UNIVERSIDADE FEDERAL DO RIO GRANDE – FURG
INSTITUTO DE OCEANOGRAFIA
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA

USO DO HABITAT E DE RECURSOS ALIMENTARES PELA TARTARUGA-CABEÇUDA (*Caretta caretta*) NO ATLÂNTICO SUL OCIDENTAL

CELINA CAROLINA GAY DE ALMEIDA

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Orientador: Profa. Dra. Danielle da Silveira Monteiro

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ATA DE DEFESA DE DISSERTAÇÃO DE MESTRADO – 05/2025

Às quatorze horas do dia vinte e nove de agosto do ano de dois mil e vinte e cinco, de forma virtual sala https://meet.jit.si/defesa_mestrado_Celina, Presencial – Sala 5102 – Pav. 5 – C. CARREIROS/FURG, reuniu-se a Comissão Examinadora de Dissertação de Mestrado da Acad. **Celina Carolina Gay de Almeida**, composta pelos seguintes membros: Profa. Dra. Danielle Monteiro – Orientadora - (PPGOB/IO/FURG); Profa. Dra. Gabriela Vélez-Rubio - Coorientadora - (UDELAR, Uruguai); Prof. Dr. Alexandre Miranda Garcia - (PPGOB/IO/FURG); Profa. Dra. Camila Domit (CEM/UFPR) e Dra. Luciana Medeiros (CIMATEC). Título da Dissertação: **"**USO DO HABITAT DA TARTARUGA-CABEÇUDA (Caretta caretta) NO ATLÂNTICO SUL OCIDENTAL"**.** Dando início à reunião, a orientadora, agradeceu a presença de todos e fez a apresentação da Comissão Examinadora. Logo após, explicou que a candidata teria um tempo de 45 a 60 min. para explanação do tema, e cada membro da Comissão, um máximo de 30 min. para perguntas. Dando prosseguimento, passou a palavra à candidata que apresentou o tema e respondeu às perguntas formuladas. Após explanação, a Comissão aprovou o que segue: As sugestões de todos os membros da Comissão Examinadora, que seguem em pareceres em anexo, foram aceitas pela orientadora/candidata para incorporação na versão final. Foi atribuída a seguinte classificação a candidata: Prof. Dr. Alexandre Miranda Garcia - Classificação: Aprovada; Profa. Dra. Camila Domit - Classificação: Aprovada e Dra. Luciana Medeiros - Classificação: Aprovada. A candidata foi considerada APROVADA por UNANIMIDADE. Nada mais havendo a tratar eu, Clabisnei Moura de Melo – Secretário do PPGOB lavro a presente ata que após lida e aprovada, será assinada pela Comissão Examinadora, pela aluna e pela Coordenadora do PPGOB.

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ÍNDICE

RESUMO ……...…05
ABSTRACT ……...….07
1. INTRODUÇÃO ……...…...08
1.1. Objetivos e hipóteses ……...……20
2. MATERIAIS E MÉTODOS ……...….21
2.1. Área de estudo ……...……...21
2.2. Coleta das amostras ……...…...21
2.3. Processamento das amostras ……...…….22
2.4. Análise dos dados (Artigo 1) ……...……25
2.5. Análise dos dados (Artigo 2) ……...……28
3. RESULTADOS ……...……30
3.1. Artigo 1 ……...…….30
3.2. Artigo 2 ……...……...……..37
4. CONCLUSÕES PRINCIPAIS ……...….39
5. REFERÊNCIAS BIBLIOGRÁFICAS ……...….41
ANEXO I ……...….53
ANEXO II ……...……...….96

RESUMO

O Atlântico Sul Ocidental (ASO) é uma importante área de alimentação e desenvolvimento para indivíduos de tartarugas-cabeçuda (*Caretta caretta*). O objetivo deste estudo foi caracterizar os padrões de uso do habitat e de recursos alimentares pela espécie na região, com base na análise de isótopos estáveis de carbono e nitrogênio em amostras sucessivas do escudo da carapaça. Foram analisadas 42 tartarugas encontradas mortas no litoral do estado do Rio Grande do Sul (RS, Brasil) (n = 13) e do Uruguai (n = 22), além de indivíduos capturados incidentalmente por espinhel pelágico (n = 5) e arrasto de parelha (n = 2). As análises isotópicas permitiram reconstruir o uso do habitat e de recursos alimentares durante um longo período da vida dos indivíduos, distinguindo três principais estágios de vida: juvenis oceânicos, juvenis neríticos e adultos. Modelos lineares mistos indicaram um aumento significativo nos valores de $\delta^{13}C$ e $\delta^{15}N$ com o avanço no estágio de vida, refletindo a mudança do habitat oceânico para o nerítico. Esse padrão também foi observado na comparação do nicho isotópico entre os grupos, sugerindo que juvenis neríticos e adultos ocupam níveis tróficos mais elevados do que juvenis oceânicos. Identificou-se que os valores isotópicos de tartarugas-cabeçuda machos e fêmeas no ASO são semelhantes, mas as fêmeas geralmente exibem valores de $\delta^{13}C$ mais deplecionados em comparação aos machos. Modelos de mistura isotópica revelaram que, ao longo da ontogenia, juvenis oceânicos apresentaram dieta dominada por presas pelágicas, como salpas. Os juvenis neríticos e adultos, por sua vez, se alimentam majoritariamente de invertebrados bentônicos, como crustáceos, peixes e gastrópodes. Nos indivíduos classificados como recrutas, observou-se a transição do ambiente oceânico para o nerítico, marcada por uma mudança na dieta, de presas pelágicas para bentônicas. Essa transição variou entre indivíduos, indicando dois padrões principais de recrutamento: discreto (mudança abrupta) e facultativo (transição gradual). Tartarugas de todos os estágios de vida apresentaram alto grau de especialização individual e consistência temporal no uso dos recursos, indicando que, embora a população do ASO seja considerada generalista, é composta por indivíduos especialistas ao longo de todo o ciclo de vida. Os resultados encontrados ampliam a compreensão sobre as variações na história de vida da tartaruga-cabeçuda e destacam a utilidade dos escudos da carapaça no estudo dessa variação. A análise sequencial desse tecido fornece um método valioso para reconstruir padrões de uso do habitat e de recursos alimentares ao longo de vários anos,

fornecendo uma visão mais ampla da ecologia de uma espécie marinha longeva e ameaçada de extinção.

Palavras-chave: ecologia trófica, isótopos estáveis, mudanças ontogenéticas, tartaruga-cabeçuda

ABSTRACT

The Southwestern Atlantic Ocean (SWAO) is an important feeding and developmental area for loggerhead turtles (*Caretta caretta*). This study aimed to characterize habitat and resource use patterns of the species in the region based on carbon and nitrogen stable isotope analysis of successive scute samples. A total of 42 turtles were analyzed, including individuals found dead along the coast of Rio Grande do Sul, Brazil (n = 13) and Uruguay (n = 22), as well as individuals incidentally caught by pelagic longline fisheries (n = 5) and bottom pair trawl fishery (n = 2). Isotopic analyses enabled a retrospective reconstruction of habitat and resource use throughout the life history of each turtle, distinguishing three main life stages: oceanic juveniles, neritic juveniles, and adults. Linear mixed models indicated a significant increase in $\delta^{13}C$ and $\delta^{15}N$ values with ontogenetic stage, reflecting the shift from oceanic to neritic habitats. This pattern was also evident in the comparison of isotopic niches among groups, suggesting that neritic juveniles and adults forage at higher trophic levels than oceanic juveniles. It was found that the isotopic values of male and female loggerhead turtles in the SWAO were similar, but females generally exhibited more depleted $\delta^{13}C$ values compared to males. Isotopic mixing models revealed that, throughout ontogeny, oceanic juveniles exhibited a diet dominated by pelagic prey, such as salps. In contrast, neritic juveniles and adults fed primarily on benthic invertebrates, including crustaceans, fish, and gastropods. Among individuals classified as shifters, a transition from oceanic to neritic habitats was observed, marked by a dietary shift from pelagic to benthic prey. This transition varied among individuals, indicating two main ontogenetic shift patterns: discrete (abrupt shift) and facultative (gradual transition). Turtles from all life stages exhibited a high degree of individual specialization and temporal consistency in resource use, suggesting that although the SWAO loggerhead population is considered generalist, it is composed of individually specialized turtles throughout the life cycle. The results contribute to a better understanding of life-history variation in loggerhead sea turtles and highlight the value of carapace scutes for studying this variation. Sequential analysis of this tissue provides a valuable method for reconstructing habitat and resource use patterns over multiple years, offering a broader view of the ecology of a long-lived and endangered marine species.

