

**UNIVERSIDADE FEDERAL DO RIO GRANDE - FURG
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**ENCALHES DE TARTARUGAS MARINHAS E
USO DO HABITAT POR *CARETTA CARETTA*
NO SUL DO BRASIL**

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Ao meu filho Francisco e à minha amiga Neca Marcovaldi

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RESUMO

A região subtropical do Atlântico Sul Ocidental (ASO) é utilizada pelas tartarugas marinhas como área de alimentação e desenvolvimento. Este estudo teve como objetivo caracterizar os padrões de uso do habitat pela tartaruga-cabeçuda (*Caretta caretta*) nesta região e determinar a magnitude e padrão espaço-temporal dos encalhes de tartarugas marinhas na região costeira do Rio Grande do Sul (RS). O padrão espaço-temporal dos encalhes foi descrito com base em modelos lineares generalizados. A duração do estágio oceânico, o grau de especialização individual no uso dos recursos, as áreas preferenciais de uso e a sobreposição entre as áreas utilizadas pelas tartarugas com as áreas utilizadas pela pesca foram determinadas a partir de análises de isótopos estáveis de carbono e nitrogênio nas linhas de crescimento nos úmeros ($n = 35$) e rastreamento por satélite dos movimentos de indivíduos de *C. caretta* ($n = 17$). Observou-se que as tartarugas-cabeçuda, verde (*Chelonia mydas*) e de-couro (*Dermochelys coriacea*) são as espécies com maior número de encalhes na costa do RS. Além disso, constatou-se um aumento significativo no número de encalhes de *C. caretta* e *C. mydas* nos últimos 10 anos relacionado, provavelmente, com ambos um crescimento no número de fêmeas nas áreas de reprodução e uma maior sobreposição entre as áreas usadas pelas tartarugas e pela atividade pesqueira na região costeira. Observou-se um aumento significativo nos valores de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ com a idade e o tamanho dos indivíduos de *C. caretta*, condizente com a mudança para o habitat nerítico. O recrutamento para o habitat nerítico ocorre a uma idade média estimada em 13 anos, variando entre 8 e 18 anos. Contudo, este recrutamento não é abrupto e pode ser reversível, também corroborado por dados de telemetria. Indivíduos de *C. caretta*, em ambos os estágios de vida – oceânico e nerítico – apresentaram alto grau de especialização individual no uso dos recursos. Com o uso da telemetria por

satélite observou-se extensa permanência de indivíduos de *C. caretta* no RS e uma plasticidade no uso do habitat. Os grandes juvenis utilizam a região oceânica como área de alimentação por longos períodos, mas, principalmente no inverno, quando a temperatura superficial do mar na plataforma esteve abaixo de 20 °C. A combinação de análises de isótopos estáveis e telemetria por satélite revelou que a história de vida de *C. caretta* na região subtropical do ASO é complexa e com diferentes estratégias de forrageio que não estão relacionadas com o tamanho dos indivíduos. O alto percentual de sobreposição entre as áreas de maior uso por *C. caretta* com a pescaria de arrasto de parelha no verão (75%) e com esta pescaria e com o emalhe de fundo no outono (64%) sugerem a necessidade de implementação de medidas de gestão pesqueira que reduzam esta sobreposição e consequentemente a mortalidade de tartarugas marinhas na costa do RS.

Palavras-chave: ecologia trófica, interação com a pesca, isótopos estáveis, mudanças ontogenéticas, tartaruga-cabeçuda, telemetria por satélite

ABSTRACT

The subtropical Southwestern Atlantic Ocean (SWAO) is used as a feeding and development area by sea turtles. The objective of this study was to characterize the habitat use patterns of loggerhead sea turtles (*Caretta caretta*) in this region and to determine the magnitude and spatio-temporal pattern of strandings of this species on the Rio Grande do Sul state (RS) coast. The spatial-temporal pattern of the strandings was described based on generalized linear models. The duration of the oceanic stage, the degree of individual specialization in the use of resources, the areas of preferential use and the overlap between the areas used by turtles and fisheries were determined via stable isotope analyzes of carbon and nitrogen from chronologically ordered growth lines of the turtles humerus ($n = 35$) and satellite tracking of movements of individual turtles ($n = 17$). Loggerhead, green (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*) turtles were the species with the highest number of strandings on the RS coast. In addition, there was a significant increase in the number of stranded *C. caretta* and *C. mydas* in the last 10 years, probably related to both an increase in the number of females in the breeding areas and a greater overlap between the areas used by turtles and fishing activity in the coastal region. A significant increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was observed with age and size of loggerhead sea turtles, consistent with a shift to the neritic habitat. Recruitment to neritic habitat occurred at an estimated mean age of 13 years, ranging from 8 to 18 years. However, this recruitment is not abrupt and can be reversible, as evidenced by telemetry data. Individuals of *C. caretta* presented a high degree of individual specialization in the use of resources in both oceanic and neritic life stages. The use of satellite telemetry allowed to depict an extensive presence of individuals of *C. caretta* in RS and a plasticity in habitat use. Large juveniles use the oceanic region as a feeding area for long periods, but

especially in winter when the sea surface temperature on the platform has dropped below 20°C. The combination of stable isotope analyzes and satellite telemetry revealed that the life history of *C. caretta* in the subtropical SWAO is complex, with different foraging strategies that are not related to the size of individuals. The high percentage of overlapping between areas of greater use by loggerheads with the trawling operations in summer (75%) and with this fishery and the bottom gillnetting in fall (64%) suggest the need to implement fisheries management measures to reduce this overlap and consequently the mortality of loggerhead sea turtles on the RS coast.

Keywords: interaction with fishing, loggerhead sea turtle, ontogenetic changes, satellite telemetry, stable isotopes, trophic ecology

1. INTRODUÇÃO

1.1. Características gerais das tartarugas marinhas

Atualmente existem sete espécies de tartarugas marinhas, divididas em duas famílias: Cheloniidae, com seis representantes, a tartaruga-verde, *Chelonia mydas*, a tartaruga-cabeçuda, *Caretta caretta*, a tartaruga-de-pente, *Eretmochelys imbricata*, a tartaruga-oliva, *Lepidochelys olivacea*, a tartaruga-de-kemp, *L. kempii* e a tartaruga-australiana, *Natator depressus*, e Dermochelyidae com apenas uma espécie, a tartaruga-de-couro, *Dermochelys coriacea* (Pritchard, 1997). Com exceção de *L. kempii*, endêmica da costa leste dos Estados Unidos e Golfo do México e *N. depressus*, com ocorrência apenas no sudoeste do Pacífico e sudoeste do Índico, incluindo a costa da Austrália, as demais espécies apresentam distribuição circunglobal (Márquez, 1990). Existe uma grande variação na história de vida entre e dentro das sete espécies. As tartarugas marinhas possuem um ciclo de vida complexo, marcado por mudanças ontogenéticas nos padrões de uso do habitat e na dieta, e migrações de longa distância. A maturação sexual é tardia e extremamente variável entre as espécies, populações e até mesmo entre indivíduos de uma mesma população, variando, por exemplo de 15 a 50 anos em *C. mydas*, e de 12 a 22 anos em *D. coriacea* (Avens & Snover, 2013). O intervalo entre desovas é variável, geralmente de um a cinco anos, de acordo com a aquisição dos recursos energéticos para a ovulação e formação dos embriões (Miller, 1997). Apresentam elevada filopatria e fidelidade, pois, ao atingirem a maturidade sexual, retornam para desovar onde nasceram, geralmente em praias tropicais (Carr, 1975), e fidelidade aos locais de desova, pois, a cada temporada reprodutiva retornam às mesmas áreas (Miller, 1997).

Imediatamente após a eclosão, que ocorre geralmente à noite, as tartarugas marinhas rumam em direção ao mar aberto, iniciando a fase de desenvolvimento oceânico. Nesta

fase, que pode durar vários anos, conhecida como “anos perdidos”, as tartarugas deslocam-se, geralmente, acompanhando o sentido das correntes e giros oceânicos. Quando se tornam grandes juvenis, recrutam para áreas de desenvolvimento nerítico em regiões tropicais e subtropicais. Próximo da maturidade sexual, migram para habitats de forrageamento de adultos (Musick & Limpus, 1997; Fig. 1).

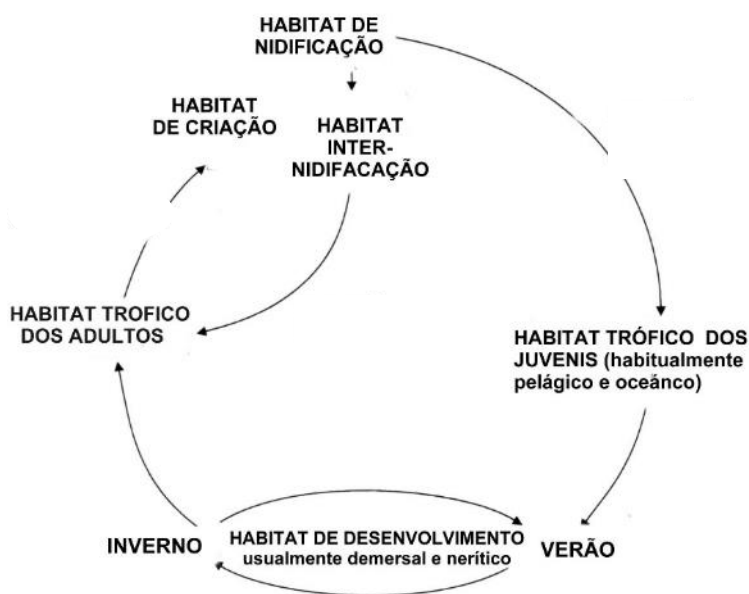


Figura 1. Modelo ontogenético dos habitats utilizados pelas tartarugas marinhas. Extraído e adaptado de Musick & Limpus (1997).

Bolten (2003) propõe três padrões para a história de vida do estágio de desenvolvimento juvenil: Tipo 1: estágio de desenvolvimento completo na zona nerítica, observado em *N. depressus*; Tipo 2: estágio de desenvolvimento inicial, com juvenis menores na zona oceânica e posterior desenvolvimento de juvenis maiores na zona nerítica, padrão apresentado por *C. mydas*, *C. caretta*, *E. imbricata* e *L. kempii*; Tipo 3: desenvolvimento completo na zona oceânica, modelo proposto para *D. coriacea*. Em

relação a *L. olivacea*, pouco se sabe sobre a ecologia dos juvenis e sugere-se que esta espécie apresenta estágios de desenvolvimento dos Tipos 2 e 3, dependendo da população (Bolten, 2003).

Para *C. mydas*, *C. caretta* e *E. imbricata* as mudanças ontogenéticas no habitat também são marcadas por mudanças ontogenéticas na dieta. No Atlântico Norte, por exemplo, antes de recrutarem para zonas neríticas, indivíduos destas espécies são onívoros ou carnívoros alimentando-se oportunisticamente de presas pelágicas (Bjorndal, 1997; Bolten, 2003; Boulon 1994). Após o recrutamento para o ambiente nerítico, mudam para uma alimentação bentônica, na qual *C. mydas* torna-se herbívora, alimentando-se principalmente de fanerógamas marinhas (Bjorndal 1997); *C. caretta* alimentando-se de crustáceos e moluscos (Bolten 2003); e *E. imbricata* de esponjas, em recifes de coral (Meylan, 1988).

Todas as espécies de tartarugas marinhas, com exceção de *N. depressus* que consta como dados deficientes, estão listadas como ameaçadas de extinção na lista vermelha de espécies ameaçadas da União Internacional para a Conservação da Natureza – IUCN, na qual *C. caretta*, *L. olivacea* e *D. coriacea* foram classificadas como vulneráveis; *C. mydas* como em perigo; e, *E. imbricata* e *L. kempii* como em perigo crítico (IUCN, 2016).

Dentre as principais ameaças atuais destacam-se a alteração e a perda dos habitats de desova, a poluição por óleo e a ingestão e o emaranhamento em materiais de origem antropogênica, as mudanças climáticas e a captura incidental na pesca (Lutcavage *et al.*, 1997; Hamann *et al.*, 2010). A captura incidental na pesca, tanto artesanal quanto industrial, é considerada a maior ameaça à sobrevivência das populações de tartarugas marinhas em nível global (Hall *et al.*, 2000; Wallace *et al.*, 2013).

Por passarem a maior parte da vida no mar, o que dificulta a coleta de dados e monitoramento de longo prazo, a maior parte dos estudos com tartarugas marinhas são realizados com fêmeas em áreas de desova. Sendo assim, existem ainda várias lacunas referentes a aspectos da ecologia das tartarugas marinhas em áreas de alimentação (Hamann *et al.*, 2010). Neste sentido, ferramentas que possibilitem compreender os padrões de uso do habitat e dieta das tartarugas, como a telemetria por satélite e marcadores bioquímicos são extremamente úteis para o avanço no conhecimento sobre aspectos da ecologia espacial e trófica, relevantes para a conservação destes animais. A identificação de áreas de ocupação e sítios preferenciais de forrageio podem auxiliar na elaboração de estratégias de conservação que reduzam os conflitos com as atividades impactantes, como a pesca.

1.2. Ferramentas para o estudo da ecologia de tartarugas marinhas em áreas de alimentação

O uso de novas ferramentas, como a telemetria por satélite e a análise de isótopos estáveis em estruturas ósseas que demarcam o crescimento, de forma cronologicamente ordenada, confirmaram, em alguns casos, o conhecimento inicial sobre a vida das tartarugas marinhas, e, em outros, redefiniram paradigmas biológicos (Jones & Seminoff, 2013). A partir da obtenção destas novas informações, observou-se que as estratégias ecológicas de algumas espécies são mais diversas do que se considerava até recentemente. Como por exemplo para as espécies *C. mydas* e *C. caretta* postulava-se que estas seguiam um padrão de desenvolvimento oceânico-nerítico (Bjorndal, 1997; Bolten, 2003), e agora reconhece-se que indivíduos de algumas populações são habitantes de alto-mar, mesmo quando adultos (Hatase *et al.*, 2002, 2006; McClellan *et al.*, 2010).

1.2.1. Telemetria por satélite

Os primeiros estudos utilizando rastreamento por satélite de tartarugas marinhas iniciaram no final da década de 70, com a publicação do primeiro trabalho em 1982, no qual as áreas utilizadas por oito indivíduos de *C. caretta*, após o período reprodutivo, foram identificadas na Geórgia, Estados Unidos (Stoneburner, 1982). Com esta tecnologia é possível acompanhar as tartarugas em tempo real e reconstruir as rotas utilizadas e suas áreas de uso preferencial (ver Godley *et al.*, 2008 para uma revisão).

O sistema usa transmissores denominados PTTs (*Platform Terminal Transmitters*) que enviam periodicamente, em intervalos de aproximadamente 60 segundos, um sinal curto de rádio (tipicamente 360–920 ms; 401.650 mHz), chamado *uplink*, para satélites em órbita-polar do NOAA. A localização do transmissor é então calculada a partir de uma mudança Doppler na frequência das transmissões recebidas por um satélite à medida que se aproxima e, em seguida, se afasta do transmissor numa única passagem (Hays *et al.*, 2001).

Desde o primeiro trabalho em 1982 até o presente, o rastreamento por satélite vem sendo amplamente utilizado para demonstrar migrações de longa distância (e.g. Benson *et al.*, 2007), fidelidade às áreas de forrageio ao longo de múltiplos anos (e.g. Broderick *et al.*, 2007; Hawkes *et al.*, 2011), sobreposição entre as áreas utilizadas pelas tartarugas com as áreas de pesca (e.g. Mangel *et al.*, 2011; Fossette *et al.*, 2014). Estas informações aumentaram de forma marcante o conhecimento sobre a ecologia espacial e quebraram alguns paradigmas relacionados aos modelos de história de vida das tartarugas marinhas (e.g. Hatase *et al.*, 2002; James *et al.*, 2005; Hawkes *et al.*, 2007; McClellan *et al.*, 2010).

1.2.2. Esqueletocronologia

Esqueletocronologia é o estudo de marcas de crescimento nos ossos de anfíbios e répteis (Castanet & Smirina, 1990). O princípio básico da esqueletocronologia é que o crescimento ósseo é cíclico, tem periodicidade e pode ser observado (Castanet et al. 1993). Com tartarugas marinhas, esta técnica foi aplicada pela primeira vez por Zug et al. (1986) em tartarugas-cabeçuda. Estes autores analisaram elementos esqueléticos do crânio e dos membros anteriores das tartarugas marinhas e determinaram que o úmero era mais adequado para estudos de esqueletocronologia, devido à capacidade de retenção de um número maior de marcas de crescimento periosteal em comparação com os outros ossos. A deposição anual destas marcas de crescimento foi validada primeiramente em *C. caretta*, através da injeção do antibiótico tetraciclina (Klinger & Musick, 1992; Coles et al., 2001) e posteriormente a partir de técnicas de validação indiretas em *L. kempii* (Snover & Hohn, 2004) e em *C. mydas* (Goshe et al., 2010; Snover et al., 2011).

Através da esqueletocronologia, a estimativa da idade e a duração do estágio de vida das tartarugas marinhas são determinadas pela contagem das marcas de crescimento (Snover et al., 2007; Avens & Snover, 2013). Uma marca de crescimento esquelético, correspondente a um ano de crescimento em tartarugas marinhas é composta por uma linha fina e manchada de crescimento retido (*Line of Arrested Growth* - LAG) e uma zona mais larga e mais clara, representando a região de crescimento ativo (Castanet et al., 1993; Snover & Hohn, 2004). Entretanto, em juvenis maiores e adultos, as marcas iniciais de crescimento são inteiramente substituídas por remodelação e crescimento endosteal, em um processo chamado reabsorção (Zug et al., 1986). Para resolver este problema, diversos fatores de correção vêm sendo desenvolvidos para estimar o número de LAGs perdidas em cada úmero (Parham & Zug, 1997; Avens et al., 2012; Petit et al., 2012). Portanto,

a estimativa de idade é obtida contando o número de LAGs observados em indivíduos que mantiveram a primeira marca de crescimento (*annulus*), que parece mais próxima ao centro do osso como uma linha difusa (Castanet *et al.* 1993) ou adicionando a estimativa do número de LAGs perdidas ao número de LAGs observadas (Avens *et al.*, 2012).

Nas últimas duas décadas, a técnica de esqueletocronologia vem sendo amplamente utilizada em tartarugas marinhas, para estimar idade, idade de maturação sexual, taxas de crescimento e duração de estágios de vida (ver Avens & Snover, 2013 para uma revisão).

1.2.3. Isótopos estáveis

Isótopos são átomos do mesmo elemento químico que possuem o mesmo número de prótons e elétrons, mas diferem no número de nêutrons. Com isso sua massa difere. Os isótopos estáveis compreendem menos de 10% dos isótopos conhecidos (Fry, 2006) e poucos são usados em estudos de ecologia, principalmente carbono, nitrogênio, oxigênio, hidrogênio e enxofre (Fry, 2006).

A razão de dois isótopos estáveis, um pesado e um leve, por exemplo ($^{15}\text{N}/^{14}\text{N}$) é quantificada nas amostras em relação a um padrão internacionalmente aceito e expressa em partes por mil (‰) com a notação δ (Michener & Lajtha, 2007). Os materiais de referência padrão mais utilizados são o *PeeDee Bee limestone* para carbono e o ar atmosférico para nitrogênio (Peterson & Fry, 1987). Aumentos nos valores de δ denotam acréscimo na quantidade do isótopo pesado em relação ao padrão e estas amostras são então chamadas de enriquecidas. Os isótopos leves ocorrem naturalmente em maior abundância do que os pesados, principalmente porque os isótopos pesados reagem mais devagar por conta da energia adicional necessária para quebrar as moléculas (Fry, 2006). Sendo assim, os isótopos mais pesados são retidos e utilizados na formação dos diferentes

tecidos, enquanto os isótopos mais leves são preferencialmente eliminados em atividades como excreção e respiração (Peterson & Fry, 1987).

O uso de isótopos estáveis no campo da ecologia é mais recente e tem se mostrado uma ferramenta apropriada para investigar, por exemplo redes tróficas (Mancini & Bugoni, 2014), dieta (Newsome *et al.*, 2009), uso do habitat (Rubenstein & Hobson, 2004) e migrações (Hobson, 1999).

Os valores de isótopos estáveis de um consumidor são diretamente influenciados pela dieta assimilada. O processo de fracionamento ou discriminação nas reações metabólicas faz com que os consumidores apresentem valores isotópicos sistematicamente diferentes em relação às suas dietas. Desta forma, os tecidos dos consumidores são frequentemente enriquecidos em ^{15}N e ^{13}C em comparação com suas dietas, permitindo, por exemplo, o cálculo do nível trófico (DeNiro & Epstein, 1977, 1981; Minagawa & Wada, 1984; Post, 2002). A discriminação isotópica é o processo pelo qual um isótopo é discriminado em relação ao outro, ou é absorvido preferencialmente de modo que o produto possui um valor de δ diferente da fonte. Tipicamente, os fatores de discriminação de carbono são menores, em geral 1.1‰ (DeNiro & Epstein, 1977) e são utilizados para diferenciar recursos alimentares de distintos habitats (oceânico versus nerítico, pelágico versus bentônico), enquanto que os fatores de discriminação de nitrogênio são maiores, 3–5‰, e têm sido tipicamente usados para estimar a posição trófica, particularmente quando os valores de base são conhecidos (DeNiro & Epstein, 1981; Peterson & Fry, 1987; Post, 2002). Todavia, os fatores de discriminação podem variar em função da forma de excreção de resíduos nitrogenados, dos tecidos, da qualidade e composição isotópica da dieta (Vander Zanden & Rasmussen, 2001; Vanderklift & Ponsard, 2003; Caut *et al.*, 2009).

O tempo que o valor isotópico das fontes (dieta) demora para refletir nos tecidos dos consumidores é chamado de taxa de reposição ou *turnover* (Newsome *et al.*, 2010). Diferentes tecidos apresentam diferentes taxas de renovação. Pele e músculo são, por exemplo, tecidos de renovação rápida e integram valores da dieta das últimas semanas ou de alguns meses (Seminoff *et al.*, 2007; Reich *et al.*, 2008). Por outro lado, tecidos considerados metabolicamente inertes, como por exemplo, vibrissas (Newsome *et al.*, 2009), penas (Cherel *et al.*, 2008), dentes (Botta *et al.*, 2012), escudos da carapaça, no caso das tartarugas marinhas (Reich *et al.*, 2007) integram informação de longo prazo e no caso do úmero, podem fornecer o histórico de uso do habitat e da dieta de toda a vida do animal (Avens *et al.*, 2013; Ramirez *et al.*, 2015).

Nos estudos sobre a ecologia de tartarugas marinhas, os isótopos estáveis têm sido utilizados para determinar migração, uso do habitat e dieta (Hatase *et al.*, 2002; Reich *et al.*, 2007; Seminoff *et al.*, 2009). Recentemente, isótopos estáveis foram aliados à esqueletocronologia para reconstruir o histórico de forrageio dos indivíduos (Avens *et al.*, 2013; Ramirez *et al.*, 2015, Turner Tomaszewicz *et al.*, 2016b). A combinação destas duas técnicas foi aplicada no Capítulo 2 desta tese.

1.3. Tartarugas marinhas no Atlântico Sul Ocidental

Cinco espécies de tartarugas marinhas utilizam a região do Atlântico Sul Ocidental como local de reprodução e alimentação. As áreas de reprodução estão restritas a regiões tropicais, localizadas principalmente do norte do estado do Rio de Janeiro ao Rio Grande do Norte e também nas ilhas oceânicas de Trindade, Atol das Rocas e Fernando de Noronha (Marcovaldi & Marcovaldi, 1999; Fig. 2). Durante a última década, observaram-se aumentos consideráveis no número de fêmeas nas áreas de desova de *C. caretta*, *L.*

olivacea e *E. imbricata* (Marcovaldi & Chaloupka, 2007; Marcovaldi *et al.*, 2007; Silva *et al.*, 2007), enquanto *C. mydas* e *D. coriacea* mantiveram-se estáveis (Thomé *et al.*, 2007; Almeida *et al.*, 2011a).

Estudos com telemetria satelital permitiram identificar que as principais áreas de alimentação das fêmeas adultas de *C. caretta*, que desovam no Brasil estão localizadas no litoral do Ceará (Marcovaldi *et al.*, 2010). Para *E. imbricata* as principais áreas estão localizadas no Rio Grande do Norte, Ceará e Pará (Marcovaldi *et al.*, 2012). Para *L. olivacea* foram identificadas como áreas de forrageamento, o litoral norte do Espírito Santo, Alagoas, Pernambuco, Rio Grande do Norte e Pará, além de áreas oceânicas no Oceano Atlântico tropical (Silva *et al.*, 2011). Com relação a *D. coriacea* as áreas de alimentação utilizadas são mais amplas, distribuindo-se do Espírito Santo ao norte da Argentina (Almeida *et al.*, 2011b). Todavia, pouco se sabe sobre os padrões de forrageio dos indivíduos imaturos, que representam a maior parcela das populações de tartarugas marinhas.

As águas costeiras do sul do Brasil, Uruguai e Argentina proporcionam um importante habitat de alimentação e desenvolvimento, particularmente para juvenis de *C. mydas* e juvenis e adultos de *C. caretta* e *D. coriacea* (Bugoni *et al.*, 2003; López-Mendilaharsu *et al.*, 2009; Almeida *et al.*, 2011a; González Carman *et al.*, 2012, 2016). Análises do DNA mitocondrial revelaram que estas áreas de alimentação são compostas por estoques mistos de *C. mydas*, provenientes principalmente de Ascensão, Ilha de Aves/Suriname e Trindade (Proietti *et al.*, 2012; Prosdocimi *et al.*, 2012); de *D. coriacea*, oriundas principalmente da África (Vargas *et al.*, 2008; Prosdocimi *et al.*, 2014; Vargas dados não publicados) e *E. imbricata* (Proietti *et al.*, 2014). No entanto, em relação a *C. caretta*, a análise do DNA mitocondrial de espécimes encalhados nas praias ou capturados em

pescarias costeiras revelou que a maioria dos indivíduos pertence às áreas de desova do Brasil (Caraccio *et al.*, 2007; Araújo, 2012; Prosdocimi *et al.*, 2015). Porém, no ambiente oceânico também é observada a presença de estoques mistos de *C. caretta*, com indivíduos de colônias brasileiras e da costa oeste africana (Shamblin *et al.*, 2014).

As espécies *L. olivacea* e *E. imbricata*, por apresentarem distribuição mais restrita a regiões tropicais, são registradas com menor frequência ao sul da latitude 20°S (Bugoni *et al.*, 2003; González Carman *et al.*, 2011; Vélez-Rubio *et al.*, 2013).

Semelhante a outras partes do mundo, as tartarugas marinhas que utilizam as regiões costeira e oceânica do sul do Brasil como áreas de alimentação são afetadas por diversas ameaças antrópicas, principalmente pela ingestão de resíduos sólidos antropogênicos (Bugoni *et al.*, 2001; Tourinho *et al.*, 2011) e pela captura incidental na pesca (Domingo *et al.*, 2006; Sales *et al.*, 2008). Taxas elevadas de capturas incidentais de *D. coriacea* e *C. caretta* foram documentadas na pescaria com espinhel pelágico (Pons *et al.*, 2010), e nas redes de emalhar de deriva e de espera (Fiedler *et al.*, 2012; Ramos & Vasconcellos, 2013). No entanto, pouco se sabe sobre a mortalidade das tartarugas marinhas nas pescarias de arrasto (Monteiro *et al.*, 2013), tampouco há dados suficientes sobre os padrões espaciais e temporais de captura incidental nessas pescarias. Contudo, encalhes de indivíduos de *C. caretta*, *C. mydas* e *D. coriacea* são comuns na região costeira do Rio Grande do Sul, principalmente nos meses de primavera e verão (Monteiro *et al.*, 2006; Silva *et al.*, 2011), estando estes encalhes provavelmente relacionados à captura incidental na pesca.

A tartaruga-cabeçuda, *C. caretta*, foco de dois dos três capítulos desta tese, é a espécie mais abundante no Brasil, com desovas regulares da Bahia ao Rio de Janeiro (Marcovaldi & Chaloupka, 2007). No entanto, informações sobre as áreas de alimentação desta espécie

no Brasil são escassas. Marcovaldi *et al.* (2010) sugerem o litoral do Ceará como área de alimentação para fêmeas que desovam na Bahia. Ocorrências de indivíduos em diferentes estágios de vida são registradas na costa de diversos estados do Brasil, em áreas costeiras ou oceânicas (Santos *et al.*, 2011). Entretanto, encalhes de *C. caretta* são raros, com exceção do sul do Brasil (Marcovaldi & Chaloupka, 2007), sugerindo que esta região provavelmente é uma área importante de alimentação desta espécie. Análises do conteúdo gastrointestinal revelou que a dieta de juvenis oceânicos é composta principalmente por salpas, enquanto juvenis neríticos alimentam-se predominantemente de crustáceos, e também de moluscos e peixes (Barros, 2010). No entanto, ainda é desconhecido o momento do recrutamento ao ambiente nerítico. O rastreamento por satélite de indivíduos juvenis capturados na pescaria de espinhel pelágico na região oceânica do Uruguai e do sul do Brasil indicaram o uso de grandes áreas oceânicas e também o uso da região nerítica por parte destes indivíduos (Barceló *et al.*, 2013). Por outro lado, o rastreamento de indivíduos juvenis, capturados na Argentina revelou o uso quase exclusivo da região costeira (González Carman *et al.*, 2016).

1.4. Objetivos e hipóteses

Objetivo geral

Caracterizar os padrões de uso do habitat por *C. caretta* no Oceano Atlântico Sul Ocidental e determinar a magnitude e padrão espaço-temporal dos encalhes de tartarugas marinhas na região costeira do Rio Grande do Sul.

Objetivos específicos

- 1) Determinar a distribuição espacial e temporal dos encalhes de tartarugas marinhas na região costeira do Rio Grande do Sul;
- 2) Determinar a idade e tamanho de recrutamento ao ambiente nerítico dos indivíduos de *C. caretta* no Rio Grande do Sul;
- 3) Avaliar a variabilidade individual no uso do habitat e nos hábitos alimentares nos indivíduos de *C. caretta*;
- 4) Identificar as áreas preferenciais de uso pelos indivíduos de *C. caretta* na plataforma continental do Rio Grande do Sul, e
- 5) Avaliar o grau de sobreposição espacial e temporal entre as áreas de maior uso pelos indivíduos de *C. caretta* e as áreas de atuação da pesca.

De acordo com o exposto anteriormente e com base nos objetivos apresentados, este estudo visou testar as seguintes hipóteses:

- i)** A sazonalidade dos encalhes está relacionada com a dinâmica das atividades pesqueiras;
- ii)** Os indivíduos de *C. caretta* são especializados quanto ao uso do habitat e aos hábitos alimentares;
- iii)** Os recrutas de *C. caretta* utilizam exclusivamente a plataforma continental como área de alimentação demersal, e
- iv)** Nos períodos com menores temperaturas da água (entre o fim do outono e o início da primavera) estes recrutas deslocam-se para regiões mais tropicais.

2. MATERIAL E MÉTODOS

2.1. Coleta dos dados

Os dados utilizados no Capítulo 1 foram obtidos a partir de saídas mensais de monitoramento de praia, de janeiro de 1995 a dezembro de 2014, realizadas pela equipe do Núcleo de Educação e Monitoramento Ambiental – NEMA (de 1995 a 2014) e do Laboratório de Ecologia e Conservação da Megafauna Marinha – EcoMega/FURG (de 2009 a 2014). Nestas saídas, foram percorridos, em torno de 355 km de costa, desde a Lagoa do Peixe (31°21'S; 051°02'W) até o Chuí (33°44'S; 053°22'W). A costa foi dividida em duas áreas: a área sul, que compreende 220 km, desde a desembocadura do estuário da Lagoa dos Patos até o Chuí, e a área norte, com 135 km, da Barra da Lagoa do Peixe até o Chuí (Fig. 2). As saídas de campo foram realizadas com um veículo 4 × 4 a uma velocidade de aproximadamente 30 km.h⁻¹, com dois a quatro observadores buscando visualmente pelas tartarugas encalhadas, desde a região intermareal até a base das dunas.

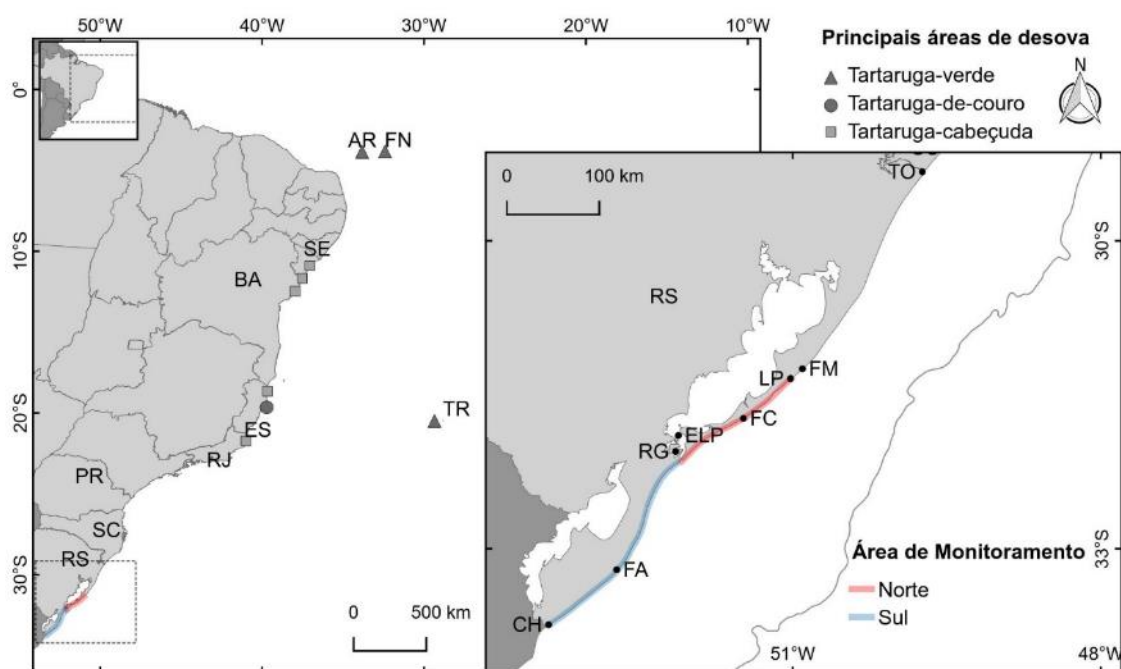


Figura 2. Principais áreas de desova da tartarugas-cabeçuda (*C. caretta*), tartaruga-verde (*C. mydas*) e tartaruga-de-couro (*D. coriacea*) no Brasil. AR = Atol das Rocas, FN = Fernando de Noronha e TR = Trindade. Mapa em destaque: Área de estudo ao longo da costa do Rio Grande do Sul com a indicação das áreas de monitoramento norte, entre a Lagoa do Peixe (LP) e a Barra de Rio Grande (RG) e a área de monitoramento sul, da Barra de Rio Grande até o Chui (CH). FM = Farol de Mostardas, FC = Farol Conceição, ELP = Estuário da Lagoa dos Patos e FA = Farol do Albardão.

Para cada tartaruga encalhada, a identificação da espécie foi realizada de acordo com Pritchard & Mortimer (1999) e anotadas a data, latitude, longitude e comprimento curvilíneo da carapaça (CCC). Também foram registrados sinais de interação com atividades pesqueiras, como cabos, restos de redes ou anzóis presos às tartarugas.

As amostras de úmeros de tartarugas-cabeçuda utilizadas no Capítulo 2 foram obtidas de espécimes encontrados mortos em saídas de monitoramento de praia ($n = 19$), na mesma região de estudo do Capítulo 1, e também capturadas incidentalmente na pescaria de espinhel pelágico no sul do Brasil ($n = 16$). Todas estas amostras foram coletadas nos anos de 2008 e 2009.

Para as análises do Capítulo 3, transmissores de satélite foram instalados em 17 tartarugas-cabeçuda (*C. caretta*) entre 2013 e 2015, das quais 15 foram capturadas incidentalmente na pescaria de arrasto de parelha na plataforma continental do Rio Grande do Sul e duas foram provenientes de encalhes na costa do Rio Grande do Sul. Utilizaram-se os modelos de transmissores PTT (*platform terminal transmitters*) SPOT 5

($n = 8$ tartarugas) e SPLASH-10 ($n = 9$ tartarugas), ambos da *Wildlife Computers*, com dois diferentes ciclos de programação: (1) 24 h ligado, e (2) 24 h ligado e 24 h desligado.

