhecimento sobre o comportamento da espécie e auxiliando para tomada de decisões e medidas de manejo e conservação da espécie a nível internacional.

Palavras-chave: PSATs, espinhel, marcação, sobrepesca, pesca esportiva, agulhões

Abstract

Blue marlin (*Makaira nigricans*) is a species among great pelagic fishes that occupy the top of marine food web, being its conservation important to the maintenance of ecosystem population dynamics. Atlantic blue marlin is one of the favorite species targeted by recreational fishing in the Atlantic Ocean, however being overexploited because of its frequent capture as bycatch by commercial pelagic longline fishery. The main goal of this study was to understand migratory movement and the influence of environmental factors in movement patterns and habitat utilization by blue marlins in the South Atlantic Ocean and how this species interacts with pelagic longline gear. Pop up archival tags (PSATs) were used to collect habitat utilization data monitoring animal behavior through continuous records of specified environmental parameters (temperature, pressure [depth] and luminosity), transmitting such reports via satellite after pop-off. Furthermore, was also analyzed longline gears hook depths from commercial fisheries in South Atlantic to better understand how this fishing effort overlap to marlins habitat utilization. PSATs were programmed to record depth, temperature, and light intensity for a period of 180 days until release. The horizontal net displacement for all blue marlins ranged from 374 to 1.838 km. Results presented that larger individuals (>196 cm), considered adults, achieved directional movements according to circular statistics applied, while shorter individuals (<195 cm) presented displacement as looping or non-directional. Time-at-depth histograms of blue marlin habitat utilization show that most individuals across all areas spent the majority of their time in shallow waters, above 20m, both during the day and night periods. Blue marlins spent most of their time within a relatively narrow temperature range, staying an average of 57% of their time in temperatures between 26° and 28°C. Overall, blue marlins had approximately 59% of their tracked range overlapped by the longline fishing gear. The average hook depth across all areas was 49 m with 90% percentile depth distribution of the hooks depth between 32-71 m. When this distribution was overlapped with the species vertical habitat utilization, the overlap ranged between 11 and 35% during daytime and 21 and 34% during nighttime. The results achieved in this study are relevant to better understand the biology and ecology of Atlantic blue marlins, composing an important knowledge about species behavior, which reduces current uncertainties about its biology and help to making decisions and take international conservation and management measures to the species.

Keywords: PSATs, longline, tagging, overfishing, sport fishing, billfish, conservation

Lista de figuras **Pág.**

Introdução

Artigo

Lista de tabelas **Pág.**

Artigo

Sumário

INTRODUÇÃO

No ecossistema marinho, espécies migratórias de grande porte são caracterizadas por sua vasta distribuição geográfica e complexos padrões de migração, compondo geralmente um único estoque dentro de uma bacia oceânica (Lynch et al. 2011). Muitas espécies de grandes peixes migratórios e outros organismos marinhos estão suscetíveis à captura incidental pela atividade pesqueira como mamíferos aquáticos, tartarugas, raias, tubarões e agulhões (Família Istiophoridae). No Atlântico, os agulhões são capturados frequentemente como fauna acompanhante na pesca de espinhel pelágico de atuns do gênero *Thunnus* (i.e. albacora branca, *T. alalunga* (Bonnaterre, 1788); albacora laje, *T. albacares* (Bonnaterre, 1788); albacora bandolim, *T. obesus* (Lowe, 1839); albacora azul, *T. thynnus* (Linnaeus, 1758)) e espadarte (*Xiphias gladius,* Linnaeus, 1758) (Restrepo et al. 2003; Die 2006; Kitchell et al. 2006). Os mamíferos marinhos possuem comumente uma grande empatia popular, sendo as capturas incidentais condenadas publicamente, o que pressiona a adoção de regulamentações e tecnologias para redução das taxas de mortalidade por pesca dessas espécies (Hall 1998; Hall et al. 2000). Essa reação não é tão comum em relação aos agulhões, como o agulhão negro (*Makaira nigricans*, Lacepède 1802) (Figura 1), apesar do mesmo já há alguns anos ser considerado uma espécie em sobrepesca no Atlântico (Restrepo et al. 2003).

No Oceano Atlântico, o ordenamento da pesca de grandes peixes migratórios é realizado pela Comissão Internacional para Conservação do Atum Atlântico (ICCAT), que tem como principal objetivo manter os estoques em níveis compatíveis com o Rendimento Máximo Sustentável (RMS) (ICCAT 2007a). O manejo de diferentes espécies de grandes pelágicos é muito complexo devido à sobreposição espacial e temporal de suas distribuições, causando altos níveis de captura incidental de espécies não-alvo. Além disso, o esforço de pesca pode causar respostas distintas entre as espécies por não possuírem as mesmas taxas de crescimento populacional e capacidade de suporte, levando, em muitos casos, à necessidade de uma redução do esforço de pesca para níveis abaixo do necessário para maximizar a produção sustentável das espécies alvo (Lynch et al. 2011).

Atualmente, duas espécies de agulhões do Atlântico, o branco e o negro, estão submetidas a um programa de recuperação dos seus estoques (ICCAT 2013), com regulamentações que afetam tanto a pesca comercial quanto a esportiva. Ainda não se sabe, porém, o quanto as atuais regulamentações impostas pela ICCAT para a redução da mortalidade dos agulhões serão capazes de reforçar, de fato, a recuperação dos estoques. Isto porque os desafios que envolvem o manejo dos agulhões estão relacionados à grandes incertezas que ainda perduram sobre a sua biologia e pesca, reduzindo, entre outros aspectos, a confiabilidade das avaliações de estoque até hoje realizadas (Restrepo et al. 2003; Die 2006; Webster 2006; ICCAT 2007c; ICCAT 2011).

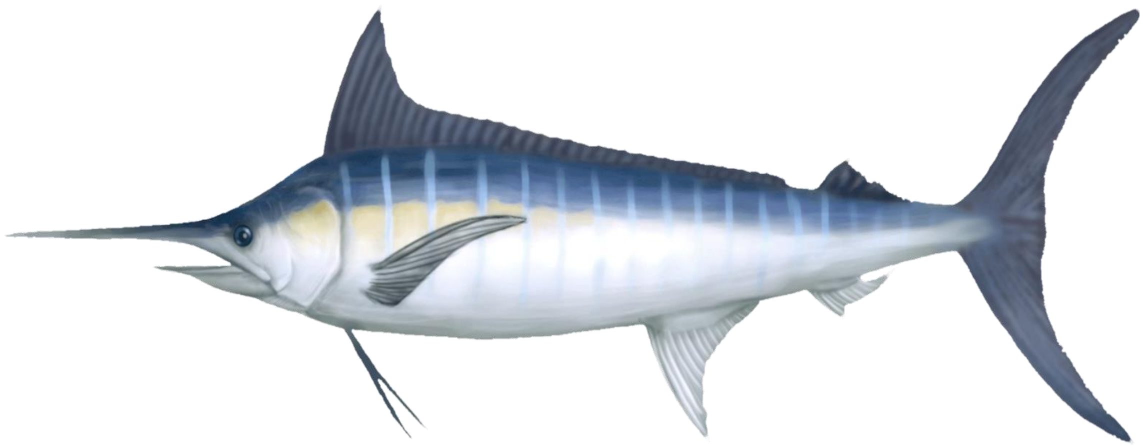

Figura 2. Desenho esquemático do agulhão negro (*Makaira nigricans*). Fonte: ICCAT

No Brasil, uma Instrução Normativa da Secretaria Especial de Aquicultura e Pesca (I.N SEAP Nº 12/2005) proíbe em todo o país a venda de agulhões brancos e negros, assim como o descarte de animais que já estiverem mortos no momento do recolhimento dos anzóis. Dessa forma, os agulhões que se encontrarem ainda vivos no momento do recolhimento devem ser devolvidos ao mar, enquanto que aqueles que já estiverem mortos devem ser embarcados, trazidos para terra e doados. Esta medida de âmbito nacional pode ter influenciado no declínio expressivo da captura por unidade de esforço (CPUE) de agulhões negros no Brasil, a partir de 2004 (Pacheco et al. 2015). A avaliação de estoque mais recente para agulhões negros do Atlântico foi realizada pelo Comitê Permanente de Pesquisa e Estatísticas (*Standing Committee for Research and Statistics- SCRS*) da ICCAT em 2011 e, apesar da redução nos desembarques e potencial estabilização nas trajetórias de biomassa, as avaliações concluíram que os estoques de agulhões negros do Atlântico permanecem em sobrepesca (ICCAT 2011). Sendo assim, em 2013, a referida comissão estabeleceu um plano plurianual para recuperação das populações, incluindo um limite de captura anual de 2.000 t de agulhões negros, para 2013 e 2014. A ICCAT recomendou pesquisas futuras em vários aspectos da pesca e dinâmica populacional dessa espécie para a redução das incertezas nas futuras avaliações de estoque e recomendações de manejo. Entre as recomendações está o levantamento de informações acerca dos movimentos migratórios e utilização do habitat dessa espécie no Oceano Atlântico, as quais podem auxiliar para que sejam realizadas avaliações de estoques mais precisas para a espécie.

Na pesca comercial os agulhões possuem menor importância econômica, sendo comumente considerados como fauna acompanhante. Apesar da atual regulamentação da ICCAT requerer que qualquer agulhão que ainda esteja vivo no momento do recolhimento do aparelho de pesca seja devolvido ao mar (ICCAT 2007b), as operações da pesca com espinhel frequentemente capturam peixes que não resistem por muito tempo nos anzóis, já se encontrando mortos no momento do recolhimento. Historicamente, o Brasil é responsável por parcelas significativas da captura de agulhões no Atlântico, sendo um dos maiores contribuintes para a mortalidade por pesca dessas espécies. Entre os anos de 1999 e 2010, o Brasil respondeu por 23% do total de capturas do agulhão negro, ficando em segundo lugar em número de agulhões desembarcados por país, com China Taipei (Taiwan) situando-se em primeiro lugar (ICCAT 2011). Por outro lado, desde meados dos anos 1800, quando a pesca esportiva de agulhões se iniciou, esta atividade tem sido uma importante fonte de renda para o turismo em várias partes do mundo (Holder 1912; Jordan & Evermann 1923; Holland et al. 1998). Em 1956, a pesca esportiva dos agulhões começou a ser promovida no Brasil com a fundação do Iate Clube Ilha Bela, em São Paulo, atuando de forma mais intensa nos Estados de São Paulo e Rio de Janeiro, incluindo a realização de campeonatos no Rio de Janeiro em 1963/64 (Arfelli et al. 1994; Amorim & Arfelli 2001; Mourato et al. 2009). Atualmente, campeonatos de pesca esportiva acontecem em toda a costa brasileira, atraindo centenas de pescadores de todo o mundo. A pesca esportiva movimenta a indústria do turismo de forma expressiva. Estima-se que no mundo inteiro, a pesca esportiva de agulhões produz entre US$ 205 milhões e US$ 340 milhões de dólares anualmente (Holland et al. 1998; Ditton & Stoll 2003). A comunidade de pesca recreativa tem reconhecido que a sustentabilidade das populações de agulhões é imprescindível para a preservação dessa prática esportiva. Como resultado, a pesca esportiva de agulhões tem se tornado essencialmente do tipo de captura e devolução (*catch-release*), visando minimizar ainda mais a mortalidade induzida pela atividade.

Infelizmente a conservação dos agulhões tem recebido relativamente uma baixa prioridade quando considerados os recursos dedicados à preservação de outras espécies da megafauna marinha, tidas como mais interessantes, tais como a albacora azul *Thunnus thynnus*, as tartarugas e os mamíferos marinhos. A conservação dos agulhões, portanto, dependerá diretamente da compreensão da sua suscetibilidade a impactos antropogênicos, particularmente à pesca, aspecto que deverá necessariamente ser reforçado com o conhecimento sobre a estrutura de tamanho e distribuição das suas populações, além do seu comportamento em relação ao habitat.

Os agulhões compõem a família Istiophoridae, que compreende cinco gêneros e nove espécies no mundo inteiro (Collette et al. 2006), entre as quais seis ocorrem regularmente no Oceano Atlântico e mares adjacentes: agulhão negro *M. nigricans*, agulhão branco *Kajikia álbida* (Poey, 1860), agulhão vela *Istiophorus platypterus* (Shaw, 1792), agulhão verde *Tetrapturus pfluegeri* (Robins & de Sylva, 1963), espadim do Mediterrâneo *T. belone* (Rafinesque, 1810) e agulhão redondo *T. georgii* (Lowe, 1841). Os agulhões negros, *M. nigricans,* estão distribuídos por águas temperadas e tropicais do oceano Atlântico, abrangendo entre 45°S no Atlântico Sul e 45°N no Atlântico Norte, e compreendendo desde o leste da Argentina até a África do Sul no hemisfério sul e do leste do Canadá até os Açores, no hemisfério norte, incluindo o Golfo do México (Nakamura 1985). É uma espécie de grande porte e de ampla mobilidade, que realiza grandes movimentos migratórios e por vezes migrações transoceânicas, sendo um dos peixes com maiores distâncias percorridas registradas em trabalhos de marcação e recaptura (Prince & Brown 1991; Ortiz et al. 2003; Orbesen et al. 2008). *M. nigricans* é uma espécie que não apresenta dimorfismo sexual, sendo difícil a diferenciação visual entre machos e fêmeas, apesar do conhecimento de que as fêmeas das espécies de agulhões atingem tamanhos bem maiores (Wilson et al. 1991; Nakamura 1983; Shimose et al. 2012). Os agulhões são predadores de topo piscívoros, embora tenha sido encontrada uma variada composição de itens alimentares nos seus estômagos, destacando-se entre as principais presas peixes e lulas epipelágicos (Brock 1984; Júnior et al. 2004; Satoh et al. 2004; Shimose et al. 2006; Shimose et al. 2010; Vaske et al. 2011). As dimensões dos itens alimentares encontrados no estômago de agulhões negros varia desde pequenos peixes de 2 cm (*Histrio histrio*) até albacoras bandolim de quase 30 kg (Strasburg 1970; Goodyear et al. 2008). São poucos os estudos que relatam a presença de itens alimentares de grandes profundidades (Strasburg 1970; Nakamura 1985; Harvey 1989; Rivas 1972), porém, as pesquisas de dieta alimentar geralmente usam agulhões capturados em superfície, por isso a composição de presas encontradas no estômago pode ser influenciada pelo local da captura (Brock 1984). Predadores de topo são ecologicamente importantes para a estruturação da teia trófica marinha, visto que seu esgotamento pode trazer impactos negativos à teia alimentar por meio do fenômeno de cascata trófica (Paine 1969; Pace et al. 1999; Kitchell et al. 2006; Casini et al. 2009; Estes et al. 2011).

As condições oceanográficas são capazes de influenciar intensamente os movimentos e a distribuição de predadores marinhos. Embora seja relativamente comum a identificação de áreas de abundância como *hotspots*, estudos quantitativos das condições que influenciam os movimentos dos grandes peixes pelágicos são ainda escassos (Queiroz et al. 2010; Queiroz et al. 2012; Bestley et al. 2013). A preferência dos agulhões por fatores específicos relacionados ao habitat pode afetar diretamente a sua distribuição e vulnerabilidade à pesca (Boyce et al. 2008). Devido ao seu extenso comportamento migratório, acredita-se que a densidade e distribuição dos agulhões do Atlântico sejam afetadas por diversas variáveis oceanográficas e biológicas, incluindo: temperatura da água, frentes oceânicas, velocidade de correntes, oxigênio dissolvido, disponibilidade de presa e abundância de zooplâncton (Brill et al. 1998; Brill & Lutcavage 2001; Prince & Goodyear 2006; Horodysky et al. 2007; Bernal et al. 2009).