Keywords: trophic ecology, stable isotopes, ontogenetic changes, loggerhead turtle

1. INTRODUÇÃO

Estudos que abordam a ecologia alimentar das tartarugas marinhas podem fornecer informações valiosas sobre a utilização dos recursos tróficos, qualidade das áreas de alimentação e de como as atividades humanas podem interferir no uso do habitat por estes animais (Bjorndal 1997). Essas informações são essenciais para orientar ações de conservação para espécies ameaçadas, pois permitem identificar habitats críticos (Bjorndal 1997, Cameron et al. 2019) e avaliar a vulnerabilidade das populações frente a diferentes ameaças (Plotkin et al. 1993, Seney & Musick 2007).

A tartaruga-cabeçuda, *Caretta caretta*, é uma das sete espécies de tartarugas marinhas conhecidas no mundo e uma das seis espécies da família Cheloniidae. Possui ampla distribuição, ocorrendo em águas temperadas, tropicais e subtropicais dos oceanos Atlântico, Pacífico e Índico (Dodd 1988, Márquez 1990). Morfologicamente, esta espécie pode ser identificada pela presença de dois pares de placas pré-frontais e uma inter pré-frontal na cabeça, além de uma carapaça de tonalidade marrom com cinco pares de escudos laterais (Fig. 1, Wyneken 2001). O nome popular "tartaruga-cabeçuda" deve-se ao tamanho desproporcional de seu grande crânio em relação ao restante do corpo e à presença de um bico córneo robusto, que lhe confere força para predar organismos de carapaça rígida, como crustáceos e moluscos.

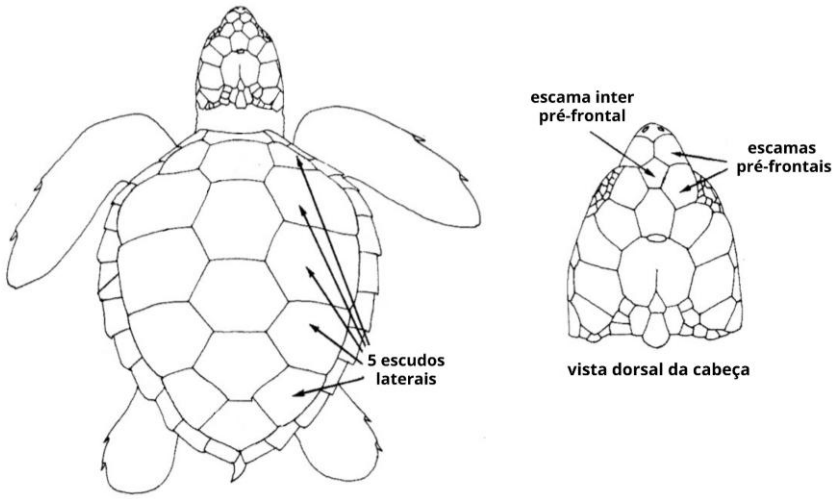


Figura 1: Características morfológicas da tartaruga-cabeçuda (*Caretta caretta*). Adaptado de Márquez (1990).

Semelhante às outras espécies de tartarugas marinhas, a tartaruga-cabeçuda possui um ciclo de vida longo e complexo. Após a eclosão dos ovos, os filhotes migram em direção ao mar aberto, iniciando a fase de desenvolvimento oceânico, onde vão permanecer no ambiente pelágico por alguns anos (aproximadamente 12 anos para populações do Atlântico sudoeste; Petitet et al. 2012). Após este período, quando se tornam grandes juvenis, recrutam para a zona nerítica em regiões tropicais e subtropicais, para completar seu desenvolvimento, fazendo migrações ao longo da fase adulta entre as áreas de forrageamento, cópula e desova (no caso das fêmeas) (Musick & Limpus 1997, Bolten 2003, Fig. 2). Entretanto, podem passar por um período de transição ontogenética complexo e de duração variável, durante o qual utilizam tanto o ambiente oceânico quanto o costeiro para alimentação e desenvolvimento (Bolten 2003, McClellan & Read 2007, Casale et al. 2008). Assim, os indivíduos podem apresentar diferentes padrões de transição ontogenética entre habitats, incluindo transições discretas (abruptas, ocorrendo em um único ano, do habitat oceânico para o nerítico); transições facultativas (graduais, caracterizadas pelo uso misto dos habitats durante vários anos); ou transições contínuas (múltiplas transições discretas ao longo do tempo), refletindo diferentes estratégias de recrutamento durante o desenvolvimento (Ramirez et al. 2015).



Figura 2: Esquema do ciclo de vida de *Caretta caretta*. Linhas contínuas representam movimentos entre estágios de vida e ecossistemas; linhas pontilhadas são especulativas. Adaptado de Bolten (2003).

Estudos de telemetria satelital reforçam este período de transição entre habitats. No Atlântico Norte, foi documentado que juvenis de tartaruga-cabeçuda podem alternar entre áreas costeiras e oceânicas, mesmo após se aventurarem em áreas de forrageamento neríticas (McClellan & Read 2007, Mansfield et al. 2009). No Atlântico Sul, juvenis capturados incidentalmente na pesca com espinhel pelágico na região oceânica do Uruguai e do Brasil, além de utilizarem a região do talude e águas internacionais adjacentes como áreas de forrageamento, realizaram deslocamentos para áreas costeiras da plataforma continental (Barceló et al. 2013). No estuário do Rio da Prata, os indivíduos juvenis exibiram uma forte fidelidade ao local de forrageamento para esta área estuarina, mas realizaram deslocamentos durante o inverno e primavera para águas costeiras do Brasil e Uruguai, e também para áreas oceânicas (González Carman et al. 2016).

Portanto, para a tartaruga-cabeçuda, mudanças ontogenéticas no habitat também são marcadas por mudanças ontogenéticas na dieta. No Atlântico Norte, por exemplo, antes de recrutar para zonas neríticas, indivíduos de *C. caretta* alimentam-se oportunisticamente de presas pelágicas, e após o recrutamento mudam para uma alimentação bentônica (Bolten 2003, McClellan et al. 2010). Assim, o comportamento alimentar da espécie pode sofrer alterações conforme a idade, mas sua dieta é principalmente carnívora durante toda a sua vida (Márquez 1990). Na fase oceânica, os filhotes são oportunistas e se alimentam de itens pelágicos/epipelágicos, principalmente de organismos gelatinosos, como salpas e pirossomos. Quando juvenis, ao migrarem para zona nerítica, começam a especializar sua alimentação em itens bentônicos, como crustáceos, moluscos e peixes, que passam a dominar sua alimentação ao longo da vida (Jones & Seminoff 2013).