Os transmissores foram aderidos no segundo escudo vertebral central (Fig. 3), pois essa é a região da carapaça que fica mais exposta quando a tartaruga sobe à superfície para respirar (Polovina *et al.* 2000) momento em que ocorre a comunicação com o satélite em órbita. Antes da fixação do transmissor foram removidos os epibiontes, e a carapaça das tartarugas foi lixada levemente, limpa com álcool e seca. Os transmissores foram aderidos utilizando pedaços de fibra de vidro e resina, de acordo com Balazs *et al.* (1996).



Figura 3. Tartaruga-cabeçuda (*C. caretta*) com transmissor de satélite.

A localização das tartarugas foi obtida por meio do sistema ARGOS que fornece dados sobre latitude, longitude, data, horário e precisão de cada localização em classes de localização – LC, onde LC 3 < 150 m; LC 2 = entre 150 e 350 m; LC 1 = entre 350 e 1000 m; LC 0 > 1000 m, e A, B e Z sem cálculo de precisão (ARGOS, 2011).

Para os Capítulos 1 e 3 foram utilizadas informações de lances de pesca. Os dados das pescarias foram obtidos a partir de cadernos de bordo preenchidos pelos mestres das embarcações de emalhe de fundo, no período de 1997 a 2009 (Capítulo 1 e 3); através de cadernos de bordo na pescaria de arrasto de parelha, de 2013 a 2015 (Capítulo 1); e de embarques de observadores científicos e cadernos de bordo na pescaria de arrasto de parelha, entre 2011 e 2016 (Capítulo 3) e na pescaria de espinhel pelágico, entre 2004 e 2015. Estes dados foram coletados como parte de programas de monitoramento das pescarias e da captura incidental de mamíferos e tartarugas marinhas conduzidos pela equipe do Laboratório de Ecologia e Conservação da Megafauna Marinha (EcoMega/FURG) para as pescarias de emalhe de fundo, pelo Núcleo de Educação e Monitoramento Ambiental (NEMA) para as pescarias de arrasto de parelha e pelas equipes do NEMA e do Projeto TAMAR para a pescaria de espinhel pelágico.

As medidas de temperatura superficial do mar foram obtidas dos dados processados do MODIS *Acqua* (L3), disponível no formato NetCDF, na Plataforma *Ocean Color* da NASA (<https://oceancolor.gsfc.nasa.gov/cms/data/seawifs>).

Nos três capítulos, a medida do comprimento curvilíneo da carapaça (CCC) das tartarugas marinhas foi tomada de acordo com Bolten (1999).

2.2. Processamento das amostras: esqueletocronologia e isótopos estáveis

Para as análises de isótopos estáveis, foi feito um corte transversal em cada um dos úmeros utilizados num estudo prévio de estimativas de idade realizado por Petit et al. (2012). O corte de cada úmero, com cerca de 1 mm de espessura, foi feito adjacente ao corte previamente realizado por Petit et al. (2012) para esqueletocronologia. Os cortes foram realizados com o auxílio de uma serra metalográfica de baixa rotação e

posteriormente colados em lâminas histológicas. As amostras foram coletadas seguindo a metodologia proposta por Turner Tomaszewicz *et al.* (2016a) utilizando um sistema de micro-amostragem. Este sistema é composto por uma broca de 10000 rpm (NSK Volvere Vmax), com uma ponteira de 0,10 mm, conectados a um microscópio (Olympus SZX10) ajustado com uma câmera (Olympus SpotFlex U-CMAD-2) para gerar uma imagem em tempo real do corte do úmero em um monitor de computador acoplado a estes equipamentos. O traçado para a coleta de cada amostra e a profundidade foram ajustados com o auxílio de um software (Carpenter Microsystems CM-2, versão 3.0.6) e a imagem do corte processado para esqueletocronologia foi usada como guia para a identificação das linhas de crescimento (Fig. 4).

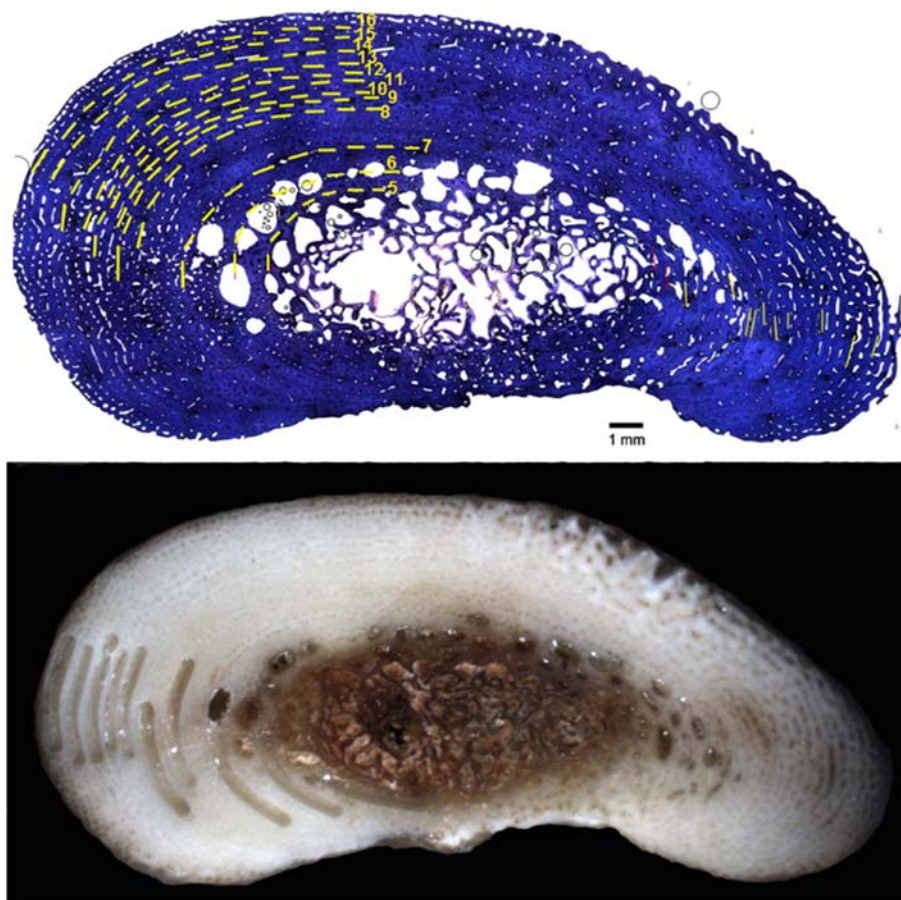


Figura 4. Imagem do corte processado histologicamente para determinação de idade, com a identificação de cada linha de crescimento retido (*line of arrested growth* – LAG) em amarelo e a idade associada a cada LAG (acima). Corte sem processamento amostrado para análises de isótopos estáveis, com a marcação dos locais de coleta (abaixo).

Para cada linha de crescimento ósseo, foi coletado aproximadamente 1,0 a 1,5 mg de pó, colocados em cápsulas de estanho e enviados para análise em um espectrômetro de massa de razão isotópica de fluxo contínuo, no Laboratório de Geoquímica de isótopos estáveis da Universidade da Florida (EUA).

Os valores de isótopos estáveis são expressos com a notação δ , em partes por mil (‰), em relação aos padrões internacionais (VPDP - *Vienna Pee Dee Belemnite limestone*) para carbono e N₂ atmosférico para o nitrogênio, de acordo com a seguinte equação (Bond & Hobson, 2012):

$$\delta X (\text{‰}) = (R_{\text{amostra}}/R_{\text{padrão}}) - 1 \quad (\text{eq. 1})$$

onde X é o valor de $\delta^{15}\text{N}$ ou $\delta^{13}\text{C}$, e R é a razão correspondente de $^{15}\text{N}/^{14}\text{N}$ ou $^{13}\text{C}/^{12}\text{C}$ (Peterson & Fry, 1987).

2.3. Análise dos dados

Modelos lineares generalizados (GLMs) foram utilizados no Capítulo 1 para modelar o número de tartarugas encalhadas na praia (Y) como uma função de nove variáveis explanatórias: mês (janeiro a dezembro), ano (1995 a 2014), área (ao sul e ao norte do estuário da Lagoa dos Patos), esforço (distância monitorada em cada saída, em km), SOI (Índice de Oscilação Sul; obtido da página

(<https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>) e quatro variáveis relacionadas à direção e velocidade do vento. Foram desenvolvidos modelos separados para as espécies *C. caretta*, *C. mydas* e *D. coriacea*. A distância monitorada em cada saída (km) foi utilizada como um fator de padronização (*offset*) do número de tartarugas encalhadas. Foram propostos 35 modelos alternativos e o modelo com melhor ajuste aos dados foi escolhido com base no menor valor do Critério de Informação de Akaike de segunda ordem - AICc (Burnham & Anderson, 2002).

O teste não-paramétrico de Wilcoxon's (Zar, 1999) foi utilizado (Capítulo 1) para detectar diferenças entre o tamanho dos indivíduos (CCC) de *C. caretta*, encalhados na praia, entre 2001 e 2007 ($n = 868$) e dos indivíduos capturados incidentalmente em 72 cruzeiros da pescaria de espinhel pelágico, no sul do Brasil, no mesmo período ($n = 894$; Monteiro, 2008). Uma análise semelhante foi realizada para comparar as diferenças no CCC das tartarugas-cabeçuda encalhadas, no período de 2012 a 2014 ($n = 492$) e das tartarugas incidentalmente capturadas em 13 cruzeiros da pescaria de arrasto de parelha ($n = 69$) (NEMA, dados não publicados).

No Capítulo 1, mapas de densidade de kernel foram produzidos para visualizar as diferenças sazonais e espaciais no padrão de encalhes das tartarugas marinhas e do esforço das pescarias de arrasto de parelha e emalhe de fundo. Os mapas foram produzidos no *software Quantum GIS*, e foi utilizada uma largura de banda (raio de influência) menor para os dados de encalhes de tartarugas (9 km), devido a menor extensão da área de abrangência dos dados, e de 28 km para os dados de pesca.

No Capítulo 2, utilizou-se o diâmetro das LAGs (*lines of arrested growth* –linhas de crescimento ósseo) do úmero de cada tartaruga para calcular o CCC correspondente a cada idade, a partir da metodologia do retro-cálculo proposta por Snover et al. (2007),

com base na Hipótese da Proporção Corporal, e utilizando o modelo de melhor ajuste obtido por Petit *et al.*, (2012). Posteriormente, estes tamanhos retro-calculados foram utilizados para determinar o tamanho (CCC) dos indivíduos na transição do ambiente oceânico para o nerítico.

Análises de agrupamento foram utilizadas, no Capítulo 2, para identificar o número de grupos que melhor ajustaram os valores de $\delta^{15}\text{N}$ e $\delta^{13}\text{C}$, juntos e em separado, obtidos das amostras das LAGs. Estas análises foram realizadas através da função *pam* no pacote *cluster* no R (Maechler *et al.*, 2015; R Core Team, 2015).

Modelos generalizados aditivos mistos (GAMMs) foram aplicados para avaliar a influência das covariáveis idade e tamanho (CCC) nos valores de $\delta^{15}\text{N}$ e $\delta^{13}\text{C}$. Os indivíduos foram utilizados como efeito aleatório e os modelos foram ajustados usando a distribuição Gaussiana, com a função de ligação identidade e as curvas de suavização (*thin plate regression splines*) como funções de suavização (Wood, 2006; Avens *et al.*, 2012). Os modelos foram implementados usando os pacotes *mgcv* e *nlme* no R (Wood, 2006; R Core Team, 2015).

O momento da mudança ontogenética foi identificado como a primeira linha de crescimento onde o valor de $\delta^{15}\text{N}$ foi superior ao valor limite de 11,20‰. Este valor é conservativo e foi baseado em ambos, no valor médio de $\delta^{15}\text{N}$ de 4,95‰ das presas pelágicas (salpas) de *C. caretta*, na região oceânica do sul do Brasil (EcoMega/FURG, dados não publicados) e nos valores da separação dos grupos em oceânico e nerítico, provenientes da análise de cluster. Nesta análise o limite superior do agrupamento oceânico foi 11,14‰ e o limite inferior do agrupamento nerítico foi de 11,27‰. Uma variação (Δ) no valor de $\delta^{15}\text{N}$ de +3‰ e superior ao limite de 11,20‰ em um ano foi definido como indicativo de um recrutamento discreto, enquanto um valor de $\Delta\delta^{15}\text{N} + 3\text{‰}$

levando mais de um ano para ocorrer, representou um recrutamento gradual (*sensu* Ramirez *et al.*, 2015).

Utilizou-se a variância nos valores de $\delta^{15}\text{N}$ e $\delta^{13}\text{C}$ para determinar o grau de especialização individual e consistência temporal no uso dos recursos pelos indivíduos de *C. caretta*. O termo “uso dos recursos” foi utilizado para refletir a integração da informação referente ao uso do habitat e à dieta, uma vez que é difícil, utilizando dados de isótopos estáveis, obter uma distinção entre estes dois componentes (Vander Zanden *et al.*, 2013). Para as tartarugas neríticas, foram utilizadas somente as LAGs indicativas da assinatura isotópica do ambiente nerítico. Conforme proposto por Roughgarden (1972), o componente de variação dentro do indivíduo (WIC) é a média da variância dentro dos indivíduos, enquanto o componente entre indivíduos (BIC) é a média da variância entre os indivíduos, e a largura total do nicho da população (TNW) é a soma de WIC e BIC e representa a variância ao longo de um eixo contínuo do uso dos recursos pela espécie (Bolnick *et al.*, 2003; Vander Zanden *et al.*, 2013). Utilizou-se a análise de variância (ANOVA) como uma aproximação para comparar estes valores dentro e entre os indivíduos, seguindo a metodologia proposta por Vander Zanden *et al.* (2013). Posteriormente, calculou-se o grau de especialização individual a partir da razão entre WIC/TNW, onde valores próximos de 0 indicam especialização individual, e próximos de 1 indicam que os indivíduos são generalistas (Bolnick *et al.*, 2002).

Para as análises do Capítulo 3, os dados do rastreamento das tartarugas foram filtrados para eliminar posições de baixa resolução, classe de localização Z e velocidades de deslocamento entre duas consecutivas posições superiores a 10 km.h⁻¹. As posições associadas às outras classes de localização (0–3, A e B) foram mantidas (González Carman *et al.*, 2012, 2016). Para reduzir a auto-correlação espacial, para cada tartaruga

selecionaram-se as posições de maior acurácia (melhor classe de localização) obtidas em intervalos de 6 h.

Estimativas de densidade de kernel, com uma largura de banda de aproximadamente 28 km, foram utilizadas para identificar as áreas de maior densidade de uso para as tartarugas-cabeçuda e para as pescarias de arrasto de parelha, emalhe de fundo e espinhel pelágico, por ano e por estação. Aplicou-se uma função linear para re-escalonar as estimativas de densidade em uma amplitude de 0 a 1. Posteriormente as superfícies de densidade foram transformadas em polígonos de densidade, representando 50, 75 e 90% dos valores mais altos de densidade entre a faixa de amplitude de 0 a 1. Calculou-se, então, o percentual de sobreposição entre as áreas de maior densidade de uso das tartarugas e das pescarias, para cada um dos três polígonos de densidade, por estação do ano. Estas análises e os mapas foram produzidos utilizando os pacotes *maps* (Minka & Deckmyn, 2016), *rgdal* (Bivand *et al.*, 2016), *kernSmooth* (Wanda, 2015) e *raster* (Hijmans, 2016) no programa R (R Core Team, 2015).

O padrão de movimentação sazonal das tartarugas foi contrastado com os dados de temperatura superficial do mar, os quais foram convertidos em isotermas de 5°C e plotados nos mapas de densidade de uso das tartarugas.

Todas as análises estatísticas e figuras foram produzidas no software R (R Core Team, 2015) versão 3.2.3.

3. SÍNTESE DOS RESULTADOS

A análise dos dados de encalhes de tartarugas marinhas, no litoral sul e médio do Rio Grande do Sul (RS) (Capítulo 1) revelou que a tartaruga-cabeçuda (*C. caretta*) é a espécie com maior número de encalhes (50,8%) seguida por *C. mydas* (40,9%) e *D. coriacea*

(6,0%). Encalhes de espécimes da tartaruga-oliva (*L. olivacea*) e da tartaruga-de-pente (*E. imbricata*) ocorreram em número reduzido, representando 0,8 e 0,5% do total de registros, respectivamente. Em relação às classes de tamanho, para *C. caretta* 73,7% dos espécimes encalhados foram indivíduos imaturos (CCC médio $\pm$ dp = $72,9 \pm 12,8$ cm). Para *C. mydas* e *E. imbricata* todos os espécimes foram imaturos com CCC médio de $39,2 \pm 6,0$ cm e $40,4 \pm 9,2$ cm, respectivamente. Para *D. coriacea* foram registrados ambos adultos e juvenis ($136,2 \pm 13,4$ cm), sendo que os juvenis representaram 53,2% dos registros, e para *L. olivacea* 23,4% dos indivíduos foram juvenis, com CCC médio de $65,4 \pm 5,3$ cm.

Para as três espécies mais frequentes, ano e mês foram as variáveis com maior percentual de explicação do número médio de encalhes. O modelo que apresentou o melhor ajuste para explicar os padrões espaço-temporais dos encalhes de *C. caretta* continha como variáveis independentes o ano, o mês, a área, o índice de oscilação sul, o componente oeste-leste do vento e a interação entre mês e área. Para *C. mydas* o melhor modelo continha as variáveis ano, mês, componente oeste-leste do vento e esforço amostral (distância percorrida por monitoramento de praia) e para *D. coriacea* o modelo continha as variáveis explanatórias ano, mês, área e índice de oscilação sul.

Observou-se um aumento significativo no número de encalhes de *C. caretta* e *C. mydas* a partir de 2004 até 2014, e uma estabilidade, com pequenas flutuações anuais, no número de encalhes de *D. coriacea* (Fig. 5). Também notou-se uma marcada sazonalidade, com cerca de 80% dos encalhes ocorrendo entre os meses de outubro e março, coincidindo com um maior esforço das pescarias de arrasto de parelha e emalhe de fundo próximo à costa do RS. Estes resultados corroboram a hipótese *i* do presente estudo. No caso da tartaruga-cabeçuda, interações negativas com esta pescaria foram

corroboradas pelos resultados apresentados no Capítulo 3, a partir da sobreposição dos lances de pesca com os dados de rastreamento por satélite de indivíduos desta espécie.

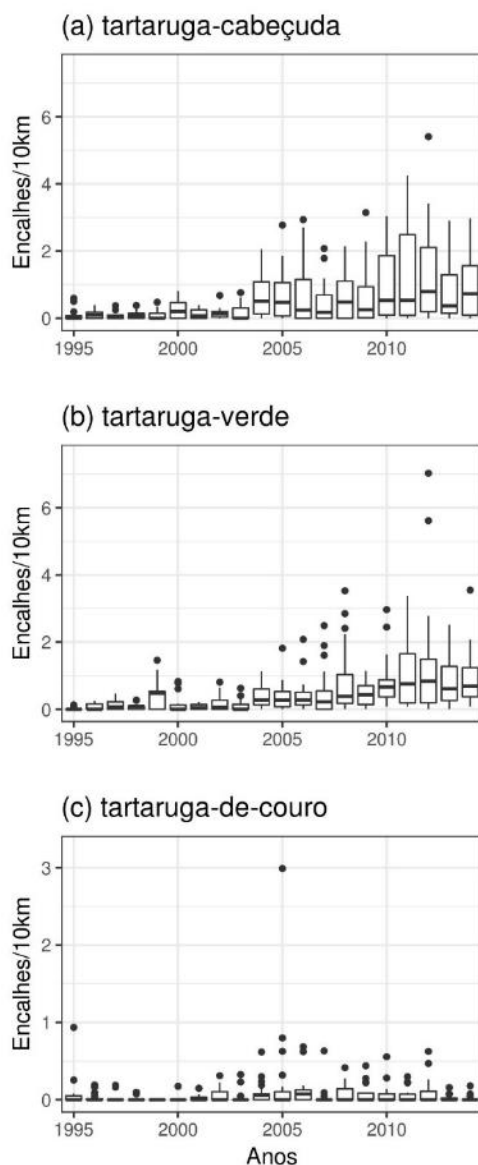


Figura 5. Variação inter-anual no número médio de encalhes de (a) tartaruga-cabeçuda (*C. caretta*), (b) tartaruga-verde (*C. mydas*) e (c) tartaruga-de-couro (*D. coriacea*) na costa do Rio Grande do Sul.

As composições de isótopos estáveis de carbono e nitrogênio amostradas sequencialmente entre as linhas de crescimento ósseo nos úmeros de indivíduos imaturos

de tartarugas-cabeçuda (Capítulo 2) com idades previamente determinadas em dois estágios de vida – oceânico e nerítico – revelaram um aumento significativo nos valores de $\delta^{15}\text{N}$ e $\delta^{13}\text{C}$ com a idade (Fig. 6) e tamanho das tartarugas, indicativos de mudança ontogenética, tanto em habitat quanto em relação à dieta.

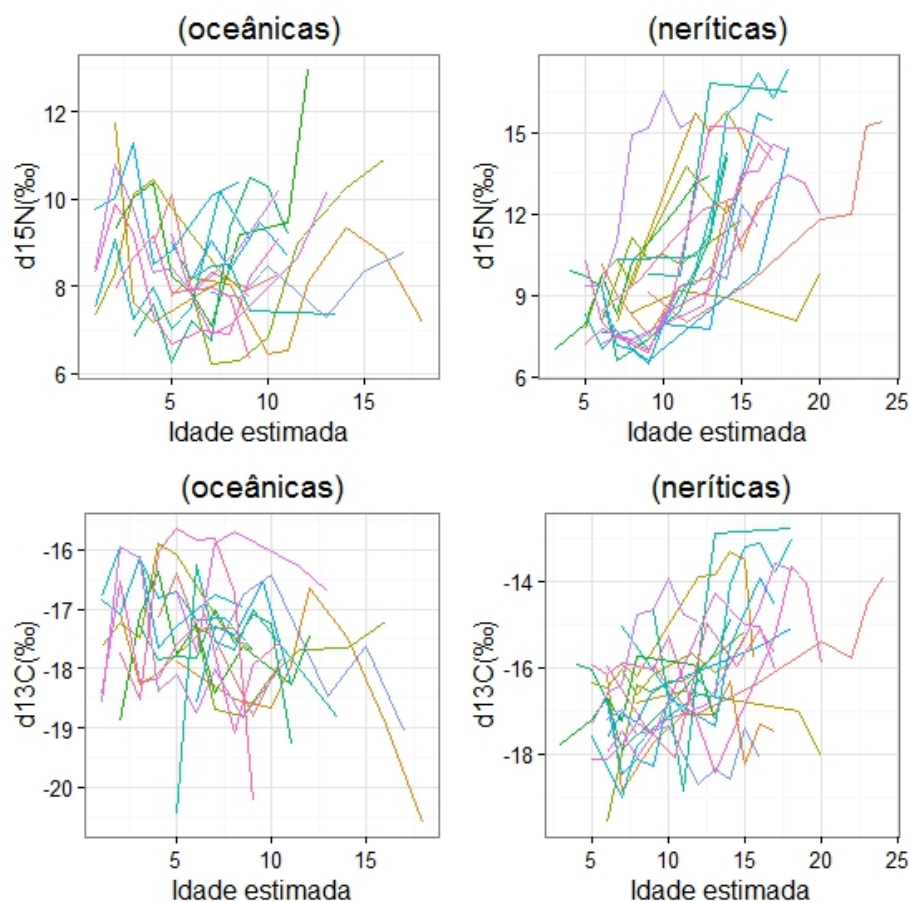


Figura 6. Valores de $\delta^{15}\text{N}$ e $\delta^{13}\text{C}$ para as idades estimadas das linhas de crescimento ósseo de tartarugas oceânicas (capturadas incidentalmente na pescaria de espinhel pelágico; n=16) e de tartarugas neríticas (encalhadas mortas na costa do Rio Grande do Sul; n=19).

Com base em informações prévias de que a dieta dos indivíduos no ambiente oceânico é composta principalmente por salpas e pirossomos, e no ambiente nerítico por

invertebrados bentônicos; e nos valores isotópicos de $\delta^{15}\text{N}$ nos tecidos das salpas (4,95‰) e do ermitão *Loxopagurus loxochelys* (10,8‰), sugere-se que o aumento marcante nos valores de $\delta^{15}\text{N}$ nas linhas de crescimento são indicativos de que ao recrutarem para o ambiente nerítico as tartarugas passam a se alimentar de presas com nível trófico superior ao ambiente oceânico.

As composições de isótopos estáveis de carbono e nitrogênio associadas às linhas de crescimento revelaram uma grande variabilidade individual na idade de recrutamento do ambiente oceânico para o ambiente nerítico, entre 8 e 18 anos de idade. Estimou-se que esta mudança ontogenética ocorre quando as tartarugas apresentam em média 13 anos de idade e 65 cm de CCC, variando de 55,7 a 77,9 cm. A média dos valores de $\delta^{15}\text{N}$ antes do recrutamento ao ambiente nerítico foi de 10,03‰ e a média após o recrutamento foi de 13,43‰. Para o carbono, a média dos valores de $\delta^{13}\text{C}$ pré-recrutamento foi de -16,72‰ e a média pós-recrutamento foi de -15,42‰.

A partir das análises de isótopos estáveis também foi possível determinar que as tartarugas-cabeçuda, em ambos os estágios do ciclo de vida, são especialistas individuais dentro de uma população generalista, alimentando-se de presas específicas ou que possuem assinaturas isotópicas semelhantes, conforme postulado na hipótese *ii*. Além disto, observou-se que existe uma consistência temporal na dieta, mantida ao longo de vários anos, sugerindo que os indivíduos apresentam fidelidade às áreas de alimentação e aos tipos de alimento ingeridos.

Os dados de rastreamento por satélite (Capítulo 3) de 16 tartarugas-cabeçuda com CCC médio de 76 cm (58 a 96 cm) revelaram uma grande plasticidade da espécie quanto ao uso do habitat. Dois padrões principais de uso do habitat foram observados: 1) tartarugas que utilizaram quase exclusivamente a região nerítica (> 80% do tempo) ($n =$

10 indivíduos); e 2) tartarugas que utilizaram as regiões nerítica e oceânica ($n = 6$), com metade dos indivíduos permanecendo mais de 50% do tempo de rastreamento no ambiente oceânico.

Para sete tartarugas rastreadas, observaram-se movimentos de ida para a região oceânica e retorno para a região nerítica ao longo do ano. O tempo que estas tartarugas permaneceram na região oceânica, sem retornar à região costeira, variou de 9 a 172 dias, indicando que estes indivíduos estavam utilizando a região oceânica como área de alimentação. Um indivíduo com 85,5 cm de CCC exibiu uma grande plasticidade no uso do habitat: após ter permanecido por 185 dias na região oceânica, esta tartaruga retornou para a região nerítica por 158 dias, novamente regressou à região oceânica por mais 117 dias e, finalmente, deslocou-se para a costa por 163 dias, até o fim da transmissão.

Os resultados do rastreamento por satélite, associados com os dados dos isótopos estáveis evidenciaram que as tartarugas-cabeçuda na região subtropical do Atlântico Sul Ocidental não apresentam uma mudança ontogenética abrupta no habitat e na dieta e que o recrutamento para o ambiente nerítico pode ser reversível. Com base nestas evidências, recusou-se a hipótese *iii*, na qual postulou-se que ao recrutarem para o habitat nerítico, os indivíduos de *C. caretta* utilizavam exclusivamente a plataforma continental como área de alimentação. Além disso, observou-se que as tartarugas-cabeçuda utilizam a região costeira ou oceânica do Rio Grande do Sul como área de alimentação ao longo do ano, contrariando o que foi postulado na hipótese *iv*, que estes indivíduos migrariam para regiões tropicais ao final do outono ou no inverno.

Registrou-se, ainda, uma variação sazonal nas áreas de maior densidade de uso pelas tartarugas-cabeçuda, às quais coincidem com as áreas de maior encalhe na costa. No verão e na primavera as áreas de maior densidade de uso estiveram localizadas entre o Farol do

Albardão e o Chuí, enquanto no outono as tartarugas utilizaram toda a plataforma continental. No inverno, a plataforma ao norte da Barra do Rio Grande, principalmente entre as latitudes 31–30°S e também a área sobre a quebra da plataforma, talude e planície abissal tiveram uso mais intenso. Estes movimentos sazonais para a região oceânica ou para a região norte na plataforma continental iniciaram no outono, quando a temperatura superficial do mar na área sul da plataforma (entre o Chuí e a Barra do Rio Grande) diminuíram abaixo de 20°C (Fig. 7).

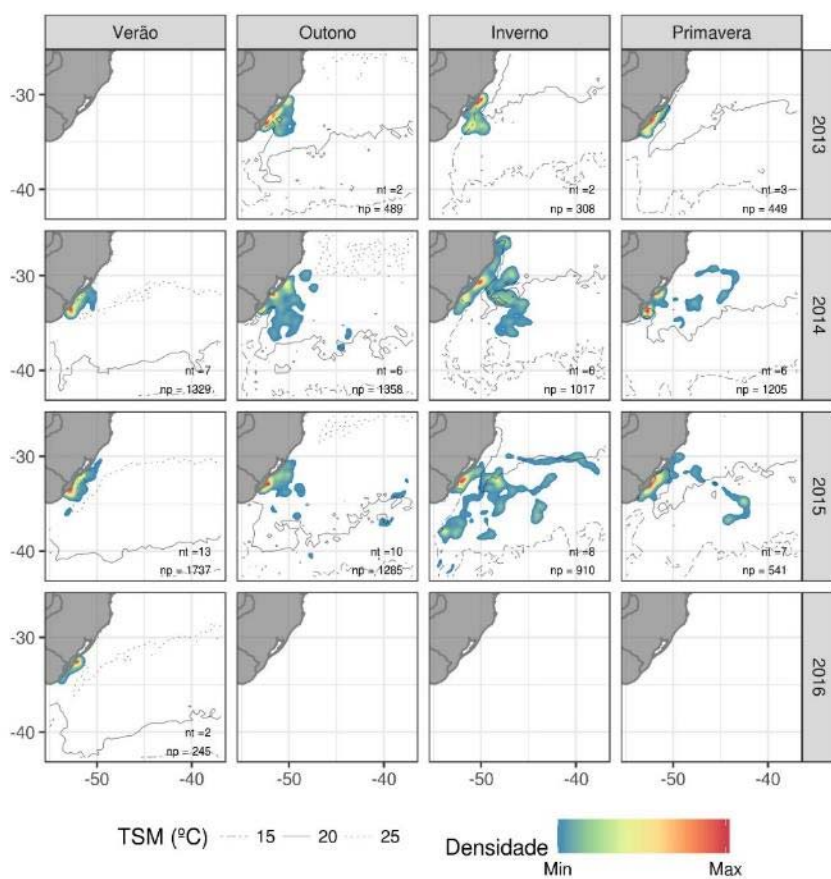


Figura 7. Áreas de maior densidade de uso pelas tartarugas-cabeçuda (*C. caretta*) na região subtropical do Atlântico Sul Ocidental, apresentados por estação do ano, entre 2013 e 2016. A linha sólida e as linhas pontilhadas representam as isotermas de 20, 15 e

25°C, respectivamente. nt = número de indivíduos rastreados e np = número de posições, após o processo de filtragem dos dados.

A partir da análise de sobreposição entre as áreas de maior densidade de uso de *C. caretta* com os dados do esforço das pescarias de emalhe de fundo, espinhel pelágico e arrasto de parelha (Capítulo 3) observou-se que no verão e na primavera as áreas utilizadas pelas tartarugas estão sobrepostas em 75% e 60%, respectivamente, com as áreas utilizadas pela frota de arrasto de parelha. Por outro lado, no outono, houve uma grande sobreposição com a pescaria de emalhe de fundo (64%) e uma sobreposição menor com o espinhel pelágico (22%) (Fig. 8).

A reduzida sobreposição entre as áreas utilizadas pelas tartarugas-cabeçuda e pelas pescarias no inverno é uma possível explicação para a quase ausência de encalhes na costa nesta estação do ano. Porém, sabe-se da existência de captura incidental de tartarugas marinhas no inverno, a partir de dados obtidos em embarques com observadores científicos e de cadernos de bordo preenchidos pelos mestres das embarcações. É provável que o número de indivíduos capturados seja menor, devido à menor sobreposição com as áreas de pesca e que mesmo ocorrendo a mortalidade, como a pescaria ocorre a uma maior distância da costa, a probabilidade de uma tartaruga capturada encalhar é reduzida.

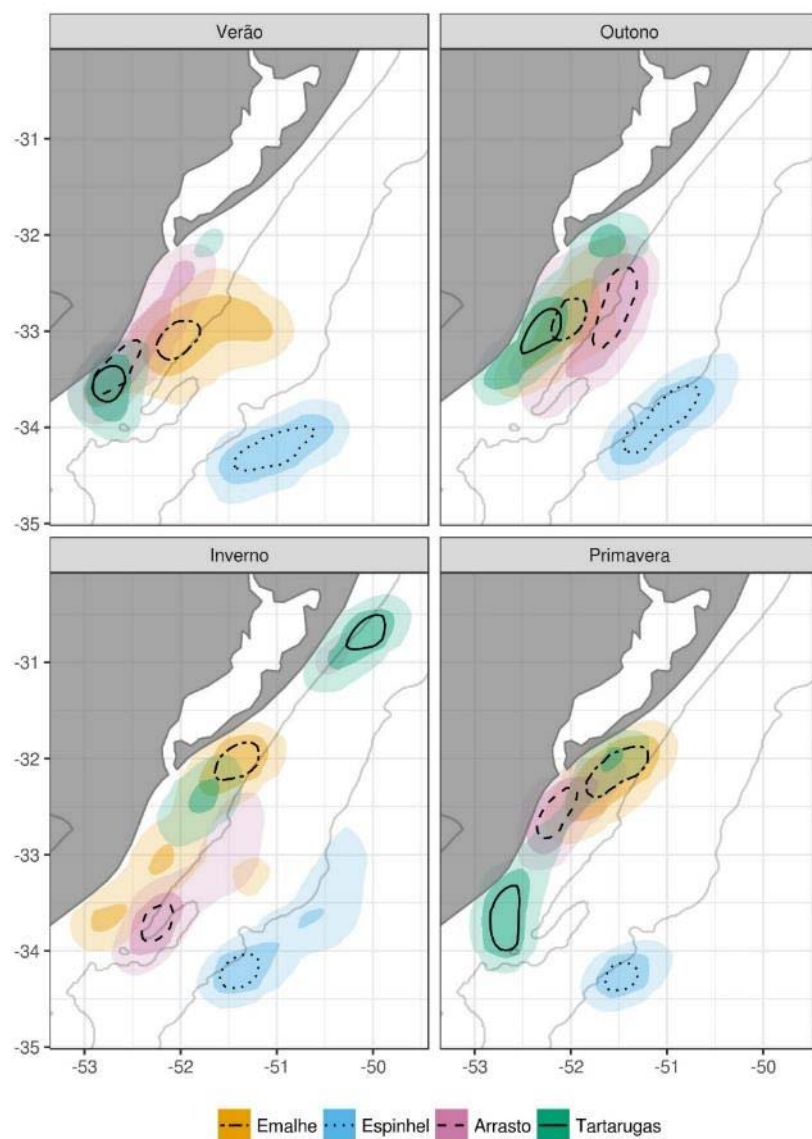


Figura 8. Polígonos de densidade, representando 50, 75 e 90% dos valores mais altos de densidade de uso pelas tartarugas-cabeçuda (*C. caretta*) e pelas pescarias de arrasto de parelha, emalhe de fundo e espinhel pelágico por estação do ano, entre 2013 e 2016, no sul do Brasil. As linhas sólidas e tracejadas representam as áreas núcleo (50%) e os polígonos com as cores mais intensas e mais transparentes representam 75 e 90% das áreas com as maiores densidades, respectivamente. As linhas cinza indicam as isóbatas de 50 e 200m.

4. CONCLUSÕES

- ✓ Os indivíduos de *C. caretta* apresentaram consistência nas áreas de maior uso do habitat e permanência nas áreas de alimentação no sul do Brasil;
- ✓ O habitat oceânico permanece importante para juvenis maiores e possíveis adultos de *C. caretta*, mesmo após o início do recrutamento para o habitat nerítico, na região subtropical do Atlântico Sul Ocidental;
- ✓ O uso de metodologias complementares como telemetria por satélite, esqueletocronologia e isótopos estáveis foi extremamente útil para melhorar a compreensão sobre as estratégias de forrageio e determinação do momento de recrutamento dos indivíduos de *C. caretta* ao ambiente nerítico;
- ✓ A duração do estágio oceânico para os indivíduos de *C. caretta* na região subtropical do Atlântico Sul Ocidental varia de 8 a 18 anos, com estimativa de recrutamento ao ambiente nerítico aos 13 anos de idade;
- ✓ As áreas de maior densidade de uso pelos indivíduos de *C. caretta* apresentam elevado percentual de sobreposição com a pescaria de arrasto de parelha, no verão e no outono, e com a pescaria de emalhe de fundo, no outono;
- ✓ O número elevado e crescente nos encalhes de tartarugas marinhas no litoral sul e médio do Rio Grande do Sul está provavelmente relacionado ao aumento na captura incidental destas espécies pela atividade pesqueira, resultado tanto do aumento no esforço de pesca na região costeira quanto no crescimento das populações fonte.