Os agulhões possuem a tendência de se distribuírem em relação à temperatura em profundidade, principalmente devido a variações na temperatura da superfície do mar (TSM) e profundidade da camada de mistura. A temperatura limita as preferências de profundidade e influencia até mesmo sua função cardíaca, reduzindo a taxa de batimentos cardíacos na medida em que o animal entra em águas com temperaturas mais frias (Brill et al. 1998; Brill & Lutcavage 2001). A luminosidade durante o dia, limitada pela profundidade, também pode atuar como um fator limitante para o comportamento dos agulhões por serem predadores visuais, apesar de suas adaptações fisiológicas, que lhe conferem uma alta sensibilidade óptica, permitirem uma boa acuidade visual em condições de pouca luz (Fritsches et al. 2003). Outra variante que pode afetar a distribuição dos agulhões é a abundância de presas em diferentes locais e profundidades, assim como baixas concentração de oxigênio dissolvido, encontradas em algumas áreas dos oceanos (Prince and Goodyear 2006; Bernal et al. 2009). Conhecer os habitats utilizados por essas espécies, portanto, é extremamente importante para compreender o seu comportamento, padrões migratórios e dinâmica populacional.

Atualmente, grande parte do conhecimento sobre a utilização de habitats por peixes pelágicos provém de estudos que utilizam PSATs (pop-up satellite archival tags) para monitorar o comportamento do animal (Block et al. 1998; Arnold & Dewar 2001; Graves et al. 2003; Luo et al. 2006; Hofmann & Gaines 2008; Musyl et al. 2011). Essa tecnologia de sensoriamento remoto vem evoluindo significativamente nos últimos dez anos, sendo utilizada em diversos tipos de pesquisa para coleta de dados. Tais equipamentos são fixados no corpo do animal e durante todo o tempo em que permanecem presos ao mesmo registram um fluxo quase contínuo de parâmetros ambientais especificados (temperatura, pressão (profundidade) e luminosidade), arquivam os dados, e transmitem a informação via satélite após se desprenderem do animal e subirem à superfície no tempo predefinido por configuração. No oceano Atlântico Norte, várias pesquisas já foram desenvolvidas para o estudo de habitat dos agulhões negros e sobre como as condições oceanográficas influenciam seu comportamento (Yang & Gong 1987; Brill & Lutcavage 2001; Graves et al. 2003; Prince et al. 2005; Boyce et al. 2008; Su et al. 2008; Dutton 2010; Kraus et al. 2011). Nos últimos anos, alguns estudos foram desenvolvidos com a tecnologia de telemetria por satélite para análises em grandes peixes pelágicos também no Atlântico Sul (Mourato et al. 2014; Carvalho et al. 2015; Tolotti et al. 2015; Afonso & Hazin 2015). Segundo Pacheco et.al. (2015), até o momento poucas pesquisas foram realizadas neste hemisfério oceânico quanto a utilização do habitat e movimentos migratórios de agulhões negros.

A compreensão do habitat dos agulhões é uma componente chave para o manejo sustentável e o adequado ordenamento da sua pesca. Os resultados de estudos desenvolvidos com a espécie sugerem que a distribuição dos agulhões está relativamente restringida a uma certa faixa de temperatura e profundidade (Graves et al. 2003; Goodyear et al. 2008; Luo et al. 2006). Embora os dados já obtidos forneçam um valioso resumo do padrão de utilização do habitat, uma compreensão mais integrada de como as populações de agulhões respondem a outros fatores ambientais em diferentes regiões e estações do ano ainda se faz extremamente necessária.

As características do espinhel comercial variam de acordo com a espécie alvo da pesca, de modo que as preferências de habitat dos animais capturados como fauna acompanhante influenciam diretamente na vulnerabilidade dos mesmos serem capturados pelos anzóis (Ward & Hindmarsh 2007; Goodyear et al. 2008). Portanto, conhecer as profundidades dos anzóis do espinhel é também necessário para reduzir as incertezas nas avaliações de estoque (Rice et al. 2007), uma vez que a profundidade dos anzóis afeta diretamente a seletividade das espécies capturadas pelo espinhel pelágico (Yang & Gong 1987; Boggs 1992; Nakano et al. 1997; Beverly et al. 2009). Sendo assim, para estimativa e predição da vulnerabilidade dos agulhões negros aos espinheis pelágicos é necessário identificar tanto o comportamento do animal na coluna d'água quanto a profundidade de pesca dos anzóis (Goodyear et al. 2003; Rice 2008).

1. OBJETIVOS

2.1. Objetivo Geral

O objetivo geral dessa pesquisa é ampliar a qualidade da informação científica disponível para o manejo e conservação dos agulhões do Atlântico, utilizando técnicas avançadas de telemetria (PSATs) e abordagens estatísticas recentemente desenvolvidas. Sendo o conhecimento do habitat vertical utilizado pelos agulhões-negros importante também para a compreensão de como essas espécies interagem com o aparelho de pesca.

2.2. Objetivos específicos

- Desenvolver um esforço de marcação de animais e coleta de dados para o Atlântico Sul para compreender os movimentos migratórios da espécie;
- Analisar os dados sobre a influência de fatores ambientais em padrões de movimento e utilização de habitat vertical pelos agulhões-negros.

- Analisar as profundidades de atuação dos anzóis do espinhel na pesca comercial de atuns e afins no Atlântico Sul, para melhor compreender quanto o esforço de pesca atualmente empregado se sobrepõe ao habitat utilizado pelos agulhões.

2. METODOLOGIA

3.1. Localização por satélite e Movimentos horizontais

Os dados de movimento foram obtidos por meio de agulhões marcados com PSATs, em quatro regiões geográficas do Atlântico Sul (NE- Área I; SE- Área II; NO- Área III; SO- Área IV). Essas regiões são dois pontos na costa Brasileira e dois pontos na costa da África, sendo em Porto Seguro, Brasil (n=4); Cabo Frio, Brasil (n=4); Bata, Guiné Equatorial (n=4); e Luanda, Angola (n=4), marcados quatro animais em cada local. Portanto, foram marcados um total de 16 agulhões-negros, capturados na pesca esportiva e marcados com PSAT (*Pop-up Satelite Archival Tag*) modelo MK10-PAT (Wildlife Computers Redmond, WA) (Fig.2). As marcas foram programadas para a captura dos dados de temperatura, luminosidade e pressão enquanto aderidas ao animal durante um período de 180 dias, sendo automaticamente liberadas e enviando os dados via satélite, após atingirem a superfície.

Os dados de movimentação horizontal foram estimados utilizando os registros de luminosidade coletados, que foram processados utilizando o software de posicionamento global WC-GPE (Wildlife Computers, Redmond, WA, USA) para obter a geolocalização diária bruta dos peixes marcados para cada dia após devolvidos ao mar. Será aplicado, então, o modelo espacial "trackit" (Nielsen and Sibert, 2007) para prever a trajetória mais provável dos agulhões marcados. O modelo trackit é montado usando software estatístico R. A distância percorrida pelos animais durante todo o período foi considerada uma linha reta entre as coordenadas geográficas do local de marcação (obtidas do equipamento GPS da embarcação) e as coordenadas da primeira transmissão de dados da PSAT após o envio de dados ao satélite (localização pop-off).

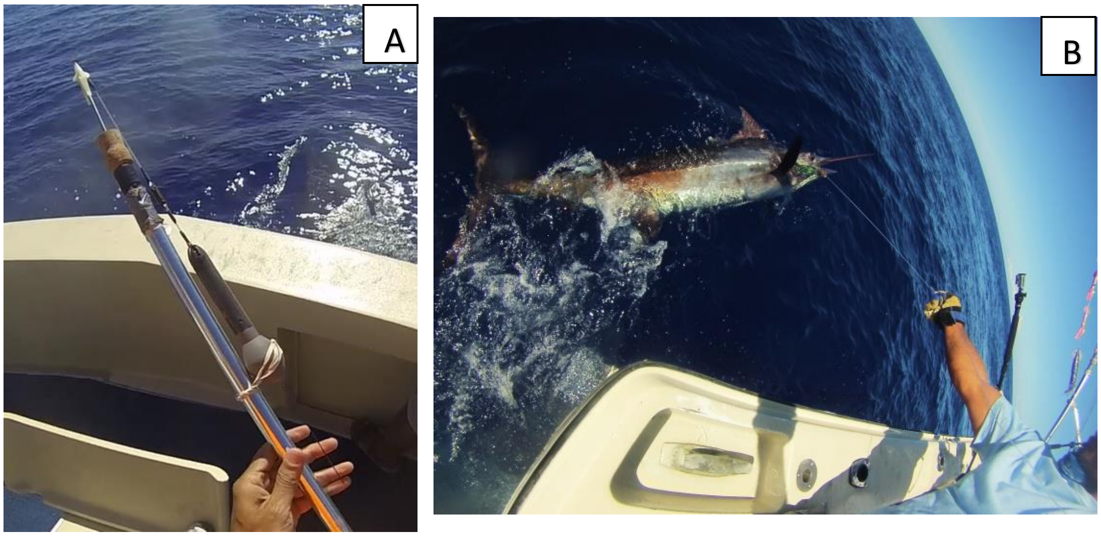

Figura 2. Procedimento de captura e marcação do Agulhão negro. (a) PSAT anexada à lança para ser fixada no dorso do animal capturado e (b) animal fisgado trazido para a lateral da embarcação.

3.2. Análises de direcionalidade

Para quantificar o direcionamento em movimentos de cada indivíduo marcado foi utilizada estatística circular, a qual compara a distribuição de ângulos de giro realizados pelo animal com a uniformidade, isto é, a probabilidade do animal ir em uma direção particular. O teste de espaçamento de Rao foi utilizado para quantificar a direcionalidade nos agulhões marcados (Zar 1984; Bergin 1991; Bonadonna et al. 2001). Esta estatística incorpora a média do vetor direcional (ϕ), o vetor de concentração angular (*r)* e o desvio padrão circular (dpc). Histogramas circulares foram gerados para cada agulhão para demonstrar graficamente a direcionalidade preferida de cada animal. Todas as estatísticas circulares são realizadas utilizando Oriana 4.0 (Kovach Computing Services).

3.3. Sobreposição de localização e dados oceanográficos

Séries temporais semanais de temperatura da superfície da água (ºC) e profundidade da camada mista foram obtidas do *Physical Oceanography Distributed Active Archive Center* (PODAAC)- *Jet Propulsion Laboratory/NASA* (La Cañada Flintridge, CA). Estes dados foram utilizados para construir uma base de dados de quadrantes de 1.0° × 1.0°, montados por dia, mês, ano, latitude e longitude para todo o Atlântico. As localizações estimadas pelo *trackit* para cada agulhão negro foram sobrepostas nos quadrantes de 1.0° × 1.0° contendo a média semanal estimada de temperatura da superfície e profundidade da camada mista para cada data específica. Em seguida, dados de temperatura da superfície e profundidade da camada mista normalmente distribuídos para quadrantes ocupados por agulhões marcados foram expressos utilizando boxplots. Com o auxílio de ferramentas de sensoriamento remoto, também foi analisada as relações entre os padrões de movimento dos animais e a variação espacial e sazonal da isoterma de 25º C.

3.4. Modelos de efeitos randômicos

As análises estatísticas geralmente assumem uma relação linear entre a variável resposta e as variáveis ambientais, quando na verdade elas provavelmente são variáveis não lineares. Os modelos aditivos generalizados (GAMs) foram propostos por Hastie e Tibshirani (1990) para superar tais dificuldades. O GAM é uma extensão de modelos lineares generalizados (GLMs), na qual uma função que descreve a variação total explicativa é modelada como uma soma das variáveis.

Em estudos de regressão os coeficientes são normalmente considerados fixos. No entanto, em alguns casos faz mais sentido assumir-se alguns coeficientes aleatórios. Esses casos são geralmente situações onde o foco é fazer inferências sobre uma população inteira de onde alguns níveis estão sendo amostrados aleatoriamente. Neste estudo, foram coletadas informações dos mesmos indivíduos ao lingo do tempo, portanto, é sensato assumir que correlações existem dentre as observações de um mesmo indivíduo. Consequentemente, será mais apropriada uma abordagem que conserve a estrutura de modelo aditivo com efeitos fixos e aleatórios (GAMM- generalized additive mixed model) para essas análises.

GAMM foram usados para investigar a influência de uma série de variáveis na utilização de habitat dos agulhões negros do Atlântico sul. As variáveis resposta binárias para a análise é presença (1) ou ausência (0) de agulhões nas quatro regiões estuadas (I, II, III, e IV). As variáveis explicativas foram TSM (contínua), PCM (contínua) e Área (categórica), sendo todas essas variáveis consideradas efeitos fixos. Visto que para cada indivíduo há múltiplas ocorrências, cada animal rastreado foi incluído nos modelos como efeitos aleatórios. A modelagem de efeitos aditivos mistos foi realizada utilizando a linguagem estatística do programa R e o pacote mgcv (Wood 2006).

3.5. Movimentação vertical e sobreposição ao esforço de pesca de espinhel

Para analisar padrões espaciotemporais no comportamento em profundidade e hábitos em temperatura, foram analisados dados da proporção de tempo em profundidade e perfis de temperatura em profundidade para cada agulhão marcado. Dados sumarizados de luminosidade identificando períodos de amanhecer e anoitecer foram utilizados para separar os dados de tempo em profundidade em dia e noite e analisar diferenças circadianas no tempo gasto em profundidade. Foi realizado o teste de Kruskal-Wallis, utilizando-se a profundidade máxima de mergulho (MDD) e a temperatura mínima de mergulho (MDT) como variáveis respostas, para investigar uma possível influência da área na distribuição vertical dos agulhões.

Paralelamente, foi conduzido um estudo no Atlântico Sul para investigarmos a potencial sobreposição dos agulhões negros à espinhéis pelágicos. Um total de 232 lances de espinhel realizados por barcos de pesca comercial foram monitorados. Para avaliarmos a sobreposição espacial horizontal (%) entre os agulhões e os lances de espinhel pelágico, a coincidência do rastreamento dos agulhões negros e o esforço de pesca dentro de cada quadrante de 0.5º x 0.5º, foi calculado com a soma do número total de quadrantes onde ocorreram agulhões e espinhéis ao menos uma vez, como uma função do número total de quadrantes. Além disso, a sobreposição entre o habitat vertical dos agulhões negros e a profundidade dos anzóis também foi estimada. Para delimitar a profundidade máxima de pesca dos espinhéis pelágicos usados por barcos pesqueiros nas quatro áreas geográficas foram implantados TDRs (Temperature and Depth Recorders – Lotek Wireless) em cada um dos 232 lances de espinhel monitorados. Os TDRs foram fixados na extremidade inferior da linha secundária central, coletando dados a cada 2 minutos, segundo a metodologia de Kerstetter e Graves (2006). O nível de sobreposição foi calculado através da análise dos dados dos TDRs e das PSATs. A média de profundidade dos anzóis foi calculada para cada lance de espinhel. Além disso, o percentil de 90% das profundidades dos anzóis registradas foi calculado e foram sobrepostos a distribuição em profundidade dos dados de PSAT dos indivíduos para calcularmos a porcentagem de tempo de sobreposição.

Todas as análises estatísticas deste estudo foram desenvolvidas no software R *Project for Statistical Computing Version* 3.0.1 (R Core Team 2013).