Ao longo de seu ciclo de vida, as tartarugas-cabeçuda estão expostas a diferentes ameaças, sendo a atividade humana o principal fator responsável pelo declínio das populações de tartarugas marinhas (Lutcavage et al. 1997). A perda de praias de nidificação e habitats de forrageamento, a poluição por óleo, a ingestão e o emaranhamento em materiais de origem antropogênica, as alterações climáticas e, principalmente, a captura incidental em pescarias artesanais e industriais representam ameaças significativas à sua sobrevivência (Lutcavage et al. 1997, Hall et al. 2000, Hamann et al. 2010, Wallace et al. 2013, López-Mendilaharsu et al. 2020). Por esta razão,

a espécie apresenta tendência populacional decrescente em nível global e está classificada como “vulnerável” na lista vermelha de espécies ameaçadas de extinção da União Internacional para a Conservação da Natureza - *IUCN* (Casale & Tucker 2017), mesma categoria atribuída nacionalmente no Brasil e no Uruguai (Vélez-Rubio et al. 2019, MMA 2022). Nesse contexto, compreender os padrões de uso do habitat e de recursos alimentares é crucial para desenvolver e manter estratégias de conservação que sejam verdadeiramente eficazes para espécies altamente migratórias, como é o caso das tartarugas marinhas (Seminoff et al. 2012, Rees et al. 2016).

No Atlântico Sul Ocidental (ASO), essa necessidade se torna ainda mais evidente, já que a região abriga importantes áreas de desova, alimentação e desenvolvimento de tartarugas-cabeçuda (Marcovaldi & Marcovaldi 1999, Vélez-Rubio et al. 2013, González Carman et al. 2016, Monteiro et al. 2016). No Brasil, essa é a espécie de tartaruga marinha mais abundante, com adultos desovando regularmente entre Sergipe e o Rio de Janeiro (Marcovaldi & Chaloupka 2007) e utilizando áreas de forrageamento ao longo da costa nordeste, especialmente no litoral do Ceará (Marcovaldi et al. 2010). Juvenis e adultos também forrageiam ao longo da costa do sul do Brasil (Bugoni et al. 2003, Monteiro et al. 2016), do Uruguai e da Argentina, próximas ao estuário do Rio da Prata (Barceló et al. 2013, González Carman et al. 2016). Essas regiões se destacam como importantes áreas de alimentação para a espécie, mas também apresentam elevadas taxas de encalhes anuais, frequentemente associados à captura incidental nas atividades pesqueiras (González Carman et al. 2011, Vélez-Rubio et al. 2013, Monteiro et al. 2016, Maruyama et al. 2024), o que reforça a necessidade de atenção em estratégias de conservação.

Diante dos desafios impostos pelas ameaças antrópicas e pela complexidade do uso do habitat e de recursos alimentares pela espécie, é essencial contar com ferramentas capazes de fornecer informações mais completas a respeito da ecologia alimentar destes animais. Nesse sentido, a análise de isótopos estáveis (AIE) tem sido amplamente utilizada, visto que auxilia na investigação da dieta (Newsome et al. 2009), relações tróficas (Hobson et al. 1994), uso do habitat (Rubenstein & Hobson 2004) e migrações (Hobson 1999). Trata-se de uma abordagem complementar às ferramentas tradicionais, como a análise do conteúdo estomacal, a qual permite identificar apenas os itens alimentares consumidos pouco antes da morte do animal ou de sua captura (Burke et al.

1993, Plotkin et al. 1993). Em contraste, a AIE possibilita a investigação da dieta de longo e curto prazo, visto que se trata de uma medida da dieta assimilada e não apenas ingerida (Peterson & Fry 1987). Além disso, essa técnica contribui para que não ocorra a superestimação de itens de difícil digestão em detrimento daqueles que são facilmente digeridos (Plotkin et al. 1993). Isto é possível devido ao fato de a composição isotópica de um predador estar diretamente relacionada com a de sua presa, através de uma dieta assimilada ao longo do tempo (Deniro & Epstein 1981).

Para entender o funcionamento da AIE, é fundamental conhecer o conceito de isótopos. Os isótopos são átomos do mesmo elemento químico que diferem entre si pelo número de nêutrons no núcleo (Fry 2006). Alguns isótopos são ditos estáveis por não apresentarem decaimento químico, ou seja, por manterem sua massa ao longo do tempo (Michener & Lajtha 2007). Atualmente, os isótopos estáveis de maior interesse em ecologia são aqueles de elementos que tem seu ciclo intimamente ligado à matéria orgânica, sendo eles o hidrogênio, carbono, nitrogênio, oxigênio e enxofre (Fry 2006). Sua aplicação é feita por meio de uma razão de dois isótopos estáveis, um pesado e um leve (por exemplo, $^{13}C/^{12}C$ e $^{15}N/^{14}N$), tanto no tecido do predador quanto no de suas presas. Essa razão isotópica é quantificada nas amostras em relação à um padrão internacionalmente aceito e expressa em partes por mil (‰) com a notação δ (Michener & Lajtha 2007). Quando os valores de δ aumentam, denotam um acréscimo na quantidade do isótopo pesado em relação ao padrão, e essas amostras são denominadas de enriquecidas, e quando ocorre o oposto, são denominadas de deplecionadas (Fry 2006).

Sendo assim, a AIE se baseia na premissa de que a composição isotópica dos predadores reflete a de suas presas, com uma diferença devido à discriminação isotópica — processo pelo qual as razões entre os isótopos estáveis da presa e do consumidor se alteram durante o processamento metabólico do material consumido (Fry 2006). O carbono possui baixa discriminação isotópica, usualmente em torno de 1‰ (DeNiro & Epstein 1978), enquanto a discriminação do nitrogênio é mais acentuada, variando entre 3 e 5‰ a cada nível trófico (DeNiro & Epstein 1981).

Visto que a razão isotópica do carbono ($\delta^{13}C$) muda pouco à medida que o carbono se move através das teias alimentares, ela é amplamente utilizada para diferenciar recursos alimentares de distintos habitats (oceânico *versus* nerítico, pelágico *versus*

bentônico) (Post 2002). Ambientes costeiros, por exemplo, onde a produção primária se baseia em macrófitas e macroalgas, apresentam valores mais enriquecidos em ^{13}C em comparação ao ambiente pelágico, onde a produção fitoplanctônica resulta em valores mais baixos de $\delta^{13}C$ (France 1995). Além disso, os isótopos estáveis de carbono podem variar com a profundidade da coluna d'água, com predadores bentônicos geralmente apresentando maior enriquecimento em ^{13}C em relação aos predadores pelágicos (Hobson et al. 1994). Por exemplo, no Uruguai foi verificado que o material orgânico particulado (MOP), representante do habitat pelágico, apresenta valores de $\delta^{13}C$ em torno de -20‰, enquanto as macroalgas, representantes do habitat bentônico, exibiram valores mais enriquecidos, em torno de –13‰ no verão e –16‰ no inverno, evidenciando a distinção isotópica entre esses habitats (Leoni et al. 2024). Em regiões estuarinas, no entanto, como no estuário do Rio da Prata e da Lagoa dos Patos, os valores de $\delta^{13}C$ são fortemente influenciados pelas contribuições de fontes de origem terrestre e marinha, acarretando em maior variação espacial e temporal (Botto et al. 2011, Troina et al. 2020, Cani et al. 2023) (Fig. 3).