5. RECOMENDAÇÕES

- ✓ A área sul da plataforma continental no Rio Grande do Sul, entre o Farol do Albardão e o Chuí, na primavera e no verão, por ser a região de maior densidade de uso por indivíduos de *C. caretta* e devido ao elevado percentual de sobreposição com a pescaria de arrasto de parelha deve ser considerada prioritária para a conservação desta espécie. Medidas mitigatórias devem ser implementadas para reduzir o esforço pesqueiro e o nível de sobreposição com as tartarugas-cabeçuda nesta região e, portanto, sua mortalidade;
- ✓ É fundamental a determinação das taxas de captura incidental e mortalidade de tartarugas marinhas nas pescarias de arrasto e emalhe de fundo;
- ✓ Recomenda-se realizar análises de isótopos estáveis de carbono e nitrogênio em tecidos de renovação mais rápida, como células vermelhas, plasma e músculo, para aumentar a resolução e a compreensão dos movimentos de ida e retorno entre os ambientes oceânico e nerítico;
- ✓ Sugere-se a realização de estudos de telemetria por satélite com indivíduos adultos de *C. caretta* que utilizam a região subtropical do Atlântico Sul Ocidental como área de alimentação, a fim de verificar se estes apresentam plasticidade quanto ao uso do habitat, semelhante ao identificado para os indivíduos imaturos.

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CAPÍTULO 1 / ANEXO 1

Long-term spatial and temporal patterns of sea turtle strandings in southern Brazil

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Long-term spatial and temporal patterns of sea turtle strandings in southern Brazil

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Abstract Strandings of marine vertebrates along beaches have been widely used to infer threats and causes of mortality in adjacent waters. Understanding the influence of anthropogenic impacts on sea turtle survival is essential for effective conservation, yet limited data are available on the magnitude and patterns of sea turtle mortalities in southern Brazil. Our study reports sea turtle stranding data obtained from monthly beach surveys undertaken from 1995 to 2014 in the state of Rio Grande do Sul, Brazil, and when possible, we identify causes of mortality associated with different fisheries. A total of 6285 turtles of five species were encountered, with the three most common species being loggerhead (*Caretta caretta*; $n = 3192$), green (*Chelonia mydas*; $n = 2572$), and leatherback turtles (*Dermochelys*

coriacea; $n = 376$). Generalized linear models demonstrated that loggerhead and green turtle strandings have increased over the last 10 years. Strandings were highest from October to March, which coincides with the greatest bottom pair trawl, gill net, and possibly double-rig trawl fishing effort near the coast. Our results provide a baseline to compare future sea turtle stranding patterns. For reducing sea turtle mortalities, we suggest that time/area closures and/or reduction in gill net, pair trawl, and possibly double-rig trawl fishing effort in coastal waters of southern Brazil during austral spring and summer be considered for future fisheries management plans.

Introduction

Understanding the status of sea turtle populations and the influence of anthropogenic mortality on their survival is essential for effective conservation (Hamann et al. 2010; Bolten et al. 2011). Identifying the life stages that are most impacted by non-natural mortality and quantifying the

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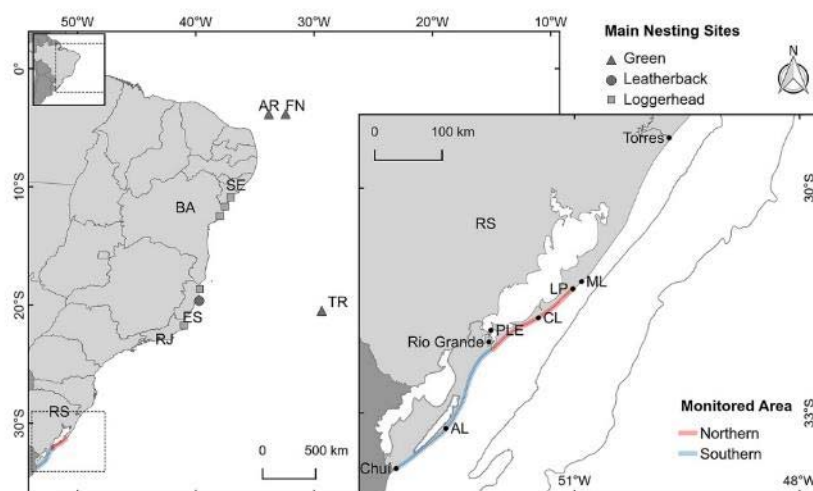


Fig. 1 Main nesting sites for loggerhead, leatherback and green sea turtles in Brazil. RS Rio Grande do Sul state, RJ Rio de Janeiro state, ES Espírito Santo state, BA Bahia state, SE Sergipe state, AR Atoil das Rocas, FN Fernando de Noronha, TR Trindade. Inside map Study

area along the coastline of Rio Grande do Sul state, southern Brazil, between Lagoa do Peixe and Chulí. AL Albardão lighthouse, PLE Patos Lagoon Estuary, CL Conceição lighthouse, LP Lagoa do Peixe and ML Mostardas lighthouse

temporal and spatial patterns of such threats are critical for assessing long-term trends and population viability (Crouse et al. 1987; Heppell 1998). This knowledge is fundamental to identify priority areas and periods for mitigation and/or intervention for the human impacts affecting sea turtles (Lewison et al. 2003; Chaloupka et al. 2008; Peckham et al. 2008).

Despite numerous efforts to estimate sea turtle mortality (Chaloupka and Limpus 2005; Tröng and Chaloupka 2007; Finkbeiner et al. 2011), existing models are based on limited data and not fully capable of depicting the effects of non-natural removal on population dynamics throughout a turtle's entire life cycle (Hamann et al. 2010). For example, mortality of juveniles, subadults, adult males, and non-breeding adult females has not been adequately estimated for most species and locations (Hamann et al. 2010), therefore limiting the accuracy of survivorship estimates.

Brazilian beaches and waters host five species of sea turtles, including the loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and leatherback (*Dermodochelys coriacea*) turtles (Marcovaldi and Marcovaldi 1999). All five species are classified in threat categories on the IUCN Red List (i.e., vulnerable, endangered, critically endangered; IUCN 2015), and all are included in the Brazilian list of threatened species (MMA 2014). During the

last decade, southwestern Atlantic Ocean populations of loggerhead, olive ridley, and hawksbill turtles have shown significant increases in abundance of nesting females (Marcovaldi and Chaloupka 2007; Marcovaldi et al. 2007; Silva et al. 2007), while green and leatherback turtle nesting populations have been stable (Thomé et al. 2007; Almeida et al. 2011a).

Whereas sea turtle nesting in Brazil is largely confined to beaches in the southeastern and northeastern regions (Fig. 1), the coastal waters of southern Brazil provide important foraging and developmental habitat, particularly for loggerhead, green, and leatherback turtles (Bugoni et al. 2003; Almeida et al. 2011a). Similar to elsewhere in the world, sea turtles foraging in southern Brazil are impacted by diverse anthropogenic threats (Lutcavage et al. 1997; Bugoni et al. 2001; Domingo et al. 2006; Tourinho et al. 2010), and sea turtles are frequently encountered stranded or caught in fishing gear (Domingo et al. 2006; Sales et al. 2008). High bycatch rates have previously been documented in the area for leatherbacks and juvenile loggerheads in pelagic longline (Pons et al. 2010) and in drift and set gill nets (Fiedler et al. 2012; Ramos and Vasconcellos 2013). However, little is known about the mortality of sea turtles in trawl gear (Monteiro et al. 2013), nor are there sufficient data on the spatial and temporal patterns of bycatch in these fisheries. This is

largely due to fragmentary spatial and temporal monitoring of fishing fleets and the scarcity of direct observations of bycatch events. However, because trawling in southern Brazil occurs over the entire continental shelf, including neritic waters, this fishery could be one of the major contributors to mortality and strandings of sea turtles. Given the logistic and economic constraints of directly monitoring fishing fleets, careful analyses of long-term stranding data from beach surveys adjacent to bycatch hotspots can be effective for understanding both spatial and temporal patterns of sea turtle mortality (e.g., Koch et al. 2006; Peckham et al. 2008).

Stranding surveys can provide important information on sea turtle distribution, demography, and cause-specific mortality via collecting data and biological samples from encountered carcasses (Chaloupka et al. 2008; Vélez-Rubio et al. 2013). In addition to the value for sea turtle status assessments, stranding data are useful for providing insights about fishery-specific impacts on sea turtle populations (e.g., Magnuson et al. 1990; Epperly et al. 1996; Casale et al. 2010). For example, in Baja California Sur, Mexico, 262 green turtles were found dead from 2006 to 2009, with 96% of stranding coinciding with the gill net fishing seasons for halibut (*Paralichthys californicus*) and guitarfish (*Rhinobatus* sp.) (Mancini et al. 2012). Also in Baja California, Mexico, Peckham et al. (2008) documented nearly 3000 dead loggerheads, between 2003 and 2007, and linked these deaths with offshore bottom-set longline and gill net fisheries for halibut via information from a coinciding onboard observer program. Similarly, Shaver (1998) encountered 3283 stranded turtles between 1980 and 1994 along the Texas, US coast, and reported that stranding rates were substantially lower during shrimp trawling closure periods.

Natural factors may also be associated with stranding events, such as climate change and temperature anomalies. For example, El Niño Southern Oscillation (ENSO) warm (El Niño) and cold (La Niña) events have a variety of effects on marine populations and ecosystems (McPhaden 2003). Inter-annual environmental variability, driven by ENSO, has profound consequences for the ecology of green turtles in Peru (Quiñones et al. 2010). Along the coast of Rio Grande do Sul, Brazil, an increased number of South American fur seals (*Arctocephalus australis*) were reported stranded during years of La Niña (Prado et al. 2016) and Magellanic penguins (*Spheniscus magellanicus*) strandings during El Niño years (Mäder et al. 2010).

In this study, we present data from sea turtle stranding surveys conducted from 1995 to 2014 along the coast of Rio Grande do Sul, Brazil. Our goal is to describe the spatial and temporal patterns of sea turtle mortality. These data can provide key information for fisheries management plans that ultimately promote the long-term conservation

and viability of sea turtles in the western South Atlantic Ocean. Moreover, we hope that these data provide a baseline against which to compare results of future surveys and mortality.

Materials and methods

Study area

The Rio Grande do Sul state coast (RSC) is 620 km long and spans from Torres (29°20'S; 049°44'W) to Chuí (33°44'S; 053°22'W), which marks the border of Brazil and Uruguay (Fig. 1). The coastline is straight with a predominant northeast–southwest orientation and is composed mostly of fine quartz sand resulting in a compacted and gentle beach slope (Pereira et al. 2010). The continental shelf of RSC is ca. 58,000 km². The broadest part is between Rio Grande and Chuí (140 km wide). This region is under direct influence of the subtropical shelf front (STSF) that is a complex thermohaline structure from mixing of Rio de la Plata waters with distinct shelf water masses (Piola et al. 2008). In austral winter, Plata Plume Water extends northeastward beyond Itajaí (~27°S), and in summer it retreats southward ~33°S (Piola et al. 2008). The mean sea surface temperature on the shelf is 18 °C in winter and 23 °C in summer (Piola et al. 2008). The low-salinity coastal waters derived from the Rio de la Plata are associated with high nutrient and chlorophyll *a* concentrations and phytoplankton (Ciotti et al. 1995), and sustain abundant demersal fishery resources (Haimovici et al. 1996). The area is considered one of the most productive fishing grounds in Brazil (Seeliger et al. 1997).

Description of fisheries

Based on prior interviews with fishermen, industrial fleets based on or landing at Rio Grande harbor identified as potentially interacting with sea turtles on the RSC are: pair trawl, otter trawl, double-rig trawl, bottom set gill netting, and pelagic longlining. The main characteristics of these fisheries are in Table S1. The trawl fleet alone accounts for 33.5 to 68.6% of the demersal fish landings in Rio Grande do Sul state, between 1997 and 2011 (CEPERG 2012). All trawl fisheries operate at day and night at a speed varying from 2 to 3.5 knots (NEMA unpubl data). We observed a relatively stable trend in the number of vessels, for pelagic longline, otter, and double-rig trawls operating in Rio Grande do Sul continental shelf and slope, from 2000 to 2014 (UNIVALI/CTTMar 2010, 2011, 2013a, b, NEMA unpubl data). A different pattern was observed for pair trawl. This fleet had decreased until 2002, but after this year presented a stable trend.

The gill net fleet size has varied from nearly 100–150 vessels, though after the mid-2000s a fraction of a much larger fleet from the neighbor state of Santa Catarina frequently fish on Rio Grande do Sul coastal areas, especially during the white croaker (*Micropogonias furnieri*) season. Although, the number of vessels remained stable over time, net length doubled from 1995 to 2003 (Secchi et al. 2004) and fourfold to 2012 (Ramos and Vasconcellos 2013; Table S1). Nevertheless, in 2012 the gill net fishery was regulated in southern and southeastern regions (Brasil 2012), and hence effort is expected to decline after 2013 when the norm was put in force. Driftnet fishery, which is also harmful to sea turtles (e.g., Fiedler et al. 2012), is no longer operating since 2009 (UNIVALI/CTTMar 2010).

Data collection and standardization

Sea turtle stranding data were obtained via monthly beach surveys from January 1995 to December 2014 along 355 km of coast, between Lagoa do Peixe (31°21'S; 051°02'W) and Chuí (33°44'S; 053°22'W), Rio Grande do Sul (Fig. 1). The visual surveys were conducted by two research groups: (1) Núcleo de Educação e Monitoramento Ambiental—NEMA (from 1995 to 2014); (2) Laboratório de Ecologia e Conservação da Megafauna Marinha, Universidade Federal do Rio Grande—EcoMega/FURG (from 2009 to 2014).

Fisheries data were obtained from logbooks completed by captains for gill net vessels from 1997 to 2009 and for bottom pair trawl from 2013 to 2015. This information was collected as part of fisheries and bycatch monitoring programs carried out by EcoMega/FURG for gill net fisheries and by NEMA for pelagic longline and all trawl fisheries.

In the present study, we define a “stranding” as any marine turtle found washed ashore, dead or alive. A total of 412 surveys covering 57,527 km were conducted along the RSC. Surveys were carried out using a four-wheel drive vehicle at an approximate driving speed of 30 km/h, with two to four observers visually scanning from the wash zone to the base of the sand dunes.

The coastline was divided into two areas: the southern area, which extends from the Patos Lagoon Estuary mouth to Chuí (220 km), and the northern area, from the estuary mouth to Lagoa do Peixe (135 km) (Fig. 1). Due to logistical constraints, survey effort was uneven across months, years, and areas (Table 1). Thus, relative stranding rates were estimated as the number of sea turtles stranded per 10 km to allow for spatial and temporal comparisons.

For each turtle, we recorded species (as per Pritchard and Mortimer 1999), date, latitude, longitude, and curved carapace length (CCL), taken from notch to tip for hard-shell turtles and from the nuchal notch to back tip of the caudal peduncle for leatherbacks turtles (Bolten 1999),

tag numbers (if present), and turtle body condition defined as: 0 = alive; 1 = freshly dead (eyes present); 2 = moderate decomposition (without eyes); 3 = intermediate decomposition (loss of carapace scutes and head scales); 4 = advanced decomposition (carapace without scutes and loss of bone plates); 5 = mummified or only bone remains. Signs of interactions with fisheries, such as entangled cables or nets, hooks, or fresh skin lesions that could be indicative of the cause of mortality, were recorded. All dead turtles were spray-painted to minimize risk of double counting in subsequent surveys. Live animals were transported to the Marine Animal Rehabilitation Center—CRAM, Oceanographic Museum at Federal University of Rio Grande (FURG), for veterinary care and rehabilitation.

Data analysis

Stranding data were stored in the Data Base Management System (DBMS) PostgreSQL. To visualize the differences in seasonal and spatial stranding patterns for loggerhead, green, and leatherback turtles, we produced weighted kernel density maps in QGIS software, with a band width of approximately 9 km. The weight of each stranding point was assigned by the inverse number of surveys which passed through that coordinate ($1/\text{number of surveys} \times 100$, calculated by spatial queries in the database).

To identify the seasonal and spatial distribution of gill net and bottom pair trawl fishing effort we produced kernel density maps in QGIS software, with a band width of approximately 28 km. We used the information of 2937 sets from 1996 to 2009 and 2171 tows from 2013 to 2015 from logbooks completed by vessels' captains for gill net and bottom pair trawl fisheries, respectively.

Individual turtles were considered juveniles if CCL was smaller than the minimum size at the nearest nesting sites for each respective species: 83 cm for loggerheads (Baptistotte et al. 2003); 90 cm for green turtles (Almeida et al. 2011a); 139 cm for leatherbacks (Thomé et al. 2007); 63 cm for olive ridleys (Silva et al. 2007), and 86 cm for hawksbills (Marcovaldi and Marcovaldi 1999).

We used a Wilcoxon's rank test (Zar 1999) to detect size differences (e.g., CCL) in loggerheads stranded between 2001 and 2007 ($n = 868$) and incidentally caught individuals in 72 pelagic longline fishing cruises with onboard observers in southern Brazil during the same period ($n = 894$; Monteiro 2008). A similar analysis was carried out to compare the differences in the CCL of stranded loggerheads from 2012 to 2014 ($n = 492$ turtles) and turtles caught during 13 bottom pair trawl fishing cruises ($n = 69$ turtles; NEMA unpubl data).

Generalized linear models (GLMs) were used to model the number of stranded loggerhead, green, and leatherback turtles (Y) as a function of nine explanatory variables: month

Table 1 Summary of sea turtle strandings and sampling effort in Rio Grande do Sul, Brazil, between 1995 and 2014

Year	Species (number of individuals)				Sampling effort				Total (km)	
	Loggerhead	Green	Leatherback	Olive ridley	Hawksbill	Mean (km/month)	SD (km/month)	Min (month) (km)		Max (month) (km)
1995	20	3	20	0	0	178	98	0 (Apr)	347 (May)	2138
1996	29	14	8	0	0	248	112	0 (Jul)	355 (Jan)	2979
1997	16	33	6	0	0	210	86	0 (Jan)	339 (Feb)	2308
1998	24	22	4	3	0	217	99	105 (Dec)	355 (Mar)	2610
1999	8	30	0	0	0	79	66	0 (Jan, Feb, Apr, Jun)	163 (Sep)	949
2000	21	13	1	1	0	65	58	0 (Aug to Dec)	120 (May)	783
2001	35	19	6	1	0	241	151	0 (Jan to Mar)	355 (Jul)	2895
2002	41	48	15	4	0	208	157	0 (Apr, Aug, Oct)	355 (May)	2495
2003	36	16	6	0	0	127	67	84 (May)	338 (Jan)	1529
2004	292	149	40	1	0	349	6	337 (Aug)	355 (Feb, Apr)	4189
2005	278	146	92	3	1	327	29	278 (Aug)	355 (Apr, Sep)	3925
2006	306	137	43	0	0	289	88	111 (Mar, Jul)	355 (Jan)	3463
2007	133	122	6	2	0	285	72	104 (Dec)	353 (Jan, Aug)	3422
2008	186	191	27	1	3	273	110	106 (Jan, Feb, Apr)	355 (Oct)	3272
2009	209	149	24	1	3	299	98	87 (Nov)	355 (Jan)	3589
2010	331	280	23	8	9	325	41	206 (Dec)	354 (May, Sep)	3894
2011	446	404	23	7	11	322	57	205 (Jan, Jul)	355 (Apr, May)	3864
2012	265	203	19	4	0	202	78	111 (Sep, Nov)	355 (Jun)	2426
2013	182	242	6	3	2	222	104	64 (Jun)	355 (Nov)	2661
2014	336	351	7	11	0	345	25	270 (Aug)	355 (Feb, Apr)	4139
Total	3192	2572	376	50	29	—	—	—	—	57,527

Table 2 Explanatory variables included in generalized linear models, with their respective type, description and data included in the models for sea turtle strandings in Rio Grande do Sul, Brazil, between 1995 and 2014

Variable	Type	Description
Year	Categorical	1995–2014
Month	Categorical	January to December
Area	Categorical	Two levels (south and north of the Patos Lagoon Estuary mouth)
SOI	Continuous	Southern Oscillation Index, where positive values indicate La Niña episodes and negative El Niño
km	Continuous	Sampling effort per survey, in km
W–E wind component	Continuous	Maximum values of wind from west during ten days before the survey date
E–W wind component	Continuous	Maximum values of wind from east during ten days before the survey date
S–N wind component	Continuous	Maximum values of wind from south during ten days before the survey date
N–S wind component	Continuous	Maximum values of wind from north during ten days before the survey date

(January–December), year (1995–2014), area (south and north of the Patos Lagoon Estuary), effort (km of coastline covered), Southern Oscillation Index (SOI; obtained from (<https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>) and four variables corresponding to wind direction and speed (Table 2), extracted from NCEP/NCAR Reanalysis 1 project using the package “mcep” from (<https://cran.r-project.org/web/packages/RNCEP/index.html>). We chose the wind dataset corresponding to a 10-day period prior to the date of every beach sampling. Prolonged periods of negative SOI values coincided with abnormally warm ocean water temperature across the eastern tropical Pacific (ETP), typical of El Niño episodes, and positive SOI values linked with cold ETP waters, typical of La Niña episodes. The length (km) of the coastline covered during each beach survey was used as a standardization factor (offset) of the number of sea turtles stranded per survey. The fit of the models to the data were performed using a negative binomial distribution (McCullagh and Nelder 1989), as shown below:

$$Y_i \sim \text{NB}(\mu_i, \theta),$$

where Y_i : number of sea turtles stranded on beach survey i , λ_i : mean number of stranded sea turtles per km of coastline on beach survey $i = (\mu_i/f_i)$, θ : over-dispersion parameter. For a negative binomial distribution, this parameter is estimated from the data.

The GLM general formula was as follows:

$$\log(\mu_i) = \log(f_i) + \beta_0 + \beta_1 \chi_{1i} + \beta_2 \chi_{2i} + \dots + \beta_n \chi_{ni} \quad (1)$$

where $\log(\mu_i)$ = link functional: logarithm of the mean number of stranded sea turtles on beach survey i , $\log(f_i)$ = offset: logarithm of the km of coastline covered on beach survey i , $\beta_0 + \beta_1 \chi_{1i} + \beta_2 \chi_{2i} + \dots + \beta_n \chi_{ni}$ = linear model, β_0 : estimated coefficient of the number of sea turtle stranded, β_i : estimated coefficient by variable i , and χ_{1i} : value of the variable i in the survey i .

Thirty-five alternative models were proposed. The best-fit model was selected using a forward stepwise approach

based on the lowest second-order Akaike information criterion—AICc value, because the relationship between the sample size and the number of parameters was less than 40 (Burnham and Anderson 2002). The models with the lowest AICc values are the models that best fit the data. The difference between the AICc value of a model “ i ” and the model with the lowest AICc value ($\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$) was also used as a model selection criteria (Table 3). Burnham and Anderson (2002) consider different levels of empirical support for model selection, based on the analysis of Δ_i , where: models with $\Delta_i = 0$ –2 are considered important models, models with $\Delta_i = 4$ –7 are considered less important models and above 10 unimportant models. All statistical analyses were performed using the software R (R Core Team 2015) version 3.2.3.

Results

Number of strandings, species and life stages

We recorded a total of 6285 strandings of five sea turtle species (Table 1). Strandings of loggerhead and green turtles were predominant with 3192 (50.8%) and 2572 (40.9%) records, respectively. Leatherback turtles were also relatively frequent, with 376 (6.0%) records. A total of 50 olive ridleys (0.8%) and 29 hawksbills (0.5%) were found, and 66 individuals could not be identified to species. Of all strandings, 3.5% were encountered alive, including 208 greens, seven loggerheads, and four hawksbills.

Loggerhead and green turtles were recorded in all 20 survey years, and leatherback strandings were observed in 19 years. Loggerhead turtles were the most frequently encountered species in 13 of the 20 survey years, whereas green turtles were the most frequent in the six years (1997, 1999, 2002, 2008, 2013 and 2014). Olive ridley and hawksbill turtles were found mostly during the last five years. An

Table 3 Five models that best fitted to the number of stranded loggerhead, green and leatherback turtles in southern Brazil, in the stepwise forwards model selection with their respective AICc (second-order Akaike information criteria) and the model percentage of deviance explained

Model	df	Loggerhead			Green			Leatherback		
		AICc	Δ AICc	% Explained	AICc	Δ AICc	% Explained	AICc	Δ AICc	% Explained
Offset (log km) + year + month	32	—	—	—	—	—	—	828.8	2.7	49.4
Offset (log km) + year + month + area + km	34	—	—	—	2008.8	12	59.2	—	—	—
Offset (log km) + year + month + area + SOI	34	—	—	—	—	—	—	826.1	0	50.9
Offset (log km) + year + month + area + SOI + west_east_wind	35	—	—	—	—	—	—	827.7	1.6	51.0
Offset (log km) + year + month + area + SOI + east_west_wind	35	—	—	—	—	—	—	827.8	1.7	51.1
Offset (log km) + year + month + area + SOI + south_north_wind	35	—	—	—	—	—	—	828.4	2.3	50.9
Offset (log km) + year + month + area + SOI + west_east_wind + month $\times$ area	46	1933.6	0	74.1	—	—	—	—	—	—
Offset (log km) + year + month + area + SOI + east_west_wind + month $\times$ area	46	1946.6	13	73.1	—	—	—	—	—	—
Offset (log km) + year + month + area + SOI + north_south_wind + month $\times$ area	46	1947.0	13.4	73.0	—	—	—	—	—	—
Offset (log km) + year + month + area + SOI + month $\times$ area	45	1945.1	11.5	73.0	—	—	—	—	—	—
Offset (log km) + year + month + area + SOI + south_north_wind + month $\times$ area	46	1945.6	12.0	73.1	—	—	—	—	—	—
Year + month + km + west_east_wind	34	—	—	—	1996.7	0	62.0	—	—	—
Year + month + area + km	34	—	—	—	2003.9	7.1	61.3	—	—	—
Year + month + area + SOI + km	35	—	—	—	2005.0	8.2	61.4	—	—	—
Year + month + km + south_north_wind	34	—	—	—	2005.4	8.6	61.2	—	—	—

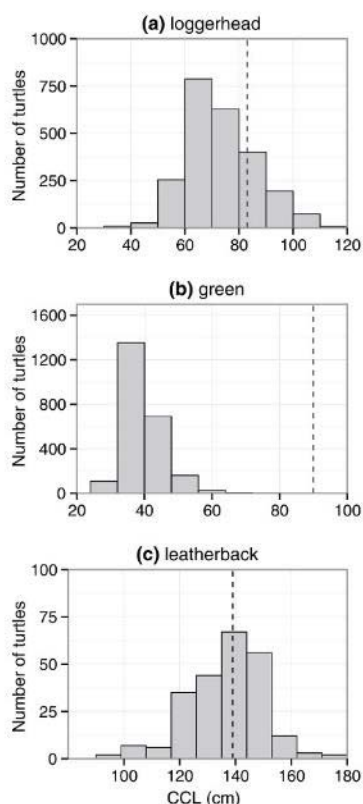
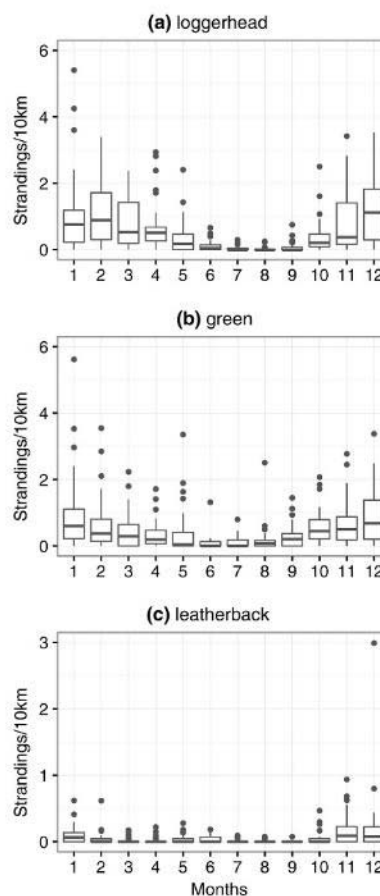
" $\times$ " refers to interaction between explanatory variables. Offset = kilometer of coastline covered during each beach survey used as a standardization factor

SOI Southern Oscillation Index, west_east_wind maximum values of wind from west, east_west_wind maximum values of wind from east, north_south_wind maximum values of wind from north, south_north_wind maximum values of wind from south, df degrees of freedom

Lower AICc are shown in boldface

Table 4 Summary of curved carapace length (CCL) for sea turtles stranded in Rio Grande do Sul, Brazil, between 1995 and 2014

Turtle species	CCL (cm)			
	<i>n</i>	Mean	SD	Range
Loggerhead	2384	72.9	12.8	24.0–115.0
Green	2354	39.2	6.0	26.0–96.0
Leatherback	235	136.2	14.3	65.0–173.0
Olive ridley	47	65.4	5.3	50.5–79.0
Hawksbill	29	40.4	9.2	29.0–60.0

**Fig. 2** Curved carapace length (CCL) of measured turtles: **a** loggerhead ($n = 2384$), **b** green ($n = 2354$) and **c** leatherback ($n = 236$). Dashed line indicates the minimum CCL of nesting females at Brazilian rookeries; 83 cm for loggerhead (Baptistotte et al. 2003), 90 cm for green (Almeida et al. 2011a) and 139 cm for leatherback (Thomé et al. 2007)**Fig. 3** Monthly variation in the number of marine turtles washed ashore on the southern Brazilian coast. **a** loggerhead, **b** green and **c** leatherback turtles. Black lines indicate the median, rectangles indicate quartiles of 25th and 75th percentiles, vertical lines indicate the maximum values and points represent outliers. Note that scales differ

anomalous mass-stranding event of 84 leatherback turtles was recorded in November–December 2005 (Table 1).

For loggerhead turtles, 73.7% of the specimens were juveniles (mean CCL $\pm$ SD = 72.9 ± 12.8 cm; Table 4; Fig. 2a). Of the adult loggerheads, five were females that had been previously marked with metallic tags at Brazilian nesting beaches (two from Espírito Santo, two from Bahia, and one from Rio de Janeiro states). For green turtles,

nearly all individuals were small juveniles (39.2 ± 6.0 cm; Table 4; Fig. 2b), and all hawksbills were small juveniles (40.4 ± 9.2 cm; Table 4). For leatherback turtles, both large juveniles and adults were recorded (136.2 ± 14.3 cm; Table 4; Fig. 2c); juveniles accounted for 53.2% of all records. For olive ridleys, 23.4% of individuals were juveniles (Table 4).

Spatio-temporal distribution and trends of strandings

The seasonality of strandings was consistent among years for loggerhead, green, and leatherback turtles. Although occurring year-round, the highest sea turtle strandings of these species were observed in austral spring and summer, from October to March (Fig. 3a–c). Although strandings were recorded throughout the study area, spatial distribution showed some areas of higher concentration, which varied among species and seasons (Fig. 4). Loggerhead turtles were found throughout most of the study area in spring, whereas in autumn and winter a higher concentration was observed in the northern area (Table S2); during the summer, most of the strandings occurred in the southern area (Fig. 4). Green turtle strandings were higher in spring and summer on the coast adjacent to the entrance of the Patos Lagoon Estuary. In autumn and winter strandings of green turtles occurred along most of the study area, but with higher densities in the northern area, near Lagoa do Peixe (Figs. 1, 4). Leatherback strandings were concentrated in the southern area in summer, autumn, and spring, whereas in winter higher rates were observed in the northern area (Fig. 4).

The number of loggerhead and green turtle strandings increased significantly during the latter years of our study (Table S2; Fig. 5). For loggerhead, green, and leatherback turtles, year and month are the explanatory variables that best explain the mean strandings number (Table 5). For loggerheads, the model that best fit the data included year, month, SOI, area, west–east wind component, and the interaction month $\times$ area as explanatory variables (Table 3). The mean number of stranded loggerheads increased significantly from 2004 ($\beta = 2.07$, $P < 0.001$) to 2014 ($\beta = 2.21$, $P < 0.001$; Fig. 5a). The loggerhead strandings were significantly lower from May to October (austral winter). Strandings were also lower when westerly winds predominated (Fig. S1) and in the southern part of the study area in May, August, and September and higher in years of positive SOI values, indicating La Niña events (Table S2). For green turtles, the model that best fit the stranding data included year, month, west–east wind component and sampling effort (km) as variables (Table 3). The mean strandings were also clearly higher starting in 2004, with peaks in 2008 and after 2010 (Fig. 5b), from October to February and in years with higher sampling effort. Similar to loggerheads, green turtle strandings were

lower when westerly winds predominated (Table S2; Fig. S1). For leatherbacks, the best-fit model included year, month, area and SOI as explanatory variables (Table 3). The mean number of stranded leatherbacks was significantly lower in 1998, 2007 and 2014. The strandings were significantly higher from November to January and in years of positive SOI values, indicating La Niña events (Table S2).

Fishing-related mortality

External examination of carcasses did not reveal cause of mortality for the vast majority of turtles recorded in this study. Most loggerheads (66%) and leatherbacks (69%) were found in advanced state of decomposition (stages 4 and 5), making it difficult to determine the cause of death. Although more than half of dead stranded green turtles were in relatively fresh (i.e., decomposition stages 1–3), the cause of mortality could not be confirmed purely from external examination and necropsies were not performed. A small fraction of the carcasses had evidence of being probably dead by causes others than mortality in fisheries (e.g., boat strike, entanglement in, and ingestion of, marine debris and, in the case of green turtles, cold stunning). A few live green turtles had external evidence of cold stunning, such as unusual amount of epibionts characteristically sessile (data not shown).

We assumed that turtles found with hooks in the beak or pieces of the main or branch lines in the flippers were caught in longline (Fig. S2), whereas those with parts of monofilament nets around the head, flippers, or carapace were considered to have been entangled in gill nets (Fig. S3). Because trawl fisherman use ropes to return heavy turtles brought onboard to the sea (Monteiro, pers obs), animals with pieces of ropes around the flippers, head or carapace were assumed to have been caught in trawl fisheries (Fig. S4). Small individuals that represent the majority of the bycatch, on the other hand, are easily handled and released back to the sea. External evidence of fishery-related mortality was observed in only 72 carcasses (1.2%).

Thirty-nine loggerheads had evidence of interaction with fisheries gear, including pelagic longlines ($n = 10$), bottom trawls ($n = 8$) and gill nets ($n = 21$). Stranded individuals had mean CCL significantly larger than those incidentally caught in the longline fishery (Wilcoxon's rank test, $W = 128,070$, $P < 0.001$). However, mean CCL of stranded turtles and individuals incidentally caught in bottom pair trawl fishery were similar (Wilcoxon's rank test, $W = 16,154$, $P = 0.516$; Fig. 6). For green turtles, we observed evidence of fisheries interaction only with gill nets ($n = 16$). For leatherbacks, we were able to identify the fishery that caused the death of 17 turtles, which included bottom trawling ($n = 12$), longlining ($n = 3$), and gill netting ($n = 2$).