3. ARTIGO

Artigo submetido à revista Marine and Freshwater Research, intitulado "Habitat utilization of south atlantic Blue marlin (*Makaira Nigricans*) and overlap with fishing effort'"

HABITAT UTILIZATION OF SOUTH ATLANTIC BLUE MARLIN (*MAKAIRA NIGRICANS*) AND OVERLAP WITH FISHING EFFORT

Crespo, O., *Carvalho, F., Pacheco, J.C., Hazin, F.

Laboratory of Fisheries Oceanography, Department of Fisheries and Aquatic Sciences, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil.

*Corresponding Author: Felipe Carvalho – (felipe.carvalho@noaa.gov)

Abstract. Research on habitat utilization for large pelagic marine species is important to better understand its biology and factors that affect fish behavior. Atlantic blue marlin (*Makaira nigricans*) is usually targeted in recreational fisheries but also captured as bycatch in pelagic longline fisheries. PSATs were deployed on sixteen blue marlins around four geographical areas of South Atlantic Ocean between October 2014 and September 2015. Longline hook depths were also evaluated, with a total of 232 longline sets in South Atlantic monitored by Temperature-depth recorders (TDRs). Results showed a range of horizontal net displacement of 374 to 1.838 km for all blue marlins. Time-at-depth histograms of marlin habitat utilization confirms that most individuals spent the majority of their time in shallow waters above 20m, both during the day and night periods. Tagged fishes had a similar pattern of vertical habitat utilization in all areas, spending most of their time within a relatively narrow temperature range, staying an average of 57% of their time in temperatures between 26° and 28°C. Overall, blue marlins had 59% of their tracked range overlapped by the longline fishing gear. The average hook depth across all areas was 49 m with 90% of the hooks depth between 32-71 m. This distribution overlap with the species vertical habitat utilization, ranging between 11 and 35% during daytime and 21 and 34% during nighttime.

Keywords: Billfish, PSAT, migration, fishing, longline, conservation

Introduction

Billfishes are large pelagic apex predators that play an ecologically important role in the food web structure of marine ecosystems. The depletion of their populations, therefore, might lead to negative cascading effects (Pace et al. 1999; Kitchell et al. 2006; Casini et al. 2009; Estes et al. 2011). Blue marlin (*Makaira nigricans*, Lacepède, 1802), is a circumtropical species widely distributed throughout tropical and temperate waters of the Atlantic Ocean, ranging from 45ºN to 45ºS, usually occupying higher latitudes in the warmer months of the year (Nakamura 1985). As a highly migratory species, blue marlins perform vast movements across the oceans, as well as transoceanic and occasionally inter-oceanic migrations, being one of the fishes with greatest recorded distances in tag-recapture and telemetry studies (Prince & Brown 1991; Ortiz et al. 2003; Orbesen et al. 2008).

Billfishes broad migratory movements expose them to a wide variation of physicochemical and biological oceanographic features that affect their vertical habitat preferences (Brill et al. 1998; Brill & Lutcavage 2001; Bernal et al. 2009). Light levels, for example, are essential for visual predators such as marlins to forage efficiently and may thus limit their swimming depths. Studies on blue marlin diet show that although they feed on a wide variety of organisms, their main prey species are epipelagic surface fishes and squids (Brock 1984; Júnior et al. 2004; Satoh et al. 2004; Shimose et al. 2006; Shimose et al. 2010). Despite studies showing the presence of deep water prey items are rare (Strasburg 1970; Nakamura 1985; Harvey 1989), diet studies usually sample marlins caught close to the surface and, therefore, prey composition may be influenced by the depth of capture (Brock 1984).

The vertical distribution of marlins is related to temperature-at-depth, which is influenced by the sea surface temperature (SST) and depth of the mixed layer (DML). Temperature may limit their depth preferences and can affect even its cardiac function, reducing its heart rate in lower water temperatures (Brill et al. 1998; Brill & Lutcavage 2001). Likewise, waters with low dissolved oxygen concentrations might also limit billfish vertical movements (Prince and Goodyear 2006; Bernal et al. 2009), which might still be influenced by prey abundance.

Several studies were already conducted in the North Atlantic to investigate how blue marlins behave in the water column and how oceanographic conditions affect their movements (Yang & Gong 1987; Brill & Lutcavage 2001; Graves et al. 2003; Prince et al. 2005; Su et al. 2008; Boyce et al. 2008; Goodyear et al. 2008; Kraus et al. 2011). However, despite the recent increase in studies using satellite telemetry in highly migratory species, few studies have been conducted in the South Atlantic (Mourato et al. 2014; Carvalho et al. 2015; Tolotti et al. 2015; Afonso & Hazin 2015; Pacheco 2015), and only one of those (Pacheco 2015) has focused on habitat utilization and movements of blue marlins.

The Atlantic blue marlin is targeted by recreational fishing in the Atlantic Ocean and it is one of the several species caught as bycatch by pelagic longline fishery targeting tunas and swordfish (*Xiphias gladius*) (Uozumi & Nakano 1996; Restrepo et al. 2003). It has been considered overexploited since 2003 (Restrepo et al. 2003) and more recent population assessments conducted by the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) indicated that the stock remains overfished and that overfishing persists, despite data deficiencies and uncertainties (ICCAT 2011). Recent research on tuna and billfish stock status reveals that Atlantic blue marlin stock is heavily depleted and have one of the highest fishing mortality rates, together with the Pacific bluefin tuna and the Atlantic sailfish stocks (Pons et al. 2016).

Fishing features of longline gear vary according to target species, and thus the vertical habitat preferences of bycatch fishes directly influence their vulnerability to longline hooks (Ward & Hindmarsh 2007; Goodyear et al. 2008). A correct understanding of the behavior of longline hooks in the water column is, therefore, very important to reduce uncertainties in the assessment of fish stocks (Rice et al. 2007), since hook depths directly affect species selectivity of longline sets (Yang & Gong 1987; Boggs 1992; Nakano et al. 1997). Therefore, for a proper estimation and prediction of marlin's vulnerability to pelagic longline gear, it is essential to identify time-at-depth behavior of marlins as well the fishing depth of hooks (Goodyear et al. 2003; Rice 2008).

The knowledge of the vertical habitats utilized by marlins is very important to elucidate how these species interact with the fishing gear. Consequently, in order to evaluate properly the species vulnerability to fishing gear, besides the geographic distribution and depth at which the fishing effort is deployed, the physical properties of the water must also be incorporated into the analysis.

Using advanced satellite telemetry techniques and a novel statistical approach, the present research will estimate, for the very first time, the migratory movements, the influence of environmental variability in movement patterns, and the habitat utilization of the blue marlin in the South Atlantic Ocean. Furthermore, it will identify the locations and depths occupied by blue marlins, underpinning a much-needed assessment of the overlap with depth ranges targeted by longline fisheries in the region.

Material and methods

Satellite Tracking

Tagging was stratified spatially and temporally. The South Atlantic was split into four quadrants, each representing a geographical area (NE- Area I; SE- Area II; NW- Area III; SW- Area IV). Sixteen blue marlins were caught by recreational fisheries and tagged with MK10-PAT (Pop-up Archival Transmitting) tags (PSATs; Wildlife Computers, Redmond, WA), off the coast of Porto Seguro, Brazil (n=4); Cabo Frio, Brazil (n=4); Bata, Equatorial Guinea (n=4); and Luanda, Angola (n=4). These locations were chosen due to their importance as a recreational fishing ground, as well as to their proximity to commercial longline hot spots. PSATs were attached to the fish by inserting the nylon anchor into the dorsal musculature, interlocking with pterygiophore bones below the dorsal fin (Graves et al. 2002; Domeier et al. 2003; Horodysky & Graves 2005). Once tagged, the fish was cut off from the fishing line and allowed to swim away from the vessel. Deployment positions of tag releases were recorded using the vessels' onboard GPS system. PSATs were programmed to record depth, temperature, and light intensity for a period of 180 days until release. Archival data from the detached tags were internally binned at 3-h intervals and the summarized data were transmitted to an Argos satellite. Light intensity records were pre-processed using the global positioning software WC-GPE (Wildlife Computers, Redmond, WA, USA) to provide daily raw geo-locations (GLS) of tagged fish for each day at-liberty.

Horizontal movement

The horizontal movements of tagged marlins were estimated by processing the data received from the Argos satellite system using the manufacturer light-based geolocation software (WC-GPE: Global Position Estimator Program suite, available at: www.wildlifecomputers.com). Intermediate positions between deployment and transmission locations were estimated by fitting the state-space model “trackit” described in Nielsen and Sibert (2007) (downloaded from: www.soest.hawaii.edu/tag-data/trackit) to time series of light data. The model was run both with and without the incorporation of sea surface temperature (SST) data, however, because convergence was rarely achieved when SST was incorporated in the model, final model fits were estimated from trackit without SST. All model runs of trackit without SST achieved convergence. Net displacement over the entire tracking period was calculated as the straight-line distance between the geographic coordinates of the PSAT deployment location (tagging locations) and the coordinates of PSAT’s location at first transmission of data (pop-off locations) using the ARGOS system.

Analysis of directionality

Directionality in the individual movements of blue marlins was quantified using circular statistics (Zar 1999). Tests were then used to compare the distribution of bearings calculated by moving from one point to another along a movement track relative to uniformity (i.e. the probability of the animal going in any particular direction is equal). Rao’s spacing test was used to quantify directionality in blue marlins (Bergin 1991; Bonadonna et al. 2001). This statistic incorporates the mean directional vector (ϕ), the angular concentration (r) and the circular standard deviation (csd). Circular histograms were generated to graphically demonstrate the preferred directionality for some individuals. All circular statistics were performed using Oriana 4.0 (Kovach Computing Services).

Space utilization distribution

A Brownian Bridge Movement Model (BBMM) was used to estimate the marlins’ Utilization Distributions (UD) across the South Atlantic Ocean (Bullard 1999; Horne et al. 2007). The BBMM estimates UDs by modeling movements between locations (i.e.

trackit estimated locations) as a conditional random walk consisting of a series of steps where the step length, direction, and time interval between steps are independent of each other and those of preceding steps (Bullard 1999; Horne et al. 2007). The time step (iteration increment) in the model was 24 hours. The BBMM also accounts for the error associated with the estimated position of the tracked animal by calculating a variance component, referred to as the ‘‘Brownian motion variance’’ (Horne et al. 2007).

A grid system consisting of 1.0° latitude × 1.0° longitude cells (~ 111 km x 111 km) was constructed for the entire South Atlantic Ocean. An animal's trajectory was modeled using 50,000 random-walk iterations to develop a probability distribution of the animal's position between actual location estimates. Each cell had its own UD value, and population level probabilities were generated by summing the cell values of all UDs for all individuals (tagged across the South Atlantic Ocean) and then re-scaling their cumulative cell values to sum to 1. All calculations were performed using the BBMM package in R 2.13.1 language for statistical computing (R Development Core Team 2011).

Overlapping tracking and oceanographic data

Weekly time-series of SST (ºC) and depth of the mixed layer (DML) were obtained from the Physical Oceanography Distributed Active Center (PODAAC)- Jet Propulsion Laboratory/NASA (La Cañada Flintridge, CA). These data were used to construct a database of 1.0° latitude × 1.0° longitude quadrats assembled by day, month, year, latitude, and longitude for the entire study area. Trackit estimated locations for each marlin were then overlapped on the 1.0° × 1.0° quadrats containing the weekly averaged estimated SST for that specific date. Continuous normally distributed SST and DML data for quadrats experienced by tagged blue marlins were expressed using boxplots. Using remote sensing data, we also explored the relationship between the movement patterns of tagged blue marlins and the seasonal and spatial variation of the isotherm of 25° C. This temperature was taken as reference following previous studies by Hazin (1993) and Amorim *et al.* (1994).

Random effect models

The inclusion of environmental variables in statistical modeling is often complex. Statistical analysis often assumes a linear relationship between the response and environmental variables (e.g. SST and DML), when actually they are very likely to be nonlinear. To overcome these difficulties, Hastie and Tibshirani (1990) proposed generalized additive models (GAMs). GAMs are extensions of generalized linear models (GLMs) in which a link function describing the total explained variance is modeled as a sum of the variables. The terms of the GAMs can be local smoothers or simple transformations with fixed degrees of freedom (Maunder & Punt 2004, Venables & Dichmont 2004).

In regression studies, the coefficients are commonly considered fixed. However, there are cases in which it makes sense to assume some random coefficients. These cases typically occur in situations where the primary focus is to make inferences on the entire population from which some levels are randomly sampled. In the present study, observations were collected from the same individuals over time. Therefore, it is reasonable to assume that correlations exist among the observations from the same individual. Consequently, an approach that conserves the additive model framework with both fixed and random effects (generalized additive mixed model - GAMM) would be more appropriate for these analyses.

GAMMs were used to investigate the influence of a series of variables on habitat use of blue marlins across the South Atlantic Ocean. The binary response variable for these analyses is presence (1) or absence (0) of blue marlins in the four geographical areas (I, II, III, and IV). The explanatory variables included SST (continuous), DML (continuous), and Area (categorical). All variables (SST, DML, and Area) were considered as fixed effects. Since there were multiple occurrences for each individual, each tracked individual was included in the models as a random effect. Additive mixed-effects modeling was conducted using R statistical language and the mgcv package (Wood 2006). First, the effect of the variable (SST and DML) was compared to the response variable for each area. Second, to determine whether the relationship differed by area, Area was added as a variable in the model. To find the most parsimonious GAMM model, standard selection criteria based on Akaike Information Criteria (AIC) (Akaike

1973) and Bayesian Information Criteria (BIC) (Schwarz 1978) were used to determine which variables best explained the variability in the data. The model was built with variables independent from each other (Stage I). The best model was selected based on AIC and BIC values and subsequently tested in the next stage. Stages II to III used the initial model, with an additional variable. Likelihood Ratio tests were also used to determine whether the inclusion of additional variables in the model significantly improved the explanatory power of the model.

Vertical movement

In order to avoid the potential for post-release behavior modification biasing any interpretation of time series, the first seven days (based on the maximum disturbance observed with a conservative temporal buffer added) of data from each tag were excluded. In order to examine spatial and temporal patterns in diving behavior and thermal habitats, the proportion of time-at-depth and temperature-depth profiles data were analyzed for each marlin tagged. Summary light data identifying periods of dawn and dusk were used to separate time at depth data into day and night periods and diel differences in time spent at depth were examined. Data where temporal bins incorporated a combination of day and night periods or transition periods between day and night at dawn and dusk were excluded. To investigate a possible influence of area on blue marlin adult and juvenile vertical distribution, Kruskal-Wallis rank sum tests were performed using maximum diving depth (MDD) and minimum diving temperature (MDT) as the response variables.

Overlap with longline fishing effort

To investigate the potential overlap of blue marlin with pelagic longline fishing gear, a parallel and independent study was conducted in the South Atlantic during the same period of time while the PSATs were being deployed. A total of 232 longline fishing sets carried out by commercial longline fishing vessels targeting swordfish (*Xiphias gladius*) were monitored (Figure 1). The fishing gear consisted of a standard US-style polyamide monofilament mainline (Watson & Kerstetter 2006) with five branch lines between floats. Deployment of gear typically starts in the late afternoon at ~17:00 h, and haulback commences the next morning ~06:00 h. To evaluate the horizontal spatial overlap (%) between blue marlins and pelagic longline fishing, the coincidence between the tracking of tagged blue marlins and longline fishing effort within each 0.5° and 0.5° grid cell, at any time within the tracking period, was calculated by counting the total number of 0.5° and 0.5° grid cells where tagged blue marlins and longliners occurred at least once, as a function of the total number of grid cells.