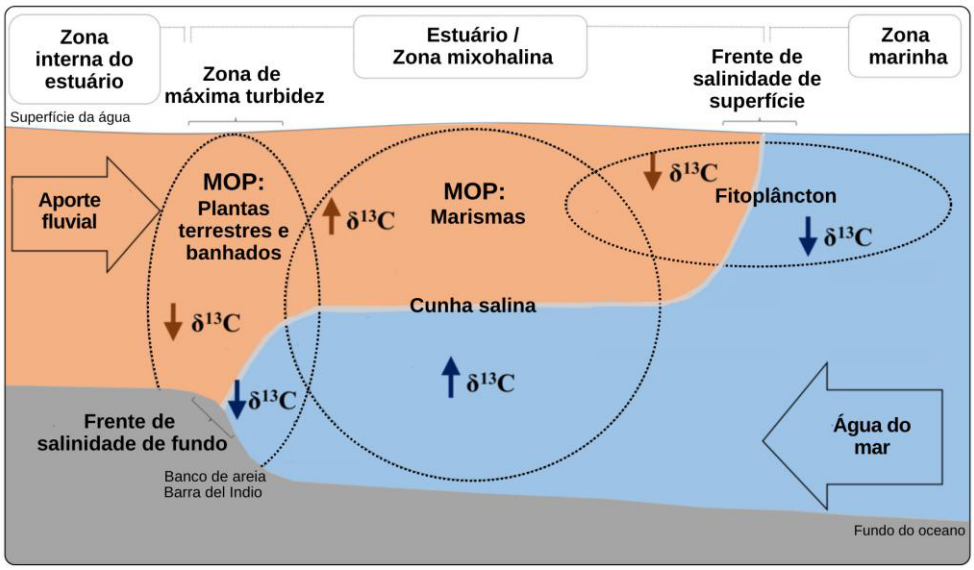


Figura 3: Variação de $\delta^{13}C$ nas diferentes regiões do estuário do Rio da Prata. Na zona interna, a zona de máxima turbidez é caracterizada por alta concentração de plantas terrestres e banhados, deplecionadas em ^{13}C (metabolismo C3), trazidas para o estuário pelo rio; na zona mixohalina, a maior parte são plantas de marismas, enriquecidas em ^{13}C (metabolismo C4); na zona marinha, o fitoplâncton marinho é predominante, também deplecionado em ^{13}C. As setas indicam a tendência geral da razão isotópica em cada região, com setas para cima representando valores enriquecidos

e setas para baixo valores deplecionados. MOP: material orgânico particulado. Adaptado de Cani e colaboradores (2023).

Diferentemente do $\delta^{13}C$, os valores de $\delta^{15}N$ tendem a aumentar gradualmente ao longo da cadeia alimentar devido à retenção do isótopo pesado – que reage mais lentamente e tende a ser utilizado na formação dos tecidos – e à eliminação do isótopo leve (por atividades como excreção e respiração) pelo predador em relação à sua presa (Fig. 4). Esse processo torna o $\delta^{15}N$ amplamente utilizado para estimar a posição trófica, particularmente quando a composição isotópica de organismos na base da cadeia alimentar (i.e., linha de base isotópica, *isotopic baseline*) é conhecida (DeNiro & Epstein 1981, Peterson & Fry 1987, Post 2002).

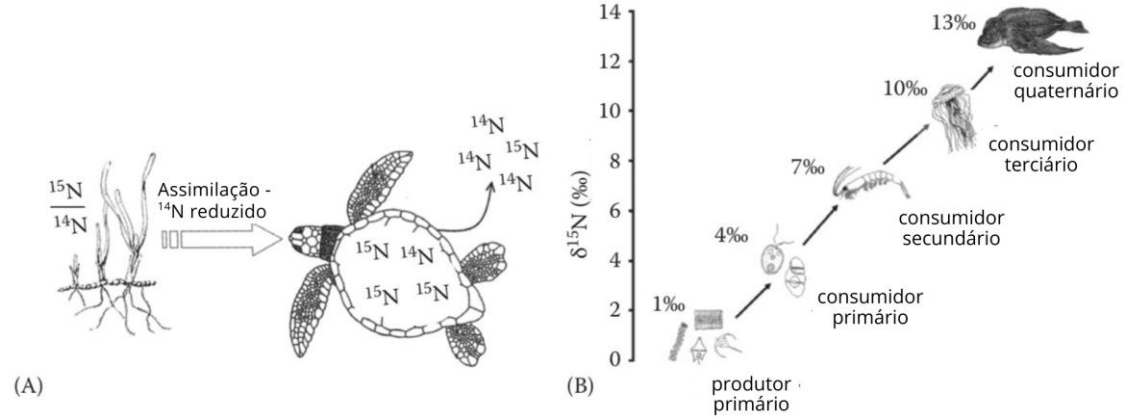


Figura 4: Esquema do enriquecimento trófico em ^{15}N em tartarugas marinhas. (A) Representação conceitual da retenção dos isótopos mais pesados de ^{15}N e da maior taxa de eliminação de isótopos mais leves de ^{14}N durante a digestão. (B) Ilustração do enriquecimento progressivo em ^{15}N, de aproximadamente 3‰ por nível trófico. Adaptado de Jones & Seminoff (2013).

O tempo necessário para que os valores isotópicos das fontes (dieta) sejam refletidos nos tecidos dos consumidores é chamado de taxa de renovação isotópica (*isotopic turnover*) e varia conforme o tecido (Newsome et al. 2010). Logo, a escolha do tecido para amostragem deve ser compatível com os objetivos da pesquisa, de modo a fornecer a janela temporal mais adequada para responder à questão investigada. Tecidos como pele e músculo, por exemplo, têm uma renovação rápida e refletem os valores da dieta das últimas semanas ou meses (Seminoff et al. 2007, Reich et al. 2008). Por outro lado, tecidos considerados metabolicamente inertes, como escudos da carapaça, no caso das tartarugas marinhas, oferecem uma abordagem alternativa para reconstruir mudanças

ontogenéticas na dieta e no habitat (Reich et al. 2007, Cardona et al. 2009, Vander Zanden et al. 2010, Vander Zanden et al. 2013, Vélez-Rubio et al. 2018, Muñoz et al. 2021, Silver-Gorges et al. 2023). Os escudos da carapaça são formados por várias camadas de queratina, onde novas camadas do tecido se formam sob as camadas mais antigas (Alibardi 2005, Fig. 6). Assim, por se tratar de um tecido que não sofre alterações físicas, químicas ou biológicas, assume-se que cada camada retém o histórico da dieta e do habitat de quando foi formada (Reich et al. 2007).

O uso dos escudos da carapaça possibilitou ampliar o conhecimento sobre o uso do habitat e de recursos alimentares durante um longo período de vida das tartarugas marinhas. No entanto, a maior parte do conhecimento disponível sobre esses animais ainda provém de estudos realizados com fêmeas adultas, devido à facilidade de acesso em áreas de desova. Em contraste, há menos conhecimento sobre as demais fases do ciclo de vida, que são mais difíceis de amostrar e acompanhar. Nos últimos anos, a AIE, aliada à telemetria satelital, revelou distintos padrões de uso de habitat e estratégias de forrageamento de tartaruga-cabeçuda (Hawkes et al. 2006, McClellan et al. 2010, Pajuelo et al. 2012, Monteiro 2017, Medeiros et al. 2019). Esses estudos indicam que a espécie pode apresentar dicotomia no uso de habitat, sendo em alguns casos associada ao tamanho corporal. Por exemplo, dimorfismos comportamentais baseados no tamanho corporal foram identificados em tartarugas-cabeçuda fêmeas adultas do Pacífico Ocidental e do leste do Oceano Atlântico, onde indivíduos maiores tendem a ocupar habitats neríticos, enquanto que os menores ocorrem preferencialmente em habitats oceânicos (Hatase et al. 2002b, Hawkes et al. 2006). Um padrão semelhante foi relatado para os machos adultos do noroeste do Pacífico, com os indivíduos maiores permanecendo em águas costeiras (Saito et al. 2015), e os menores utilizando habitats pelágicos (Hatase et al. 2002a). Entretanto, essa variabilidade não foi associada ao tamanho dos indivíduos em tartarugas-cabeçuda juvenis do noroeste do Atlântico e machos adultos do Mar Mediterrâneo (McClellan et al. 2010, Schofield et al. 2010). Essas diferenças reforçam a importância de investigar o uso do habitat e de recursos alimentares ao longo dos diferentes estágios de vida, já que mudanças nos padrões dietéticos podem expor os indivíduos a distintos tipos de ameaça, como captura incidental em pescarias com espinhel pelágico no ambiente oceânico (Sales et al. 2008), ou em pescarias de arrasto no ambiente costeiro (Monteiro et al. 2016).