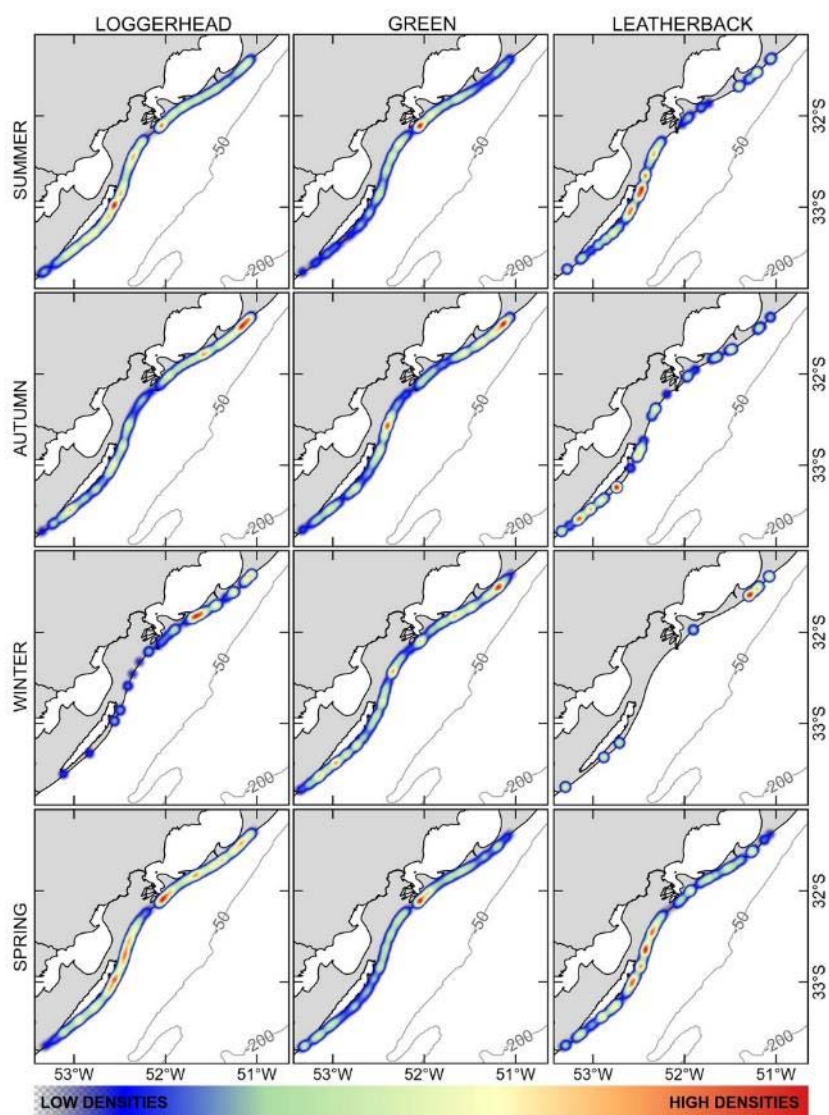


Fig. 4 Seasonal variation in the number of loggerhead, green and leatherback turtles washed ashore on the southern Brazilian coast represented by kernel density maps. Summer = January to March (loggerhead, $n = 1335$; green, $n = 778$; leatherback, $n = 81$);

Autumn = April to June (loggerhead, $n = 559$; green, $n = 450$; leatherback, $n = 48$); Winter = July to September (loggerhead, $n = 57$; green, $n = 299$; leatherback, $n = 39$); Spring = October to December (loggerhead, $n = 1187$; green, $n = 1030$; leatherback, $n = 223$)

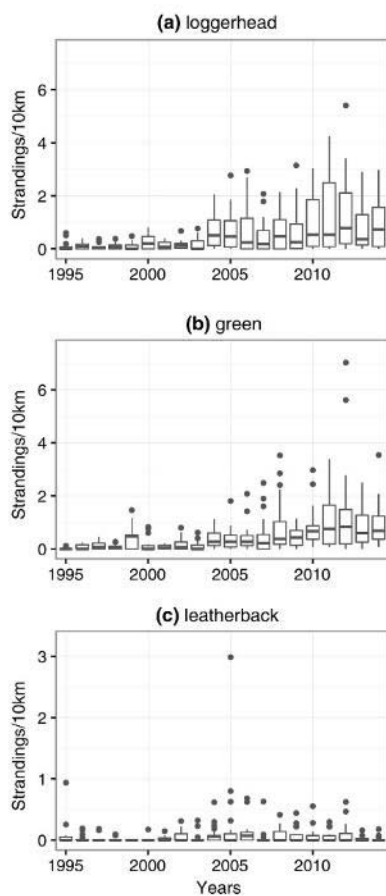


Fig. 5 Interannual variation in the number of marine turtles washed ashore on the southern Brazilian coast: **a** loggerhead, **b** green and **c** leatherback turtles. Black lines indicate the median, rectangles indicate quartiles of 25th and 75th percentiles, vertical lines indicate the maximum values and points indicate outliers. Note that scales differ

Discussion

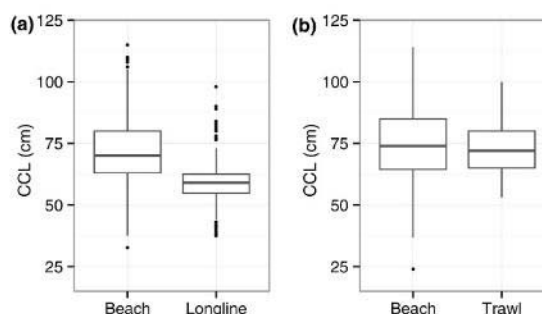
Analyses of stranding data assembled over broad spatial and temporal scales can provide insights into mortality patterns and life history of sea turtles (e.g., Witt et al. 2007; Tomás et al. 2008; Hamann et al. 2010). The current study presents the largest-ever stranding dataset for sea turtles in the southwest Atlantic Ocean, obtained during 20 years of

Table 5 Analysis of deviance for the models that best fit to the number of stranded loggerhead, green, and leatherback turtles in southern Brazil

Variables	df	Loggerhead				Green				Leatherback			
		Deviance	df of residuals	Residual deviance	% Explained	Deviance	df of residuals	Residual deviance	% Explained	Deviance	df of residuals	Residual deviance	% Explained
Null	—	—	412	1633.95	—	—	412	1156.55	—	—	412	574.40	—
Year	19	472.23	393	1161.72	28.90	470.01	393	686.54	40.64	118.92	393	455.48	20.70
Month	11	660.78	382	500.94	40.44	206.48	382	480.07	17.85	165.78	382	289.70	28.86
Area	1	10.98	381	489.96	0.67	—	—	—	—	1.85	381	287.85	0.32
SOI	1	13.21	380	476.75	0.81	—	—	—	—	5.66	380	282.19	0.99
Month × area	11	39.98	368	423.48	2.45	—	—	—	—	—	—	—	—
km	1	—	—	—	—	31.60	381	448.47	2.73	—	—	—	—
West_east_wind	1	13.29	379	463.46	0.81	9.13	380	439.34	0.79	—	—	—	—

The percent explained is calculated as deviance/residual deviance of the null model $\times 100$. “×” refers to interaction between explanatory variables
SOI Southern Oscillation Index, west_east_wind maximum values of wind from west, df degrees of freedom

Fig. 6 Curved carapace length (CCL) **a** of loggerheads incidentally captured in pelagic longline, during 2001–2007 ($n = 894$) and loggerheads stranded on the beaches during 2001–2007 ($n = 868$); **b** of loggerheads incidentally caught in bottom pair trawl during 2012–2015 ($n = 69$) and loggerheads stranded on the beaches during 2012–2014 ($n = 492$)



systematic beach surveys. From these two decades of effort we were able to generate information (e.g., spatio-temporal stranding patterns, causes of mortality) that will help inform ongoing and future conservation efforts.

Based on other studies carried out in Brazil, Uruguay, and Argentina, the number of strandings of loggerhead and leatherback turtles on the RSC is the highest reported for the southwestern Atlantic Ocean (Barata et al. 2004; González Carman et al. 2011; Vélez-Rubio et al. 2013; SITAMAR database). Although turtle demographic patterns may be skewed by seasonal fishing-related mortality, our stranding records suggest that the loggerhead turtle is the most abundant and/or the most vulnerable species in southern Brazilian waters, followed by green and leatherback turtles. Previous stranding studies for the northern part of Rio Grande do Sul coast (RSC) found (1) higher number of green turtles, followed by loggerheads and leatherbacks (Bugoni et al. 2001), and (2) a similar number of greens and loggerheads, followed by leatherbacks (Scherer et al. 2014).

Strandings of loggerhead turtles—a species that nests in southeast and northeast Brazil (Marcovaldi and Chaloupka 2007)—are uncommon in SW Atlantic, except in southern Brazil. Moreover, beach strandings of other sea turtle species (particularly juvenile green turtles) are common in the four Brazilian states where loggerheads nest (Marcovaldi and Chaloupka 2007). However, in the last seven years, loggerhead strandings were also common to the north of the state of Rio de Janeiro, in southeastern Brazil, 1550 km north of the northern edge of our study area (SITAMAR database). Whereas feeding areas for adult female loggerheads nesting in Brazil were identified as located off the Ceará coast in the northeastern region (between 2° and 5°S; 37° and 41°W; Marcovaldi et al. 2010), tag data suggest that the continental shelf of southern Brazil is also an important feeding ground for adult loggerheads from the Brazilian rookeries. Although the majority (67–85.7%) of loggerhead turtles stranded on the RSC from 1995 to 2014 were juveniles, we did encounter a substantial number of adults, including five females that

had been marked previously at the nesting sites in Brazil. Genetic studies have demonstrated that loggerhead turtles stranded along southeastern South American coasts are predominantly (Caraccio et al. 2007) or exclusively (Prosdocimi et al. 2015) from Brazilian rookeries.

Most green turtles stranded on the RSC were small juveniles. This is consistent with prior research in the same area, as well as in Uruguay and Argentina (Bugoni et al. 2001; González Carman et al. 2011; Vélez-Rubio et al. 2013; Scherer et al. 2014). The RSC may be part of a large foraging and developmental area in the SW Atlantic Ocean for turtles from Ascension, Aves/Surinam and Trindade Islands (Proietti et al. 2012). Green turtle strandings predominate in the north of Rio Grande do Sul, in Paraná and São Paulo states (Gallo et al. 2006; Gama et al. 2016).

Although leatherbacks are typically considered an oceanic species (Eckert et al. 2012), leatherbacks have been observed foraging in coastal waters of the SW Atlantic Ocean (López-Mendilaharsu et al. 2009; Almeida et al. 2011b). Southern Brazil has been shown to have the highest number of strandings of leatherback turtles along the extensive Brazilian coast (Barata et al. 2004). Considering that the number of stranded leatherbacks on the RSC is several times higher than in Uruguay and Argentina (González Carman et al. 2011; Vélez-Rubio et al. 2013), the southern Brazilian coast may represent one of the most important foraging grounds for leatherback turtles in the SW Atlantic Ocean, or alternatively, with abundance similar to adjacent areas, but with much higher mortality rates.

Spatio-temporal patterns of sea turtle strandings and fishing-related mortality

Loggerhead turtles

The size distribution as well as spatial and temporal patterns of strandings can help understand sea turtle vulnerability to different types of fishing gear. Along the RSC,

loggerhead turtles caught in longlines are smaller than those stranded or caught in the pair trawl fishery; similar results were observed in nearby Uruguay (Vélez-Rubio et al. 2013). Perhaps this difference in size is a result of different stranding probabilities for turtles interacting with each gear type. For example, despite the evidence that loggerheads are caught and drowned in pelagic longline gear in Uruguayan and Brazilian waters (Sales et al. 2008; Pons et al. 2010), these fleets operate more than 150 km from the coast, which, when considering ocean currents, reduces the likelihood that a turtle killed in a longline will wash ashore. In the RSC, bottom pair trawl and gill net fleets operate mostly over the inner continental shelf at depths less than 50 m (Fig. S5). Larger loggerheads in neritic or transitional stages spend more time near the coast to feed (Eckert et al. 2008), resulting in increased potential for interaction with fishing gear (and associated stranding). Stomach contents of stranded turtles indicate that they had been feeding and therefore were likely in good body condition and otherwise healthy upon death (Barros 2010; Monteiro pers obs).

In the best-fit model, the covariates with the most explanatory power ("month" and "year") for the variability in the mean number of loggerhead strandings were related to biological and ecological factors, including turtle population demography and fisheries dynamics. Loggerhead turtle strandings on the RSC have increased over the last 10 years of surveys. Similarly, Marcovaldi and Chaloupka (2007) reported an increasing trend in the abundance of loggerhead adult females at the Brazilian nesting sites. We acknowledge that a variety of factors such as positive trend in population growth, interannual variation in hatching success or hatchling survival can influence the observed stranding patterns. The marked increase in stranded loggerheads, particularly from the latter half of the 2000s to present, however, is not coupled with increased numbers observed in any of Brazilian nesting sites of this species. Therefore, this observed pattern of strandings is most likely explained by either a sudden increase in fishing effort or loggerheads abundance near the coast which resulted in a greater overlap in spatial distribution of this species and trawl (both pair and double-rig) fisheries. From a conservation perspective, this deserves further attention given that the majority of the stranded loggerheads were large juveniles with high reproductive value and thus of great relevance for maintaining population size (Crouse et al. 1987; Crowder et al. 1995; Wallace et al. 2008). Considering that the time at maturation for Brazilian loggerhead turtle population is approximately 32 years (Petit et al. 2012), this continuous high juvenile mortality observed in southern Brazil may lead to a decline in the number of nesting females once the affected cohorts reach reproductive ages.

Higher sea turtle strandings in the austral spring and summer are likely related to a greater abundance of turtles

and an increased fishing effort near the coast during these seasons. Loggerhead turtles that have been tagged with satellite transmitters indicate that some individuals remain in the area year-round close to the coast, while others move alongshore to the north of the study area or to deep oceanic waters in late autumn and winter (NEMA/EcoMega unpubl data). This displacement in autumn and winter could be a strategy to avoid cold waters in the inner continental shelf that result from the intrusion of Malvinas/Falklands current waters in the winter. Thus, the low number of loggerhead strandings in autumn and winter may be related to the dispersal of turtles to other areas and reduced fishing effort near the coast. During summer months, most loggerhead strandings are located in the southern area, which coincides with the highest effort for the pair and double-rig trawl fishery in this zone (Haimovici and Mendonça 1996; NEMA unpubl data; Fig. S5). Approximately 75% of the turtles bycaught in bottom pair trawl fishery were loggerhead turtles (NEMA unpubl data). A mark and recapture study to determine the probability that a turtle will wash ashore after being killed in this fishery demonstrated that 22 out of 74 turtles (30%) that were tagged were found stranded on the adjacent coast (Monteiro unpubl data). All those carcasses lack external evidences of bycatch. Based on the similar spatial and temporal patterns of bottom pair trawl fishing effort and strandings data, and also, in interviews, logbooks, and scientific cruises (NEMA unpubl data), we suggest that this fishery is responsible for the majority of loggerhead strandings, although impacts from gill nets and others trawl fisheries cannot be ruled out. Bycatch of loggerheads also occurs in double-rig trawl targeting both shrimps and fish, though the magnitude of mortality remains unknown (NEMA unpubl data). Bottom trawlers are also known to cause high mortality of turtles elsewhere (Caillouet et al. 1991; Lewison et al. 2003; Casale et al. 2010). Capture and drowning in trawl fishing gear leaves no external evidence that can easily be detected in dead stranded carcasses (Casale et al. 2010), and bycatch is usually inferred from the large numbers of stranded turtles during the fishing season (Caillouet et al. 1996; Casale et al. 2010). Tomás et al. (2008) observed that most loggerhead strandings in eastern Spain occurred in spring, summer and early autumn and were associated with the increase in longline fishing activities. In southern Brazil, effort of gill netting (e.g., Secchi et al. 1997, 2004; Boffo and Reis 2003), bottom pair, and double-rig trawling for both shrimps and fish (UNIVALI/CTTMar 2010, 2011, 2013b; Duarte 2013; NEMA unpubl data) increases in the inner continental shelf in warm months (Fig. S5). This greater fishing effort in coastal areas increases the potential overlap with the distribution of sea turtles and hence their bycatch and consequent stranding. Therefore, this combination of seasonal distribution of turtles coupled with the

dynamics of pair and double-rig trawl fisheries probably explains much of the spatial and temporal stranding patterns observed here.

The best-fit model indicates that mean number of loggerhead strandings was higher in years of La Niña (positive SOI values) and when strong easterly winds predominate. In the SW Atlantic Ocean, the continental shelf north of 45°S is characterized by high chlorophyll *a* values during El Niño events whereas the opposite pattern occurs in La Niña years (Machado et al. 2013). The relationship between sea turtle strandings and ENSO events is not clear. It is possible, however, that wind direction and speed explain part of the strandings. Wind is one the most important factors that explain the stranding probabilities of sea turtles in the northwestern Atlantic (Hart et al. 2006) and in the north-eastern Pacific (Koch et al. 2013).

Green turtles

Whereas the best-fit model includes “year,” “month,” “sampling effort,” and “west–east wind component,” “year” was the single variable that explained most of the variation in the observed number of green turtle strandings. Since the vast majority of stranded green turtles were composed of juveniles, the variation may, in part, be explained by inter-annual fluctuations in the reproductive success and survival rates of the small juveniles, hence on the recruitment to feeding areas in southern Brazil. Diet and size frequency of stranded individuals suggest that the RSC is most likely a recruitment area for green turtles from the oceanic to neritic stage. In most of the Brazilian coast green turtles feed mainly upon algae and seagrasses (Reisser et al. 2013; Santos et al. 2015; Gama et al. 2016). On the RSC, however, stomach contents from stranded green turtles largely consisted of invertebrates, with nearly half of the turtles having consumed pelagic invertebrates, such as pteropods and heteropods (Barros 2007).

Based on lack of external evidence of interaction with fisheries for most carcasses and the low observed frequency of bycatch in pair trawl (15%, NEMA unpubl data) and in almost null bycatch in pelagic longline (e.g., Monteiro 2008; Sales et al. 2008), we suggest that incidental capture in gill nets is an important source of mortality for green turtles in southern Brazil. Furthermore, the higher green turtle strandings in spring and summer coincide with the fishing season for bottom-set gill nets targeting white croaker closer to coast (e.g., Secchi et al. 1997, 2004; Ferreira et al. 2010). However, impacts of double-rig trawl fisheries cannot be ruled out as this fleet operates close to shore in warm months. A similar lack of bycatch evidence in gill nets off Baja California Sur where 84% of green turtles had no external marks is indicative of fisheries interactions, whereas almost all strandings coincided with halibut and

guitarfish fishing seasons (Mancini et al. 2012). Reports indicate a significant increase in coastal gill net fishing effort, in both fleet size and net length (Ramos and Vasconcellos 2013). Mean length of bottom gill nets targeting white croaker doubled from 1995 to 2003 (Secchi et al. 1997, 2004) and fourfold to 2012 (Ramos and Vasconcellos 2013).

Gill nets have also been implicated as the main cause of green turtle mortality on the adjacent coast of Uruguay (Lezama et al. 2004) as well as globally (Byrd et al. 2011; Mancini et al. 2012). The fact that sampling effort was not a good offset for green turtle models is possibly due to a more homogeneous spatial pattern of strandings along the study area. Thus, as expected, the number of stranded green turtles increased with surveying effort. This is likely because greens are the most coast-dependent of the sea turtle species.

Green turtle strandings on the RSC have increased significantly over the last 10 years of surveys. This may be the result of ongoing increased in annual nesting populations in the south Atlantic, and hence, an increase in juveniles at foraging areas from these nesting populations. Weber et al. (2014) observed a sixfold increase in the number of green turtle nests during 36 years of observation at Ascension Island, which is the major source of juveniles foraging in southern Brazil (Proietti et al. 2012). An increase in nesting females was observed at Aves Island (García-Cruz et al. 2015) and a stable trend at Trindade Island (Almeida et al. 2011a), which are the second and third major sources of green turtles found in southern Brazil (Proietti et al. 2012).

Leatherback turtles

Similar to loggerheads, “month” and “year” were the most important explanatory variables for the variation in the mean number of stranded leatherbacks. The higher stranding of this species from late austral spring to early summer (November to January) is probably due to higher fishing effort during this period, as mentioned above. Nevertheless, its association with jellyfish abundance and distribution cannot be overlooked. In the northeastern Atlantic, leatherbacks were most abundant during the summer when gelatinous prey is plentiful (Witt et al. 2007).

Strandings of leatherbacks were relatively consistent across years throughout the study period. Given that fishing effort has increased over time (Secchi et al. 2004; Ramos and Vasconcellos 2013), the relatively stable trend in strandings suggests that the population of leatherbacks may be declining. A negative population trend in the number of nesting females was observed in Gabon (Godgenger et al. 2008), which is the major source of leatherbacks stranded in southern Brazil (Vargas et al. 2008; Vargas unpubl data). The cause of the mass-stranding that occurred in

November–December 2005 remains unclear as almost all carcasses were severely decomposed (stages 4 and 5), thus precluding proper evaluation for cause of mortality. Unusual blooms of jellyfish were reported by fishermen and a large amount washed ashore during the period of mass stranding; thus, it is possible that jellyfish blooms promoted a leatherback aggregation nearshore, thereby increasing the risk of bycatch in coastal fisheries.

Furthermore, the mean number of leatherback strandings was higher in years of La Niña (positive SOI values). The increase in SW wind observed in La Niña years (Esteves et al. 2006) can also bring more jellyfishes from oceanic to coastal waters, hence increasing the number of turtles and the chances of incidental catches in fisheries. Indeed, leatherback distribution has previously been linked to jellyfish hotspots, in the northeast Atlantic (Houghton et al. 2006).

Conclusions

This long-term study provides information on spatial and temporal stranding patterns, and trends and anthropogenic threats to loggerhead, green, and leatherback turtles in southern Brazil. Such information can be useful to infer demographics of nearshore turtles and establish conservation strategies, especially regarding threats. Incidental mortality in fisheries is probably the most important threat to sea turtles in southern Brazil. Because visible evidence of capture in trawl and gill net fisheries can be minimal or nonexistent, in our study only 1.2% of the turtle deaths had evidence of being killed in fisheries. However, the spatial and temporal overlap between sea turtles' strandings and fisheries distribution provides circumstantial evidence to suggest that bycatch is likely responsible for the mortality of a much higher proportion of stranded turtles. This relationship is also observed in other locations (e.g., Peckham et al. 2008; Casale et al. 2010; Mancini et al. 2012; Koch et al. 2013) and is corroborated by alternative evidence such as interviews with fishermen, onboard observers in fishing vessels, and logbooks (NEMA unpubl data).

Furthermore, strandings of juvenile loggerhead and green turtles have increased over the last 10 years. Stranded carcasses, however, represent a minimum measure that usually does not exceed 10–20% of total at-sea mortality (Epperly et al. 1996; Hart et al. 2006; Koch et al. 2013; Prado et al. 2013), meaning that many more turtles were likely killed at sea than the number observed washed ashore. These findings underscore our concern that fisheries bycatch mortality may have significant negative impacts on the source nesting populations of loggerhead and leatherback turtles. Whereas adult mortality will have a near-instantaneous impact on nesting numbers, juvenile

mortality will take years or decades—until the affected cohorts mature—to manifest as declines at the nesting beaches.

The RSC represents an important part of a large foraging and development ground for sea turtles and can be considered a hotspot for loggerhead, green and leatherback turtles. The extensive overlap with fisheries and the consequent high bycatch deserve urgent attention from managers concerned with reducing sea turtle mortality in this area. Our results suggest that time-area closures or reduction in gill net, pair trawl and possibly double-rig trawl fishing effort in coastal waters of southern RSC, during austral spring and summer months, could be effective measures for consideration in future fisheries management plans. Therefore, we recommend that the establishment of fisheries management plans take into account to the information regarding the conservation status and bycatch data of other threatened species (e.g., the endangered franciscana dolphin, *Pontoporia blainvillei*—Reeves et al. 2008; Secchi 2014; the guitarfish, *Rhinobatos horkelii* and angel sharks, *Squatina* spp.—Vooren and Klippel 2005), together with the fine-scale identification of areas of high bycatch risk.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants. All applicable international, national, and institutional guidelines for the care of animals found stranded alive were followed. In our study we did not conduct experimental analysis with animals.

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ELETRONIC SUPPLEMENTAL MATERIAL (ESM)

Long-term spatial and temporal patterns of sea turtle strandings in southern Brazil

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Table S1 Description of industrial fisheries that interact with sea turtles on the Rio Grande do Sul coast. All reference points that identify fishing areas are shown in Figure 1. NA = not applicable

	Bottom gillnet for white croaker	Bottom gillnet for stripped weakfish	Pair trawl	Double-rig trawl for shrimp	Double-rig trawl for fish	Otter trawl	Pelagic longline
Target species	white croaker (<i>Micropogonias furnieri</i>)	stripped weakfish (<i>Cynoscion guatucupa</i>) and Argentine croaker (<i>Umbrina canosai</i>)	<i>C. guatucupa</i> , <i>U. canosai</i> , <i>M. furnieri</i> and southern king weakfish (<i>Macrodon atricauda</i>)	Argentine stiletto shrimp (<i>Artemesia longinaria</i>) and Argentine red shrimp (<i>Pleoticus muelleri</i>)	Flatfish (<i>Paralichthys spp.</i>), Brazilian codling (<i>Urophycis brasiliensis</i>), monkfish (<i>Lophius gastrophysus</i>) and hake (<i>Merluccius hubbsi</i>)	<i>C. guatucupa</i> , <i>U. canosai</i> , <i>M. furnieri</i> and <i>M. atricauda</i>	tuna (<i>Thunnus spp.</i>), swordfish (<i>Xiphias gladius</i>) and sharks, mainly blue (<i>Prionace glauca</i>)
Net length (m)	4500 in the mid 1990s to over 18000 in the early 2010s	4500 in the mid 1990s to over 18000 in the early 2010s	NA	NA	NA	NA	NA
Net width (m)	4	3	NA	NA	NA	NA	NA
Mesh size (cm)	14	9	8–15	1.5–2.5	9	9–12	NA
Number of hooks	NA	NA	NA	NA	NA	NA	1000–1200
Soak time (hours)	12	12	NA	NA	NA	NA	6
Towing time (hours)	NA	NA	3–7 (mean:4.38)	4–4.5	3–4	4–6	NA
Depth (m)	ca. 5–50	ca. 25–150	10–80	14–30	18–500	12–150	140–5000

Fishing Area	between Mostardas' lighthouse and Chuí	between Mostardas' lighthouse and Chuí	along the entire coast	mostly between Conceição lighthouse and Albardão (in spring), and between Conceição and Mostardas, (in summer)	along the entire coast; mostly in shallow waters in austral spring and summer	mostly between Rio Grande and Chuí	along the entire coast
Season	austral spring and summer	austral autumn and winter	year round	austral spring and summer	year round	year round	autumn, winter and spring
Reference	Secchi et al. 1997, 2004; Ferreira et al. 2010	Secchi et al. 1997, 2004; Ferreira et al. 2010	Haimovici 1997; NEMA unpubl data	Duarte 2013; NEMA unpubl data	Haimovici 1997; NEMA unpubl data	Haimovici 1997; NEMA unpubl data	Neves et al. 2006

Table S2 Estimates, standard errors and p-values of coefficients for selected generalized linear models fitted to the number of stranded loggerhead, green and leatherback turtles in southern Brazil. The last line displays the maximum likelihood estimates of Θ and their standard errors. SOI = Southern Oscillation Index; km = sampling effort in kilometers; west_east_wind = maximum values of wind from west

Parameter	Loggerhead			Green			Leatherback		
	Estimate	Std-error	p-value	Estimate	Std-error	p-value	Estimate	Std-error	p-value
intercept	-3.78	0.36	<0.001	-1.54	0.66	0.0205	-4.39	4.68x10 ⁻¹	<0.001
year 1996	0.18	0.40	0.6724	1.30	0.70	0.0628	-1.16	6.06x10 ⁻¹	0.0549
year 1997	-0.16	0.44	0.7215	2.19	0.69	0.0015	-9.88x10 ⁻¹	6.85x10 ⁻¹	0.1493
year 1998	0.13	0.41	0.7515	1.79	0.69	0.0097	-1.38	6.91x10 ⁻¹	0.0463
year 1999	-0.31	0.53	0.5545	2.66	0.69	0.0001	-3.59	1.62x10 ⁷	0.9999
year 2000	0.63	0.44	0.0148	1.91	0.74	0.0099	-1.48	1.10	0.1784
year 2001	0.63	0.40	0.1085	1.75	0.70	0.0124	-1.06	6.32x10 ⁻¹	0.0934
year 2002	0.29	0.40	0.0458	2.38	0.68	0.0005	-3.34x10 ⁻¹	5.69x10 ⁻¹	0.5571
year 2003	0.79	0.40	0.0441	1.56	0.70	0.0265	-8.89x10 ⁻¹	6.69x10 ⁻¹	0.1834
year 2004	2.07	0.34	<0.001	3.27	0.66	<0.001	4.42x10 ⁻¹	4.92x10 ⁻¹	0.3685
year 2005	1.83	0.35	<0.001	3.18	0.66	<0.001	6.42x10 ⁻¹	4.89x10 ⁻¹	0.1876
year 2006	1.73	0.35	<0.001	3.14	0.66	<0.001	3.77x10 ⁻¹	5.02x10 ⁻¹	0.4523
year 2007	1.32	0.36	<0.001	3.09	0.66	<0.001	-1.34	6.31x10 ⁻¹	0.0338
year 2008	1.53	0.36	<0.001	3.72	0.65	<0.001	-1.17x10 ⁻¹	5.32x10 ⁻¹	0.8257
year 2009	1.49	0.35	<0.001	3.43	0.66	<0.001	-1.44x10 ⁻¹	5.24x10 ⁻¹	0.7843

year 2010	2.28	0.35	<0.001	4.28	0.65	<0.001	-3.11x10 ⁻¹	5.30x10 ⁻¹	0.5565
year 2011	2.14	0.35	<0.001	4.31	0.65	<0.001	-4.18x10 ⁻¹	5.42x10 ⁻¹	0.4397
year 2012	2.33	0.35	<0.001	3.79	0.66	<0.001	1.80x10 ⁻¹	5.29x10 ⁻¹	0.7330
year 2013	1.99	0.35	<0.001	4.08	0.65	<0.001	-1.14	6.21x10 ⁻¹	0.0658
year 2014	2.21	0.34	<0.001	4.37	0.65	<0.001	-1.53	6.20x10 ⁻¹	0.0139
month 2	0.10	0.26	0.6881	-0.22	0.21	0.2818	-9.55x10 ⁻¹	3.78x10 ⁻¹	0.0114
month 3	-0.16	0.26	0.5155	-0.49	0.21	0.0223	-2.05	4.84x10 ⁻¹	<0.001
month 4	-0.15	0.27	0.5740	-0.68	0.23	0.0025	-1.73	4.54x10 ⁻¹	0.0001
month 5	-0.36	0.28	0.2554	-0.78	0.23	<0.001	-8.80x10 ⁻¹	3.73x10 ⁻¹	0.0184
month 6	-1.48	0.33	<0.001	-1.89	0.27	<0.001	-1.12	3.96x10 ⁻¹	0.0048
month 7	-2.85	0.44	<0.001	-1.74	0.26	<0.001	-2.12	5.02x10 ⁻¹	<0.001
month 8	-2.76	0.43	<0.001	-1.34	0.24	<0.001	-2.51	5.81x10 ⁻¹	<0.001
month 9	-1.86	0.32	<0.001	-0.66	0.22	0.0026	-4.12	1.04	<0.001
month 10	-0.63	0.28	0.0226	-0.13	0.22	0.5341	-8.83x10 ⁻¹	3.77x10 ⁻¹	0.0193
month 11	0.17	0.25	0.4961	0.09	0.20	0.6758	4.72x10 ⁻¹	3.11x10 ⁻¹	0.1292
month 12	0.42	0.25	0.0873	0.25	0.20	0.2157	5.19x10 ⁻¹	3.15x10 ⁻¹	0.0995
area (southern)	-0.04	0.25	0.8660				2.40x10 ⁻¹	1.78x10 ⁻¹	0.1767
SOI	0.02	0.005	<0.001	-----	-----	-----	2.52x10 ⁻²	1.02x10 ⁻²	0.0134
km	-----	-----	-----	<0.01	<0.01	<0.001	-----	-----	-----
west_east_wind	-0.05	0.01	<0.001	-0.04	0.01	0.0021	-----	-----	-----
month 2 (southern)	0.17	0.35	0.6298	-----	-----	-----	-----	-----	-----

month 3 (southern)	0.27	0.35	0.4446	-----	-----	-----	-----	-----	-----
month 4 (southern)	-0.02	0.36	0.9664	-----	-----	-----	-----	-----	-----
month 5 (southern)	-1.05	0.38	0.0059	-----	-----	-----	-----	-----	-----
month 6 (southern)	-0.79	0.46	0.0834	-----	-----	-----	-----	-----	-----
month 7 (southern)	-0.61	0.64	0.3344	-----	-----	-----	-----	-----	-----
month 8 (southern)	-2.60	1.11	0.0196	-----	-----	-----	-----	-----	-----
month 9 (southern)	-2.09	0.60	0.0006	-----	-----	-----	-----	-----	-----
month 10 (southern)	-0.26	0.38	0.4966	-----	-----	-----	-----	-----	-----
month 11 (southern)	-0.17	0.34	0.6305	-----	-----	-----	-----	-----	-----
month 12 (southern)	-0.18	0.35	0.5977	-----	-----	-----	-----	-----	-----
Θ	2.733	0.335	-----	1.970	0.224	-----	1.178	0.248	-----

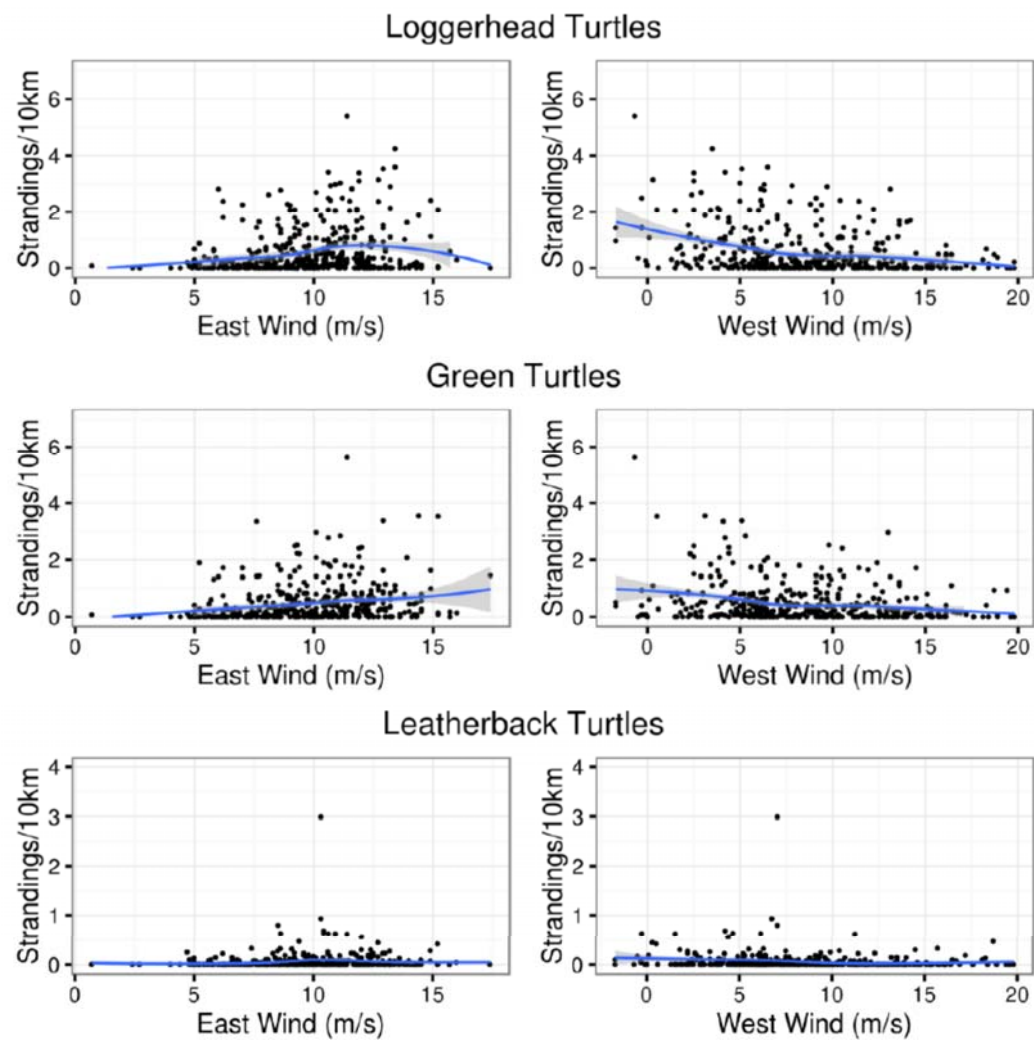


Fig. S1 Number of marine turtles washed ashore on the southern Brazilian coast in relation to wind direction and speed



Fig. S2 Sea turtles caught in trawl fishery. (a) leatherback being released to the sea after incidental capture in trawl fishery. (b) leatherback turtle washed ashore with a rope tied to its flipper. (c) loggerhead turtle stranded on the beach with rope around the flipper and neck



Fig. S3 Sea turtles found washed ashore in southern Brazil with nets around the body and neck, during monthly beach surveys in southern Brazil. (a) loggerhead; (b) leatherback and (c) green turtle



Fig S4 Loggerhead turtle washed ashore in southern Brazil with a pelagic longline hook and branch line attached to its beak

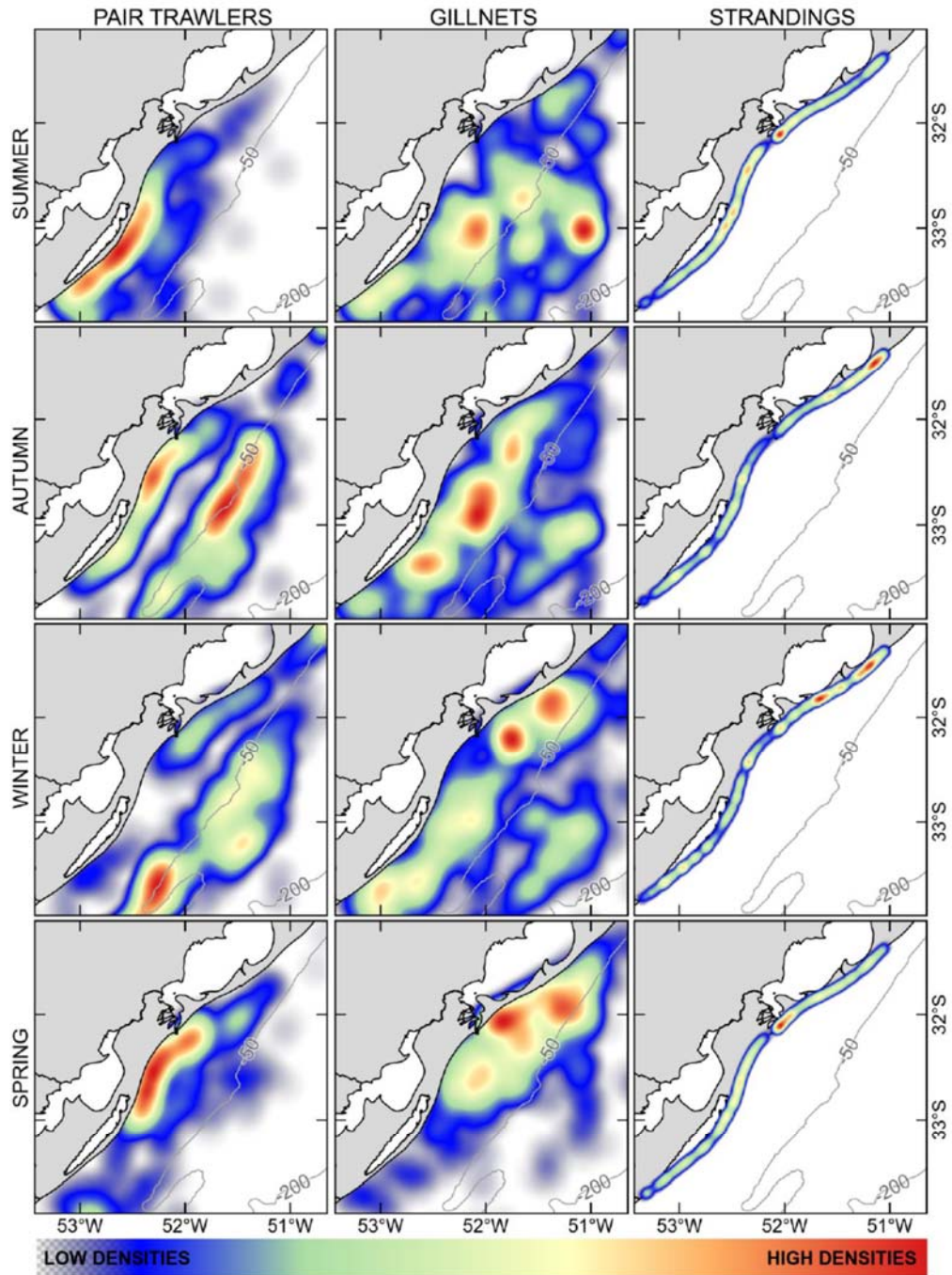


Fig. S5 Seasonal patterns in bottom pair trawl and gillnet fishing effort and sea turtle strandings in southern Brazil. Number of towns per season: summer ($n = 436$), autumn ($n = 535$), winter ($n = 624$) and spring ($n = 576$), number of gillnet sets: summer ($n = 498$), autumn ($n = 588$), winter ($n = 1010$) and spring ($n = 841$) and number of sea turtles: summer ($n = 2194$), autumn ($n = 1057$), winter ($n = 395$) and spring ($n = 2440$)

CAPÍTULO 2 / ANEXO 2

Ontogenetic habitat shifts and individual specialization in resource use by loggerhead sea turtles in the southwestern Atlantic Ocean

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Yonat Swimmer, & Eduardo R. Secchi

(Manuscrito submetido ao periódico *Oecologia*)

Ontogenetic habitat shifts and individual specialization in resource use by loggerhead sea turtles in the southwestern Atlantic Ocean

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Author Contributions: DSM, LB, JAS and ERS conceived and designed the research. DSM and CNTT performed the experiments. DSM analyzed the data and wrote the manuscript under the guidance of ERS, LB, and JAS. ERS, LB, JAS, YS, CNTT reviewed the manuscript.