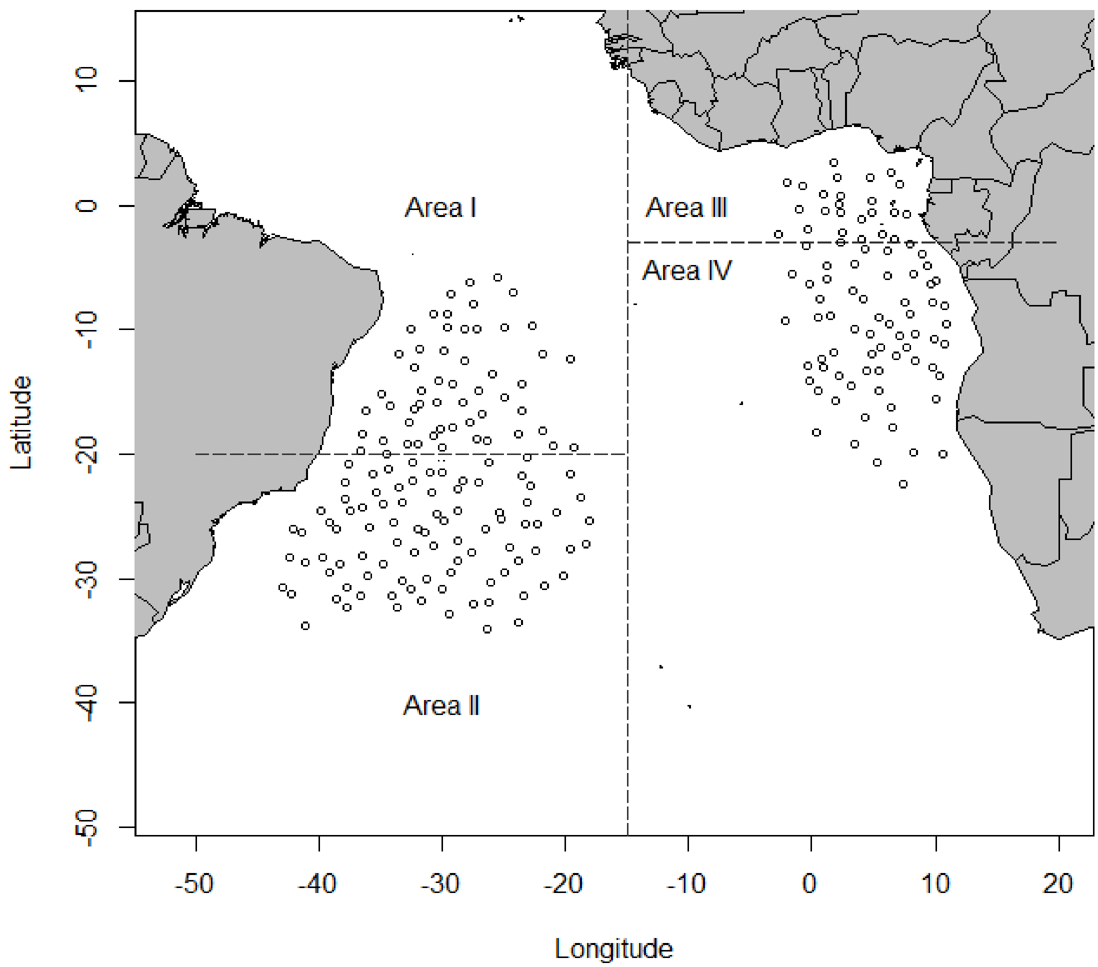

Figure 1. Location of 232 longline fishing sets monitored by TDRs in South Atlantic Ocean covering the four study Areas.

In addition, the overlap between blue marlin vertical habitat and depth of fishing gear was also estimated. To delimit the maximum effective fishing depth for the configuration of pelagic longline gear used by fishing vessels in those four geographic regions, Temperature Depth Recorders (TDRs) (Lotek Wireless) were deployed in each one of the 232 monitored fishing sets. TDRs were attached to the lower end of the middle branch within each hook basket, and collected data every 2 minutes interval, following the methodology of Kerstetter and Graves (2006). The overlap was calculated by analyzing the results from the TDRs and PSATs. The mean depth of the hooks was calculated for each longline set. In addition, the 90% percentiles of the recorded hook depths were calculated and the depth distribution of the specimens PSAT data were overlapped with the depth distribution of the fishing gear in order to calculate the percentage of overlap time.

All statistical analyses for this paper were carried out with the R Project for Statistical Computing version 3.0.1 (R Core Team 2013).

Results

Horizontal movements

Tracking results showed complex and remarkable movement patterns by blue marlins in the South Atlantic with some individuals staying near the tagging location while others performed longer migrations (Figure 2). Pop-up satellite archival tags were at liberty for 69–114 days (Table 1). Latitudinal movements were limited, with the majority of individuals estimated to move < 10°. However, some individuals moved > 10° in longitudinal movements. The net displacements were variable among individuals within a location and among locations. Displacements observed between release and transmission locations ranged from 375 to 1.838 km. The average net displacement for all blue marlins combined was 959 km. The mean net displacement for blue marlins in Area I, II, III, and IV were 833, 938, 1,133, and 931 km, respectively.

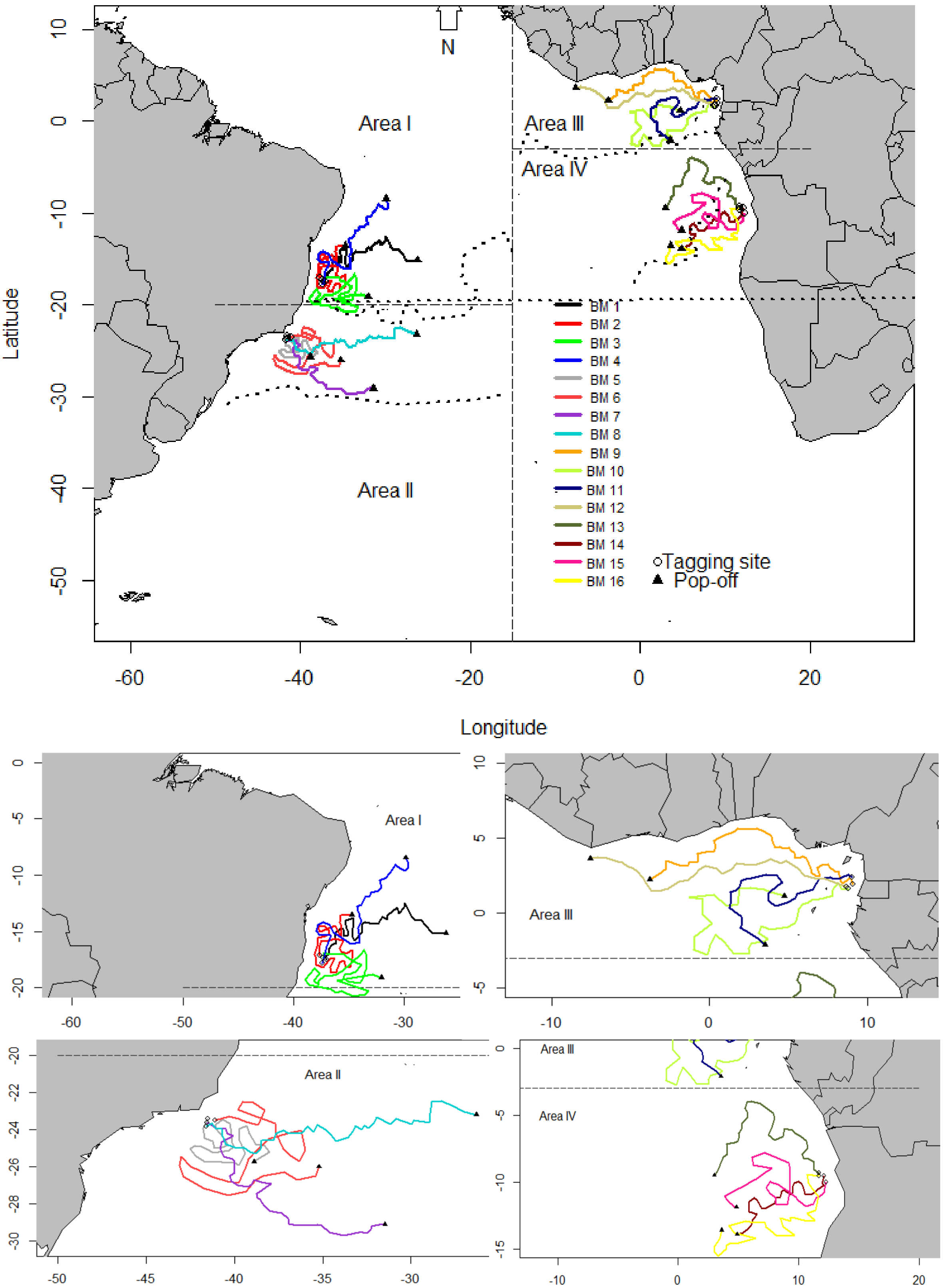

Figure 2. Most-probable track for tagged blue marlins across the South Atlantic Ocean fit with the state-space model "trackit" model. Area I top left, Area II bottom left, Area III top right, and Area IV bottom right. Dashed line in upper image represents the isotherm of 25ºC in the period of the year that marlins were tracked.

Table 1. Summary data for 16 blue marlins tagged with pop-up satellite-tags in the South Atlantic Ocean. Tagging occurred in four geographic Areas I, II, III, and IV. Size is in lower jaw fork length (LJFL). Individuals highlighted in grey represent Rao's test (*r*) statistically different from a uniform distribution, therefore implying directional movement.

ID	Size (LJFL in cm)	Area	Tagging date	Pop-up date	Days at liberty	Displacement (km)	Rao's test
1	251	I	10/03/14	01/15/15	104	1201	187.2
2	180	I	10/05/14	12/13/15	69	375	121.0
3	188	I	10/08/14	01/18/15	103	590	102.3
4	257	I	10/13/14	02/03/15	114	1169	190.5
5	176	II	01/02/15	03/14/15	71	374	104.8
6	187	II	01/08/15	04/17/15	99	653	112.7
7	224	II	01/11/15	04/22/15	101	1176	169.3
8	201	II	01/17/15	04/18/15	91	1548	172.4
9	201	III	02/08/15	05/28/15	88	1448	191.8
10	185	III	02/12/15	06/12/15	95	764	106.2
11	193	III	02/16/15	05/11/15	85	482	105.1
12	217	III	02/21/15	05/14/15	83	1838	131.4
13	197	IV	06/02/15	08/19/15	79	954	128.3
14	204	IV	06/08/15	09/11/15	95	895	199.2
15	191	IV	06/12/15	09/29/15	109	821	103.1
16	232	IV	06/15/15	09/20/15	97	1055	189.2

In Area I, adult individuals (LJFL > 195 cm) BM 1 and BM 4 performed directed movements compared to those from young individuals (BM 2 and BM 3), a result of the adult animals avoiding residency in a relatively small region. In the other hand, young individuals (LJFL < 195 cm) BM 2 and BM 3 had a uniform distribution of directional vectors, a result of the animals maintaining residency in a relatively small area. In this area adult individuals also moved longer distances than young individuals. BM 4, for example, showed a displacement of 1,169 km, while BM 3 during almost the same period had a displacement of 590 km (Table 1, Figure 3). In Area II, BM 7 and BM 8, both adult individuals, showed a directed easterly movement away from the tagging site towards the central part of the South Atlantic, while BM 5 and BM 6 traveled in loops off the southeast coast of Brazil. Similar to the results found in Area I, adult individuals in Area II showed longer displacements than juveniles. From Area III, adult individual BM 9 and BM 12, both tagged near the islands of San Tome and Principe, displayed directed westerly movements, traveling along waters close to the African coast, while BM 10 and BM 11 moved towards the central part of the Gulf of Guinea, although they had a uniform distribution of directional vectors. Satellite tracking of blue marlins tagged off the central coast of West Africa (Area IV) revealed similar displacement patterns among adult and juvenile individuals. However, adult marlins BM 14 and BM 16 showed directed southwesterly movements away from the tagging site towards the central part of the South Atlantic.

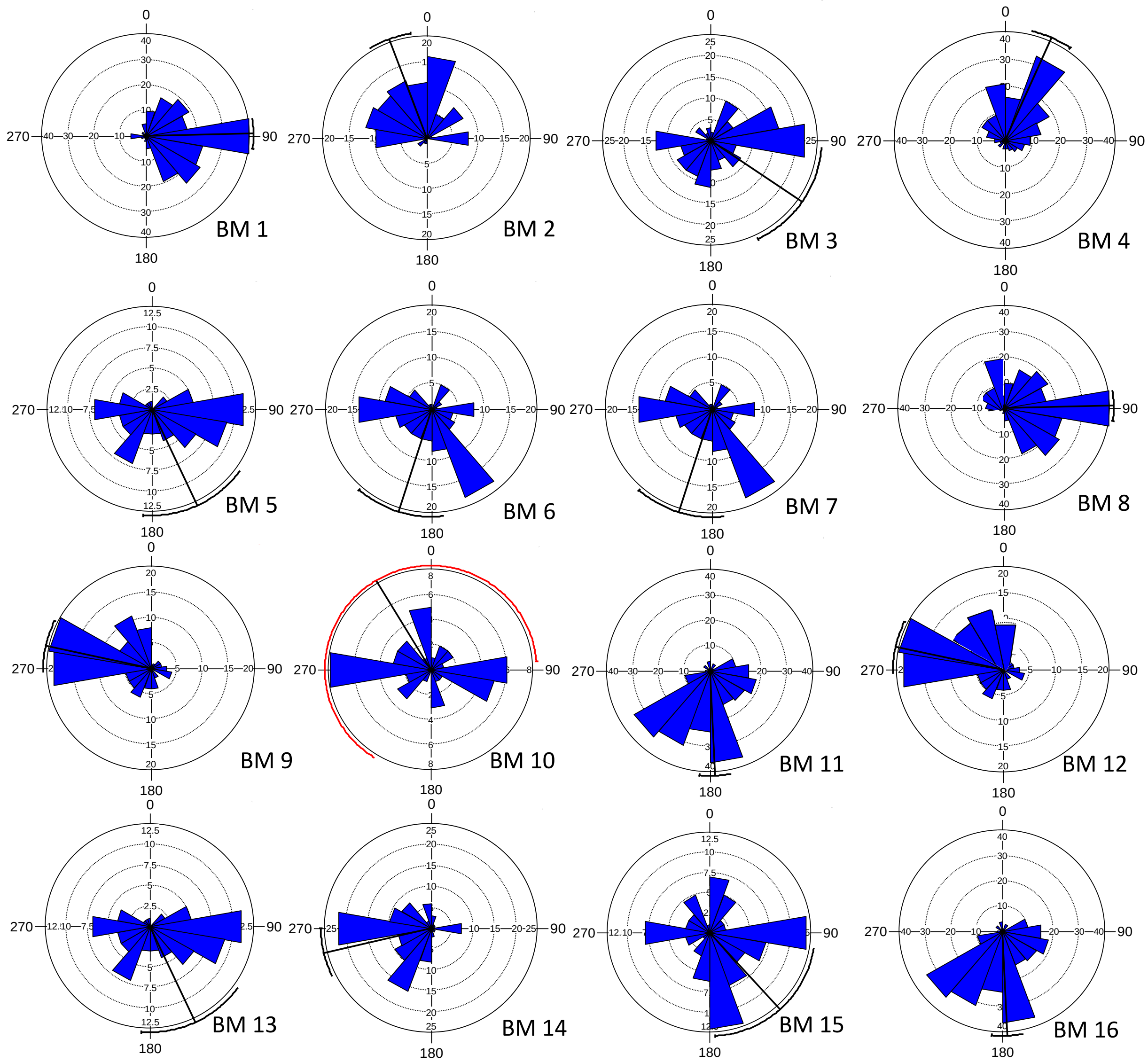

Figure 3. Rose diagrams showing the angular changes (blue histograms) for tagged blue marlins. The mean bearing direction taken by each blue marlin is given by the solid black line emanating from the center of the plot.