Apesar da ampla literatura sobre dieta e uso do habitat de fêmeas adultas de tartaruga-cabeçuda, reconhece-se que os machos estão sub-representados devido à dificuldade de acesso a essa parcela da população (Haywood et al. 2019). Ainda assim, alguns estudos indicam que machos e fêmeas podem adotar estratégias de forrageamento semelhantes. No Atlântico Noroeste, por exemplo, machos adultos de tartaruga-cabeçuda foram registrados utilizando áreas geográficas isotopicamente distintas após a temporada de acasalamento, e a concordância entre os valores isotópicos e os padrões de movimento sugere fidelidade a locais de alimentação – comportamento já descrito para fêmeas adultas (Pajuelo et al. 2012). Nesse mesmo estudo, a variação nos valores de $\delta^{13}C$ e $\delta^{15}N$ foi similar aos valores encontrados para fêmeas adultas da mesma população (Reich et al. 2010), reforçando a semelhança nas estratégias de forrageamento entre os sexos. Em outras regiões, como no noroeste e sudeste do Atlântico e no Mar Mediterrâneo, estudos de telemetria satelital também relataram que machos adultos podem apresentar alta fidelidade e comportamento de residência em áreas de alimentação (Schofield et al. 2010, Arendt et al. 2012, Casale et al. 2013, Varo-Cruz et al. 2013). No sul do Brasil (31º21′S–51º05′O até 33º44′S–53º22′O), um estudo utilizando AIE de amostras de epiderme revelou que machos adultos ocorrem predominantemente em águas costeiras, enquanto juvenis exibem maior variabilidade no uso do habitat e de recursos (Medeiros et al. 2019).

No contexto da ecologia de populações, o conceito de nicho ecológico constitui um princípio fundamental. Formalizado por Hutchinson (1957) como um espaço abstrato n-dimensional constituído por variáveis ambientais (dieta e habitat) que permitem a existência de uma espécie, essa definição facilita a compreensão do uso de recursos, diversidade geográfica e outros aspectos da composição da estrutura da comunidade (McGill et al. 2006). A utilização da AIE neste contexto se dá por meio da adoção do nicho isotópico como um *proxy* para o nicho ecológico (Bearhop et al. 2004), sendo definido como uma área isotópica (δ-espaço) delimitada por valores isotópicos (δ-valores) que funcionam como coordenadas (Newsome et al. 2007). Assim, assume-se que o espaço isotópico é comparável as n dimensões do nicho ecológico porque a composição química de um organismo é diretamente influenciada pela dieta e/ou pelo habitat onde vive (Newsome et al. 2007).

Convencionalmente, os ecologistas utilizam a teoria de nicho para descrever a ecologia de uma espécie como um todo, tratando indivíduos coespecíficos como ecologicamente equivalentes (Bolnick et al. 2003). Entretanto, existe uma literatura bastante desenvolvida sobre variação de largura de nicho, originada com a hipótese de variação de nicho de Van Valen (1965), que incorporou pela primeira vez a ideia de variação individual no uso de recursos na teoria de nicho. A especialização individual (EI) se refere ao grau em que os indivíduos usam um subconjunto restrito do nicho ecológico da população, ou base de recursos, por motivos não atribuíveis a características como idade, sexo ou variação morfológica (Bolnick et al. 2003, Araújo et al. 2011). Desta forma, indivíduos especialistas representam um extremo ao longo de um continuum de variação intrapopulacional no uso de nicho, enquanto os generalistas, aqueles que usam uma ampla porção do nicho, representam o outro extremo (Bolnick et al. 2003).

A Teoria do Forrageio Ótimo (OFT ou *Optimal Foraging Theory*) busca explicar por que os indivíduos selecionam apenas um subconjunto da diversidade de recursos disponíveis. Segundo a OFT, os indivíduos tendem a priorizar recursos mais valiosos que maximizam a ingestão de energia por unidade de tempo de procura (MacArthur & Pianka 1966, Schoener 1974), e expandem seu nicho apenas quando esses recursos preferenciais se tornam escassos. Assim, os indivíduos podem se tornar especialistas, dedicando mais tempo à busca de uma presa, da qual obtêm o maior retorno energético; ou generalistas, quando teoricamente o ganho energético é menor, mas o consumo ocorre com maior frequência (Morse 1982). De acordo com o modelo conceitual sobre uso de recursos proposto por Vander Zanden e colaboradores (2010) (Fig. 5), as populações podem ser classificadas como generalistas, compostas por indivíduos generalistas ou especialistas; ou especialistas, compostas de indivíduos especialistas.

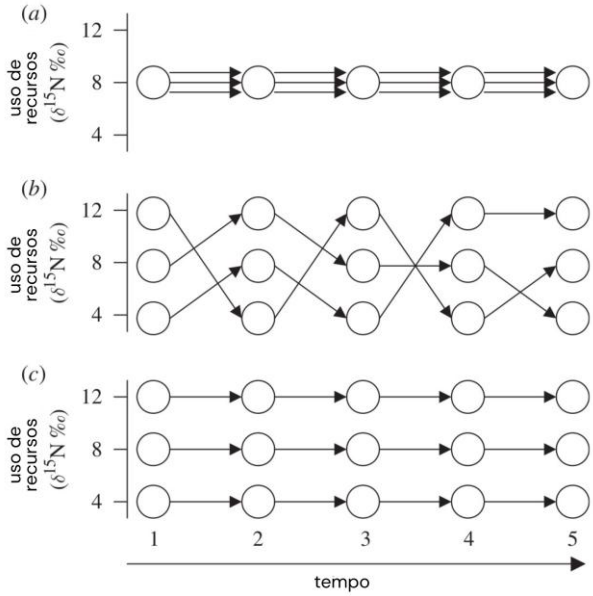


Figura 5: Modelo conceitual de três padrões populacionais representando o uso de recursos ao longo do tempo. As setas representam os indivíduos e cada círculo representa o valor de δ^{15}N para uma camada de tecido inerte, que reflete o uso de recursos (integração de dieta, habitat e localização geográfica). Legenda: (a) População especialista composta de indivíduos especialistas; (b) População generalista composta de indivíduos generalistas; (c) População generalista composta de indivíduos especialistas. Adaptado de Vander Zanden e colaboradores (2010).

Mecanismos ecológicos que levam à especialização individual podem estar relacionados à competição intra e interespecífica, oportunidade ecológica (e.g. abundância e diversidade de recursos) e predação (Araújo et al. 2011). Esses fatores provavelmente alteram a disponibilidade de recursos, o que, por sua vez, modifica a amplitude do nicho populacional e o grau de variação entre indivíduos. Por exemplo, se as presas preferenciais se tornam menos abundantes (devido ao aumento da competição intraespecífica) ou a população tem acesso a uma maior diversidade de presas (devido a diminuição da competição interespecífica ou predação, ou em decorrência do aumento das oportunidades ecológicas), os indivíduos tendem a incluir recursos alternativos em suas dietas, o que pode aumentar a divergência entre eles e, consequentemente, aumentar o grau de especialização individual (Araújo et al. 2011). Em contraste, se as presas secundárias forem itens que foram originalmente consumidas por outros, a variação entre indivíduos diminui à medida que os indivíduos ampliam sua dieta, e a especialização individual se reduz (Araújo et al. 2011).