Abstract

Ontogenetic habitat and diet shifts are related to energetic requirements and predation risk at different life stages. Oceanic stage duration, habitat and diet shifts, and individual specialization in resource use by loggerhead sea turtles (*Caretta caretta*) from the southwestern Atlantic Ocean (SWA) were determined through the analysis of carbon and nitrogen stable isotope ratios of growth increments in their humeri. The turtles were incidentally killed in pelagic longline fishery ($n=16$) or were found stranded on the Rio Grande do Sul coast ($n=19$). Cluster analysis and generalized additive mixed models (GAMM) were applied to identify the number of clusters that best fit the data of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios and to evaluate the influence of age and size in isotope values, respectively. Oceanic individuals had lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than those in the neritic turtles. Values increased significantly with age and size, and are consistent with a shift in diet towards higher trophic level preys. The mean age and length at transition was estimated at 13 years (range: 8 to 18) and 65 cm of curved carapace length (range: 55.7 to 77.9cm), respectively. Low within individual component/total niche width ratios indicate that this generalist population of loggerheads is composed of specialist individuals. Resource use by individual turtles was consistent over years within both neritic and pelagic life stages. The high variability in age and size at recruitment and the high degree of individual specialization can have consequences in population dynamics and, hence, information provided here is useful to guide conservation strategies.

Keywords: recruitment, trophic ecology, stable isotopes, ecological niche, *Caretta caretta*.

Introduction

Ontogenetic habitat and diet shifts are well documented for many vertebrates, such as fish (Dahlgren and Eggleston 2000), amphibians (Duellman and Trueb 1986), mammals (Newsome et al. 2009) and sea turtles (Bjorndal et al. 1997; Bolten 2003) and are likely related to energetic requirements and predation risk at different life stages (Werner and Gilliam 1984). For some species, shifts are linked to abrupt morphological changes, such as metamorphosis, or changes to very different areas or habitats (e.g. in anadromous fish or flatfishes). In other species, changes are not linked to marked morphological changes, but the mechanisms that trigger the onset of the ontogenetic niche shift remain largely unknown, and timing can vary among individuals within a population (e.g. Miller and Rudolf 2011).

Most trophic studies have considered all individuals as equal and the niche as a property of the species or population as a whole (Bolnick et al. 2003), whereas in fact many generalist populations are composed by specialized individuals of similar age and sex, whose niches are small subsets of the overall population niche (Bolnick et al. 2002). The degree of individual specialization may vary across life stages within a single species (Nshombo 1994; Kim et al. 2012; Vander Zanden et al. 2013), particularly if ontogenetic diet shifts occur. Determining the timescale over which niche variation persists is important because the temporal consistency of individual specialization will have implications for both evolution and ecology. Resource competition and selection will operate very differently when inter-individual variation is stochastic, temporary, or a permanent feature of the individuals in the population (Bolnick et al. 2003).

In sea turtles, the understanding of stage duration and how individuals within a population use resources in oceanic vs. neritic regions is limited. The duration of each life stage and its variation will influence the mean age at reaching sexual maturity and stage-specific survival rates, and therefore, their determination is essential for modeling population dynamics (Heppell et al. 2003). Mark-recapture of individuals or length-frequency analyses had been used to estimate these parameters. For example, the oceanic stage duration was inferred to occur between 6.5 and 11.5 years for loggerhead turtles in Northwestern Atlantic, based on length-frequency analyses (Bjorndal et al. 2000).

One technique that can yield insights on life stage duration in sea turtles is skeletochronology, the study of annually-deposited growth rings in their humerus bones

(Zug et al. 1986; Snover and Hohn 2004; Avens and Snover 2013). Through the skeletochronology technique, age estimation of sea turtles is determined by counting the growth marks (e.g. Snover et al. 2007; Avens and Snover 2013). A skeletal growth mark for one year of growth in sea turtles is composed by one thin and darkly stained line of arrested growth (LAG) and one broad lighter stained zone, representing the region of active growth (Castanet et al. 1993; Snover and Hohn 2004). However, in large individuals, early growth marks are entirely replaced by remodeling and endosteal growth, in a process called resorption (Zug et al. 1986). There are correction factors to estimate the number of LAGs lost due to resorption in each humerus (Parham and Zug 1997; Avens et al. 2012; Petitet et al. 2012). Therefore, the age is directly assigned by counting the number of observed LAGs in individuals that retained the first growth mark (annulus), which appears closest to the center of the bone as a diffuse line (Castanet et al. 1993) or can be estimated by adding the estimated number of lost LAGs to the number of observed LAGs (Parham and Zug 1997, Avens et al. 2012).

Examining annual growth layers can also provide insights on long-term diet and habitat use during the respective years of deposition. This is accomplished using stable isotope analysis under the assumption that the isotopic composition of consumer tissues, such as bone collagen, reflects the stable isotope values within its food sources (Fry 2006). Nitrogen (N) and carbon (C) stable isotopes are the most used elements in diet and habitat use studies. The $^{15}\text{N}/^{14}\text{N}$ ratio, expressed as $\delta^{15}\text{N}$ increases about 3-5‰ each trophic level due to preferential excretion of the lighter isotope and, therefore, is appropriate to indicate trophic position (Post 2002) and stage-related diet shift (Lajtha and Michener 1994). The $^{13}\text{C}/^{12}\text{C}$ ratio, expressed as $\delta^{13}\text{C}$, has a small enrichment of around 1.1‰ through each step of the food chain in marine environments (Post 2002). Nevertheless, the limited variation along the trophic chain and the typical coastal-to-pelagic and latitudinal gradients in $\delta^{13}\text{C}$ values (Michener and Schell 1994; Hobson et al. 1995) make this isotope useful to indicate location of feeding grounds and hence migratory and habitat usage patterns (e.g. Reich et al. 2007).

Stable isotopes retained in inert materials such as dentin, keratin, and collagen provide records of diet on annual or even lifetime scales (Newsome et al. 2009; Vander Zanden et al. 2010). Snover et al. (2010) observed a change in the pattern of growth marks when the loggerhead turtles (*Caretta caretta*) shift to neritic habitat, in addition to

changes in isotopic ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ collagen in bones, resulting from the change in diet and habitat. In recent studies, SIA has been used simultaneously with skeletochronology to identify the timing of habitat and diet shifts (Snover et al. 2010; Avens et al. 2013; Ramirez et al. 2015, Turner Tomaszewicz et al. 2016b). Based on sequential analysis of annual growth marks using these complementary approaches we are able to determine changes in habitat and diet for each individual, at each age and/or size, and therefore reconstruct long-term foraging ecology and habitat use.

Two metrics have been used to address aspects of individual resource use within a population: individual specialization (Roughgarden 1972) and temporal consistency (Vander Zanden et al. 2013). Individual specialization within the so-called generalist populations seems to be the rule rather than the exception (e.g. Araújo et al. 2011). Indirect dietary proxies, such as stable isotopes, offer alternatives for observing and understanding patterns of dietary variation in wildlife species (Newsome et al. 2009). In addition, isotopic niche is adopted as a proxy of ecological niche of a consumer (Bearhop et al. 2004). Although ecological and isotopic niches cannot be directly translated, isotopic variation within and among individual consumers of a particular species or population is a proxy for niche width (Bearhop et al. 2004; Newsome et al. 2007). Long-term individual variation in foraging behavior has been observed in many taxa, such as sea otters (Newsome et al. 2009), fur seals (Kermaleguen et al. 2012), seabirds (Bearhop et al. 2006) and sea turtles (Hatase et al. 2006; Reich et al. 2007). In green (*Chelonia mydas*) and loggerhead sea turtles, the degree of consistency and specialization in resource use at different ages is highly variable between individuals (Vander Zanden et al. 2013; Pajuelo et al. 2016).

Loggerhead turtles are highly migratory marine reptiles with a carnivorous diet in all life stages. Small juvenile loggerheads may spend more than a decade in oceanic habitat feeding upon epi-pelagic prey; they recruit to neritic habitats at larger sizes, often shifting to a demersal foraging strategy after this transition (Bolten 2003; Hopkins-Murphy et al. 2003, Turner Tomaszewicz et al. 2015). Recruitment to neritic environments, however, may not come with a concomitant sudden change in diet. For example, in northwestern Atlantic Ocean, juvenile loggerheads that had recruited to neritic environments maintained oceanic isotopic signatures during overwintering periods, indicating a continued feed on oceanic-pelagic organisms (McClellan et al.

2010). Later, Ramirez et al. (2015) identified two major patterns of recruitment, a gradual one, and another based on a sudden transition from oceanic to neritic environment, referred to as facultative and discrete shifts, respectively. Facultative ontogenetic shifts were also observed in loggerhead sea turtles in northeastern Pacific (Hatase et al. 2002), and in the Mediterranean (Casale et al. 2008).

The loggerhead is the most abundant sea turtle species among Brazilian rookeries (Marcovaldi and Marcovaldi 1999). While foraging grounds of adults are concentrated along the northeastern coast (Marcovaldi et al. 2010), pelagic and neritic waters of the southern Brazil are important foraging grounds for juveniles (e.g. Barros 2010; Monteiro et al. 2016). Oceanic juvenile turtles (mean curved carapace length - CCL of ca. 58 cm) are often incidentally caught in longline fisheries in the continental shelf-break and slope of southern Brazil (Sales et al. 2008), whereas neritic turtles (mean CCL of ca. 73 cm) are frequently bycaught in trawl fisheries and washed ashore (Monteiro et al. 2016). Thus, susceptibility to incidental mortality in different fisheries varies according to the developmental stages. In addition, juvenile loggerhead turtles from the neritic environment that were tracked via satellite telemetry showed two patterns of habitat use. While some individuals demonstrated a permanent habitat shift to neritic coastal waters where they remained throughout the year, others showed a reversible habitat shift, returning to oceanic habitat, mainly during austral autumn and winter months (Monteiro et al. unpubl. data).

Analyses of gut contents from loggerhead turtles found stranded on the coast and bycaught in longline fishery in southern Brazil revealed over 45 prey items and ontogenetic changes in diet, supporting the hypothesis of a generalist species. The oceanic juveniles preyed upon pelagic organisms, mainly salps and pyrosoms, whereas the diet of neritic turtles was predominantly composed of benthic hermit crabs and gastropods (Bugoni et al. 2003; Barros 2010).

In this study we determine for the first time the oceanic life stage duration, temporal consistency in resource use (diet and habitat), and degree of individual specialization in each life stage (oceanic and neritic) of loggerhead turtles in Southwestern Atlantic Ocean. For such, analysis of carbon and nitrogen stable isotope ratios of sequentially sampled bone tissue from growth increments in humerus of the turtles was performed. This study contributes to our understanding about patterns of

recruitment of a large marine vertebrate, which involves a marked shift in use of both spatial and trophic resources.

Materials and methods

Sampling and skeletochronology

Between January 2008 and December 2009, humerus bones were removed from loggerhead turtles stranded dead ($n = 19$) along the Rio Grande do Sul coast (herein referred to as neritic turtles) and from individuals incidentally caught in the longline fishery ($n = 16$) of southern Brazil (herein referred to as oceanic turtles) (Fig. 1). Curved carapace length (CCL) was measured from nuchal notch to posterior tip (Bolten 1999). Stranding and bycatch locations were recorded. Humeri were processed and histologically prepared for a previous skeletochronology study (Petitet et al. 2012), from which estimated age and observable LAG diameter results were used. The diameter of the LAGs for each turtle were used to back-calculate CCLs at each successive growth increment (Snover et al. 2007). We applied the best-fitted model to describe the relationship between curved carapace length and humerus diameters as proposed by Petitet et al. (2012). Then, we back-calculated body size estimates at each LAG as described in Snover et al. (2007) by applying the body proportional hypothesis (BPH)-corrected allometric equation, developed by Francis (1990) and adapted by Snover et al. (2007), using the best-fitted model as f (Petitet et al. 2012) and the formula below:

$$L_b = [f(D_b)] [L_{final}] [f(D_{final})]^{-1}$$

where L_b is the back-calculated length; D_b is a given diameter; L_{final} is the CCL of a turtle at death; and $f(D_{final})$ is the back-calculated CCL based on humerus diameter. This age/size at each LAG was aligned to growth layers sampled for SIA (Fig. 2) and this information was used to determine the length at transition from oceanic to neritic environments and size-related diet shift.

Stable isotope analysis

A cross-section of ca. 1.0 mm thick, adjacent to the section used for skeletochronology, was cut from each humerus for stable isotope analyses using an Isomet slow speed saw fitted with a diamond-embedded blade. Each section was mounted onto microscope slides and the sampling of bone powder was conducted following the steps and methodology

presented by Turner Tomaszewicz et al. (2016a). In brief, we used an Olympus SZX10 microscope fitted with an Olympus SpotFlex camera (U-CMAD-2) to display a live image of the bone section on the computer monitor that was interfaced with a computer-guided micromilling system (Carpenter Microsystems CM-2, version 3.0.6). Sampling paths and depths for extracting bone powder were programmable and we used an NSK Volvere Vmax drill at 10,000 rpm, fitted with a 0.10 mm carbide dentist bit for sample collection. For identifying annual growth layers in the bone sections, we used a transparency film with the skeletochronology-derived image as an “annual layer guide”.

Approximately, 1.0 to 1.5 mg of bone dust was collected from each annual growth layer. Composite (i.e. multiple year) samples were collected when adjacent LAGs were very narrow. The samples were weighted in tin capsules and the carbon and nitrogen isotope ratios were measured by combustion in a Carlo Erba NA 1500 CNS elemental analyzer interfaced via a ConFlow II device to a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer. These analyzes were performed in the Stable Isotope Geochemistry Lab at the University of Florida, Gainesville, USA.

Stable isotopes values are expressed in δ notation as parts per thousand (‰) differences from the international standard material, Vienna Pee Dee Belemnite limestone and atmospheric nitrogen for carbon and nitrogen, respectively, according to the following equation (Bond and Hobson 2012):

$$\delta X (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}}) - 1$$

where X is the ^{15}N or ^{13}C value, and R is the corresponding ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ (Peterson and Fry 1987). Laboratory reference materials (USGS40) were calibrated at regular intervals against the standards. The average precision for these data was determined using the standard deviations around the means for the internal laboratory standards run at set intervals and was 0.13‰ for $\delta^{15}\text{N}$ and 0.08‰ for $\delta^{13}\text{C}$.

Data analysis

We applied cluster analysis to identify the number of groups that best fit the data. Clusters were evaluated for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values together and separated using the function *pam* in the package *cluster* in R (Maechler et al., 2015; R Core Team, 2015). Euclidean distance was used to calculate dissimilarities, and average silhouette width was used to identify the best fit for numbers of clusters. Silhouette width is a measure for clustering

validity and indicates the strength of cluster membership for each observation (Kaufman and Rousseeuw 1990), where values between 0.7 and 1 indicate a strong structure within the dataset.

Generalized additive mixed models (GAMM) were used to evaluate the influence of the covariates age and size (CCL) in nitrogen and carbon values. The factors CCL and age were separated into different models because high degree of concavity, which can confound statistical inference (Arens et al. 2012). Therefore, model GAMM_δ¹⁵N_CCL incorporated only the covariates δ¹⁵N and CCL, whereas GAMM_δ¹⁵N_Age included Age and δ¹⁵N. We used GAMMs to account for the incorporation of multiple annual growth intervals from each turtle and the models included turtle identification as a random individual-specific effect (Wood 2006; Arens et al. 2012, 2013). The model was structured using a Gaussian distribution, identity link function, and smoothed curves (thin plate regression splines) as smoothing functions. Models were implemented using the *mgcv* and *nlme* packages in R (Wood 2006; R Core Team, 2015). Significance of GAMM model factors was determined by non-parametric *F*-ratio test.

Mean age and back-calculated CCL at transition were estimated at the beginning of an ontogenetic shift based on turtle-specific δ¹⁵N data. These estimated ages and CCLs were visually compared with the GAMM fit for neritic turtles only. The timing of an ontogenetic shift was identified as the first growth increment where the δ¹⁵N value surpassed the threshold determined based both on the mean δ¹⁵N value of pelagic prey and on the cluster analysis where the lower and upper δ¹⁵N values split the data into neritic and oceanic groups. The mean δ¹⁵N value of salps in the oceanic environment of southern Brazil was $4.95 \pm 1.56\text{‰}$ ($n = 8$; EcoMega/FURG unpubl. data). Assuming an enrichment of 3 to 5‰ (Post 2002), the δ¹⁵N value in the predator's tissues feeding in this area on this prey should be around 8 to 10‰. A variation (Δ) in δ¹⁵N value of +3‰ that surpasses the threshold in one year indicates a discrete recruitment, whereas a $\Delta\delta^{15}\text{N}$ value of +3‰ that takes a multiple years to occur, represent an gradual recruitment (see Ramirez et al. 2015). When necessary, changes in δ¹³C values were used as supporting evidence of a habitat shift. When multiple growth layers were sampled, the isotopic value from these “composite layers” was attributed to the mean age/and size of the corresponding LAGs or between the prior and posterior LAGs.

To determine the degree of individual specialization and temporal consistency in resource use by oceanic and neritic loggerheads we used the variance in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Because both habitat and diet influence stable isotope values, we employ the term “resource use” to reflect the integration of these two factors in the foraging history of the animal (Vander Zanden et al. 2013). In the case of neritic turtles, only the LAGs indicative of neritic signatures were included. Based on the framework proposed by Roughgarden (1972), the within-individual component (WIC) is the mean variance within individuals, while the between-individual component (BIC) is the variation among individuals and the total niche width (TNW) of the population represents the variance along a continuous axis of the species’ resource use is a sum of WIC + BIC (Bolnick et al. 2003; Vander Zanden et al. 2013). The degree of individual specialization is determined by the ratio of WIC/TNW, where values close to 0 indicate specialist individuals, and values close to 1 indicate generalist individuals (Bolnick et al. 2002). We used an ANOVA framework as a proxy for these values to compare variation within and between individuals (Matich et al. 2011), as did Vander Zanden et al. (2013) for North Atlantic green turtles, using carapace scutes. The mean sum-of-squares within individuals (MSW) measures the variability within individuals, which we used as a proxy for WIC, and was calculated through the equation:

$$\text{MSW} = \frac{\sum_i \sum_j (x_{ij} - \bar{x}_i)^2}{(N - k)}$$

and the mean sum-of-squares between individuals (MSB) measures the variability among individuals and was the proxy for BIC, and was calculated as:

$$\text{MSB} = \frac{\sum_i \sum_j (x_i - \bar{x})^2}{(k - 1)}$$

where i represents an individual, j represents a single growth increment, N is the total number of observations, and k is the number of individuals. The sum of MSB + MSW was a proxy for TNW (Vander Zanden et al. 2013). In this study, we also used WIC to evaluate temporal consistency, that is the variation within individuals over time, where small WIC values indicate that individuals are consistent in resource use through time (Vander Zanden et al. 2013). All statistics were performed using the software R (R Core Team 2015) version 3.2.3.

Results

Sixteen oceanic turtles and 19 neritic turtles were studied. The oceanic turtles were incidentally caught in the Brazilian longline fishery and ranged from 51.5 to 66.5 cm (mean = 59.8, SD = 4.2 cm) of CCL and from 9 to 19 years of age. The neritic turtles, found washed ashore in southern Brazil, were 64.5 to 88 cm (mean = 75.0, SD = 6.8 cm) long and 13 to 24-year old (Fig. 1).

A total of 302 growth increments were sampled and analyzed for stable isotopes from all 35 loggerhead humeri (mean = 9; range = 5 to 13 LAGs per turtle). A total of 66 samples were composites of two ($n = 28$), three ($n = 2$) or four ($n = 1$) LAGs.

Ontogenetic shift

Two clusters, based on $\delta^{15}\text{N}$ only, best fit the distribution of stable isotope signatures for loggerhead turtles. The average silhouette of 0.69 is indicative of a strong structure within the dataset. The more enriched $\delta^{15}\text{N}$ cluster (mean $\delta^{15}\text{N} = 14.03$, SD = 1.62 ‰; mean $\delta^{13}\text{C} = -15.10$, SD = 1.31 ‰; $n = 61$) was separated approximately at $\delta^{15}\text{N} = 11.20$ ‰ from the more depleted $\delta^{15}\text{N}$ cluster (mean = 8.35, SD = 1.22 ‰; mean $\delta^{13}\text{C} = -17.32$, SD = 1.01 ‰; $n = 206$) (Table 1; Fig. 3).

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values ranged, respectively, from 6.23 ‰ to 12.96 ‰ (mean = 8.49, SD = 1.27 ‰) and from -20.59 ‰ to -15.64 ‰ (mean = -17.52, SD = -0.98 ‰) in the oceanic turtles (Fig. 4). Almost all LAGs from oceanic turtles had $\delta^{15}\text{N}$ values below the $\delta^{15}\text{N}$ threshold of 11.20 ‰ and were placed in the depleted $\delta^{15}\text{N}$ cluster. Only one turtle exhibited a much higher value for nitrogen (i.e. 12.96 ‰) in its last LAG (corresponding to an inferred age of 12 years and a CCL of 65 cm) compared to all other oceanic turtles. Two other turtles also showed $\delta^{15}\text{N}$ values higher than the threshold, though the difference was much smaller (11.30 and 11.73 ‰) and occurred at initial ages of 2 and 3 years. Although we observed four oceanic turtles with a marked increase in $\delta^{15}\text{N}$ values that surpassed the 3 ‰ after the first years, these values were lower than the threshold of 11.20 ‰ that identify the shift from oceanic to neritic habitat (Fig. S1). Four oceanic turtles were older than the estimated mean age at transition of 13 years (Table 2).

Based on CCL-at-age relationships and skeletal growth increment stable isotope analysis of $\delta^{15}\text{N}$, the mean age at transition was estimated at 13 years (range from 8 to 18 years). For the neritic turtles, $\delta^{15}\text{N}$ values ranged from 6.47 ‰ to 17.32 ‰ (mean = 10.80,

SD = 2.98 ‰) and $\delta^{13}\text{C}$ values ranged from -19.58 ‰ to -12.77 ‰ (mean = -16.27 , SD = -1.48 ‰) (Fig. 4). We observed a marked increase of ca. 3.40‰ in $\delta^{15}\text{N}$ values for 18 of 19 turtles, which is consistent with a transition from oceanic to neritic habitat. The only turtle that did not show an increased $\delta^{15}\text{N}$ value was 21-years old and 75 cm long. The estimated mean CCL at transition was 65 cm, ranging from 55.7 to 77.9 cm (Table 2). The mean pre-shift of $\delta^{15}\text{N}$ values was 10.03‰ and the mean post-shift was 13.43 ‰ (Table 2). For 11 turtles we observed a concomitant increase in $\delta^{13}\text{C}$ values, indicative of a shift from oceanic to neritic habitats (Table 2, Fig. S2). The mean pre-shift of $\delta^{13}\text{C}$ values was -16.72 ‰ and the mean post-shift was -15.42 ‰ (Table 2). For 11 neritic turtles, a likely recruitment to neritic habitat was observed (Table 2; Fig. S2). At least five neritic turtles exhibited sharp increases in $\delta^{15}\text{N}$ values of ca. 3 ‰ in one year and were classified as discrete turtles. Four turtles were facultative, with gradual increases $\delta^{15}\text{N}$ values, which increased by at least 3 ‰ over the course of more than one year. Nine individuals could not be classified, because we were unable to sampling single LAG just post-shift growth increment layer.

GAMMs incorporating the growth increment-specific isotopic data revealed a significant correlation of both age and back-calculated CCL-at-age with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Table 3). The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values increase significantly with both age and back-calculated CCL-at-age (Table 3; Figs. 5 and 6).

Temporal consistency and individual specialization

Temporal consistency in resource use was observed in both oceanic and neritic phases and the degree of within-individual variability was similar between these two phases (Table 4). The degree of individual specialization (WIC/TNW) was higher in neritic than in oceanic turtles (Table 4). The overall results indicate that loggerhead turtle population is generalist composed by specialist individuals.

Discussion

Many marine organisms undergo one or more ontogenetic habitat shifts as they grow to maximize growth rates while minimizing predation risks. Several ecological processes can influence these shifts, including size-specific predation, size-specific limitations to habitat exploitation, and density dependence (e.g. Werner and Gilliam 1984; Snover

2008). In addition, organisms can adopt different foraging strategies between and within life stages (Bolnick et al. 2003), and the general patterns can be more complex than previously thought. This complexity is probably due the intrinsic heterogeneity among individuals that lead to great variability in the onset and patterns of the recruitment process, as demonstrated for loggerhead sea turtles in this present study. Our results revealed that the combined analysis of nitrogen and carbon stable isotope ratios improved the resolution for tracking diet and habitat shifts in sea turtles. Although $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values showed convergent patterns for most individuals (see Figs. S1, S2), $\delta^{15}\text{N}$ performed better in identifying ontogenetic shifts, as observed in loggerheads sea turtles in northwestern Atlantic Ocean (Ramirez et al. 2015), and in the North Pacific Ocean (Turner Tomaszewicz et al. 2016b).

In our study, each growth increment-specific LAG was an integration of information over an entire year, thus reflecting the mean dietary stable isotope value for that time interval (Avens et al. 2013; Ramirez et al. 2015; Turner Tomaszewicz et al. 2016b), or multiple years in cases of composite samples. With the analyses of this tissue from sequential LAGs we were able to reconstruct retrospectively and depict important differences in the diet and habitat use for individual loggerhead sea turtles beginning in their early life stages in oceanic waters, the transition period and ending in their neritic phase.

Ontogenetic niche shift

The increase in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with age is consistent with the recruitment to neritic habitat and a shift in diet from low to high trophic levels. With the exception of one individual, all stranded turtles presented a marked increase ($> 3\text{‰}$) in $\delta^{15}\text{N}$ values, likely reflecting a transition from oceanic to neritic habitats. More than half (61%) of these turtles had a concomitant increase in $\delta^{13}\text{C}$ values ($> 1.31\text{‰}$), as expected for oceanic-to-neritic habitat shifts. The only turtle that did not show an increased $\delta^{15}\text{N}$ value was 21-years old and 75 cm of CCL. Although information is not available for the last very narrow LAG, all other sampled layers presents oceanic signature, including the growth increment corresponding to age 20 ($\delta^{15}\text{N} = 9.75\text{‰}$ and $\delta^{13}\text{C} = -18.03\text{‰}$). Thus, it is very likely that this turtle was probably a late first year recruit to the neritic habitat. Long oceanic stage duration was also observed in three oceanic turtles that had not recruited

until the age between 17 and 18 yrs. The late recruitment to neritic habitat may lead to delayed maturation, that is consistent with the estimated mean age at maturation for this population at 32 year of age (Petitet et al. 2012). Individuals that settle early and remain in neritic habitat are likely to attain sexual maturity at younger ages as they will feed on prey of higher energetic value (3.07 to 5.50 KJ/g) compared to those preyed upon in the oceanic environment (0.37 to 0.95 KJ/g - Barros 2010). In sea turtles the shift from oceanic to neritic habitat is most frequently explained to maximize growth rates (Snover 2008; Avens et al. 2013). Therefore, this change in diet promotes faster growth and energy storage to meet energetic requirements for reproduction.

In the present study, mean age and size at transition to neritic habitat for loggerhead sea turtles in southwestern Atlantic Ocean was estimated at 13 years and 65 cm CCL, respectfully. Our results were similar to those observed in the western North Atlantic (Avens et al. 2013; Ramirez et al. 2015). For loggerhead sea turtles at Baja California Mexico, in the North Pacific Ocean, a bimodal age (and size) distribution in timing of recruitment from oceanic to neritic coastal waters was observed, with a group of turtles shifting with mean age of 7.5 years and another group with 15.6 years (Turner Tomaszewicz et al. 2016b), showing yet another pattern of ontogenetic shift variability in a loggerhead population and demonstrating the high plasticity of the species to explore resources.

We observed that individuals that use offshore waters have lower $\delta^{15}\text{N}$ than those using neritic habitats. Since baseline $\delta^{15}\text{N}$ values are similar between particulate organic matter (POM) sampled from surface waters over the continental shelf ($5.94\text{‰} \pm 2.22\text{‰}$; $n = 19$) and in deep waters ($5.53\text{‰} \pm 3.23\text{‰}$; $n = 19$) of southern Brazil (EcoMega/FURG unpubl. data), the significant changes in $\delta^{15}\text{N}$ values within turtles indicate an ontogenetic shift in diet with neritic turtles feeding upon prey of higher trophic level. The mean difference in pre- and post-shift $\delta^{15}\text{N}$ values ($3.4\text{‰} \pm 1.56\text{‰}$) found in this study was consistent with observed 3-5‰ enrichment in ^{15}N per trophic level within food webs (Post 2002). A similar pattern was observed in loggerhead turtles from the northwestern Atlantic, where stable isotope values, mainly $\delta^{15}\text{N}$ of the prey items consumed by loggerhead turtles in the oceanic habitat, were significantly lower than those consumed in the neritic habitat (Snover et al. 2010).

Among all oceanic turtles sampled, a single individual exhibited a much higher value for nitrogen (12.96‰) in its last LAG, corresponding to an inferred age of 12 years and a CCL of 65 cm. This suggests that the turtle had started its transition to the neritic habitat and was feeding upon demersal prey of higher trophic level. Although the resolution of growth increment-specific $\delta^{15}\text{N}$ values is likely insufficient to depict back and forward movements between oceanic and neritic habitat lasting a few months, it seems clear that that turtle was performing this movement pattern as it presented a high $\delta^{15}\text{N}$ value in its last LAG and was killed far offshore in the pelagic longline fishery (see Fig. S1, individual ID = ES009). Analyses of gut contents from these oceanic individuals showed typical items from neritic environments such as benthic crabs in two turtles, thus supporting the notion of neritic foraging, followed by movement offshore, prior to capture in the fishery. Similarly, items of pelagic origin, such as salps, pteropods and *Lepas* spp. were found in three turtles stranded on the beach with CCLs of 57, 68 and 69 cm (Barros 2010), suggesting offshore foraging followed by movement to neritic habitats. Three turtles that had already recruited to the neritic environment (based on $\delta^{15}\text{N}$ values > 11.2 ‰) showed a slight decrease (ca. 1.2‰) in $\delta^{15}\text{N}$ values in their most recent (outer) bone growth layers. This evidence of back and forth movement is consistent with five loggerhead turtles (three adults and two juvenile) that were tracked with satellite telemetry in the neritic environment and spent up to 50% of the time in the oceanic habitat (Monteiro et al. unpubl. data). In another study that deployed satellite transmitters in oceanic loggerheads incidentally caught in longline fishery, 48% (n=13) of the tracked individuals returned to neritic habitat (Barceló et al. 2013). In the western North Atlantic, juvenile loggerheads were observed using oceanic habitat for long periods of time and moving back and forth between coastal and oceanic environments (e.g. McClellan and Read 2007; Mansfield and Putman 2013). Elsewhere, seasonal variability in habitat use has been observed, with loggerheads overwintering and feeding in oceanic areas (McClellan et al. 2010; Hawkes et al. 2011). Analyses of stable isotopes in carapace scutes from male loggerheads in western North Atlantic did not detect cyclical changes in $\delta^{13}\text{C}$ values, thus lacking to support seasonal variability in habitat use (Pajuelo et al. 2016).

Our results indicate that the time at and duration of the ontogenetic diet and habitat shift of loggerhead turtles in the southwestern Atlantic Ocean is highly variable and

ranges between 8 and 18 years. Consequently, an overlap in age and size between oceanic and neritic turtles was observed. This intra-specific variation in ontogenetic shifts demonstrates individual variability in resource use by loggerhead turtles. The observed variability in age and size at recruitment to neritic habitat can be related with interdependent factors, such as environmental variability (Mansfield and Putman 2013), and individual genotypes (Piovano et al. 2011). Congdon et al. (1992) suggested that differential habitat use associated with age or size in turtles may be due to changes in diet, distribution of food resources of appropriate size, size-specific risks to predation, or a combination of these factors. Hatase et al. (2002) proposed an analogy with anadromous salmonids and hypothesized that immature female loggerhead sea turtles encountering rich patches of food in offshore areas settled there and remained oceanic throughout their life, whereas those experiencing food scarcities during their oceanic stage became neritic.