Overall the utilization distributions obtained from the BBMM (Figure 4) showed smaller use areas for juvenile blue marlins compared to the areas used by adult individuals. In Area I juveniles concentrated in a region characterized by the presence of seamounts (Royal Charlote Bank), while in Area II they concentrated off the coast of Cabo Frio, in Rio de Janeiro state. In areas I and II adults showed a more dispersed movement without a clear core area of use. In Area III, adults showed a high utilization area spread along waters off the coast of Nigeria, Benin, Togo, and Gana, while juvenile preferred areas in the central part of Gulf of Guinea. A relatively large "core" utilization area for both adult and juvenile was identified in Area IV.

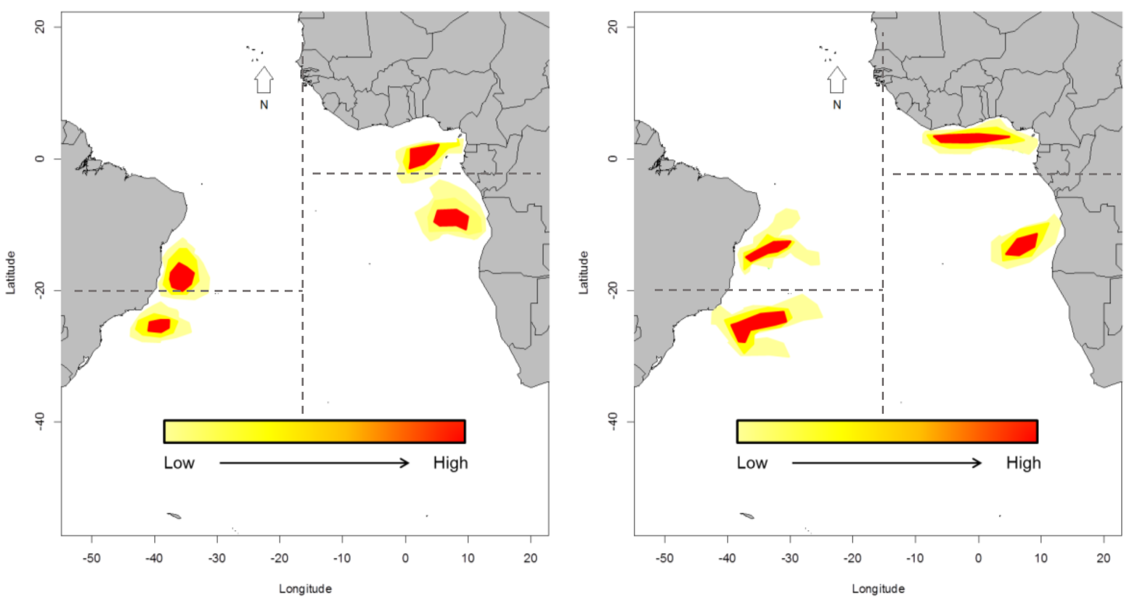

Figure 4. Utilization distributions for juvenile (left panel) and adult (right panel) blue marlins tagged with PSATs in the South Atlantic Ocean. Patches of red and dark yellow indicate where blue marlins occurred in 30-50% of all of their estimated locations, indicating "core" areas of use.

Vertical distribution

Time-at-depth histograms of blue marlin habitat utilization show that most individuals across all areas spent the majority of their time in shallow waters both during the day and night periods (Figure 5). Overall, tagged blue marlin spent most of their tracking time in the top 20 m of the water column. Blue marlins tagged in Area IV spent the least amount of time in the upper 20 m (60% during the day and 64% during the night), while blue marlins tagged off northeast coast of Brazil spent the highest proportion of time in shallow depths (72% during the day and 77% during the night).

Blue marlins tagged off Area II and III were intermediate with regard to the time spent in the upper 20 m. A secondary peak of higher occurrence at 60- 80 m depth during daytime was also observed for blue marlins in Area II. Occasionally, tagged blue marlins went to depths larger than 120 m. Most of these deep descents were recorded during the day, and more frequently in Areas I, II, and III. The deepest descents recorded for blue marlin was 630 m by BM 2 tagged in Area I.

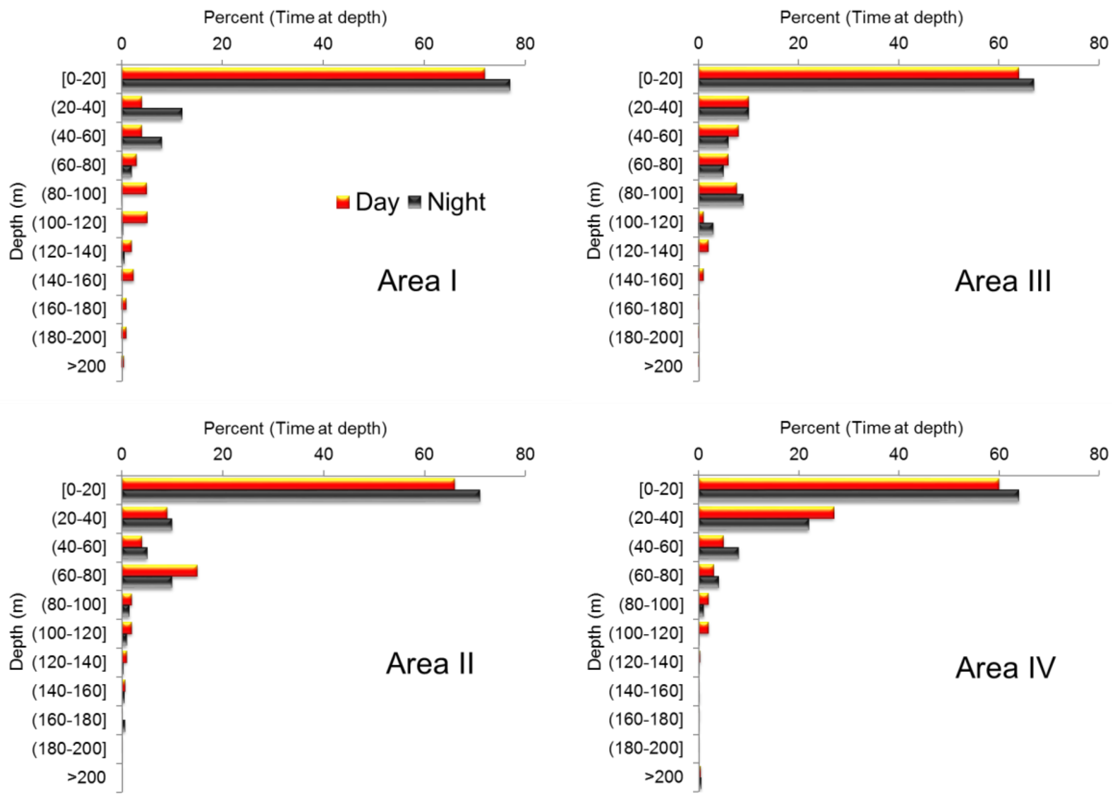

Figure 5. Time-at-depth histogram for blue marlin tagged across the South Atlantic Ocean, separated by nighttime (black bars) and daytime (yellow/red bars).

The patterns of habitat utilization for blue marlins followed the general trend of occupying both shallow and deep waters during the day and night. Kruskal-Wallis tests detected no significant differences in MDD (p = 0.079) and MDT (p = 0.082) across areas. However, after a detailed visual inspection of the dive profiles from all tagged blue marlins significant differences were noted in some individuals. Specifically, for BM 2 and BM 11 the range of vertical habitat utilization was larger during the day than during the night (Figure 6). During five straight days BM 2 showed mean depth during daytime of 37.5 m (SD = 28.8 m), while during the nighttime the mean depth was 23.2 m (SD =

15.1 m). This same pattern was also found in BM 11, which exhibited a mean depth during daytime of 36.4 m (SD = 26.1), while during nighttime the mean depth was 22.7 m (SD=16.6).

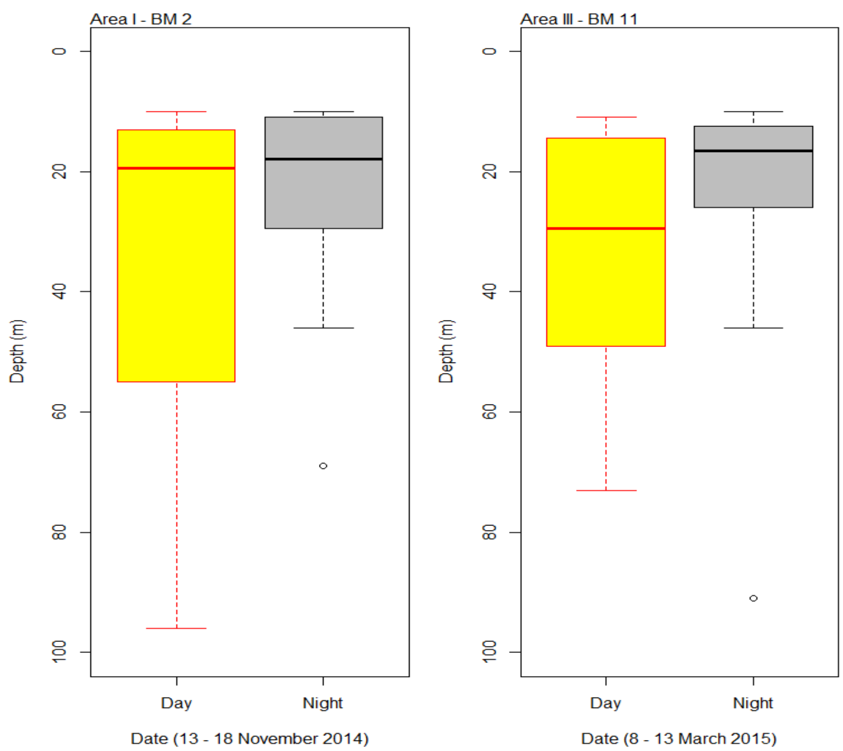

Figure 6. Boxplot of depth experienced by BM 2 and BM 11 during a period of five days. Outliers are represented by a dot at either end of the plot.

Blue marlins spent most of their time within a relatively narrow temperature range, staying an average of 57% of their time in temperatures between 26° and 28°C. In Area I, blue marlins remained in water temperatures between 24° and 29°C for 90% of the day and 92% of the night, while blue marlins in Area II remained between 24° and 29°C, for 88% and 91% of the day and night, respectively (Figure 7). Blue marlins in Area III exhibited a similar behavior pattern to blue marlins in Areas I and II, remaining in water temperatures between 24° and 29° C for 88% of the day and 91% of the night. Blue marlin in Area IV also showed similar temperature preferences observed in the other areas, however a peak can be observed in cooler waters between 22° and 24°C (Figure 7).

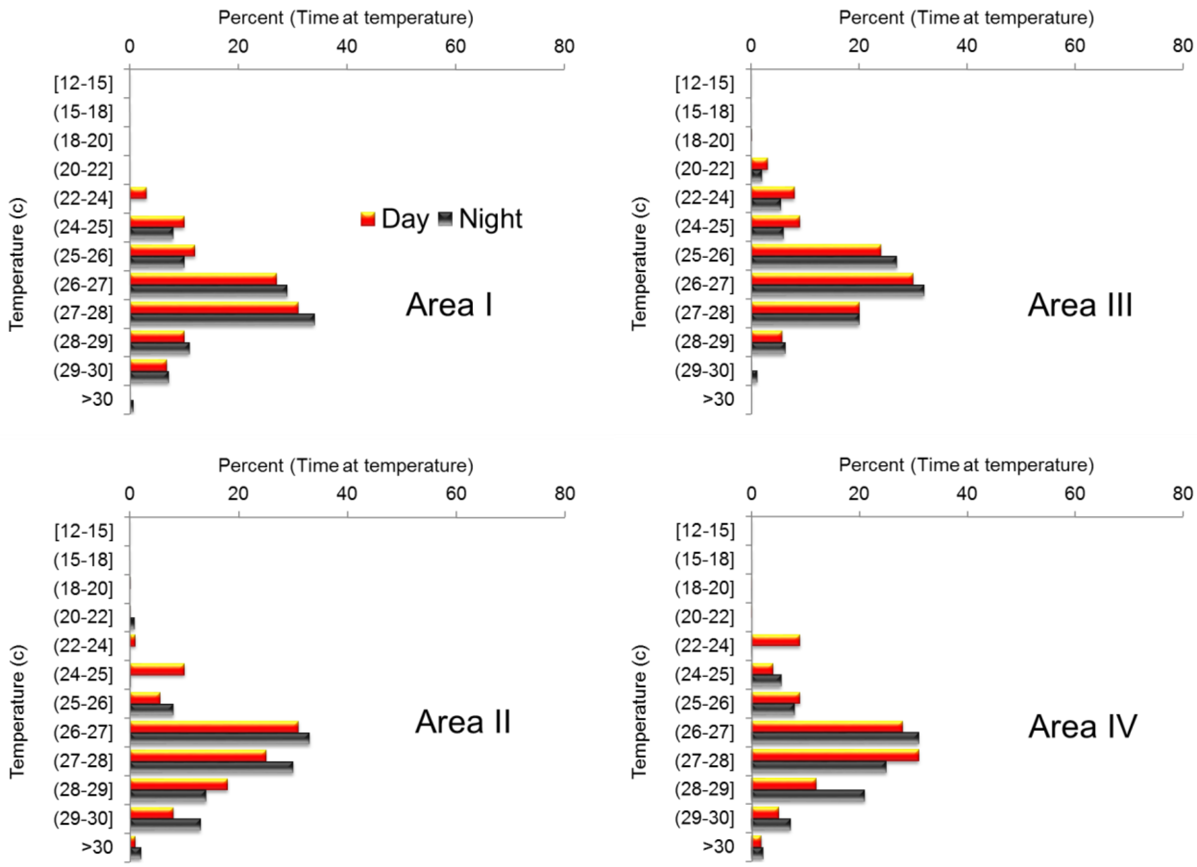

Figure 7. Time-at-temperature histogram for blue marlin tagged across the South Atlantic Ocean, separated by nighttime (black bars) and daytime (yellow/red bars).

Overlap with fishing effort

Some monitored pelagic longline sets were located in the same four areas where blue marlin PSATs were deployed. Not surprisingly perhaps, as both longliners and recreational marlin anglers tend to select productive habitats. Overall, blue marlins had approximately 59% of their tracked range overlapped by the longline fishing gear, with Area II showing the highest overlap frequency (68%), followed by Area I, Area IV, and Area III (Table 2). The average hook depth across all areas was 49 m with 90% percentile depth distribution of the hooks depth between 32-71 m. When this distribution was overlapped with the species vertical habitat utilization, the overlap ranged between 11 and 35% during daytime and 21 and 34% during nighttime. Except in Area I, the overlap between the blue marlin vertical habitat and fishing gear deployment was higher during the day (Table 2).