Uma estrutura quantitativa amplamente utilizada para avaliar a variação de nicho intrapopulacional foi proposta por Roughgarden (1972, 1974), propõe que a largura total do nicho (TNW ou *Total Niche Width*) de uma população pode ser dividida em dois componentes: a variação intraindividual (WIC ou *Within Individual Component*) e a variação entre indivíduos (BIC ou *Between Individual Component*), de modo que TNW = WIC + BIC. A razão WIC/TNW é usada como uma métrica para determinar o grau de especialização individual, variando de 0, quando são especialistas e usam apenas uma parte do recurso usado pela população em geral, a 1, quando são generalistas típicos que usam todo esse recurso (Bolnick et al. 2003). Além da especialização individual, a consistência temporal pode ser avaliada pelos valores WIC ao longo do tempo (Vander Zanden et al. 2013). Como o WIC mede a variância intraindividual, a análise da consistência temporal fornece a capacidade de determinar o quão variáveis os indivíduos são em seu uso de recursos ao longo do tempo, diferente do grau de especialização individual, o qual é usado para comparar o uso de recursos dos indivíduos ao da população (Vander Zanden et al. 2013).

A variação individual na composição da dieta tem importantes implicações evolutivas, ecológicas e de conservação. No entanto, poucos estudos de tartarugas marinhas examinaram o comportamento de forrageamento de longo prazo de indivíduos. No Atlântico Norte, com base na AIE de escudos da carapaça, a população de machos e fêmeas adultos de tartaruga-cabeçuda foi classificada como uma população generalista com indivíduos especialistas (Vander Zanden et al. 2010, Pajuelo et al. 2016, Fig. 5c). *C. caretta* juvenis residentes em águas estuarinas ao longo da Carolina do Norte demonstraram consistência em sua seleção de recursos ao longo do tempo e foram especializados no uso de recursos em relação à população, com base na AIE de plasma sanguíneo de tartarugas recapturadas diversas vezes (Hall et al. 2015). Altos graus de especialização individual também foram encontrados em populações de tartarugas-cabeçuda adultas do noroeste da África (Cardona et al. 2017) e de subadultos e adultos do Japão (Muñoz et al. 2021). Tartarugas-verde (*Chelonia mydas*) adultas de uma praia de nidificação da Costa Rica também foram demonstradas como formando uma população generalista com indivíduos especialistas com base na AIE de escudos (Vander Zanden et al. 2013). Tartarugas-oliva (*Lepidochelys olivacea*) do leste do Oceano Pacífico e da costa indiana foram classificadas como populações generalistas por isótopos estáveis

de tecido epidérmico e estudos dietéticos, respectivamente (Behera et al. 2014, Peavey et al. 2017). No Brasil, estudos baseados na AIE de úmeros revelaram que tartarugas-oliva adultas da região Nordeste e tartarugas-cabeçuda juvenis oceânicas e neríticas da região Sul são especialistas dentro de populações generalistas (Monteiro 2017, Petitet et al. 2023).

Embora as pesquisas acerca do uso do habitat e de recursos alimentares pela tartaruga-cabeçuda no ASO estejam em expansão (Barceló et al. 2013, González Carman et al. 2016, Mansfield et al. 2017, Monteiro 2017, Medeiros et al. 2019), este é o primeiro estudo na região a investigar as diferenças no uso do habitat e de recursos alimentares e o grau de especialização individual entre sexos e estágios de vida da tartaruga-cabeçuda.

1.1. Objetivos e hipóteses

1.1.1. Objetivo Geral

Caracterizar os padrões de uso do habitat e de recursos alimentares por *Caretta caretta* no Oceano Atlântico Sul Ocidental (31º - 34º S).

1.1.2. Objetivos Específicos

1) Determinar a composição isotópica de carbono e de nitrogênio no escudo da carapaça de *C. caretta* ao longo da vida dos indivíduos;
2) Identificar os habitats preferenciais de uso pelos indivíduos de *C. caretta*;
3) Investigar se existem diferenças no uso do habitat e de recursos alimentares entre estágios de vida e sexos;
4) Identificar os padrões de recrutamento e mudanças ontogenéticas no uso de recursos;
5) Avaliar a existência e o grau de especialização individual entre estágios de vida e sexos.

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

i) Os indivíduos juvenis de *C. caretta* utilizam habitats neríticos e oceânicos, enquanto os adultos utilizam o habitat nerítico;

ii) Os indivíduos machos apresentam padrões semelhantes ao das fêmeas em relação ao uso do habitat e de recursos alimentares;

iii) Os indivíduos juvenis apresentam padrão de recrutamento ontogenético com transição facultativa;

iv) Os indivíduos são especializados quanto ao uso do habitat e de recursos alimentares.

Com base nesses objetivos e hipóteses, o estudo foi estruturado em duas partes, apresentadas nos Anexos I e II. Os objetivos de 1 a 4, relacionados à caracterização isotópica, à identificação dos padrões de uso do habitat e de recursos alimentares e padrões de recrutamento são abordados no Anexo I. Já o objetivo 5, que trata da avaliação da especialização individual entre estágios de vida e sexos, é detalhado no Anexo II.

2. MATERIAIS E MÉTODOS

2.1. Área de estudo

A área de estudo compreende o litoral sudoeste do Atlântico Sul, entre o Parque Nacional da Lagoa do Peixe, no Rio Grande do Sul (31º21′S–51º05′O, Brasil) e o Departamento de Montevideo (34º55'S–56º09'O, Uruguai). Essa região é influenciada pela Convergência Subtropical, a qual é formada pela confluência entre as águas frias ricas em nutrientes da Corrente das Malvinas (CM), que fluem para o norte, e as águas tropicais oligotróficas da Corrente do Brasil (CB), que fluem para o sul (Garcia 1997, Piola et al. 2008). As correntes de limite oeste (CM e CB) recebem sazonalmente grandes escoamentos continentais de água doce da bacia de drenagem do Rio da Prata e, através do estuário da Lagoa dos Patos, da Bacia hidrográfica da Lagoa dos Patos-Mirim, beneficiando a produtividade da região (Garcia 1997, Odebrecht & Castello 2001, Piola et al. 2008), o que favorece a disponibilidade de alimento para diversos organismos marinhos (Muelbert et al. 2008). Em função disso, é considerada uma importante área de alimentação e desenvolvimento para algumas espécies de tartarugas marinhas (Bugoni et al. 2003, Martinez Souza 2009).

2.2. Coleta das amostras

Amostras de escudos da carapaça de tartarugas-cabeçuda foram obtidas de espécimes encalhados mortos na costa do estado do Rio Grande do Sul (13 amostras) e

Uruguai (22 amostras), entre 2013 e 2024, durante saídas de monitoramento de praia realizadas pela equipe do Núcleo de Educação e Monitoramento Ambiental - NEMA (de 2013 a 2023) e pela Asociación Civil Karumbé (de 2015 a 2024), respectivamente (veja Vélez-Rubio et al. 2013 e Monteiro et al. 2016 para mais informações sobre os monitoramentos de praia). Também foram obtidas amostras de espécimes capturadas incidentalmente na pescaria de espinhel pelágico (n=5) e arrasto (n=2) no sul do Brasil, entre 2014 e 2022, a partir de programas de monitoramento de pesca e captura incidental realizados pelo NEMA. Para cada tartaruga encontrada, a identificação da espécie foi realizada de acordo com Pritchard & Mortimer (1999). Para cada espécime, foi obtido o comprimento curvilíneo da carapaça (CCC), medido com uma fita métrica, da linha média da incisura nucal até a extremidade posterior do escudo marginal posterior (Bolten 1999). O sexo foi determinado pela análise macroscópica das gônadas durante a necropsia (Wyneken 2001) e/ou pelo comprimento da cauda, para adultos > 83 cm de CCC, tamanho mínimo das fêmeas que desovam no Brasil (Baptistotte et al. 2003).