The determination of life stage duration is difficult because the shift can last several years instead of being discrete in time (Casale et al. 2008; Ramirez et al. 2015). Some studies have shown evidence that this shift is not abrupt in sea turtles and could be reversible during development (Hatase et al. 2002; McClellan and Read 2007). In the Mediterranean Sea, loggerhead sea turtles start to feed upon benthic prey in neritic waters early in life (Casale et al. 2008). In the western North Atlantic, Ramirez et al. (2015) estimated that 37% of loggerhead turtles that exhibited an ontogenetic shift were “facultative shifters” and that the transition may last up to five years. In our study, a gradual increase in $\delta^{15}\text{N}$ values was observed spanning between two and four years, indicative of the continuum transition, though sampling of individual growth increment was only possible in four turtles.

Temporal consistency and individual specialization

Oceanic juveniles presented similar temporal consistency to neritic juveniles, with lower within individual component (WIC) than neritic turtles. We observed that individual specialization in resource use of loggerhead turtles varied between life stages. The degree of individual specialization was higher (lower WIC/TNW ratio) in neritic turtles than in oceanic turtles. A high degree of individual specialization was observed for other loggerhead sea turtle populations. In North Carolina, USA, individual turtles in the neritic habitat were specialized in resource use relative to the population (Goodman-Hall et al.

2015). Adult females from Florida (Vander Zanden et al. 2010) and adult males from South Carolina/Georgia (Pajuelo et al. 2016) presented a high degree of individual specialization. For green turtles, the degree of individual specialization was highest in adult females and higher in neritic turtles than in oceanic turtles (Vander Zanden et al. 2013).

Loggerhead sea turtles are considered the most generalist sea turtle species (Bjorndal 1997, 2003), and our results indicate that in the southwestern Atlantic Ocean, the generalist population is composed of specialist individuals in both oceanic and neritic life stages. Analyses of gut contents showed that loggerhead sea turtles stranded in southern Brazil were generalists, consuming up to 45 prey species (Barros 2010); the mean number of prey consumed by an individual turtle was 5.5 (D. Monteiro, pers. obs. calculated from same data used by Barros 2010).

The higher WIC/TNW observed in oceanic versus neritic turtles is likely due to greater variation in stable isotopes baselines of oceanic environments used by these individuals. The nearest loggerhead rookery is located 1550 km to the north of our study area. Younger turtles were probably feeding in tropical oceanic areas close to their natal home, before migrating south to their feeding grounds in the subtropical waters near southern Brazil. However, the long-term consistency in resource use suggests that neritic loggerhead turtles exhibit some degree of fidelity to their foraging areas. Assuming that these oceanic and neritic individuals exhibited fidelity to these foraging grounds, we suggest that changes in $\delta^{13}\text{C}$ and especially $\delta^{15}\text{N}$ values within (WIC) and between (BIC) turtles in each respective life stage represent variation in resource use within the foraging area.

Although there is growing evidence about individual specialization in several taxa and the relevance in understanding this process (Araújo et al. 2011), variation in resource use among and within individuals remains poorly understood. It has been suggested that intra- and inter-specific competition influences foraging decisions of individuals over time, which leads to increased individual specialization (Bolnick et al. 2003; Araújo et al. 2011). Our findings indicate that individual specialization in resource use by loggerhead sea turtles is consistent over years; that is, individuals forage on the same prey items or groups of prey with similar isotope values over a long period of time.

Ecological and conservation implications

The high variability in age and size at recruitment, the high degree of individual specialization and temporal consistency present in both oceanic and neritic life stages observed in the present study have ecological and conservation implications. Differential habitat use and foraging behaviors at various life stages within a population can have consequences for survivorship, stage duration, time to maturity and reproductive success (e.g. Snover 2008). Kim et al. (2012) found significant variability in the degree and timing of shifts with age among individuals of white-shark (*Carcharodon carcharias*) in California and suggested that this pattern may be a mechanism to increase foraging success in species experiencing high intraspecific competition (i.e., the niche variation hypothesis; Van Valen 1995). Instead of individuals using all resources equally, individual foraging patterns diverge to create a spectrum of specialists that do not differ in survival or reproductive success (Bolnick et al. 2003; Estes et al. 2003; Newsome et al. 2009). Sea otters (*Enhydra lutris nereis*), for example, have highly individualized diets, with most individuals maintaining unique dietary patterns through time (Newsome et al. 2009) and these individual dietary preferences, observed in the Monterey Bay sea otter population, can transcend generations through the cultural transmission from mothers to offspring (Estes et al. 2003).

For loggerhead sea turtles the optimal size at the pelagic-to-neritic habitat shift may vary considerably over time and sources of mortality vary within and between oceanic and neritic habitats (Snover 2008). In southern Brazil, loggerhead sea turtles are highly vulnerable to bycatch in longline fisheries during their oceanic phase, whereas the main source of mortality for turtles in neritic stage is the incidental capture in trawl fisheries that operate along the continental shelf (Monteiro et al. 2016). Individuals that transit between these two habitats, therefore, may be exposed to both sources of mortality at variable degrees, depending on the duration of residence in each area.

Populations composed by long-term specialist individuals are less able to quickly respond to environmental changes (Bolnick et al. 2003). On the other hand, this behavior can bring benefits to population. Consistent use of a known foraging ground that provides sufficient resources is probably a more beneficial strategy than wandering through unexplored new areas (Schofield et al. 2010). Highly variable populations may be more

stable in the face of competition or predation (Lomnicki 1984) and can be more resilient to environmental changes and anthropogenic impacts (Perez et al. 2016).

Describing a species as the sum or the average of its parts can vastly simplify both empirical data collection and theoretical models (Bolnick et al. 2003). Population models for sea turtles, in general, use fixed stage duration (Crouse et al. 1987; Heppell et al. 2003). The inclusion of observed uncertainty in stage duration improves the reliability of those models and predictions about population status on a probabilistic framework.

The results presented here highlight the importance of combining methodologies for elucidating life history patterns and improve the resolution of inter-individual variability of loggerhead sea turtles foraging behavior. Our findings corroborate that indirect proxies for resource use, such as stable isotopes, offer alternatives for documenting patterns of variation in numerous species (Bearhop et al. 2004; Newsome et al. 2007, 2009) and that inert tissues, such as bones, are useful to reconstruct animal trajectories (e.g. Avens et al. 2013, Ramirez et al. 2015, Turner Tomaszewicz et al. 2016b). Moreover, this approach can be applied to other taxa for which age determination and sequential sampling of chronologically ordered growth increments are possible.

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Ethical approval: This article does not contain studies with human participants. In our study we did not conducted experimental analysis with animals alive. We were sampled animals found stranded dead at beach or incidentally killed in fisheries.

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Table 1. Determination of numbers of clusters based on average silhouette widths using the *pam* partitioning algorithm. Bold value indicates best fit

Number of clusters	$\delta^{15}\text{N}$ only	$\delta^{13}\text{C}$ only	$\delta^{15}\text{N}$ & $\delta^{13}\text{C}$
2	0.69	0.55	0.63
3	0.61	0.47	0.46
4	0.60	0.54	0.33

Table 2. Estimated age and CCL for neritic loggerhead turtles ($n = 18$) pre and post-shift from oceanic to neritic habitat and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values pre and post-shift

Turtle_ID	Age pre- shift	Age post- shift	CCL pre- shift	CCL post- shift	$\delta^{15}\text{N}$ pre- shift	$\delta^{15}\text{N}$ post-shift	$\delta^{13}\text{C}$ pre-shift	$\delta^{13}\text{C}$ post-shift	Difference $\delta^{15}\text{N}$	Difference $\delta^{13}\text{C}$
PR033	7	8	53.93	57.58	11.01	14.90	-16.39	-14.79	3.89	1.61
PR004	8	12	64.07	71.93	9.68	15.70	-16.19	-13.89	6.02	2.30
PR010	8	11	51.58	55.65	10.20	12.32	-15.73	-15.90	2.12	-0.17
PR007	9	11.5	56.57	59.40	10.99	13.78	-16.17	-15.65	2.79	0.52
PR043	10.5	13	56.21	60.95	8.82	15.23	-16.41	-14.29	6.41	2.12
PR050	10.5	12.5	61.82	67.12	10.99	12.14	-18.08	-14.97	1.15	3.11
PR008	11	15	66.89	68.64	10.15	11.80	-16.31	-15.14	1.65	1.17
PR013	11	12	74.63	77.88	9.70	13.02	-18.84	-15.81	3.32	3.03
PR016	12	14	56.79	65.02	9.88	14.27	-16.63	-16.73	4.39	-0.10
PR021	12	13	64.10	67.11	10.44	11.27	-16.26	-16.71	0.83	-0.45
PR037	12.5	15	60.97	64.84	8.60	13.54	-16.85	-15.31	4.94	1.54
PR003	13	14	59.10	62.00	9.66	12.41	-17.07	-16.32	2.75	0.75
PR011	13	14	56.72	57.68	11.14	14.04	-15.67	-14.90	2.90	0.77
PR044	13	17	64.06	66.50	9.21	13.03	-18.41	-15.29	3.82	3.12
PR022	14	16	62.47	68.49	11.09	15.69	-15.50	-13.93	4.60	1.57
PR026	14	15	67.73	70.38	9.60	12.37	-18.59	-17.39	2.77	1.20
PR002	15.5	20	59.56	63.37	9.46	11.78	-16.43	-15.39	2.32	1.04
PR023	16	18	NA	NA	9.92	14.44	-15.49	-15.07	4.52	0.42
mean	11.67	13.28	61.01	64.97	10.03	13.43	-16.72	-15.42	3.40	1.31

Table 3. Statistical output from the generalized additive mixed models (GAMMs) for age and all back-calculated growth-increments. Edf = estimated degrees of freedom; CCL = curved carapace length

Model	<u>Smooth terms</u>			
	Variable	Edf	<i>F</i>	Prob (<i>F</i>)
GAMM_ $\delta^{15}\text{N}_{\text{CCL}}$	CCL	6.105	60.56	<0.001
GAMM_ $\delta^{15}\text{N}_{\text{Age}}$	Age	4.899	59.80	<0.001
GAMM_ $\delta^{13}\text{C}_{\text{CCL}}$	CCL	3.544	22.40	<0.001
GAMM_ $\delta^{13}\text{C}_{\text{Age}}$	Age	2.534	18.86	<0.001

Table 4. Within-individual variation (WIC), between-individual variation (BIC) and total niche width (TNW) for nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope values of lines of arrested growth (LAG's) of juvenile loggerhead turtles in southern Brazil

Life stage	<i>N</i>	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		WIC	BIC	TNW	WIC/TNW	WIC	BIC	TNW	WIC/TNW
Oceanic juveniles	16	1.49	2.37	3.86	0.39	0.85	1.74	2.60	0.33
Neritic juveniles	13	1.53	6.67	8.20	0.19	0.84	4.91	5.74	0.15

FIGURE CAPTIONS

Figure 1. The sampling locations of dead loggerhead sea turtles in southern Brazil: (1) neritic individuals stranded on Rio Grande do Sul coast; (2) oceanic individuals incidentally caught by the longline fisheries

Figure 2. (A) Histologically processed and (B) micro-milled humerus bone cross-sections from a juvenile loggerhead sea turtle stranded dead on Rio Grande do Sul coast, with a curved carapace length of 74.0 cm and an estimated age of 16 years. Dashed lines delimit the outer edge of each line of arrested growth (LAG)

Figure 3. Comparison of $\delta^{15}\text{N}$ values with estimated age from loggerhead sea turtles ($n = 35$) from southern Brazil. Dashed horizontal line separates ^{15}N -depleted cluster (circles) and ^{15}N -enriched cluster (triangles) at $\delta^{15}\text{N} = 11.20 \text{ ‰}$

Figure 4. Oceanic ($n = 16$) and neritic ($n = 19$) loggerhead turtle-specific $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values by estimated age

Figure 5. Generalized Additive Mixed Model (GAMM) smoothing splines and 95% confidence interval fit to $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) and estimated age of loggerhead sea turtles from southern Brazil

Figure 6. Generalized Additive Mixed Model (GAMM) smoothing splines and 95% confidence interval fit to $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) and estimated CCL of loggerhead sea turtles from southern Brazil.

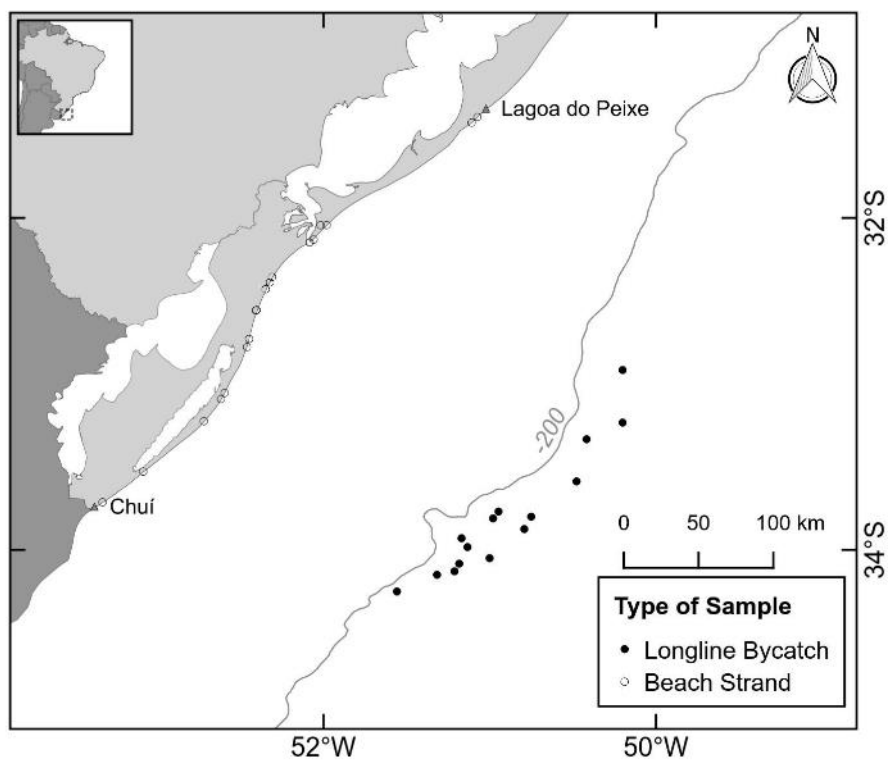


Figure 1.

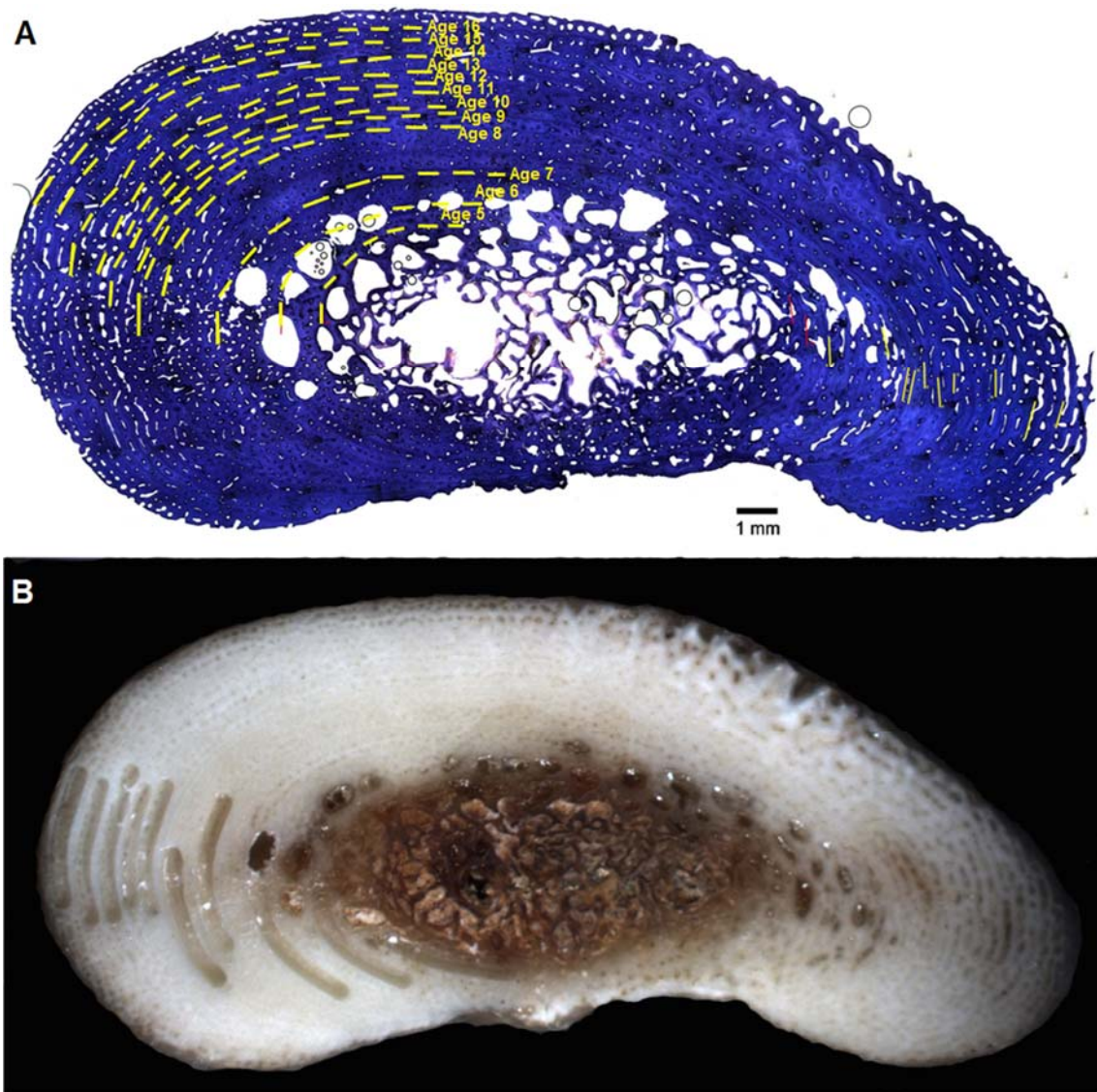


Figure 2.

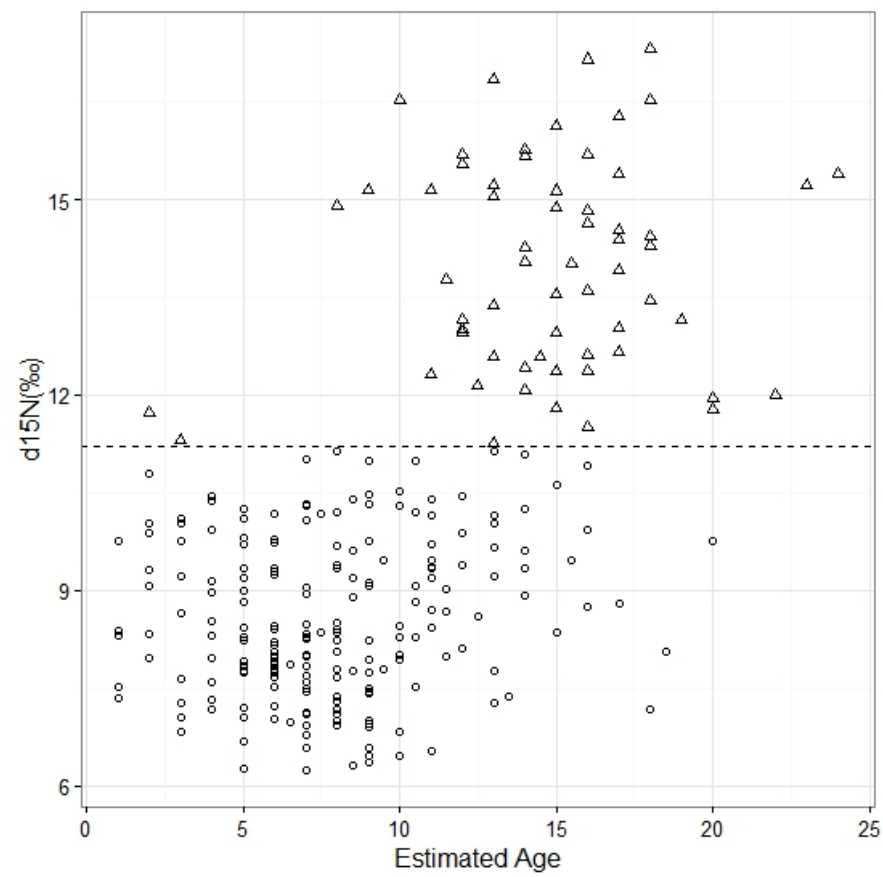


Figure 3.

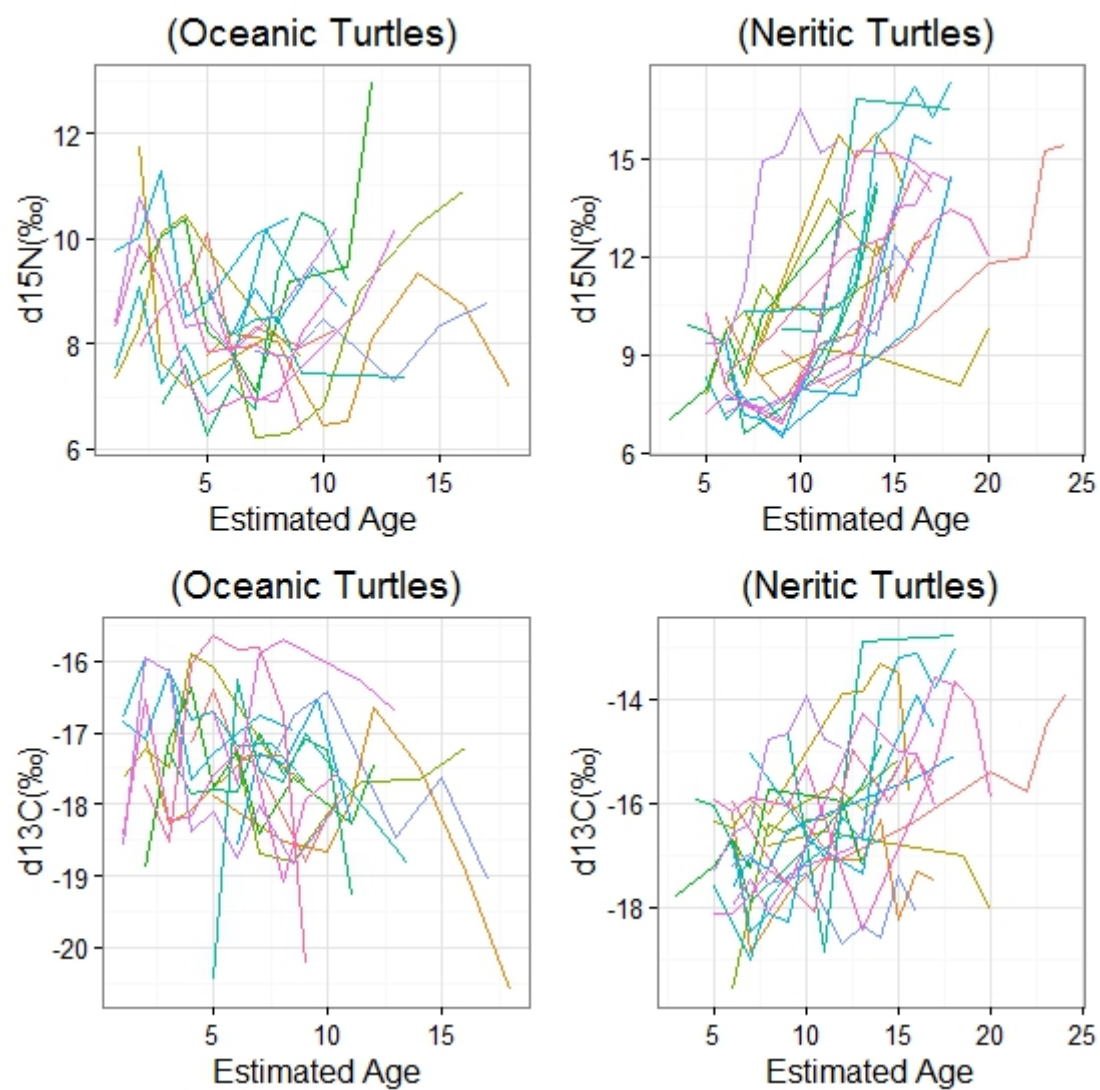


Figure 4.

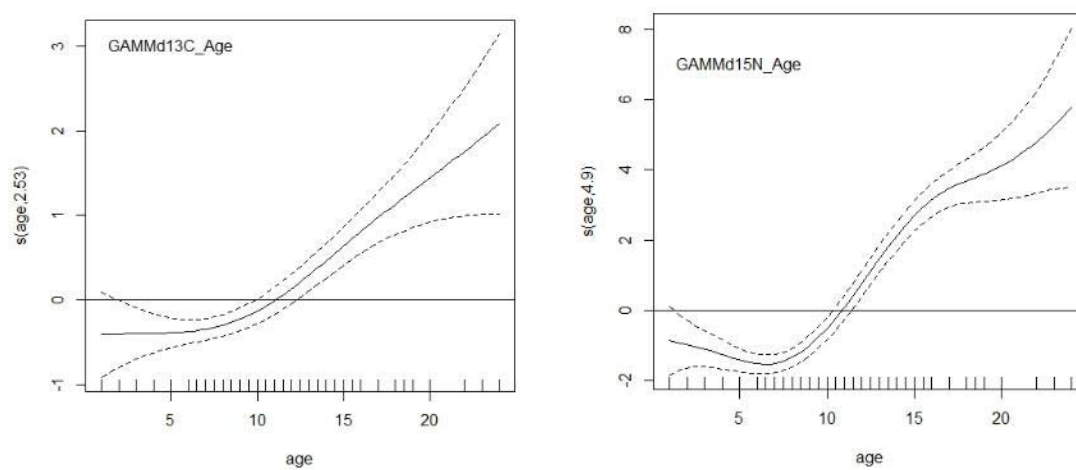


Figure 5.

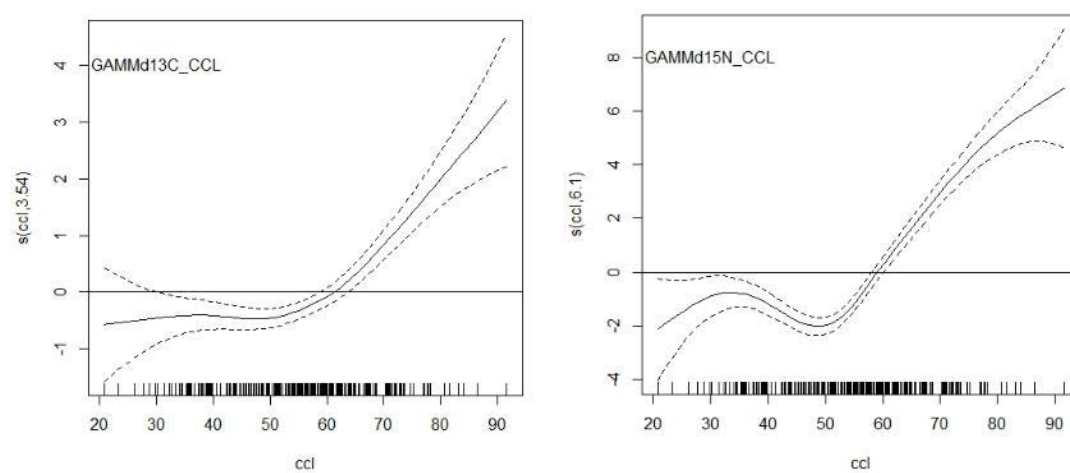


Figure 6.

ELETRONIC SUPPLEMENTAL MATERIAL (ESM)**Ontogenetic habitat shifts and individual specialization in resource use by loggerhead sea turtles in the southwestern Atlantic Ocean**

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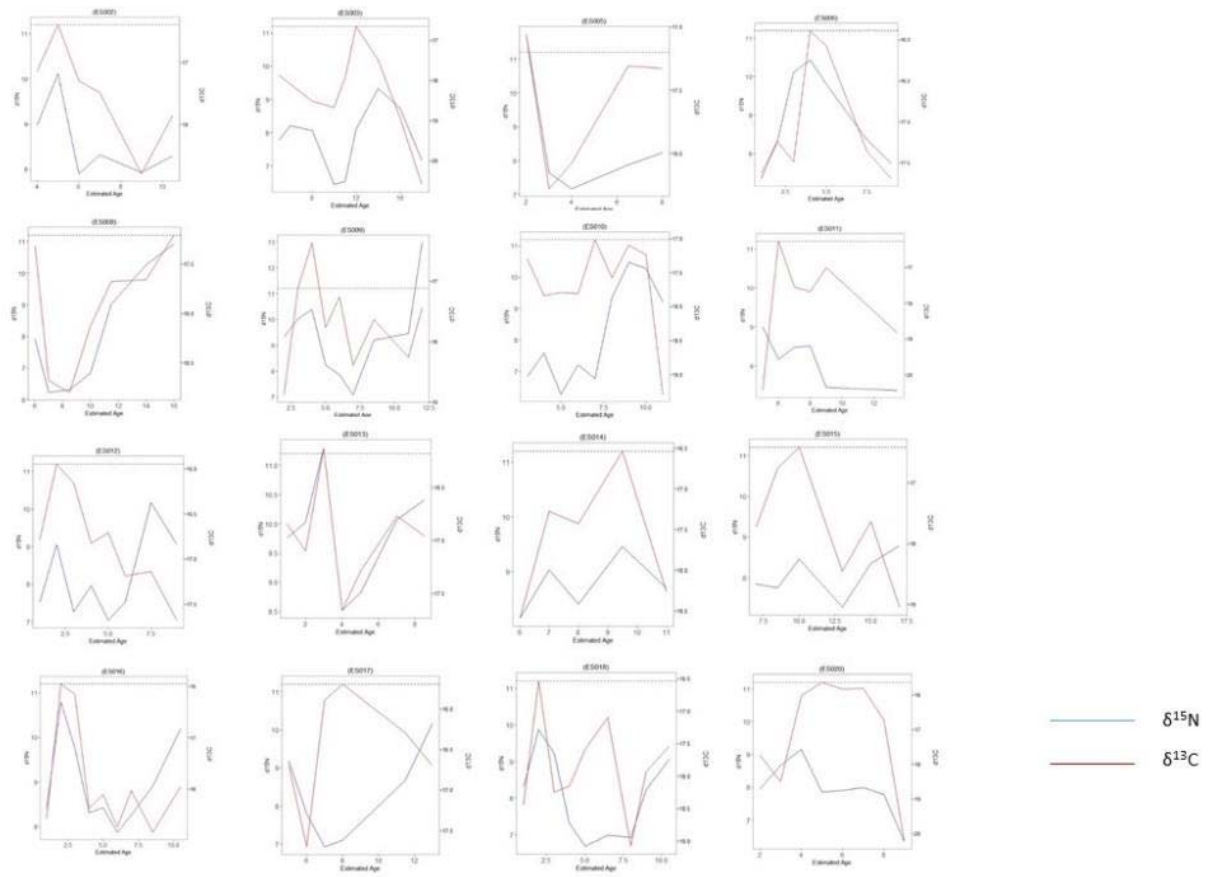


Figure S1. Oceanic loggerhead turtles: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values by estimated age ($n = 16$) for each individual turtle sampled. Dashed horizontal line indicates $\delta^{15}\text{N}$ threshold value of 11.20 ‰

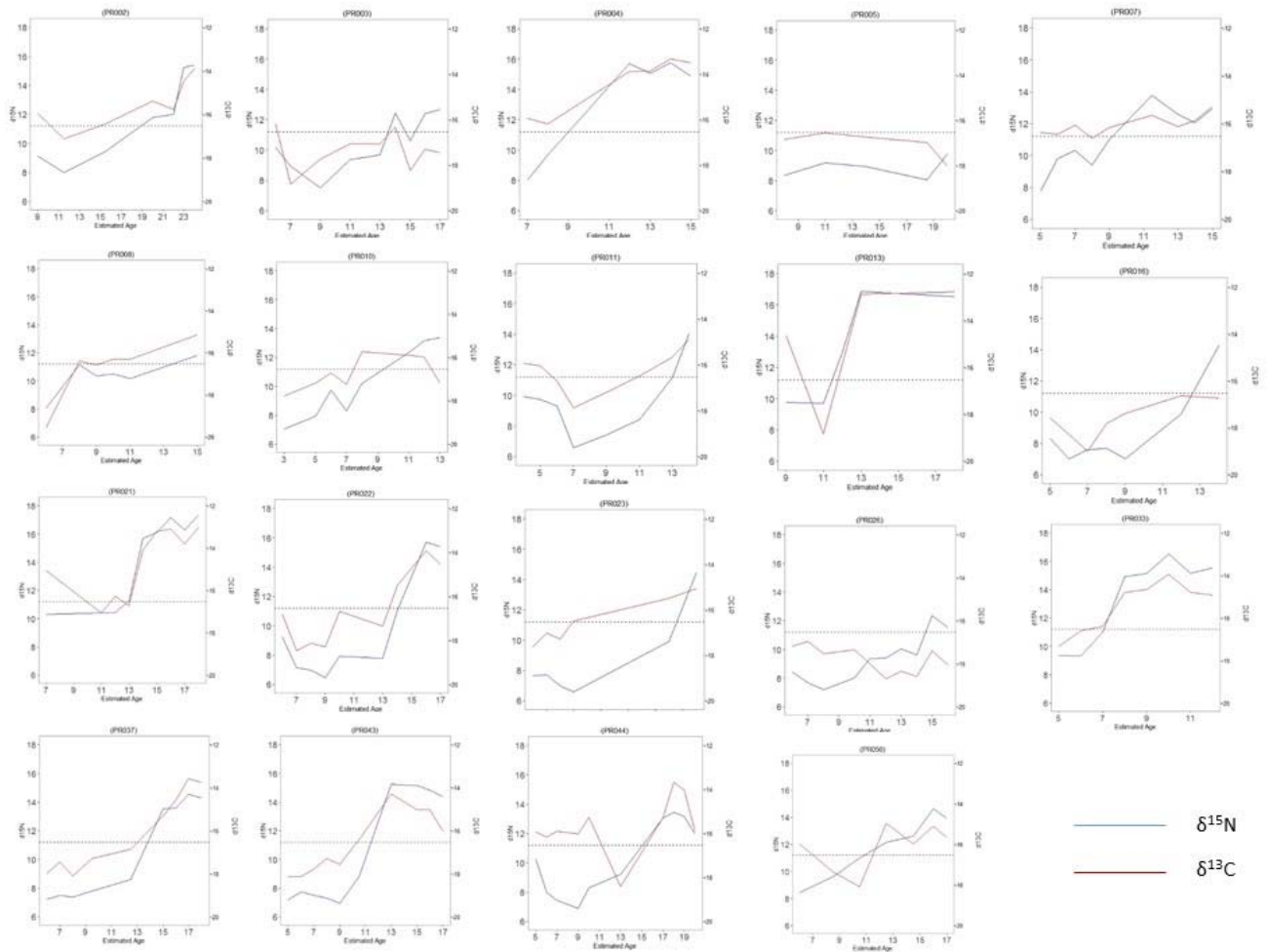


Figure S2. Neritic loggerhead turtles: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values by estimated age ($n = 19$) for each individual turtle sampled. Dashed horizontal line indicates $\delta^{15}\text{N}$ threshold value of 11.20 ‰

CAPÍTULO 3 / ANEXO 3

Satellite tracking reveals habitat use patterns and extent of overlap between loggerhead sea turtles and multiple fisheries in the subtropical southwestern Atlantic Ocean

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(Manuscrito a ser submetido ao periódico *Biological Conservation*)

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ABSTRACT

It is widely recognized that incidental mortality of non-target species is often unsustainable in areas of high overlap with fisheries. The subtropical Southwestern Atlantic Ocean – SWAO is an important area for foraging juvenile loggerhead sea turtles (*Caretta caretta*) and multiple small and large scale fisheries. Nevertheless, the degree of spatial and temporal overlap between areas used turtles and fisheries remain to be determined. Such information can strongly support conservation strategies. Therefore, between 2013 and 2016, movement patterns, habitat use and the degree of overlap of loggerheads (mean curved carapace length = 76 cm; SD = 15.6cm) with the major fisheries in the area - bottom pair trawl, bottom set gillnet and pelagic longline - were determined based on 16 satellite-tracked turtles. Extended permanence of large juveniles in southern Brazilian waters and a plasticity in habitat usage were determined. Turtles exhibited two major movement patterns: (1) year-round movement, spending over 80% of time in neritic waters and (2) seasonal displacement between neritic and oceanic environments. Individual variability in movement patterns was not related to size/age and indicates that a discrete ontogenetic shift is not performed by loggerheads in subtropical SWAO. Seasonal movements into offshore waters or to the northern portions of area started when sea surface temperature in the southern continental shelf dropped below 20°C and make loggerheads vulnerable to different fisheries. Overlap between main usage areas of turtles was high with bottom pair trawl in summer (75%) and with this and gillnet fishing grounds in autumn (64%). These seasonal areas of high overlap can subside proper fishery-specific management strategies, such as spatial-temporal fishing closures, for the conservation of loggerhead sea turtles in the SWAO.