Table 2. Overlap in percentage of time (%) between the vertical and horizontal habitat of blue marlin, and the depth of operation of shallow water pelagic longlines targeting swordfish.

Area	Average observed depth (90% percentile)	Track range Overlap (%)	Depth overlap (%)	
			Day	Night
I	47 (31 – 68) m	62	11	22
II	49 (34 – 66) m	68	28	25
III	54 (37 – 75) m	47	24	21
IV	47 (30 – 73) m	55	35	34

Habitat use and mixed models

Habitat use varied among individuals in all Areas (Figs 8 and 9). SSTs (mean= 27.43ºC) and DMLs (mean= 65.13m) experienced by tagged blue marlin in Area I were relatively similar. In Area II, BM 7 occurred in waters with significantly colder SST (mean= 25.03°C) and deeper DML (mean= 58.54m), when compared to BM 5, BM 6, and BM 8 (SST =26.71°C; DML=41.65m). In Area III BM 9 and BM 12 used areas close to shore with warmer SST (mean = 26.88°C) and shallower DML (mean= 33.81m), while BM 10 and 11, spent most of their time in locations with cooler SST (mean= 25.76 °C) and significantly deeper DML (mean= 52.37m). In Area IV, BM 14, 15 and 16 also occurred in waters with cooler SST (mean= 25.9°C) and deeper DML (mean= 48,65m), when compared to BM 13 (SST= 26.96°C; DML= 39.67m).

Both SST and DML had a statistically significant influence on GAMM predictions, and lowered AIC and BIC values for all areas (Table 3). The best-fit model that described the effect of the variables on the presence or absence of tagged blue marlins in a specific quadrant was obtained for Area II (R^2 = 0.78), followed by Area III (R^2 = 0.74), Area I (R^2 = 0.60), Area IV (R^2 = 0.52), and all Areas combined (R^2 = 0.51) (Table 4). The output of the fifth GAMM model, investigating the effect of Area on the presence or absence of tagged blue marlins in a specific quadrant (i.e. all Areas model), showed that Area has no significant effect as a variable (Table 4). In all models, SST was the most important variable explaining the variance.

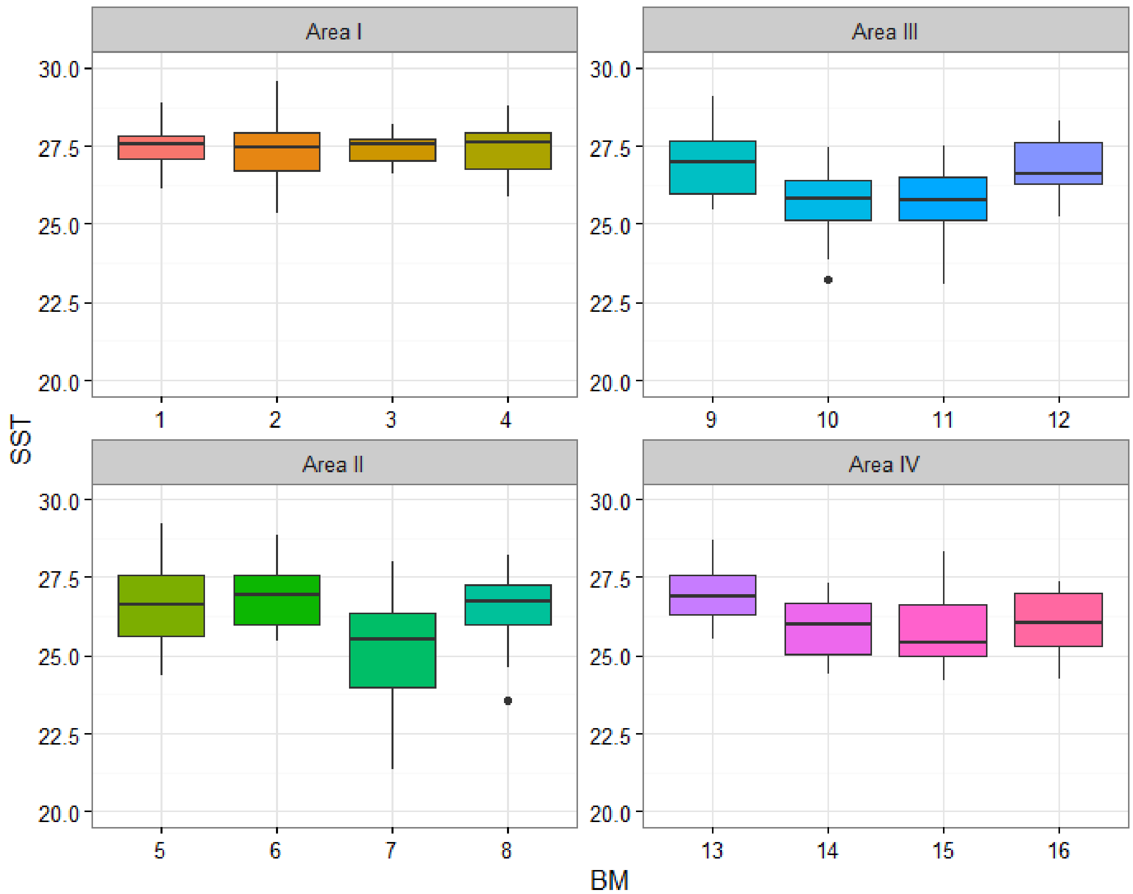

Figure 8. Boxplot of sea surface temperature (SST) experienced by tagged blue marlins for each area across the South Atlantic Ocean. Outliers are represented by a dot at either end of the plot.

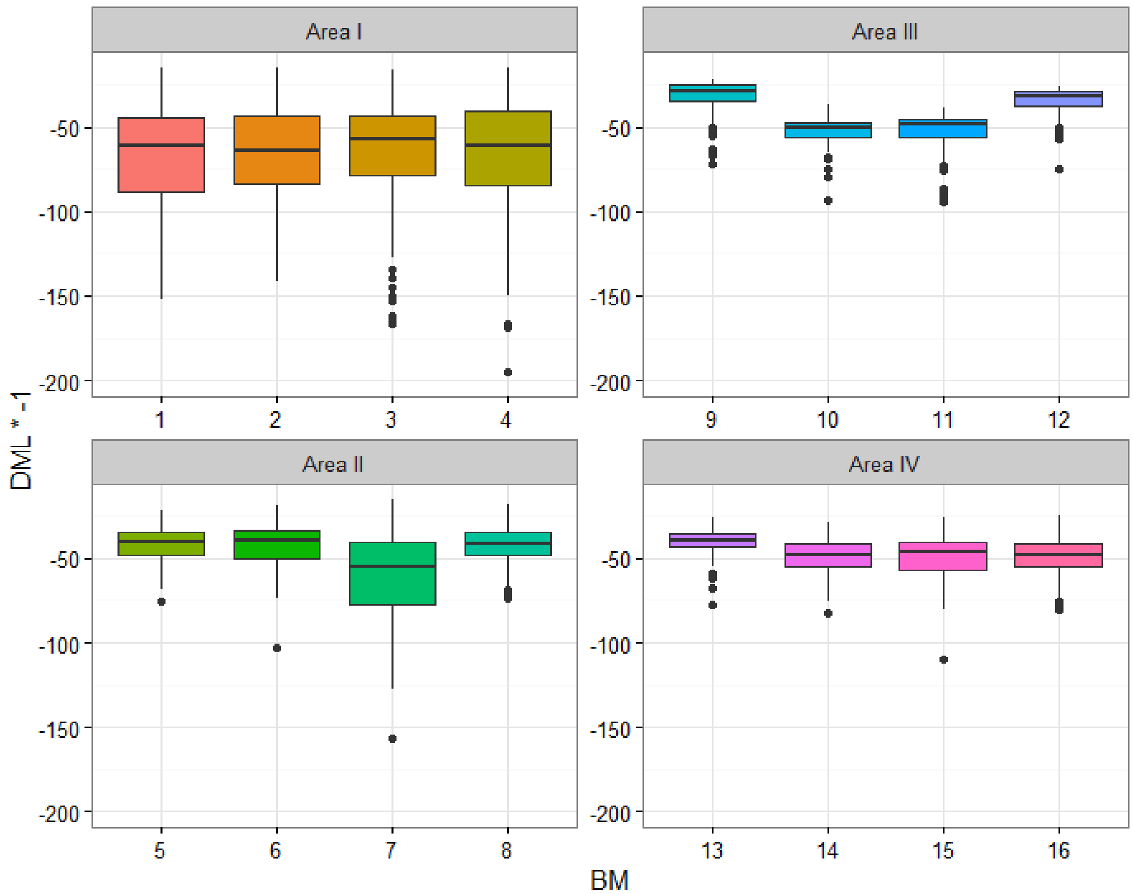

Figure 9. Boxplot of depth of the mixed layer (DML) experienced by tagged blue marlins for each area across the South Atlantic Ocean. Outliers are represented by a dot at either end of the plot.

Table 3. Results from the generalized additive mixed models (GAMMs) for presence and absence of tagged blue marlins in areas across the South Atlantic Ocean. The best-fit model is highlighted in grey. R^2 is the adjusted coefficient of determination and Lr is likelihood ratio test.

	Model	R^2 (%)	AIC	BIC	Lr	Lr (p-value)
Area I						
Stage I	1) SST	0.56007	3938.27	3956.05	NA	NA
	2) DML	0.54229	4301.49	4302.76	NA	NA
Stage II	3) SST + DML	0.60071	3661.41	3663.95	3 vs. 1	19.35 (<0.0001)
Area II						
Stage I	1) SST	0.77216	5358.13	5368.29	NA	NA
	2) DML	0.73152	5478.78	5483.86	NA	NA
Stage II	3) SST + DML	0.78613	5086.35	5093.97	3 vs. 1	8.27 (0.026)
Area III						
Stage I	1) SST	0.72644	6047.74	6061.71	NA	NA
	2) DML	0.7112	6365.24	6372.86	NA	NA
Stage II	3) SST + DML	0.74041	5728.97	5734.05	3 vs. 1	12.31 (0.007)
Area IV						
Stage I	1) SST	0.51181	4516.12	4532.63	NA	NA
	2) DML	0.508	4621.53	4625.34	NA	NA
Stage II	3) SST + DML	0.52451	4215.13	4215.13	3 vs. 1	18.33 (<0.0001)
All areas						
Stage I	1) SST	0.49784	3853.18	3862.07	NA	NA
	2) DML	0.46863	4271.01	4300.22	NA	NA
	3) Area	0.44577	4583.43	4587.24	NA	NA
Stage II	4) SST + DML	0.51816	3693.16	3704.59	4 vs. 1	15.04 (0.003)
	5) SST + Area	0.49149	4716.78	4723.13	NA	NA
Stage III	6) SST + DML + Area	0.45847	4872.99	4883.15	6 vs. 4	4.91 (0.185)

Table 4. Results from the generalized additive mixed models (GAMMs) for presence and absence of tagged blue marlins in areas across the South Atlantic Ocean. Estimated degrees of freedom (Edf) and *F*-values for smooth-term variables are given. All variables selected were significant in the models (p < 0.001).

	Edf	*F*	*p-value*
Area I			
Smoother term			
SST	5.033	4.39 E + 01	–<0.0001
DML	2.445	4.12 E + 01	–<0.0001
Area II			
Smoother term			
SST	6.045	2.37 E + 01	–<0.0001
DML	3.114	2.04 E + 01	–<0.0001
Area III			
Smoother term			
SST	6.308	2.11 E + 1	–<0.0001
DML	2.561	88.42	0.0031
Area IV			
Smoother term			
SST	5.023	4.02 E + 01	–<0.0001
DML	3.491	6.71 E + 01	–<0.0001
All areas			
Smoother term			
SST	7.993	2.03 E + 01	–<0.0001
DML	4.872	19.465	0.0041

Discussion

This research is the largest spatially-stratified satellite tagging study of South Atlantic blue marlin to date. Blue marlins showed intermediate levels of residency to core areas, with smaller individuals in some areas that swam in loops staying near the tagging site. These results support a growing number of studies indicating that pelagic species show site fidelity within core areas, although some individuals also undertake long-range movements (Kohler et al. 2002; Weng et al. 2005; Campana et al. 2011; Howey-Jordan et al. 2013). Unfortunately, we were not able to develop an all-explanatory movement model for blue marlins in the South Atlantic Ocean. However, based on the highly directed long distance movements of larger individuals, it is very likely that blue marlins perform partial migrations where only such individuals migrate, like other animals that have an extended period of growth prior to reproduction (Jonsson & Jonsson 1993; Chapman et al. 2012). Long distance migrations between waters associated with foraging and those associated with reproduction have been recorded in many pelagic animals including sea turtles (James et al. 2005), fish (Patterson et al. 2008), sharks (Weng et al. 2008), seabirds (Shaffer et al. 2006) and mammals (Mate et al., 2007). The timing of such long distance migrations has been associated with seasonal peaks in ocean productivity and with seasonal changes in temperatures that are favorable for reproduction (Shaffer et al. 2006; Patterson et al. 2008). Such long distance migrations are presumably a trade-off between the energy expended during migration, the energetic returns gained while on foraging grounds and the benefits on reproductive success (Alerstam et al. 2003; Evans et al. 2012). If regions close to areas suitable for reproduction are productive and likely to sustain regional populations, there may be less of a requirement to undertake large movements away from those areas. However, conducting a tagging study to tease apart the contributing factors for an animal movement requires selecting the appropriate spatial and temporal scales to analyze. We selected the entire South Atlantic Ocean, which was an appropriate spatial scale, but an appropriate temporal scale would cover a much longer period (e.g. 2 or 3 years).

Even with tags attached for a relatively short period, interesting movement patterns of blue marlins in the South Atlantic Ocean could be detected, such as the more pronounced long-distance and directed movements in larger blue marlins (LJFL > 200 cm). Hazin et al. (1993) was the first to hypothesize the migratory behavior of blue marlins in the Southwest Atlantic Ocean by analyzing spatial and seasonal patterns in CPUE of blue marlins caught by the Brazilian longline fishery in the southwest Atlantic. They found higher rates of blue marlin off northeast region of Brazil (Area I in this study) in the 3rd quarter of the year (July to September), and in the southeast region (Area II in this study) during the 1st (January to March) and 4th quarters (October to December). Amorim et al. (1994), using preliminary information on the reproductive biology of individuals caught in the Brazilian longline fishery, suggested that adult blue marlin spawn off the southeast coast of Brazil during the first quarter of the year. More recently, Frédou et al. (2012), using data across a broad spatial and temporal scale, described the size composition of the blue marlin in the equatorial and southwestern Atlantic Ocean, and proposed that adult individuals move from the southeast coast to the northeast coast of Brazil during the second quarter and then eastward towards the equatorial in the third quarter. This is consistent with some of our findings, for example BM 1 and BM 4, both adult individuals, were tagged in Area I in the very beginning of the fourth quarter and started moving away from the northeast coast of Brazil right after. Although, some information was available on blue marlin migratory dynamics off the coast of Brazil, very little was known about their behavior in the other side of the Atlantic, off the west coast of Africa. Results from Area III and IV presented here add few more pieces to the puzzle. For example, both adult blue marlins tracked in Area IV during the third and fourth quarter of the year, seem to show a directed movement towards Area II, if those individuals actually kept moving in that direction they would eventually arrive in Area II during the first quarter of the year, corroborating with Amorim et al. (1994). The data of seasonal and spatial variation of the 25° C isotherm in each area indicate that blue marlins horizontal movements are most likely related to this isotherm displacement. This result supports the findings of Amorim *et al.* (1994) that blue marlins move southward off Brazilian coast following the displacement of 25° C isotherm to spawn in this area in the first quarter of the year.