2.3. Processamento das amostras

Todas as amostras foram armazenadas congeladas a -4ºC, sem nenhum preservante até o processamento. Foram coletadas biópsias da região póstero-medial do terceiro escudo lateral esquerdo de cada indivíduo, próximo à margem posterior, utilizando um punch de biópsia de 6 mm de diâmetro (Fig. 6, 7a), seguindo Reich e colaboradores (2007). Foram utilizadas apenas as amostras de biópsia que atravessaram todo o escudo e alcançaram a camada mais interna. Os escudos foram enxaguados com água destilada no laboratório antes da análise.

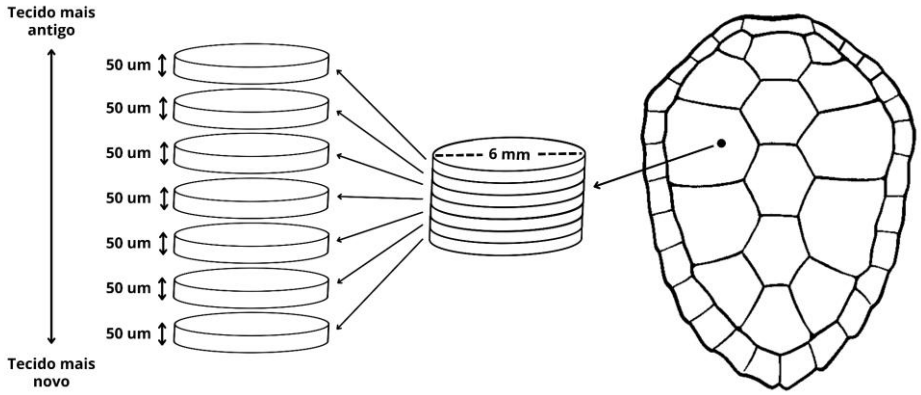


Figura 6: Esquema representativo do local de amostragem (terceiro escudo costal esquerdo).

Seguindo a metodologia proposta por Vélez-Rubio e colaboradores (2018), cada amostra foi incorporada em O.C.T. (Composto de temperatura de corte ideal, Tissue-Teck®) com o lado dorsal (tecido mais antigo) para baixo, congelado a -20°C e subamostrado em camadas sucessivas de 50 µm usando um micrótomo (Leica SM2000 R) (Fig. 7b, 7c). Foi estimado que cada camada de 50 µm corresponde a um período de aproximadamente 0,6 anos para indivíduos adultos (Vander Zanden et al. 2010). O número de camadas obtido foi proporcional à espessura do escudo. Cada camada foi posteriormente enxaguada durante 24 h com água destilada e guardada separadamente. As amostras foram secas a 60°C por 24 h. Cada camada foi analisada independentemente para as proporções de isótopos estáveis de carbono e nitrogênio. As amostras foram pesadas em cápsulas de estanho em uma balança de precisão (aproximadamente 0,3 mg de amostra) e analisadas em espectrômetro de massa de razão isotópica de fluxo contínuo (modelo *EA Flash 2000 Delta V Advantage e TC/EA, da ThermoFisher Scientific*™) no CIA/FURG. Nos casos em que camadas individuais não forneceram material suficiente para a análise de isótopos estáveis, essas camadas foram excluídas da amostragem, a fim de evitar a combinação de camadas adjacentes e, assim, preservar a resolução temporal (ou seja, manter cada camada como uma unidade de tempo de aproximadamente 0,6 anos).

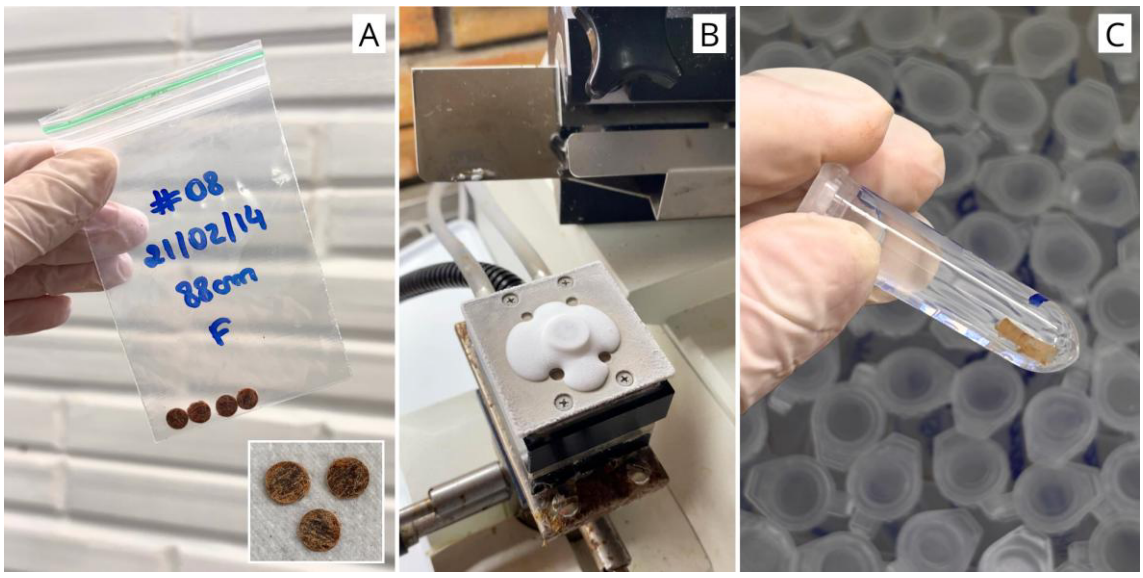


Figura 7: Etapas do processamento das amostras. (A) Coleta de amostras do escudo por meio de punchs de 6 mm de diâmetro; (B) Amostra congelada em O.C.T. e seccionamento no micrótomo; (C) Camada de 50 µm obtida do escudo de um indivíduo para posterior análise isotópica.

As abundâncias de isótopos estáveis são expressas na notação δ de acordo com a seguinte equação:

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

onde X é ^{13}C ou ^{15}N, $R_{amostra}$ é a razão isotópica do isótopo pesado em relação ao isótopo leve da amostra ($^{13}C/^{12}C$ ou $^{15}N/^{14}N$), e $R_{padrão}$ é a razão isotópica dos padrões internacionais. O CIA/FURG utiliza a cafeína, ácido glutâmico, acetanilida, NBS22, açúcar de cana, açúcar de beterraba, N_1 e N_2 como padrões internacionais, os quais são certificados pela Agência Internacional de Energia Atômica.

Dado que a presença de lipídios pode alterar os valores de $\delta^{13}C$ (Post et al. 2007), um experimento foi realizado para avaliar o efeito da extração de lipídios nos valores de $\delta^{13}C$ e $\delta^{15}N$ das amostras. Para isso, foram utilizadas duas subamostras de 10 espécimes, separados em dois grupos. Foram utilizados apenas indivíduos adultos (CCC entre 94 - 101 cm), uma vez que a dieta desses animais apresenta maior teor lipídico em comparação aos juvenis oceânicos (Barros 2010). Para garantir a comparabilidade entre os grupos, foram selecionadas as camadas centrais do escudo, correspondentes à mesma posição na sequência de camadas obtidas no micrótomo (Fig. 8). No primeiro grupo, os lipídios foram extraídos com uma solução de clorofórmio/metanol (2:1) (~1,5 mL) (Medeiros et al. 2019); o segundo grupo, o grupo controle, não passou por nenhum processo de extração (Fig. 8). As extrações foram realizadas em eppendorfs, trocando a solução Chl:Met três vezes ao dia. Após a última extração, as amostras foram secas a 60°C por 24 h e em seguida foi realizada a análise independente das proporções de isótopos estáveis de C e N.