Keywords: *Caretta caretta*, marine turtles, fisheries interaction, satellite telemetry, spatial ecology

INTRODUCTION

The affinities of individuals to specific breeding or foraging sites, when assessed at the population-level, can reveal aggregation sites that are probably relevant for conservation purposes (e.g. McClellan et al. 2014). Nevertheless, depicting important aspects of the spatial ecology of large marine vertebrates is challenging due to the wide spatio-temporal scales of their life cycles (Rees et al. 2013). The understanding of the spatio-temporal patterns of habitat usage and the susceptibility to spatially explicit threats are fundamental for determining effective conservation strategies for threatened species (Fossette et al. 2014).

Loggerhead sea turtles (*Caretta caretta*) are long-distance migrants that exhibit high variability in migration destinations among individuals of a same population and among populations (McClellan and Read 2007; Godley et al. 2008). Upon leaving the nesting beach, hatchlings begin an oceanic phase, floating passively in major current systems (gyres) for several years (Carr 1986; Mansfield et al. 2014). Many juveniles then recruit from oceanic waters to neritic developmental habitats, rich in benthic food resources where they forage and grow until maturity (Musick and Limpus 1997). However, evidence shows that this shift to neritic habitats is reversible during development (Witzell et al. 2004; McClellan and Read 2007; Hawkes et al. 2011; Monteiro et al. Chapter 2) and not obligatory for all individuals in a population (Hatase et al. 2002; Reich et al. 2010; Ramirez et al. 2015).

Sea turtles residing in coastal and offshore areas are often exposed to different threats (Bolten et al. 2011), such as bycatch in multiple fisheries, which have been identified as the main source of non-natural mortality and a reason for concern regarding the conservation of many populations (Wallace et al. 2010). The bycatch of loggerheads is highest among sea turtles worldwide (Moore et al. 2009; Wallace et al. 2013) and occurs in both artisanal and industrial fisheries such as trawling, longlining and gillnetting (Finkbeiner et al. 2011; Fiedler et al. 2012; Wallace et al. 2013).

The spatial ecology of sea turtles had been initially investigated through flipper tagging (Balazs 1976; Limpus et al. 1992). The use of satellite telemetry has expanded the understanding on the behavior of turtles in pelagic environments, revealing fine-scale movements of juveniles of a variety of species (McClellan and Read 2007; Godley et al. 2008; Mansfield et al. 2009). Further, because satellite telemetry yields spatio-temporal patterns of turtle distribution, the resultant movement tracks can be integrated with information on fisheries effort to elucidate the potential overlap between turtles and

fisheries and identify areas of higher risk of bycatch (Fossette et al. 2014). A fundamental impediment to sea turtle population recovery is that most individuals spend large time periods in areas where they are susceptible to incidental capture in fishing gear. It had been shown that the frequency of interactions depends on the degree of overlap between turtles and fishing activities (Wallace et al. 2008; Fossette et al. 2014). Therefore, a key step for conservation purposes is to map the spatio-temporal distribution of the species and the extent of interactions with fisheries (Mangel et al. 2011; Zydels et al. 2011; Fossette et al. 2014).

The southwestern Atlantic Ocean - SWAO provides important foraging grounds for loggerheads and hosts one of the largest nesting rookeries in the Atlantic. Adults nests on the subtropical and tropical beaches of Brazil (Marcovaldi and Chaloupka 2007; Paes e Lima et al. 2012) and forage along the northern Brazilian coast (Marcovaldi et al. 2010), whereas juveniles, after recruitment to neritic zones, feed along the Uruguayan and Argentinian coasts, near the Rio de La Plata estuary (Barceló et al. 2013; González Carman et al. 2016) and in southern Brazil (Bugoni et al. 2003; Monteiro et al. 2016). Mass-strandings of loggerheads were observed on the southern Brazilian coast and bycatch in fisheries had been suggested as the main source of mortality (Monteiro et al. 2016). Despite the intense fishing activities and high bycatch rates in this region (Domingo et al. 2006; Sales et al. 2008; Pons et al. 2010; Monteiro et al. 2013, 2016), few data are available concerning loggerhead distribution in the area (Barceló et al. 2013; González Carman et al. 2016).

In the current study, we tracked loggerhead sea turtles via satellite telemetry in order to characterize seasonal patterns of habitat use, to identify high-usage areas and to determine the spatial-temporal overlaps with main fisheries in their foraging areas within the subtropical western South Atlantic. The results provided here demonstrated for the first time two major spatio-temporal patterns of habitat use and high seasonal variation in the degree of overlap of large juvenile loggerhead sea turtles with industrial fisheries in SWAO. Therefore, the present study elucidates important aspects on the spatial ecology and the vulnerability of the species to bycatch in fisheries, with clear implications for its conservation.

MATERIALS AND METHODS

Study area

The southern Brazil, Uruguay and northern Argentina continental shelves are wide (over 200 km in width in some portions), with a gentle declivity (Calliari 1998; Mahiques et al. 2010). The shelf break, in southern Brazil, is located between the isobaths of 100 and 180 m (Mahiques et al. 2010) and the slope can extend up to 4000 m of depth. Located approximately 600 nautical miles off the coast, in the abyssal plain, is the undersea mountains chain known as the Rio Grande rise, an important area for several species, including marine turtles (Sales et al. 2008). The ocean dynamics over the continental shelf is mostly influenced by the Subtropical Shelf Front (STSF) formed by the encounter of the La Plata River Plume (LPRP), the cold and nutrient-rich SubAntarctic Water (SAW) and the warm and oligotrophic Tropical Water (TW) (Muelbert et al. 2008; Piola et al. 2008). The surface waters over the continental slope and beyond are mostly influenced by the TW of the Brazil Current. This current flows south and meets the northward flowing Malvinas/Falkland current forming the Brazil-Malvinas/Falkland Confluence. The latitudinal location of this offshore front varies seasonally around 34–35°S (Matano et al. 2010). The low salinity coastal waters derived from the Rio de la Plata are associated with high nutrient and phytoplankton concentrations (Ciotti et al. 1995) that sustain an important demersal fishery (Haimovici et al. 1997).

Spatial distribution of the fisheries

The continental shelf and slope of southern Brazil represents important fishing grounds for a variety of both artisanal and large-scale fisheries (Haimovici et al. 1997; Castello et al. 2009). Nevertheless, based on prior studies, only pair trawl, otter trawl, double-rig trawl, bottom set gillnetting, and pelagic longlining were identified as potentially interacting with sea turtles (e.g. Domingo et al. 2006; Monteiro et al. 2016). The main spatial and temporal characteristics of these fisheries are in Table 1. In brief, the trawl fleet alone accounts for 33.5% to 68.6% of the demersal fish landings in Rio Grande do Sul state, southern Brazil, between 1997 and 2011 (CEPERG 2012). Except for the bottom pair trawl, information is limited. This fishery takes place throughout the year over the continental shelf, at depths ranging from 15 to 80 m (Haimovici 1998). The southern Brazil is also the main fishing ground for the Brazilian pelagic longline fleet during the autumn, winter and the early spring (Travassos and Hazin 2003; Mayer and Andrade 2005). The pelagic longline vessels operate near the continental shelf-break and

beyond. The bottom-set gillnet fleet operates throughout most of the year, though fishing locations vary seasonally according to the target species and are closer to coast during summer and spring (Secchi et al. 1997; Ferreira et al. 2010).

Satellite telemetry and fisheries data

Between March 2013 and April 2015, we deployed satellite transmitters on seventeen loggerhead turtles, of which two were found stranded on the coast and rehabilitated, and fifteen were incidentally caught in bottom pair trawl fishery operating on the continental shelf off Rio Grande do Sul, southern Brazil (Table 2). One of these turtles was captured again by another pair trawl after eight days from the first capture and was not included in the analysis. The curved carapace length – CCL was measured from notch to tip (Bolten 1999) for all tagged turtles. The captured turtles were brought on board and their health condition was evaluated. Satellite transmitters were installed only on turtles that appeared to be in good conditions (e.g. with active movements on the vessel deck for at least 12 h) to survive after release. Turtles stranded on beach were moved to the Marine Animal Rehabilitation Center, Oceanographic Museum at the Federal University of Rio Grande (CRAM-FURG), for veterinary care and rehabilitation. After recovery, the turtles had the tags attached and were released into the sea, near Patos Lagoon estuary mouth.

We instrumented turtles with Wildlife Computers SPOT 5 (n=8) and SPLASH-10 (n=9) platform terminal transmitters (PTT). Transmitters had two different duty cycles: (1) no duty cycle and (2) 24 h on and 24 h off (Table 1). Satellite tags were adhered to the second anterior central scutes of turtles carapace using fiberglass and resin (Balazs et al. 1996). Prior to attaching transmitters, we removed epibionts, slightly sanded and cleaned the carapace with ethanol, and allowed to air dry. Data provided by ARGOS were filtered and stored initially in the STAT program (Satellite Tracking and Analysis Tool, seaturtle.org - Coyne and Godley 2005) and then in database in PostgreSQL.

Fisheries data were obtained from logbooks completed by skippers of gillnet vessels from 1996 to 2009 and from logbooks and onboard scientific observer programs for bottom pair trawl from 2011 to 2016 and for pelagic longline from 2004 to 2015. These data were collected as part of fisheries and bycatch monitoring programs carried out by EcoMega/FURG for gillnet, by NEMA for bottom pair trawl, and by NEMA and TAMAR for pelagic longline fisheries.

Data analysis

Transmitters returned 28501 positions, all quality pooled. Data were filtered to eliminate low quality locations. First we calculated turtles displacement speed between two consecutives positions and eliminated positions that resulted speeds over 10 km h^{-1} and location classes Z. All other location classes (0 to 3, A and B) remained (González-Carman et al. 2012, 2016). These first filters removed 8669 positions. To reduce effects of spatial autocorrelation of consecutive positions provided in short time interval, we selected locations for each turtles in intervals of 6 h. For such, the median of latitude and longitude were calculated from the most accurate location classes acquired in that time interval. After this procedure, 10874 positions remained.

The kernel density estimation (KDE), with a bandwidth of 0.25° (approximately 28 km) and spatial resolution 0.05° (ca. 5.5 km), was used to identify high usage areas of loggerhead turtles and fisheries by season and year. A linear function was used to rescale the density surfaces within the range between 0 and 1 and high usage areas were identified based on the density values close to 1. For loggerheads we used all the post-filtering positions ($n=10874$). For the fisheries, positions of 2838 bottom gillnet sets from 1996 to 2009, 3170 pair trawl tows from 2011 to 2016 and 1553 pelagic longline sets from 2004 to 2015 were used.

The Spearman coefficient was applied to assess the correlation between the areas used by turtles and fisheries on a seasonal basis. Pixels of very low density value (<0.025) were eliminated and the correlation was performed pixel by pixel. Furthermore, the density surfaces were transformed in three classes of density polygons, representing 50, 75 and 90% of the highest density values. Therefore, the area ranged by the 90% and 50% highest values were considered representative and core areas, respectively (e.g. Parra 2006). Then, the percent of area overlap between turtles and fisheries density polygons were calculated for each of the three classes of density for each season.

Turtle movement patterns were contrasted with sea surface temperature (SST) data that were obtained through processed data from MODIS Aqua (L3), available in NetCDF format at NASA's Ocean Color Platform (<https://oceancolor.gsfc.nasa.gov/cms/data/seawifs>). The SST data were transformed in 5°C isotherm and plotted in the same seasonal density surface maps.

The statistical analyses and figures were performed using the packages *maps* (Minka and Deckmyn, 2016), *rgdal* (Bivand et al. 2016), *kernSmooth* (Wanda 2015) and *raster* (Hijmans, 2016) in R software (R Core Team 2015) version 3.2.3.

RESULTS

Turtle movements

The mean CCL of satellite tracked loggerhead turtles was 76 ± 15.6 cm (range: 58 to 96 cm). Ten individuals were juveniles of unknown sex and seven were larger than 83 cm, minimum CCL of loggerheads nesting in Brazilian rookeries (Baptistotte et al. 2003) and, hence, possibly adults (Table 2). The mean track duration was 334.2 days (range: 51 to 775 days, $n = 16$). Seven turtles transmitted for more than one year (Table 2). The distance traveled varied from 1473.34 to 33325.00 km (mean = 9969.52 ± 8762.40 km) and the average speed ranged between 1.31 and 2.78 km h⁻¹ (mean = 2.14 ± 1.73 km h⁻¹). Tracks ranged between 26 and 42°S, and between 36 and 54°W (Fig. 1). Among tracked turtles, Turtle D, traveled the farthest south, reaching 42°40'S (Argentina) in February 2015. Turtle G traveled the farthest north, reaching 25°30' S (Paraná State), in November 2014 and Turtle I traveled the farthest into offshore waters, reaching 37°40' W in August 2015 (Fig. 2).

Overall, turtles exhibited two major movement pattern: (1) a year-round movement restricted to neritic waters and (2) a seasonal displacement between neritic and oceanic environments (Fig. 3; Table 3). Eleven turtles spent most of the time over the continental shelf and five of them remained the whole time in neritic waters (Figs. 3 and S1). On the other hand, five turtles spent most of the time in offshore waters over the continental slope (Table 3); four of them used the slope during late autumn and/or winter only (Figs. 3 and S1). Turtles that returned to offshore waters remained there between 13 and 360 days (Table 3), and two of those individuals (Turtles F and P) remained there until the transmission ceased. Turtle P was recently found dead on the coast (December 2016; 15 months after the last transmission) and had the digestive tract full of hermit crabs. However, back and forward movements between neritic and oceanic habitat were observed for seven turtles. The time that these turtles remained in oceanic habitat until returning to neritic region ranged from 9 to 172 days. Turtle D spent 185 days in the oceanic habitat, returned to coastal waters for 158 days and then migrated back to open ocean for 117 days, and finally returned to neritic habitat for 163 days, when the transmissions ceased.

These two major movement patterns were not related to size (Table 3). For instance, turtle I, the largest turtle tracked (CCL = 96 cm) and the turtle P (CCL = 86 cm) remained 63% and 80% of the time in the oceanic region, respectively. Whereas, two other large turtles (G and K) spent 87% and 100% of the time in the continental shelf.

Among juveniles, turtles A, B, C, E, M and N spent more than 90% of their time in continental shelf, whereas turtles F and J remained 79% and 46% of time in offshore waters.

High-usage areas

Our results showed a clear extended permanence in southern Brazilian waters. Ten turtles used this region during all tracking period. The kernel distributions indicated that the high-usage areas were highly consistent between years, but varied seasonally, and that core areas were much smaller in the continental shelf than in the oceanic region (Fig. 3). High usage areas in austral summer are located on the continental shelf, between Albardão lighthouse and Chuí. In 2015, we observed a secondary small core area located near Patos Lagoon estuary mouth. In autumn, turtles used the entire continental shelf and offshore waters. In winter, the high use areas were located in the northern portion of the study area, near 30°S. In spring, turtles return to the same areas used in previous summer (Fig. 3). The autumn/winter movements into offshore waters or northern portions of the study area started on autumn, when SST in the southern portion of the continental shelf (34-31° latitude) dropped below 20°C (Fig. 4; S1).

Overlap with fisheries

We observed a positive correlation between areas of high usage by sea turtles and different fisheries. The correlation was strong with bottom pair trawl in summer ($r_s = 0.87$) and spring ($r_s = 0.74$), and moderate with bottom pair trawl ($r_s = 0.53$) and with set-gillnet in autumn ($r_s = 0.63$). A weak positive correlation was observed with gillnet in spring ($r_s = 0.46$) and summer ($r_s = 0.38$), and with pelagic longline in autumn ($r_s = 0.33$). On the other hand, we observed a moderate negative correlation with pelagic longline fishery in summer ($r_s = -0.54$).

The overlap with different fisheries varied seasonally (Table 4; Fig. 5). Based on the 50% density polygon, the overlap between high usage area by turtles and bottom pair trawl fishery was high in summer (75% of the turtle area) and autumn (64%). On the other hand, higher overlap between turtles and bottom gillnet fishery was restricted to autumn (64%) (Table 4).

DISCUSSION

Habitat use

Our results showed that the life history of loggerhead sea turtles from the Southwestern Atlantic Ocean (SWAO) is more complex than previously thought. The large juveniles exhibit plasticity in habitat use with two major movement patterns. Some turtles remained year-round in neritic waters while others performed seasonal displacement between neritic and oceanic environments. This individual variation in movement patterns seems not related to size (or age) and is a strong evidence that loggerheads do not undergo a discrete ontogenetic shift as previously thought (Bjorndal et al. 2000). Patterns of habitat usage depicted from stable isotope analysis in humeri of individuals sampled in this region (Monteiro et al. Chapter 2) also indicated such individual variation.

Other studies also showed that juvenile loggerheads explore both neritic and oceanic habitats in the SWAO. Barceló et al. (2013) observed that 13 out of 27 (mean CCL = 61.8 cm; range 49 to 83) turtles incidentally caught in longline fisheries in offshore waters used the neritic region and suggested that these individuals were in a transitional stage (*sensu* Bolten 2003). On the other hand, González Carman et al. (2016) satellite-tracked six juvenile loggerheads (mean CCL = 59.4 cm; range 46.5 to 66.5 cm) incidentally captured in artisanal gillnet fisheries in Argentinian coastal waters and five turtles remained the entire period on the continental shelf, mostly in the Rio de La Plata estuary, and a single one used oceanic waters in austral winter. Although turtles tracked in these two previous studies were smaller than those tracked for the current study and could be in a transitional stage, some turtles followed in our study, large juveniles or adults, also returned to the pelagic habitat. The overall finding of these studies underscores the plasticity of loggerhead sea turtles, with high individual variability in habitat use and foraging strategies of juvenile, large juvenile and possibly adult loggerhead sea turtles in SWAO and corroborate patterns observed with the combined skeletochronology and stable isotopes analysis (Monteiro et al. under review). Plasticity in habitat use were also demonstrated for juvenile loggerhead sea turtles in North Carolina, USA, where individuals move back into coastal waters and then return to the open ocean, sometimes for multiple years (McClellan and Read 2007). Mansfield et al. (2009) observed two movement patterns performed by juvenile loggerhead sea turtles in foraging grounds of the western North Atlantic: a seasonal shelf north-south migratory pattern, and a year-round oceanic dispersal strategy. Several individuals returned to their

seasonal foraging grounds during subsequent summers (Mansfield et al. 2009). On the other hand, in waters off Peru and Chile, juvenile loggerhead turtles (mean CCL = 60.6 ± 7.7 cm) maintained a pelagic lifestyle for the duration of tracking, spending most of the time beyond the 1000 m isobath (Mangel et al. 2011). In western North Pacific, some adult female loggerheads were observed using oceanic areas after nesting season, whereas others used neritic areas, potentially mediated by female habitat selection as a function of body size (Hatase et al. 2002). In the Northeastern Atlantic, around Cape Verde Islands, smaller post-nesting loggerheads were found foraging in oceanic regions, whereas larger post-nesting individuals foraged in coastal habitats (Hawkes et al. 2006).

The factors responsible for this observed variation in life-history strategies for both adults and juveniles are not yet clear (Hatase et al. 2010; McClellan et al. 2010). Thermal conditions and other environmental features, such as primary productivity and prey availability have been considered important factors to explain seasonal variability in turtle movements (Godley et al. 2008; Howell et al. 2010; Mansfield and Putman 2013). In our study, size does not explain the differences in habitat use. The inshore-offshore or south-north movements started in late austral autumn and winter, just when a drop in the water temperature occurred. In winter, mean SST on the inner continental shelf of southern Brazil is 18°C, whereas in summer SST rises to 23°C (Piola et al. 2008). In spring those turtles returned to coastal waters. Therefore, these movements probably occurred to avoid thermal stress caused by the cold waters on the continental shelf during this period. Similarly, in Uruguay, Barceló et al. (2013) observed strong seasonality in turtle movements related to changes in SST, with individuals using northern areas during austral winter. González Carman et al. (2016) also observed juvenile loggerheads moving from foraging areas in La Plata River estuary to overwinter in warmer waters of Brazil and Uruguay. Mangel et al. (2011) suggested that the absence of loggerhead turtles on the continental shelf of Peru may be explained by the dominance of upwelling driven cold waters, ranging from 15 to 17°C in winter and 15 to 19°C in summer. A similar pattern was observed in western North Atlantic, where turtles started fall/winter southward movements when SST dropped below 20°C and return to northern areas when both SST and primary productivity increased (Mansfield et al. 2009).

In our study, while some turtles moved to offshore waters only in autumn and winter, two turtles remained there almost year-round. Morreale and Standora (2005) suggested that some juvenile loggerheads migrate seasonally between coastal habitats and warmer offshore waters, in northwestern Atlantic. McClellan et al. (2010), in North

Carolina, also observed juvenile loggerheads exhibiting a seasonal movement pattern to offshore waters in winter where individuals preyed upon pelagic items. Association of loggerhead turtles with eddies and frontal systems had been observed in the Pacific Ocean (Polovina et al. 2000, 2006). Kobayashi et al. (2008) also found that latitudinal movements correspond to variations in chlorophyll *a*. In northwestern Atlantic, the permanence of two turtles for one and three years within an oceanic habitat was associated with mesoscale features and frontal systems (Mansfield et al. 2009). Although our studies suggest that temperature and currents may play a role on habitat use by turtles, additional studies are needed to understand the influence of oceanographic features on the habitat use patterns of loggerhead sea turtles in the SWAO.

The low number of loggerhead strandings in austral winter in the area (range: zero to 14 individuals per year) suggested that individuals leave the area during this season (Monteiro et al. 2016). However, the use of satellite telemetry showed that most turtles remained year-round in southern Brazilian waters. The permanence of turtles in this area is probably related to the high productivity in coastal and oceanic waters from southern Brazil to Argentina. The use of smaller core areas in neritic habitat than in oceanic region is likely due the higher abundance and/or aggregated distribution of hermit crabs and mollusks, the main prey items of loggerheads in southern Brazil. In general, resident areas of juveniles in oceanic zones are much wider than in neritic zones (Cardona et al. 2005; Mansfield et al. 2009) a similar pattern observed for adults (Hawkes et al. 2006; Schofield et al., 2010). Coastal areas are typically more productive than pelagic areas (Saba et al. 2008).

Although feeding areas of adult female loggerheads are located in northeastern and northern Brazil (Marcovaldi et al. 2010), this study confirms that coastal and oceanic waters of southern Brazil are a key foraging ground for juvenile and possibly adult loggerhead turtles.

Overlap with fisheries

Here we performed the first integrated analysis of spatio-temporal distribution of loggerhead turtles in the subtropical SWAO and the degree of overlap with the three major industrial fishing fleets operating in southern Brazil.

Based on this analysis, the bottom pair trawl fishery showed the greatest overlap with loggerhead turtles. The high degree of overlap between turtles high usage areas and bottom pair trawl fishery in summer and spring is coincident with the high number of

loggerhead strandings on the Rio Grande do Sul coast (Monteiro et al. 2016). This high overlap increases the chances of turtle bycatch, pointing to this fishery as the most likely responsible for most of loggerhead strandings, and confirming previous findings (Monteiro et al. 2013, 2016). A high degree of overlap between turtles high usage areas and bottom gillnet fishery in autumn may be related with loggerhead strandings in that season. On the other hand, the low overlap between turtles and fisheries density areas in austral winter can explain the lack of loggerhead strandings in that season (Monteiro et al. 2016).

Although low overlap between turtles and pelagic longline high-density areas was observed, high bycatch rates of loggerhead in this fishery are documented for southern Brazilian and Uruguayan waters (Pons et al. 2010). This is possibly because we tracked only turtles that were captured in coastal trawl fisheries. These individuals had either started their ontogenetic shift or completely recruited to neritic habitats, hence did not spend much time in oceanic waters.

Other studies highlighted similarly large overlap between sea turtles and fisheries. In the eastern Pacific, loggerhead turtles spent 75% of their time within previously defined Peruvian small-scale longline fishing grounds (Mangel et al. 2011). In the Atlantic Ocean, a high overlap was observed between leatherback turtles and pelagic longline fisheries (Fossette et al. 2014).

Fisheries bycatch is recognized as a major threat for sea turtle populations around the world (Hamann et al. 2010; Bolten et al. 2011). Southern Brazil provide relatively high productivity neritic and oceanic regions within the preferred SST range of loggerheads, therefore the high degree of overlap with fisheries in southern Brazil can reverse the upward population trend observed for loggerhead turtles from Brazilian nesting sites (Marcovaldi and Chaloupka 2007).

The reversible behavior in habitat use showed in our study can have ecological and conservation implications. The differences in foraging strategies may affect, for example, survival rate, stage duration, time to maturity and reproductive success (e.g. Snover 2008). The use of several foraging habitats exposes loggerheads to a range of threats, including the interaction with multiple fisheries, effects of which accumulate throughout life stages in the populations (Bolten et al. 2011). In this case, population models should consider that juvenile or adult loggerheads may not restrict to neritic or oceanic habitats during life stages.

Crouse et al. (1987) suggest that the most effective way to enhance population growth of loggerhead sea turtles is to increase large juvenile survivorship. In the present study we were able to identify the areas and seasons of highest vulnerability of large juvenile loggerhead turtles to negative interactions with fisheries. Thus, there is clearly a need for a comprehensive assessment of loggerhead turtles bycatch at least in bottom pair-trawl and gillnet fisheries. Once the magnitude of bycatch is evaluated and the most harmful fishing gear identified, proper spatial and/or temporal fisheries management strategies, such as area closures, can be defined for the conservation of sea turtles. We suggest that the areas of high use by turtles and overlap with fisheries, identified in this study, be considered as priority for the conservation loggerhead sea turtles.

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Table 1 Spatial and temporal characteristics of industrial fisheries that interact with sea turtles on the Rio Grande do Sul continental shelf and adjacent offshore waters. All reference points that identify fishing areas are shown in Figure 1.

	Bottom gillnet for white croaker	Bottom gillnet for stripped weakfish	Pair trawl	Pelagic longline
Target species	White croaker (<i>Micropogonias furnieri</i>)	Stripped weakfish (<i>Cynoscion guatucupa</i>) and Argentine croaker (<i>Umbrina canosai</i>)	<i>C. guatucupa</i> , <i>U. canosai</i> , <i>M. furnieri</i> and southern king weakfish (<i>Macrodon atricauda</i>)	Tuna (<i>Thunnus</i> spp.), swordfish (<i>Xiphias gladius</i>) and sharks, mainly blue (<i>Prionace glauca</i>)
Depth (m)	ca. 5–50	ca. 25–150	10–80	140–5000
Fishing Area	Between Mostardas lighthouse and Chuí	Between Mostardas lighthouse and Chuí	Along the entire coast	Along the entire coast
Season	austral spring and summer	austral autumn and winter	year round	autumn, winter and spring
Reference	Secchi et al. 1997; Ferreira et al. 2010	Secchi et al. 1997; Ferreira et al. 2010	Haimovici et al. 1997	Neves et al. 2006

Table 2. Summary table with information of 16 satellite tracked loggerhead turtles in the subtropical SW Atlantic Ocean deployed between 2013 and 2015. Dates given as yyyy/mm/dd. CCL: curved carapace length. Duty cycle: (1) no duty cycle; (2) 24 h on, 24 h off.

Turtle ID	CCL (cm)	Sex	Deployment date	Last location date	PTT model	Duty cycle	Track duration (days)	Distance traveled (km)	Mean speed (km h⁻¹)	Time over continental shelf (%)
A	63	U	2013-03-22	2014-03-25	SPOT 5	1	368	10858.03	2.11	90.7
B	63	U	2013-03-30	2014-09-18	SPOT 5	1	537	15681.29	2.10	100
C	67.8	U	2013-12-08	2015-03-26	SPOT 5	1	473	19658.50	2.78	91.6
D	85.5	F	2014-01-20	2016-03-13	SPOT 5	1	775	33324.98	2.47	53.6
E	61	U	2014-01-23	2015-10-14	SPOT 5	1	629	16858.05	2.32	99.8
F	60	U	2014-01-27	2015-01-19	SPOT 5	1	357	13525.29	2.22	21.1
G	87	F	2014-02-24	2015-03-24	SPOT 5	1	393	15284.14	2.30	87.0
H	79	U	2014-12-24	2015-03-31	SPLASH 10	2	97	2053.85	1.72	100
K	92	F	2015-02-13	2015-10-21	SPLASH 10	2	250	3204.23	1.31	100
I	96	M	2015-01-28	2015-10-11	SPLASH 10	2	256	7400.75	1.83	36.8
J	68.5	U	2015-02-06	2016-02-24	SPLASH 10	2	373	8189.11	1.62	54.1
L	75	U	2015-03-17	2015-06-01	SPLASH 10	2	76	1473.34	1.74	100
M	61.5	U	2015-03-19	2015-12-22	SPLASH 10	2	278	1817.52	1.44	100
N	58	U	2015-03-19	2015-12-10	SPLASH 10	2	266	4098.99	1.53	99.7
O	84	F	2015-03-20	2015-05-10	SPLASH 10	2	51	1755.33	2.09	74.2
P	86	F	2015-04-09	2015-09-25	SPLASH 10	2	168	4328.97	1.81	20.2

Table 3. Summary of the movements of loggerhead sea turtles, including the number of days (d), total distance (km), and mean speed (km h⁻¹). The zones were defined as internal shelf (0 to 30 m), external shelf (>30 to 200 m), slope and oceanic region (> 200 m). CCL: curved carapace length (cm); (-): no data.

Turtle ID	CCL (cm)	Inner shelf			Outer shelf			Slope and oceanic region		
		Duration	Distance	Speed	Duration	Distance	Speed	Duration	Distance	Speed
A	63	196	5735.36	2.15	129	3474.95	1.86	33	1647.73	2.44
B	63	367	13373.72	2.27	167	2307.57	1.08	-	-	-
C	67.8	60	3138.76	2.91	372	14821.25	2.83	40	1698.50	2.19
D	85.5	312	12097.61	2.51	103	4819.79	2.50	360	16407.59	2.44
E	61	434	14596.53	2.39	194	2186.30	1.66	1	75.22	3.16
F	60	38	1250.03	2.32	37	1002.48	1.98	282	11272.79	2.24
G	87	172	7509.68	2.43	170	6023.08	2.18	51	1751.38	1.96
H	79	95	1928.79	1.69	3	125.06	2.85	-	-	-
K	92	203	2654.62	1.34	48	549.61	1.09	-	-	-
I	96	9	369.02	2.49	85	1664.44	1.62	162	5367.29	1.88
J	68.5	57	1417.57	1.67	145	2960.49	1.75	171	3811.04	1.50
L	75	15	213.92	1.17	61	1259.41	1.82	-	-	-
M	61.5	268	1746.75	1.42	9	70.76	1.87	-	-	-
N	58	185	2555.85	1.53	80	1515.53	1.56	1	27.60	1.34
O	84	-	-	-	38	1273.05	2.17	14	458.68	1.86
P	86	23	162.81	0.86	11	216.65	1.37	134	3949.51	1.87

Table 4. Summary table of turtles and fisheries density areas, in km², for three classes of density polygons, representing 50, 75 and 90% of the highest density values, and percent of overlap between turtles and fisheries density areas for each season.

Season	Density areas (%)	Turtles area (Km²)	Pair Trawl area (Km²)	Gillnet area (Km²)	Longline area (Km²)	Pair Trawl overlap (%)	Gillnet overlap (%)	Longline overlap (%)
Summer	90	11161	9695	15737	13953	83	88	0
Summer	75	6653	6341	10487	5910	83	76	0
Summer	50	2111	3584	4855	2868	75	35	0
Autumn	90	22585	16557	13696	13925	59	50	22
Autumn	75	10029	10299	8515	6035	68	60	0
Autumn	50	3827	5403	3452	2966	64	64	0
Winter	90	36100	16258	18814	15960	37	38	11
Winter	75	10390	9279	11723	8980	46	49	<1
Winter	50	3514	3799	5244	3903	14	41	0
Spring	90	11911	9924	9015	15605	79	61	<1
Spring	75	7709	5903	5542	4730	68	52	0
Spring	50	3868	2299	3042	1479	33	38	0

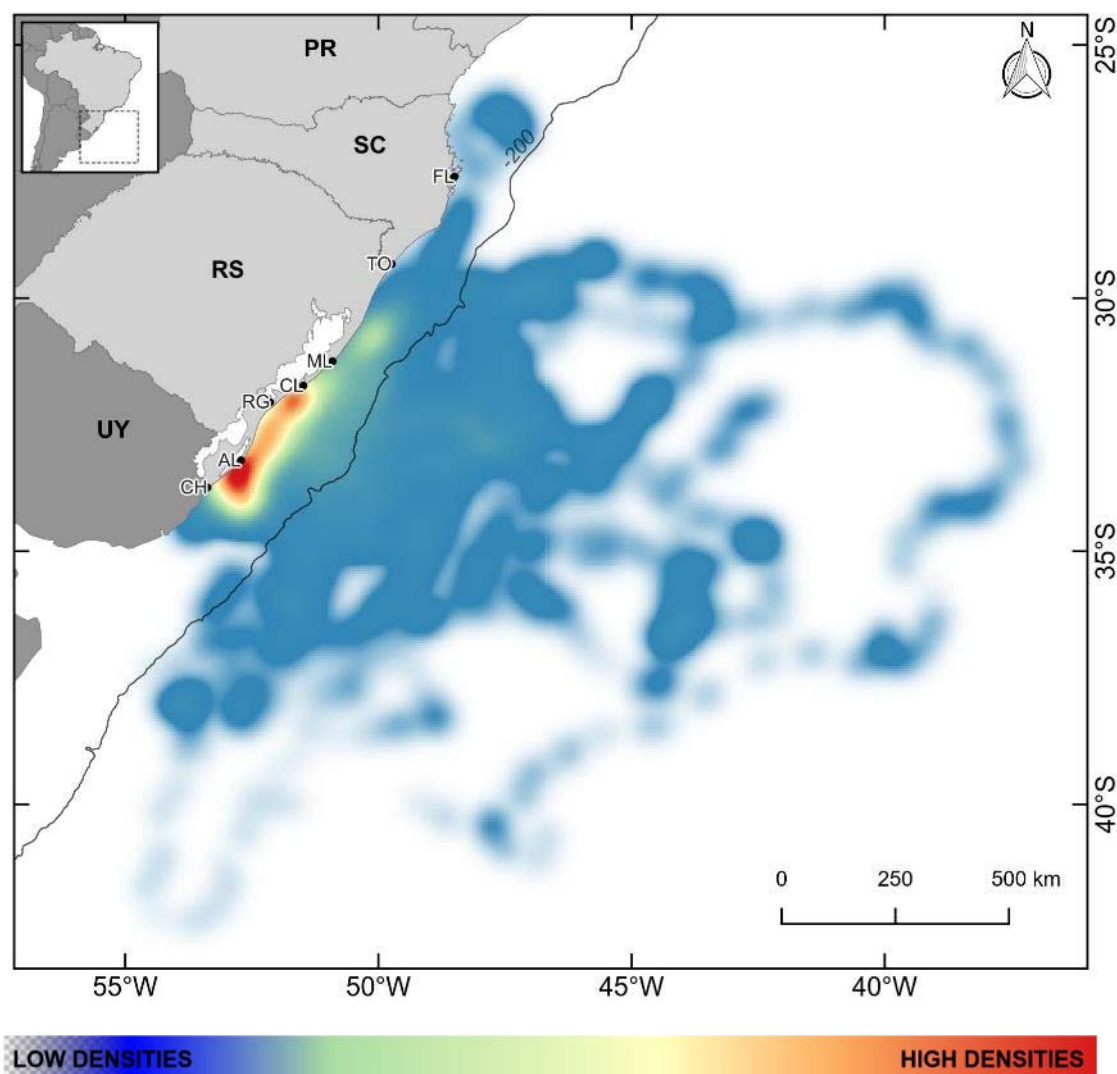


Figure 1. Study area: southern Brazil, Uruguay and northern Argentina continental shelves and offshore waters; and, kernel density estimation of the all loggerhead turtles tracked ($n = 16$), between 2013 and 2016. The locations mentioned in the text are indicated. FL = Florianópolis, TO = Torres, ML = Mostardas lighthouse, CL = Conceição lighthouse, RG = Rio Grande, AL = Albardão lighthouse and CH = Chui

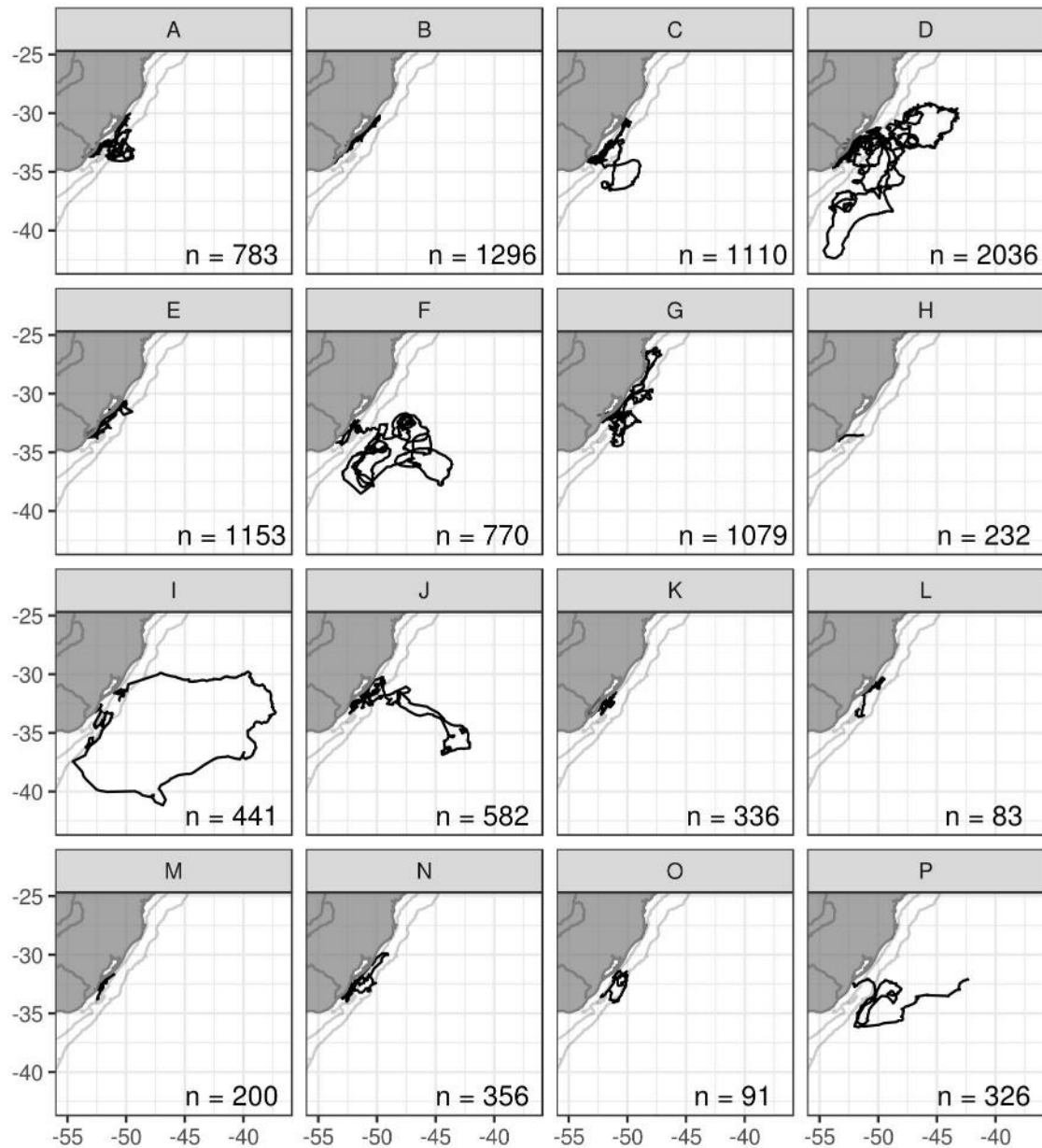


Figure 2. Individual movements for each loggerhead turtle tracked ($n = 16$) in subtropical southwestern Atlantic Ocean between 2013 and 2016. The letters indicate individual turtles and n represents the number of positions after filtering process. Gray lines are the 50 and 200m isobaths.