This study also revealed a cross-Atlantic marked preference of tagged blue marlin to occupy the upper 20 m of the water column during all times of day, and have a narrow temperature distribution. Some large individuals also occurred in waters with shallower mixed layers, which may also be related to selecting warmer surface waters, as shallow DML are generally associated with warmer surface waters. This pattern was very clear among blue marlins tagged in Area III, where large individuals selected warmer waters off the coast of Northwest Africa, which is also near to a highly productive zone due the coastal upwelling system (Summerhayes et al. 1995; Chavez & Messié 2009). These patterns are consistent with previous studies using acoustic and pop-up tags on blue marlin (Holland et al. 1990; Block et al. 1992; Graves et al. 2002; Kerstetter et al. 2003; C. P. Goodyear et al. 2008), and other istiophorids, including: white marlin (Graves et al. 2003; Prince et al. 2005; Prince & Goodyear 2006; Horodysky et al. 2007), striped marlin (Domeier *et al.* 2003, Sippel *et al.* 2007), black marlin (Gunn *et al.* 2003, Prince and Goodyear 2006), and sailfish (Hoolihan 2004, Kerstetter and Graves 2006, Prince and Goodyear 2006, Hoolihan and Luo 2007).

Time at temperature data fell within ranges reported in all other tagging studies of blue marlin. Previous studies have shown that blue marlin spend the vast majority of time in the uniform temperature surface layer, above the thermocline, indicating how important is this variable for the habitat utilization of billfishes (Yuen *et al.* 1974, Block 1990, Horodysky *et al.* 2007, Goodyear *et al.* 2008). Moreover, temperature directly limits cardiac output and swimming performance in tunas and billfishes (Brill *et al.* 1998). Here, the vast majority of blue marlins stayed within a 5^0C range of water temperature (24°- 29°C).

The amount of dissolved oxygen has also been considered to affect the vertical distribution of istiophorids, acting as a physical barrier to limit vertical movement and increasing predator-prey interactions due to habitat compression (Prince & Goodyear 2006; Prince et al. 2010; Stramma et al. 2011). According to Prince *et al.* (2010) and Stramma *et. al* (2011), the east tropical Atlantic has a low dissolved oxygen (DO) area below the thermocline, contrasting to much higher DO concentrations in the southwest Atlantic (Castro & Miranda 1998; Braga & Niencheski 2006). However, our study showed that there were no significant differences in blue marlin vertical behavior among the four study areas. This might suggest that temperature is more relevant than DO as a limiting factor for blue marlin vertical habitat utilization.

Although the majority of the time spent by blue marlin was restricted to warmer waters near the surface, the data showed diel patterns of vertical distribution for some individuals diving deeper during the day and swimming near the surface at night, which is possibly related to the variation of light level range since they are visual predators. This high presence in the surface layer is also reflected in the blue marlin diet, which consists mainly of epipelagic fishes and squids (Brock 1984, Garcia de las Salmones *et al.* 1989, Junior *et al.* 2004). However, few studies have reported prey items that typically inhabit deeper water (Strasburg 1970, Nakamura 1985, Harvey 1989).

An important prerequisite for estimating local fishing impacts is to assess how much of fish core habitats, estimated from survey data (e.g. animal tracks and depth preference), overlap with areas used by the fisheries (Vinther & Eero 2013). We believe that more than 16 tags would be needed to fully understand the migratory patterns of blue marlin and its interaction with fishing gears across the South Atlantic Ocean. However, the broad reaching nature of the PSATs data and the detailed information about horizontal and vertical movements that these tags can provide are unique. Our study showed that areas used by tagged blue marlins directly overlapped with major fishing grounds for a variety of tuna longline fishing fleets in the South Atlantic Ocean, which is reflected in the presence of blue marlin catches in the commercial longline fisheries operating in the South Atlantic, and especially off the coast of Brazil. On the other hand, the low vertical overlap between blue marlins and pelagic longline gear found in this study might suggest that for most of the time this interaction can be avoided. Thus, this negative effect of horizontal overlap could be smoothed out by taking measures of time-area closure for example.

In 2013, Brazil was one of the top three nations to report the largest catches of blue marlin in the Atlantic, only behind Japan and Chinese Taipei (ICCAT 2011). In addition, there is a growing concern about the high levels of blue marlin fishing mortality on a developing artisanal longline fishery operating off the Brazilian coast between 18^0 and 30^0S Latitude (Amorim et al., 2013).

The continuing problem of exploited blue marlin population in the South Atlantic requires new information to support stock assessments and imposes new challenges for population modeling. One of these challenges requires the incorporation of spatial patterns of blue marlin into stock assessment modeling. As shown here, there is variability in the depth fished by pelagic longlines, which can also influence marlins and fishing gear encounters, causing catch rates to be a weak estimator of abundance (Ward & Hindmarsh 2007; C. P. Goodyear et al. 2008). Standardizing catch rates for factors other than abundance is needed, since catch rates are used as a critical source of information for the majority of fish stock assessments (Bigelow & Maunder 2007).

In the mid 90's, Hinton and Nakano (1996) tried for the first time to account for changes in depth of longline fishing over time by standardizing catchability by depth. This method, known as habitat-based standardization (HBS), represents a modeling approach whereby catch rates are standardized by estimating effective longline effort from information on the vertical distribution of the hooks and the species-specific depth preference (Maunder, 2006). In its last blue marlin assessment, ICCAT (2011) tested this technique to blue marlin catch series from the Atlantic Ocean using vertical habitat data from nine blue marlins tracked in the central Pacific Ocean with acoustic tags (Holland et al. 1990; Block et al. 1992). ICCAT scientists deemed the use of HBS premature for assessments of Atlantic Ocean blue marlin, because the habitat data available had been obtained from another ocean basin. The data collected as part of this study, therefore, may facilitate the use of HBS methods in the Atlantic to develop indices of relative abundance useful for future stock assessments.

Acknowledgements

This study was financed by the Science Without Borders (SWB) program from CNPq, National Oceanic and Atmospheric Administration (NOAA) and Guy Harvey Foundation. We are thankful to Charlene da Silva and Henning Winker from the Department of Agriculture Forestry and Fisheries of South Africa Government for their support on tagging process in African coast. We are also grateful to all contributors to the field work process and data collection.

5. CONCLUSÃO

A presente pesquisa revela que o agulhão negro possui uma distribuição vertical no Oceano Atlântico Sul ocupando águas superficiais de até 20 m de profundidade em sua maior porcentagem de tempo, porém com capacidade de mergulhos esporádicos profundos para além dos 600 m. O comportamento vertical dos animais se mostrou semelhante nas quatro áreas de estudo. Este padrão de ocupação da camada superficial pelos animais faz com que a sobreposição vertical com os anzóis de espinhel pelágico seja reduzida em razão destes permanecerem numa profundidade média superior aos 45 m. Por outro lado, os dados de movimentação horizontal apresentados pelo presente estudo mostraram uma ampla distribuição ao longo das quatro áreas estudadas, causando um nível significativo (47-68%) de sobreposição horizontal com os lances de espinhel no Atlântico Sul. Padrões de dispersão maiores e direcionais nos indivíduos de maior tamanho (>200 cm), considerados adultos, foram também observados, com os espécimes de menor porte apresentando um comportamento de residência na grande área de marcação. O padrão de ocupação horizontal dos animais marcados mostrou-se fortemente relacionado à variação sazonal da isoterma de 25ºC (TSM), encontrando-se em sua maioria em águas de temperatura superficial acima da mesma.

As pesquisas relacionadas à utilização de habitat por grandes pelágicos no atlântico sul estão, nos últimos anos, ganhando mais força e expressividade, tornando-se extremamente relevantes para a conservação das espécies alvo e de fauna acompanhante da pesca comercial. Por esse motivo, apesar da grande quantidade de informações aqui obtidas, o problema da sobrepesca para a espécie só pode ser amplamente analisado com pesquisas adicionais que utilizem os dados para avaliação do estoque pesqueiro e modelagem populacional.

Os resultados obtidos na presente pesquisa são relevantes para uma melhor compreensão da biologia e ecologia dos agulhões negros no oceano Atlântico Sul. Apesar da necessidade de uma coleta de dados em maior escala temporal, as informações já obtidas aportam um conhecimento importante sobre o comportamento da espécie, contribuindo para reduzir as atuais incertezas sobre sua biologia e auxiliando, consequentemente, na tomada de decisões sobre medidas de manejo e conservação da espécie ao nível internacional.

6. REFERÊNCIAS

Afonso, A.S. & Hazin, F.H. V., 2015. Vertical Movement Patterns and Ontogenetic Niche Expansion in the Tiger Shark, *Galeocerdo cuvier*. *Plos One*, 10(1), p.e0116720. Available at: http://dx.plos.org/10.1371/journal.pone.0116720.

Alerstam, T., Hedenstrom, A. & Akesson, S., 2003. Long-distance migration: evolution and determinants. *Oikos*, 103(May), pp.247–260.

Amorim, A. et al., 1994. Blue marlin (*Makaira nigricans*) fisheries off Brazilian coast by national and leased longliners (1971-1991). *Col. Vol. Sci. Pap. ICCAT*, 41, pp.208–213.

Amorim, A.F. & Arfelli, C.A., 2001. Analysis of the Santos fleet from Sao Paulo, southern Brazil (1971-1999). , pp.263–271.

Arfelli, C.A., Amorim, A.F. & Graca-Lopes, R., 1994. Billfish Sport Fishery Off Brazilian Coast. *Col. Vol. Sci. Pap. ICCAT*, 41, pp.214–217.

Arnold, G. & Dewar, H., 2001. Electronic tags in marine fisheries research: a 30-year perspective. In J. R. Sibert & J. L. Nielson, eds. *Electronic tagging and tracking in marine fisheries*. Kluwer Academic Publishers, pp. 7–64.

Bergin, T.M., 1991. A Comparison of Goodness-of-Fit Tests for Analysis of Nest Orientation in Western Kingbirds (*Tyrannus verticalis*). *The Condor*, 93(1), pp.164–171. Available at: http://www.jstor.org/stable/1368619.

Bernal, D. et al., 2009. The eco-physiology of swimming and movement patterns of tunas, billfishes, and large pelagic sharks. In *Fish Locomotion–an etho-ecological perspective*. Science Publishers, Enfield, pp. 436–483.

Bestley, S. et al., 2013. Integrative modelling of animal movement: incorporating in situ habitat and behavioural information for a migratory marine predator. *Proceedings. Biological sciences / The Royal Society*, 280(1750), p.20122262. Available at: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3574443&tool=pmcentrez&rendertype=abstract.

Beverly, S. et al., 2009. Effects of eliminating shallow hooks from tuna longline sets on target and non-target species in the Hawaii-based pelagic tuna fishery. *Fisheries Research*, 96(2–3), pp.281–288.

Bigelow, K. a & Maunder, M.N., 2007. Does habitat or depth influence catch rates of pelagic species? *Canadian Journal of Fisheries and Aquatic Sciences*, 64(11), pp.1581–1594.

Block, B.A., Booth, D.T. & Carey, F.G., 1992. Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Marine Biology*, 114(2), pp.175–183.

Block, B. a et al., 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proceedings of the National Academy of Sciences of the United States of America*, 95(16), pp.9384–9389.

Boggs, C.H., 1992. Depth, capture time, and hooked longevity of longline-caught pelagic fish: timing bites of fish with chips. *Fishery Bulletin*, 90(4), pp.642–658.

Bonadonna, F. et al., 2001. Foraging ground fidelity and route-choice tactics of a marine predator: The Antarctic fur seal *Arctocephalus gazella*. *Marine Ecology Progress Series*, 223, pp.287–297.

Boyce, D.G., Tittensor, D.P. & Worm, B., 2008. Effects of temperature on global patterns of tuna and billfish richness. *Marine Ecology Progress Series*, 355, pp.267–276.

Brill, R.W., Lowe, T.E. & Cousins, K.L., 1998. How Water Temperature Really Limits the Vertical Movements of Tunas and Billfishes - It's the Heart Stupid. *Pelagic Fisheries Research Program, JIMAR, SOEST*, (October), p.4.

Brill, R.W. & Lutcavage, M.E., 2001. Understanding Environmental Influences on Movements and Depth Distributions of Tunas and Billfishes Can Significantly Improve Population Assessments. *American Fisheries Society Symposium*, pp.179–198.

Brock, R.E., 1984. a Contribution To the Trophic Biology of the Blue Marlin *Makaira nigricans* in Hawaii Usa. *Pacific Science*, 38(2), pp.141–149.

Bullard, F., 1999. Estimating the home range of an animal: a Brownian bridge approach. *Doctoral Dissertation.* Master thesis.

Campana, S.E. et al., 2011. Migration Pathways, Behavioural Thermoregulation and Overwintering Grounds of Blue Sharks in the Northwest Atlantic. *PLoS ONE*, 6(2), p.e16854. Available at: http://dx.doi.org/10.1371%2Fjournal.pone.0016854.

Carvalho, F. et al., 2015. Using pop-up satellite archival tags to inform selectivity in fisheries stock assessment models: a case study for the blue shark in the South Atlantic Ocean. *ICES Journal of Marine Science*.

Casini, M. et al., 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(1), pp.197–202.

Chapman, B.B. et al., 2012. Partial migration in fishes: Causes and consequences. *Journal of Fish Biology*, 81(2), pp.456–478.

Chavez, F.P. & Messié, M., 2009. A comparison of Eastern Boundary Upwelling Ecosystems. *Progress in Oceanography*, 83(1–4), pp.80–96. Available at: http://dx.doi.org/10.1016/j.pocean.2009.07.032.

Collette, B.B., Mcdowell, J.R. & Graves, J.E., 2006. Phylogeny of recent billfishes (Xiphioidei). , 79(3), pp.455–468.

Die, D.J., 2006. Are Atlantic marlins overfished or endangered? Some reasons why we may not be able to tell. *Bulletin of Marine Science*, 79(3), pp.529–543.

Ditton, R.B. & Stoll, J.R., 2003. Social and economic perspective on recreational billfish fisheries. *Marine and Freshwater Research*, 54, pp.545–554.

Domeier, M.L., Dewar, H. & Nasby-Lucas, N., 2003. Mortality rate of striped marlin (*Tetrapturus audax*) caught with recreational tackle. *Marine and Freshwater Research*, 54(4), pp.435–445.

Dutton, D.J., 2010. Habitat Utilization and Dive Characterization of Blue Marlin (*Makaira nigricans*) and White Marlin (*Kajikia albida*) in the Western Atlantic Ocean. *PhD Dissertation, College of Willian and Mary.* Available at: http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:No+Title#0 [Accessed September 5, 2014].

Estes, J. a et al., 2011. Trophic downgrading of planet Earth. *Science (New York, N.Y.)*, 333(6040), pp.301–6. Available at: http://www.ncbi.nlm.nih.gov/pubmed/21764740 [Accessed July 10, 2014].

Evans, K. et al., 2012. Spatial dynamics of swordfish in the south Pacific Ocean inferred from tagging data. *WCPFC document WCPFC-SC8-2012/SA-IP-05*, (August), p.36.

Frédou, T. & Frédou, F.L., 2012. Length Composition and Spatio-Temporal Distribution of Blue Marlin (*Makaira Nigricans*) in the South Atlantic Ocean. , 68(4), pp.1524–1530.

Fritsches, K.A., Marshall, N.J. & Warrant, E.J., 2003. Retinal specializations in the blue marlin: Eyes designed for sensitivity to low light levels. *Marine and Freshwater Research*, 54(4), pp.333–341.