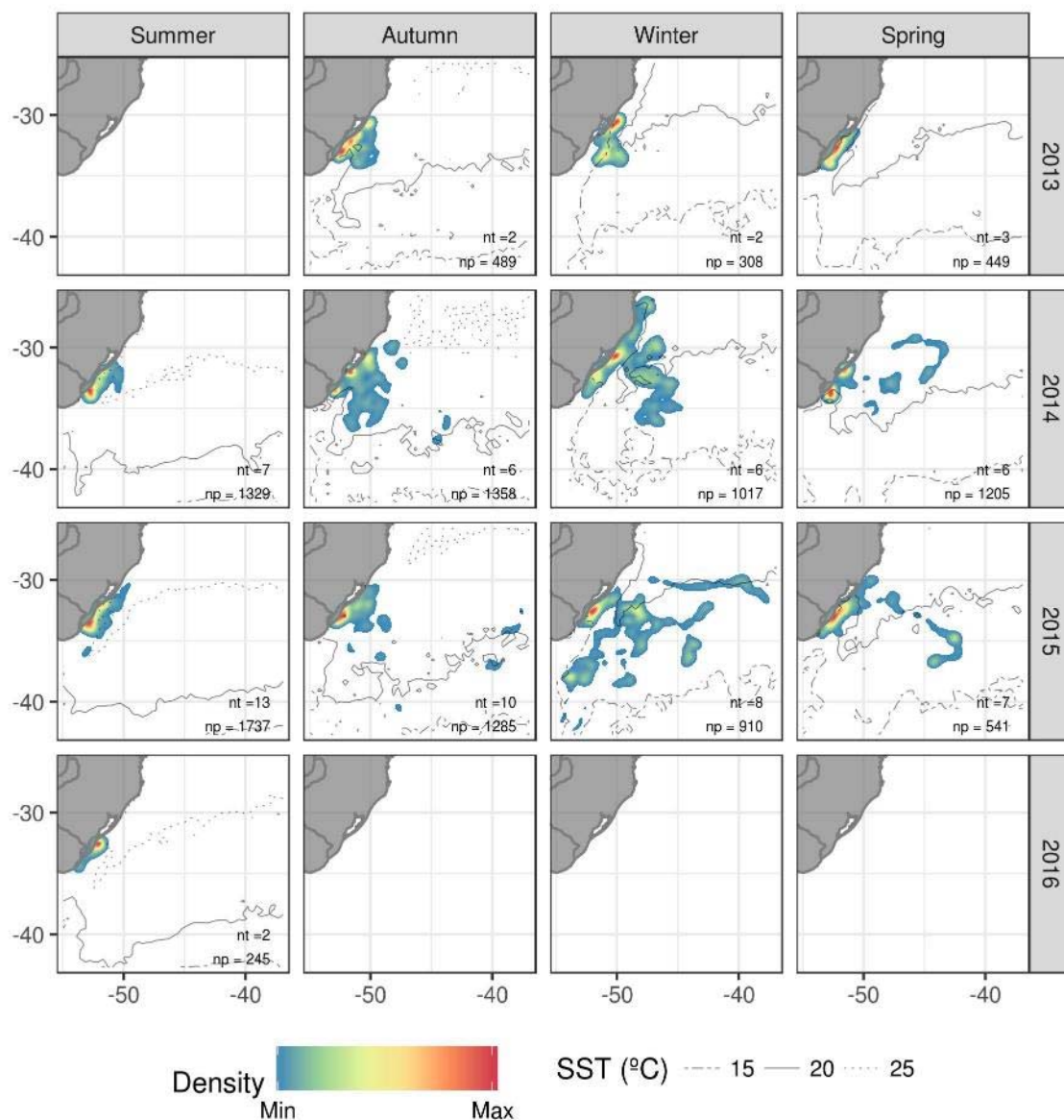


Figure 3. Kernel density estimation for all loggerhead turtles tracked, by year and season, in subtropical southwestern Atlantic Ocean, between 2013 and 2016. The number of tracked turtles (nt) and the number of positions after filtering process (np) are indicated. Solid and dashed lines represent 15, 20 and 25 °C isotherms.

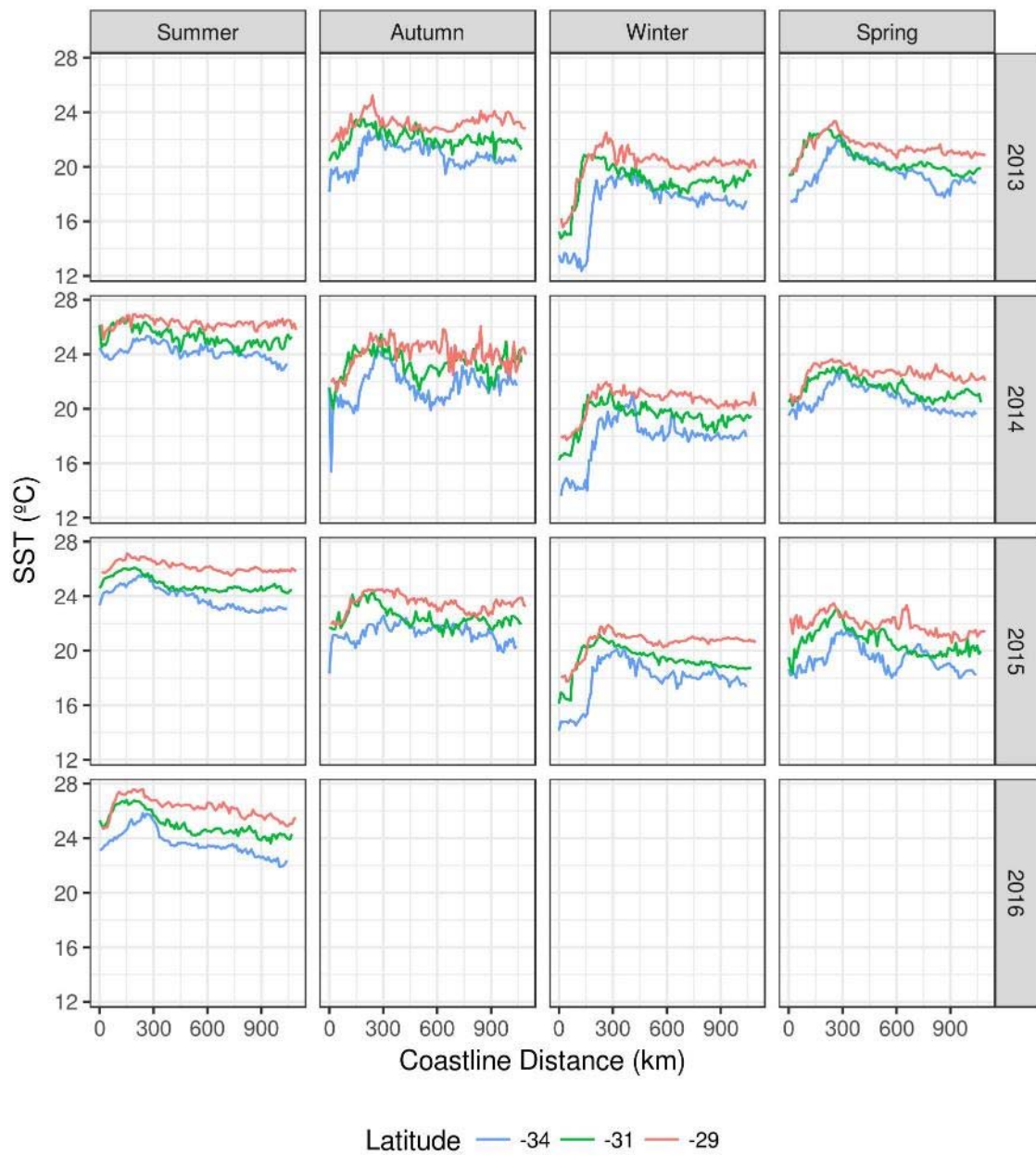


Figure 4. Mean sea surface temperature (SST) by season and year for three locations in southern Brazil, between 2013 and 2016: -34°S (near Chuí, the southern limit of RSC); -31°S (near of Patos Lagoon estuary mouth) and -29°S (near Torres, the northern limit of RSC) according to distance from coast.

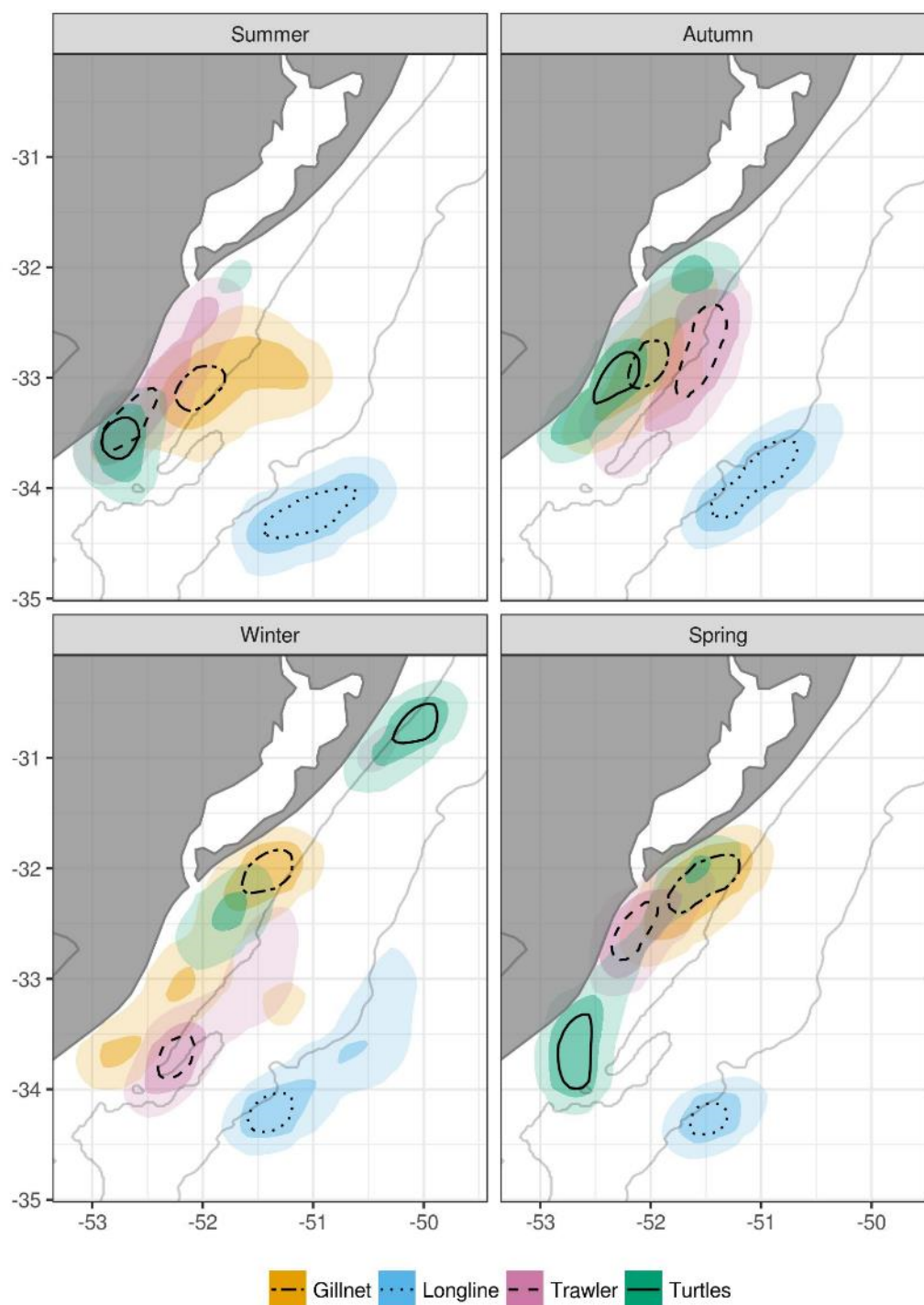


Figure 5. Turtles and fisheries polygons of 50, 75 and 90% of the highest density values by season in southern Brazil, between 2013 and 2016. The solid and dashed lines represent the core areas (the 50% highest values). The darker and lightest colors show polygons of representative areas with 75% and 90% of highest values. Gray lines represent 50 and 200m isobaths.

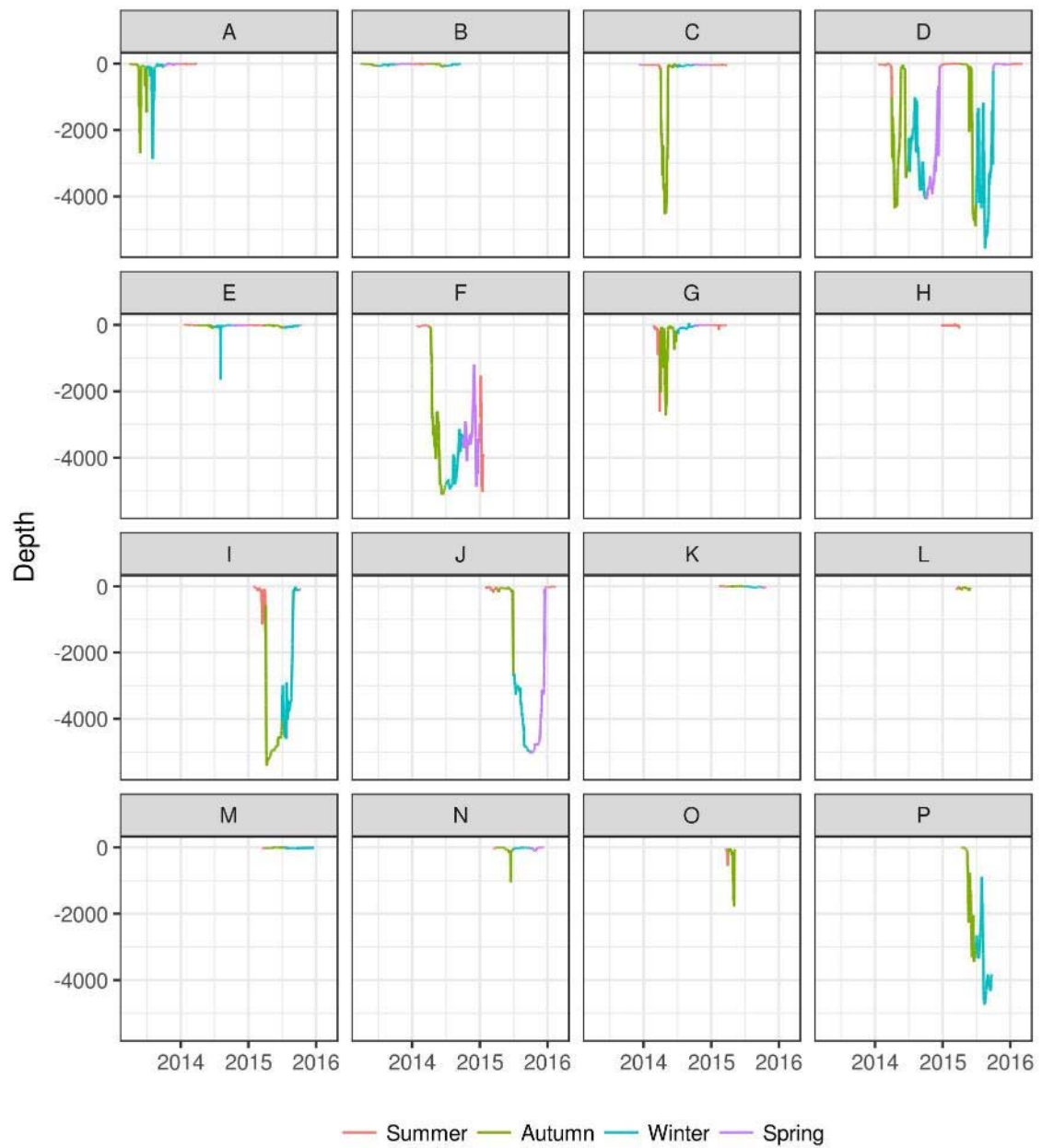


Figure S1. Movements of individual loggerhead sea turtles by season and year in relation to seafloor depth in subtropical southwestern Atlantic Ocean, between 2013 and 2016.

APÊNDICE 1

Rotinas utilizadas para a análise dos dados no Programa R

###Capítulo 1###

###Rotina para os modelos lineares generalizados (GLM) para os encalhes de tartarugas###

###Y=ncc (número de encalhes de *Caretta caretta* por saída) ou ncm (*Chelonia mydas*) ou ndc (*Dermochelys coriacea*)###

###Variáveis explicativas categóricas: ano= 20 níveis; mes= 12 níveis; dir (Direção da saída)= 2 níveis (Sul ou Norte)###

###Variáveis explicativas contínuas: km= km percorridos na saída; soi = índice de oscilação sul (El Niño e La Niña); uwmax10 = valor máximo do vento da direção oeste, 10 dias antes da data da saída de monitoramento; uwmin10 = valor máximo do vento da direção leste, 10 dias antes da saída; vwmax10 = valor máximo do vento da direção sul, 10 dias antes da saída; vwmin10 = valor máximo do vento da direção norte, 10 dias antes da saída###

###Offset (fator de padronização)= km percorridos por saída###

###Para importar a tabela dos dados###

```
saidas=read.table("dados_glm_wind.txt",header=T)
```

###Para informar que o ano, o mês e a direção são variáveis categóricas###

```
saidas$ano=as.factor(saidas$ano)
```

```
saidas$mes=as.factor(saidas$mes)
```

```
saidas$dir=as.factor(saidas$dir)
```

###Para carregar a biblioteca da Binomial Negativa###

```
library(MASS)
```

Modelos para *Caretta caretta*

###o asterisco (*) significa a interação entre duas variáveis###

```
caretta1.nb=glm.nb(ncc~offset(log(km)),data=saidas)
```

```
caretta2.nb=glm.nb(ncc~offset(log(km))+ano,data=saidas)
```

```

caretta3.nb=glm.nb(ncc~offset(log(km))+mes,data=saidas)
caretta4.nb=glm.nb(ncc~offset(log(km))+dir,data=saidas)
caretta5.nb=glm.nb(ncc~offset(log(km))+soi,data=saidas)
caretta6.nb=glm.nb(ncc~offset(log(km))+ano+mes,data=saidas)
caretta7.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir,data=saidas)
caretta8.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi,data=saidas)
caretta9.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+ano*mes,data=saidas)
caretta10.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+ano*dir,data=saidas)
caretta11.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+mes*dir,data=saidas)
caretta12.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+ano*soi,data=saidas)
caretta13.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+km,data=saidas)
caretta14.nb=glm.nb(ncc~ano,data=saidas)
caretta15.nb=glm.nb(ncc~mes,data=saidas)
caretta16.nb=glm.nb(ncc~dir,data=saidas)
caretta17.nb=glm.nb(ncc~km,data=saidas)
caretta18.nb=glm.nb(ncc~ano+mes,data=saidas)
caretta19.nb=glm.nb(ncc~ano+mes+dir,data=saidas)
caretta20.nb=glm.nb(ncc~ano+mes+dir+km,data=saidas)
caretta21.nb=glm.nb(ncc~ano+mes+dir+km+soi,data=saidas)
caretta22.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi+mes*dir,data=saidas)
caretta23.nb=glm.nb(ncc~ano+mes+dir+soi+mes*dir,data=saidas)
caretta24.nb=glm.nb(ncc~ano+mes+dir+km+soi+mes*dir,data=saidas)
caretta25.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi+ano*dir,data=saidas)
caretta26.nb=glm.nb(ncc~offset(log(km))+uwmax10,data=saidas)
caretta27.nb=glm.nb(ncc~offset(log(km))+vwmax10,data=saidas)

```

```

caretta28.nb=glm.nb(ncc~offset(log(km))+uwmin10,data=saidas)

caretta29.nb=glm.nb(ncc~offset(log(km))+vwmin10,data=saidas)

caretta30.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi+uwmax10+mes*dir,data=saidas)

caretta31.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi+vwmax10+mes*dir,data=saidas)

caretta32.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi+uwmin10+mes*dir,data=saidas)

caretta33.nb=glm.nb(ncc~offset(log(km))+ano+mes+dir+soi+vwmin10+mes*dir,data=saidas)

caretta34.nb=glm.nb(ncc~offset(log(km))+ano+dir+soi+uwmax10,data=saidas)

caretta35.nb=glm.nb(ncc~offset(log(km))+mes+uwmax10,data=saidas)

####Para listar os valores do critério de informação de Akaike de segunda ordem (AICc)####

####Para carregar a biblioteca necessária####

library(MuMIn)

AICc(caretta1.nb,caretta2.nb,caretta3.nb,caretta4.nb,caretta5.nb,caretta6.nb,caretta7.nb,caretta8.
nb,caretta9.nb,caretta10.nb,caretta11.nb,caretta12.nb,caretta13.nb,caretta14.nb,caretta15.nb,care
tta16.nb,caretta17.nb,caretta18.nb,caretta19.nb,caretta20.nb,caretta21.nb,caretta22.nb,caretta23.
nb,caretta24.nb,caretta25.nb,caretta26.nb,caretta27.nb,caretta28.nb,caretta29.nb,caretta30.nb,car
etta31.nb,caretta32.nb,caretta33.nb,caretta34.nb,caretta35.nb)

####Para visualizar os resultados de cada modelo####

summary(caretta30.nb)

####Para visualizar os resíduos####

plot(fitted(caretta30.nb), residuals(caretta30.nb), xlab="fitted values",ylab="residuals")

####Observação: os mesmos passos foram repetidos para C. mydas e D. coriacea####

```

```
#####
```

###Capítulo 2###

###Rotina para os modelos generalizados aditivos mistos (GAMM)###

```
###Para carregar a biblioteca necessária###
```

```
library(mgcv)
```

```
###Preparação dos dados###
```

```
data2<-read.table("silags.txt", header=TRUE)
```

```
age <- c(data2$age)
```

```
c <- c(data2$c)
```

```
id <- as.factor (data2$id)
```

```
n <- c(data2$n)
```

```
###Análise exploratória dos dados###
```

```
par(mfrow=c(2,2))
```

```
plot(age, c, xlab="age", ylab="c")
```

```
plot(age, n, xlab="age", ylab="n")
```

```
par(mfrow=c(2,2))
```

```
boxplot(age, xlab="age")
```

```
boxplot(c, xlab="c")
```

```
boxplot(n, xlab="n")
```

```
###Teste de Colinearidade###
```

```
panel.cor <- function(x, y, digits=2, prefix="", cex.cor)
```

```
{
```

```
usr <- par("usr"); on.exit(par(usr))
```

```
par(usr = c(0, 1, 0, 1))
```

```
?pairs

r = (cor(x, y, use="complete"))

txt <- format(c(r, 0.123456789), digits=digits)[1]

txt <- paste(prefix, txt, sep="")

if(missing(cex.cor)) cex <- 0.8/strwidth(txt)

text(0.5, 0.5, txt, cex = cex * abs(r))

}

plot(data, lower.panel=panel.smooth, upper.panel=panel.cor)
```

```
###Modelo Aditivo Misto para carbono e idade###
```

```
c1 <- gamm(c ~ s(age), random = list(id =~ 1), data = data2)

summary(c1$gam)

summary(c1$lme)

par(mfrow=c(1,1))

plot(c1$gam, scale = FALSE)

abline(h=0)

text(5,3,"GAMMd13C_Age")

c2 <- gam(c ~ s(age), data = data)

predict(c1$gam)

write.csv(predict, "Loggerhead.d13C predictvalues.csv")
```

```
###Teste de autocorrelação dos resíduos###
```

```
Ec <- resid(c1$lme, type = "normalized")

EAllc <- vector(length = length(c))

EAllc[] <- NA
```

```
Ic <- !is.na(c)
```

```
EAllc[Ic] <- Ec
```

```
library(lattice)
```

```
xyplot(EAllc ~ age | id, col = 1, ylab = "Residuals")
```

###Observação: os memos passos foram repetidos para os modelos para nitrogênio e idade###

###rotina para o modelo com o comprimento da carapaça da tartaruga###

```
library(mgcv)
```

###Preparação dos dados###

```
data<-read.table("size.txt", header=TRUE)
```

```
age <- c(data$age)
```

```
ccl=c(data$ccl)
```

```
c <- c(data$c)
```

```
id <- as.factor (data$id)
```

```
n <- c(data$n)
```

###gráfico relação age and ccl###

```
ggplot(data, aes(x=age, y=ccl)) +
```

```
  geom_point(shape=1) + #use hollow circles#
```

```
  geom_smooth(method=lm) + #Add linear regression line #(by default includes 95%
  confidence region)#
```

```
  xlab("Estimated Age") + ylab("Estimated CCL") +
```

```
  theme_bw()
```

###Modelo Aditivo Misto para carbono e comprimento curvilíneo da carapaça da tartaruga (ccl, da sigla em inglês)###

```
c2 <- gamm(c ~ s(ccl), random = list(id =~ 1), data = data)
```

```
summary(c2$gam)
```

```
summary(c2$lme)
```

```
par(mfrow=c(1,1))
```

```
plot(c2$gam, scale = FALSE)
```

```
abline(h=0)
```

```
text(30,4,"GAMMd13C_CCL")
```

```
###Modelo Aditivo Misto para nitrogênio e ccl###
```

```
n2 <- gamm(n ~ s(ccl), random = list(id =~ 1), data = data)
```

```
summary(n2$gam)
```

```
summary(n2$lme)
```

```
par(mfrow=c(1,1))
```

```
plot(n2$gam, scale = FALSE)
```

```
abline(h=0)
```

```
text(30,8,"GAMMd15N_CCL")
```

```
###Rotina para o retro-cálculo do comprimento curvilíneo da carapaça (CCC)###
```

```
###Entrada dos dados# planilha com os dados do diâmetro do úmero e CCC da tartaruga ao  
morrer###
```

```
data_cc <- read.table("bph_cc.txt", header=T)
```

```
lop <- 4.778982 #CCC médio dos filhotes recém-eclodidos
```

```
dop <- 1.9 #diâmetro médio do úmero dos filhotes recém-eclodidos
```

```
###Dados de entrada###
```

```

attach(data_cc)

data_cc <- list (L=length(l),x=log(d - dop) , y=log(1 - lop))

detach(data_cc)

###Definição dos parâmetros###

parametros <- list("B","b", "c", "sigma")

inicio <- function(){

    list(b=0,c=0,sigma=1)

}

###O modelo###

sink("bph1.txt")

cat("model {

    b ~ dnorm(0,.001)I(-10,10)

    c ~ dnorm(0,.001)I(-10,10)

    sigma ~ dunif(0,10)

    tau <- 1/(sigma*sigma)

    B<-exp(b)

for (i in 1:L){

    mu[i] <- b + c*x[i]

    y[i] ~ dnorm(mu[i],tau)

}

} ")

sink()

```

```
####Para carregar as bibliotecas necessárias####
```

```
library(R2WinBUGS)
```

```
library(BRugs)
```

```
ajuste_1_cc <- bugs(data_cc,inicio,parametros,model.file="bph1.txt",
                    n.chains=1,n.iter=31000,n.burnin=21000,n.thin=2, program="OpenBUGS",
                    debug=TRUE, DIC=TRUE)
```

```
print(ajuste_1_cc,dig=3)
```

```
plot(ajuste_1_cc)
```

```
####DIAGNOSTICOS####
```

```
library(coda)
```

```
sapo <- mcmc(ajuste_1_cc$sims.matrix)
```

```
plot(sapo,trace=T,density=F)
```

```
plot(sapo,trace=F,density=T)
```

```
autocorr.plot(sapo)
```

```
crosscorr.plot(sapo)
```

```
####Geweke diagnostics (single chain)
```

```
geweke.diag(sapo)
```

```
####Usando o ajuste acima segue a sintaxe para descobrir
```

```
####o valor de x quando y = 19 (por exemplo)####
```

```
b.post <- ajuste_1_cc$sims.matrix[, "b"]
```

```
c.post <- ajuste_1_cc$sims.matrix[, "c"]
```

```

####CCC estimado do diametro do úmero####

banco.2 <- read.table("tc.txt", header=T)

attach(banco.2)

dados.2 <- list (L=length(l),l=l, d=d, d.hat2=d.hat2)

ccc.est <- function(l,d,d.hat2)

{ x <- log(d-dop)

  y.pred <- b.post + c.post*x

  x.hat <- log(d.hat2-dop)

  y.hat <- b.post + c.post*x.hat

  l.hat <- exp(y.hat)+lop

  list(L=length(l), l.hat=l.hat)

}

objeto <- numeric()

outro.obj <- numeric()

for(i in 1:69) {

  saidas <- ccc.est(l[i],d[i],d.hat2[i])

  outro.obj[i] <- mean(saidas$l.hat)

}

outro.obj

as.data.frame(outro.obj)

####CCC_ estimado das LAGs####

est <- read.table("lags.txt", header=T)

attach(est)

```

```

dados.4 <- list (L=length(l),l1=l1, d1=d1, d.hat4=d.hat4)

ccc.est <- function(l1,d1,d.hat4)

{ x <- log(d1-dop)

  y.pred <- b.post + c.post*x

  taxa <- l1/(exp(y.pred)+lop)

  x.hat <- log(d.hat4-dop)

  y.hat <- b.post + c.post*x.hat

  l.hat2 <- exp(y.hat)+lop

  l.hat4 <- l.hat2*taxa

  list(L=length(l), l.hat4=l.hat4, taxa=taxa)

}

outro.obj2 <- numeric()

objeto <- numeric()

for(i in 1:791) {

  saidas2 <- ccc.est(l1[i],d1[i],d.hat4[i])

  outro.obj2[i] <- mean(saidas2$l.hat4)

  objeto[i] <- mean(saidas2$taxa)

}

outro.obj2

as.data.frame(outro.obj2)

###para exportar o data frame em planilha de excel no diretório de trabalho###

write.csv(outro.obj2,"CCCs estimados.csv")

```

```
#####
```

###Capítulo 3###

###Rotina para as análises de densidade – kernel###

###Carregando os pacotes necessários###

```
library(maps)
library(rgdal)
library(sqldf)
library(RPostgreSQL)
library(ggplot2)
library(KernSmooth)
library(raster)
```

###Conexão ao BD###

```
options(sqldf.RPostgreSQL.user="usuario_do_bd",
        sqldf.RPostgreSQL.password="senha",
        sqldf.RPostgreSQL.dbname ="nome_do_bd",
        sqldf.RPostgreSQL.host ="ip_do_servidor_do_bd",
        sqldf.RPostgreSQL.port =porta)
```

###Carregando os dados para calcular as superfícies kernel###

###Estes dados estão organizados no SGBD Postgres, com acesso externo###

###As credenciais não foram publicadas neste trabalho, uma vez que os dados ainda não são públicos###

###tartarugas

```
turt<-sqldf("select lon, lat, season, prof from ttags6h")
```

###espinhel

```
long<-sqldf("select lon,lat, season, prof from aespinhelg")
```

###arrasto

```
traw<-sqldf("select st_x(geom) as lon, st_y(geom) as lat, season, prof from aarrastog")
```

#emalhe

```
gill<-sqldf("select st_x(geom) as lon, st_y(geom) as lat, season, prof from aemalhe where
season is not null")
```

```

####Definindo o retângulo de extensão das análises####
minlon<-min(turt$lon-.5)
maxlon<-max(turt$lon+.5)
minlat<-min(turt$lat-.5)
maxlat<-max(turt$lat+.5)

####Definindo o número de linhas e colunas dos kernel (resolução espacial de 0,05 graus de lat e
lon)####
nx<-as.integer((maxlon-minlon)/.05)
ny<-as.integer((maxlat-minlat)/.05)

####Elaboração de mapas de densidade kernel####
####Tartarugas no verão####
####Calculando o kernel####
dens <- bkde2D(turt[which(turt$season=='Summer'),], # nome da variável com lat, lon#
               bandwidth=c(0.25,0.25), #maior distância de influência de cada ponto, neste caso em
               graus#
               gridsize=c(nx,ny), #número de linhas e colunas (resolução) do arquivo gerado#
               range.x=list(c(minlon,maxlon),c(minlat,maxlat))) #coordenadas mínimas e máximas
do cálculo#

####Transformando em raster####
dens.raster = raster(list(x=dens$x1, y=dens$x2, z=dens$fhat))
projection(dens.raster) <- CRS("+init=epsg:4326")
xmin(dens.raster) <- minlon
xmax(dens.raster) <- maxlon
ymin(dens.raster) <- minlat
ymax(dens.raster) <- maxlat

####Normalizando as densidades para valores entre 0 e 1 (Transformação Linear)####
kde.turtles.summer <- (dens.raster-cellStats(dens.raster,"min"))/(cellStats(dens.raster,"max")-
cellStats(dens.raster,"min"))

```

####Repetir as linhas de comando para cada tipo de dado (tartaruga, espinhel, arrasto, emalhe) e cada estação (verão, outono, inverno e primavera)

####Fazendo tabela de correlação de spearman entre o kernel das tartarugas e da pesca por estação do ano####

####para carregar a biblioteca necessária####

library(Hmisc)

####r.df.su é um dataframe com lat, lon, kernel de tartarugas, kernel do espinhel, kernel do emalhe, kernel do arrasto de parelha, no verão

rcorr(as.matrix(r.df.su), type="spearman") #para o verão#

rcorr(as.matrix(r.df.au), type="spearman") #para o outono#

rcorr(as.matrix(r.df.wi), type="spearman") #para o inverno#

rcorr(as.matrix(r.df.sp), type="spearman") #para a primavera#