Goodyear et al., 2008. Vertical habitat use of Atlantic blue marlin *Makaira nigricans*: Interaction with pelagic longline gear. *Marine Ecology Progress Series*, 365, pp.233–245.

Goodyear, C.P. et al., 2003. Habitat standardization of CPUE indices: Research needs. *ICCAT*, 55(2), pp.613–623.

Goodyear, C.P. et al., 2008. Vertical habitat use of Atlantic blue marlin *Makaira nigricans*: interaction with pelagic longline gear. *Marine Ecology Progress Series*, 365, pp.233–245. Available at: http://www.int-res.com/abstracts/meps/v365/p233-245/ [Accessed September 5, 2014].

Graves, J.E. et al., 2003. Habitat preferences of istiophorid billfishes in the western north atlantic : applicability of archival tag data to habitat- based stock assessment methodologies. , 55(2), pp.594–602.

Graves, J.E., Luckhurst, B.E. & Prince, E.D., 2002. An evaluation of pop-up satellite tags forestimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fishery Bulletin*, 100, pp.134–142.

Hall, M.A., Alverson, D.L. & Metuzals, K.I., 2000. By-catch: Problems and solutions. *Marine Pollution Bulletin*, 41(1–6), pp.204–219.

Hall, M. a., 1998. An ecological view of the tuna-dolphin problem: impacts and trade-offs. *Review in Fish Biology and Fisheries*, 8, pp.1–34.

Harvey, G.C., 1989. An historical review of recreational and artisanal fisheries for billfish in Jamaica, 1976-1988. *Col. Vol. Sci. Pap. ICCAT*, 30(2), pp.440–450.

Hazin, F.H. V., 1993. Fisheries-oceanographical study on tunas, billfishes and sharks in the southwestern equatorial Atlantic Ocean. University of Fisheries, Tokyo.

Hofmann, G.E. & Gaines, S.D., 2008. New Tools to Meet New Challenges: Emerging

Technologies for Managing Marine Ecosystems for Resilience. *BioScience*, 58(1), p.43.

Holder, C., 1912. *The game fishes of the world*, New York: Hodder and Stroughton.

Holland, K., Brill, R. & Chang, R.K.C., 1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fishery Bulletin*, 88(2), pp.397–402.

Holland, S.M., Ditton, R.B. & Graefe, A.R., 1998. An Ecotourism Perspective on Billfish Fisheries. *Journal of Sustainable Tourism*, 6(2), pp.97–116. Available at: http://www.tandfonline.com/doi/abs/10.1080/09669589808667305.

Horne, J.S. et al., 2007. Analyzing animal movements using Brownian bridges. *Ecology*, 88(9), pp.2354–2363.

Horodysky, A.Z. et al., 2007. Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean : inferences from short duration pop-up archival satellite tags. , pp.240–256.

Horodysky, A.Z. & Graves, J.E., 2005. Application of pop-up satellite archival tag technology to estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank (“J”) hooks in the western North Atlantic recreational fishery. *Fishery Bulletin*, 103(1), pp.84–96.

Howey-Jordan, L.A. et al., 2013. Complex Movements, Philopatry and Expanded Depth Range of a Severely Threatened Pelagic Shark, the Oceanic Whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. *PLoS ONE*, 8(2), p.e56588. Available at: http://dx.doi.org/10.1371%2Fjournal.pone.0056588.

ICCAT, 2007a. *ICCAT Basic Texts* 5th ed., Madrid.

ICCAT, 2007b. *Report for biennial period, 2006-07 PART I (2006)- Vol. 1*,

ICCAT, 2007c. Report of the 2006 Iccat Billfish Stock Assessment. *Col. Vol. Sci. Pap. ICCAT*, 60(5), pp.1431–1546.

ICCAT, 2011. Report of the 2011 Blue Marlin Stock Assessment. *Collective Volume of Scientific Papers ICCAT*, pp.1–75.

James, M.C., Ottensmeyer, C.A. & Myers, R.A., 2005. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: New directions for conservation. *Ecology Letters*, 8(2), pp.195–201.

Jonsson, B. & Jonsson, N., 1993. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, 3(4), pp.348–365.

Jordan, D.S. & Evermann, B.W., 1923. American food and game fishes.

Júnior, T.V., Maria Vooren, C. & Paula Lessa, R., 2004. Feeding habits of four species of Istiophoridae (Pisces: Perciformes) from northeastern Brazil. *Environmental Biology of Fishes*, 70(3), pp.293–304.

Kerstetter, D.W. et al., 2003. Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear. *Fishery*

Bulletin, 101(4), pp.939–948.

Kerstetter, D.W. & Graves, J.E., 2006. Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. *Fisheries Research*, 80, pp.239–250.

Kitchell, J.F. et al., 2006. Billfishes in an ecosystem context. *Bulletin of Marine Science*, 79(3), pp.669–682.

Kohler, N.E. et al., 2002. Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*) and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. *International Commission for the Conservation of Atlantic Tunas, Collective Volume of Scientific Papers SCRS/2001/64*, 54(4), pp.1231–1260.

Kraus, R., Wells, R.J.D. & Rooker, J., 2011. Horizontal movements of Atlantic blue marlin (*Makaira nigricans*) in the Gulf of Mexico. *Marine Biology*, 158(3), pp.699–713. Available at: http://dx.doi.org/10.1007/s00227-010-1593-3.

Luo, J. et al., 2006. Vertical habitat utilization by large pelagic animals: a quantitative framework and numerical method for use with pop-up satellite tag data. *Fisheries Oceanography*, 15(3), pp.208–229. Available at: http://doi.wiley.com/10.1111/j.1365-2419.2006.00360.x.

Lynch, P.D., Graves, J.E. & Latour, R.J., 2011. Challenges in the Assessment and Management of Highly Migratory Bycatch Species : A Case Study of the Atlantic Marlins. *Sustainable Fisheries: Multi-Level Approaches to a Global Problem*, (Nmfs 2007), pp.197–225.

Mourato, B.L. et al., 2014. Short-term movements and habitat preferences of sailfish, Istiophorus platypterus (Istiophoridae), along the southeast coast of Brazil. *Neotropical Ichthyology*, 12(4), pp.861–870. Available at: http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1679-62252014000400861&lng=en&nrm=iso&tlng=en.

Mourato, B.L. et al., 2009. Standardized CPUE of Atlantic Sailfish (*Istiophorus platypterus*) caught by the recreational fishery in southern Brazil (1996-2007). *Collective Volumes of Scientific Papers*, 64(6), pp.1941–1950.

Musyl, M. et al., 2011. Performance of pop-up satellite archival tags. *Marine Ecology Progress Series*, 433(1998), pp.1–28. Available at: http://www.int-res.com/abstracts/meps/v433/p1-28/.

Nakamura, I., 1985. FAO Species Catalogue. Vol. 5: Billfishes of the World. An Annotated and Illustrated Catalogue of Marlins, Sailfishes, Spearfishes and Swordfishes Known to Date. *FAO Fisheries Synopsis.*, 125, p.65 pp.

Nakamura, I., 1983. Systematics of the billfishes (Xiphiidae and Istiophoridae). *Publications of the Seto Marine Biological Laboratory*, 28(5–6), pp.255–396.

Nakano, H., Okazaki, M. & Okamoto, H., 1997. Analysis of catch depth by species for tuna longline fishery based on catch by branch lines. *Bulletin-National Research Institute of Far Seas Fisheries (Japan).*

Nielsen, A. & Sibert, J.R., 2007. State–space model for light-based tracking of marine animals. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(8), pp.1055–1068.

Orbesen, E.S. et al., 2008. Transboundary Movement of Atlantic Istiophorid Billfishes Among International and U.S. Domestic Management Areas Inferred from Mark-Recapture Studies. *Marine Fisheries Review*, 70(1), pp.14–23. Available at: http://search.proquest.com/docview/20180454?accountid=14874\nhttp://unicat.bangor.ac.uk:4550/resserv?genre=article&issn=00901830&title=Marine+Fisheries+Review&volume=70&issue=1&date=2008-03-01&atitle=Transboundary+Movement+of+Atlantic+Istiophorid+Billfish.

Ortiz, M. et al., 2003. Global overview of the major constituent-based billfish tagging programs and their results since 1954. *Marine and Freshwater Research*, 54(4), pp.489–507.

Pace, M. et al., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution*, 14(12), pp.483–488. Available at: http://www.ncbi.nlm.nih.gov/pubmed/10542455.

Pacheco, J.C., 2015. *Estudo do comportamento dos agulhões branco (Kajikia albida - Poey, 1860) e negro (Makaira nigricans – Lacepede, 1802)*. Universidade Federal Rural de Pernambuco.

Pacheco, J.C. et al., 2015. Standardized catch rates of White Marlin and Blue Marlin caught by the brazilian tuna longline fleet (1978-2012) using generalized linear mixed models (GLMM) with a delta log approach. *Collect. Vol. Sci. Pap. ICCAT*, 71(5), pp.2338–2354.

Paine, R.T., 1969. A Note on Trophic Complexity and Community Stability. *The American Naturalist*, 103(929), pp.91–93. Available at: http://www.jstor.org/stable/2459472.

Patterson, T.A. et al., 2008. Movement and behaviour of large southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop-up satellite archival tags. *Fisheries Oceanography*, 17(5), pp.352–367.

Pons, M. et al., 2016. Effects of biological, economic and management factors on tuna and billfish stock status. *Fish and Fisheries*, pp.1–21. Available at: http://doi.wiley.com/10.1111/faf.12163.

Prince, E.D. et al., 2005. Movements and spawning of white marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) off Punta Cana, Dominican Republic. *Fishery Bulletin*, 103, pp.659–669.

Prince, E.D. et al., 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fisheries Oceanography*, 19(6), pp.448–462.

Prince, E.D. & Brown, B.E., 1991. Coordination of the ICCAT enhanced research program of billfish. *American Fishery Society symposium*, 12(MARCH 1991), pp.13–18.

Prince, E.D. & Goodyear, C.P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography*, 15(OCTOBER), pp.451–464.

Queiroz, N. et al., 2010. Short-term movements and diving behaviour of satellite-tracked blue sharks Prionace glauca in the northeastern Atlantic Ocean. *Marine Ecology Progress Series*, 406, pp.265–279.

Queiroz, N. et al., 2012. Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation Y. Ropert-Coudert, ed. *PLoS ONE*, 7(2), p.e32374. Available at: http://dx.plos.org/10.1371/journal.pone.0032374.

R Core Team, 2013. R: A language and environment for statistical computing. Available at: http://www.r-project.org/.

Restrepo, V. et al., 2003. ICCAT stock assessments of Atlantic billfish. *Marine and Freshwater Research*, 54(4), pp.361–367.

Rice, P.H., 2008. *Factors Affecting the Catch of Target and Bycatch Species During Pelagic Longline Fishing*.

Rice, P.H. et al., 2007. Use of Catenary Geometry to Estimate Hook Depth during Near-Surface Pelagic Longline Fishing: Theory versus Practice. *North American Journal of Fisheries Management*, 27(4), pp.1148–1161. Available at: http://www.tandfonline.com/doi/abs/10.1577/M06-114.1 [Accessed October 10, 2014].

Rivas, L.R., 1972. Proceedings of the international billfish symposium. In *Synopsis of biological data on blue marlin, Makaira nigricans Lacepede, 1802.* Kailua-Kona, Hawaii, pp. 9–12.

Satoh, K. et al., 2004. Preliminary stomach contents analysis of pelagic fish collected by Shoyo-Maru 2002 research cruise. *Collect. Vol. Sci. Pap. ICCAT*, 56(3), pp.1096–1114.

Shaffer, S. a et al., 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America*, 103(34), pp.12799–12802.

Shimose, T. et al., 2012. Sexual difference in the migration pattern of blue marlin, Makaira nigricans, related to spawning and feeding activities in the western and central North Pacific Ocean. *Bulletin of Marine Science*, 88(2), pp.231–249. Available at: http://www.scopus.com/inward/record.url?eid=2-s2.0-84861427257&partnerID=40&md5=68fe20b56d9a6c50cbd8338317ca7aab.

Shimose, T., Shono, H. & Yokawa, K., 2006. Food and feeding habits of blue marlin , *Makaira nigricans* , around Yonaguni island , southwestern Japan. , 79(3), pp.761–775.

Shimose, T., Yokawa, K. & Saito, H., 2010. Habitat and food partitioning of billfishes (Xiphioidei). *Journal of Fish Biology*, 76(10), pp.2418–2433.

Stramma, L. et al., 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, 2(1), pp.33–37. Available at: http://dx.doi.org/10.1038/nclimate1304.

Strasburg, D.W., 1970. A report on the billfishes of the central pacific ocean. *Bulletin of marine science*, 20(3), pp.575–604.

Su, N.J. et al., 2008. Environmental and spatial effects on the distribution of blue marlin (*Makaira nigricans*) as inferred from data for longline fisheries in the Pacific Ocean. *Fisheries Oceanography*, 17(6), pp.432–445.

Summerhayes, C.P. et al., 1995. Variability in the Benguela Current upwelling system over the past 70,000 years. *Progress in Oceanography*, 35(3), pp.207–251.

Tolotti, M.T. et al., 2015. Vulnerability of the Oceanic Whitetip Shark to Pelagic Longline Fisheries. *Plos One*, 10(10), p.e0141396. Available at: http://dx.plos.org/10.1371/journal.pone.0141396.

Uozumi, Y. & Nakano, H., 1996. A historical review of Japanese longline fishery and billfish catches in the Atlantic Ocean. *Collective volume of scientific papers. Report of the second ICCAT Billfish Workshop.*, 243, p.233â€“243.

Vaske, T.J. et al., 2011. Diet of the blue marlin (*Makaira nigricans*, Lacepède 1802) (Perciformes: Istiophoridae) of the southwestern equatorial Atlantic Ocean. *Brazilian Journal of Aquatic Science and Technology*, 15, pp.65–70.

Ward, P. & Hindmarsh, S., 2007. An overview of historical changes in the fishing gear and practices of pelagic longliners, with particular reference to Japan's Pacific fleet. *Reviews in Fish Biology and Fisheries*, 17(4), pp.501–516.

Watson, J.W. & Kerstetter, D.W., 2006. Pelagic longline fishing gear: a brief history and review of research efforts to improve selectivity. *Marine Technology Society Journal*, 40(3), pp.6–11.

Webster, D.G., 2006. The Marlin Conundrums : Turning the Tide for By-catch Species. , 79(3), pp.561–575.

Weng, K.C. et al., 2008. Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Marine Ecology Progress Series*, 372(Longhurst 1998), pp.253–264.

Weng, K.C. et al., 2005. Satellite Tagging and Cardiac Physiology Reveal Niche Expansion in Salmon Sharks. *Science*, 310.

Wilson, C.A. et al., 1991. An examination of sexual dimorphism in Atlantic and Pacific blue marlin using body weight, sagittae weight, and age estimates. *Journal of Experimental Marine Biology and Ecology*, 151(2), pp.209–225.

Yang, W. & Gong, Y., 1987. The vertical distribution of tunas and billfishes, and fishing efficiency between Korean regular and deep longlines in the Atlantic Ocean. *Col. Vol. Sci. Pap. ICCAT*, 26(1), pp.184–187. Available at: http://iccat.int/Documents/CVSP/CV026_1987/no_1/CV026010184.pdf [Accessed September 10, 2014].

Zar, J.H., 1999. *Biostatistical Analysis*, Prentice Hall, Upper Saddle River, NJ, USA.