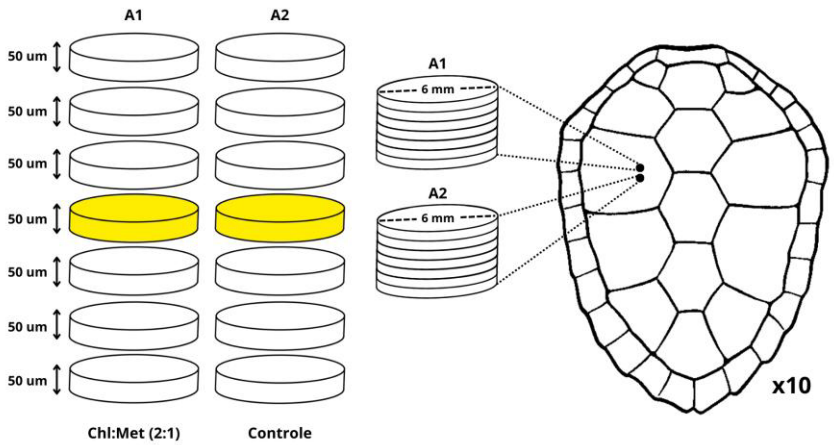


Figura 8: Esquema representativo do teste de extração lipídica. Foram obtidas duas amostras (A1 e A2) do escudo de 10 indivíduos adultos. Cada amostra foi seccionada em camadas sucessivas de 50 μm, e as camadas centrais correspondentes (destacadas em amarelo) foram selecionadas para análise de isótopos estáveis (AIE), de modo que representassem a mesma posição na sequência de camadas. As camadas do grupo teste foram submetidas à extração lipídica utilizando solução de clorofórmio/metanol (Chl:Met) (2:1), enquanto as camadas do grupo controle não foram submetidas a nenhum tratamento.

2.4. Análise dos dados (Artigo 1)

O teste t de Student pareado foi utilizado para testar se havia diferenças significativas nos valores de $\delta^{13}C$ e $\delta^{15}N$ entre camadas pareadas com e sem extração lipídica, após a verificação dos pressupostos de normalidade e homocedasticidade, por meio dos testes de Shapiro-Wilk e Levene, respectivamente.

Para identificar o número de grupos que melhor se ajustam aos dados, foi realizada uma análise de agrupamento. Essa análise considerou separadamente e em conjunto os valores de $\delta^{13}C$ e $\delta^{15}N$, utilizando a função *pam* do pacote *cluster* no R (Maechler et al. 2025). As dissimilaridades entre os indivíduos foram calculadas com base na distância euclidiana, e o melhor ajuste para o número de agrupamentos foi determinado a partir da largura média da silhueta. Essa medida é importante na validação do agrupamento, pois reflete a força de associação de cada observação ao seu respectivo grupo (Kaufman & Rousseeuw 1990). Valores de silhueta entre 0,7 e 1 indicam uma estrutura forte dentro do conjunto de dados.

Para avaliar a influência do estágio de vida, sexo e de sua interação nos valores isotópicos de $\delta^{13}C$ e $\delta^{15}N$ dos indivíduos de *C. caretta*, utilizamos Modelos Lineares (ML) e Modelos Lineares Mistos (MLM). Para lidar com as repetidas amostragens do mesmo escudo ou indivíduo, o indivíduo foi tratado como termo aleatório, enquanto o sexo, estágio de vida e sua interação foram tratados como termos fixos. Indivíduos com sexo indeterminado foram excluídos da análise, a fim de permitir a avaliação adequada do efeito do sexo e da interação entre os termos. Partindo de um modelo inicial simples, incluindo apenas um termo fixo (estágio de vida), modelos subsequentes foram gerados através da inclusão progressiva dos demais termos. O modelo mais apropriado foi selecionado com base nos menores valores do Critério de Informação de Akaike de

segunda ordem (AICc) (Burnham & Anderson 2002). Por fim, comparações múltiplas par a par foram realizadas com ajuste de Tukey, por meio do pacote *emmeans* no R (Lenth 2025).

A classificação dos estágios de vida adulto e juvenil foi definida com base no comprimento curvilíneo da carapaça: indivíduos com CCC > 83 cm, correspondente ao tamanho mínimo das fêmeas desovantes no Brasil (Baptistotte et al. 2003), foram classificados como adultos. Entretanto, visando considerar que o escudo armazena informações de vários anos da vida do animal, foi realizada uma análise retrospectiva do crescimento para estimar, dentro de cada indivíduo adulto, a camada em que teria atingido a fase adulta, com aproximadamente 83 cm. Para isso, utilizaram-se as taxas médias de crescimento por classe de tamanho descritas por Petitet e colaboradores (2012), aplicadas de forma retrospectiva, estimando o tamanho corporal correspondente a cada camada com base na suposição de que cada uma representa aproximadamente 0,6 anos (Vander Zanden et al. 2010). Com base nessa estimativa, as camadas mais externas (formadas quando o animal ainda não havia atingido 83 cm de CCC) foram classificadas como pertencentes ao estágio juvenil nerítico, enquanto as camadas mais internas (formadas após o animal atingir 83 cm de CCC) foram classificadas como adultas. Isso minimizou, mas não eliminou, a chance de classificar incorretamente os estágios de vida nos indivíduos analisados. Já os indivíduos com CCC < 83 cm foram considerados juvenis, sendo sua classificação como oceânicos ou neríticos realizada com base na análise de agrupamento dos valores de $\delta^{15}N$ das camadas do escudo. O ponto de recrutamento foi definido como a primeira camada em que o valor de $\delta^{15}N$ foi superior ao valor limite do ponto de corte estabelecido.

Modelos de mistura isotópicos Bayesianos (*Bayesian stable isotope mixing models*, pacote MixSIAR) (Stock et al. 2018), foram utilizados para estimar a contribuição das presas na dieta da tartaruga-cabeçuda, com base nos valores de $\delta^{13}C$ e $\delta^{15}N$ e com intervalo de credibilidade de 95%. Esse pacote possibilitou a inclusão de uma covariável contínua (espessura do escudo), de modo a representar as variações ontogenéticas no uso de recursos. A seleção das presas foi baseada em estudos anteriores sobre a dieta de *C. caretta* no sul do Brasil e Uruguai (Martinez Souza 2009, Barros 2010), priorizando os quatro grupos mais representativos da dieta da espécie: crustáceos,

moluscos, peixes e salpas. Além desses, os cnidários também foram incluídos nas análises, pois estudos de conteúdo estomacal frequentemente subestimam sua presença como alimento de tartarugas marinhas, já que as medusas são compostas principalmente por água e digeridas rapidamente, tornando sua detecção nos métodos tradicionais limitada (Van Nierop & Den Hartog 1984). Apesar de geralmente serem registrados em baixa ou nenhuma proporção nos estudos de conteúdo estomacal na área de estudo (Bugoni et al. 2003, Martinez Souza 2009, Barros 2010), há registros de seu consumo em outras regiões, como na costa do Atlântico Norte, Mar Mediterrâneo e Austrália (Jones & Seminoff 2013).

Após definidos os grupos de presas, selecionou-se como representante de cada grupo o menor nível taxonômico disponível (espécie, gênero ou família) que apresentasse a maior contribuição na dieta da espécie segundo o Índice de Importância Relativa (IIR) reportado nos estudos consultados, servindo como *proxy* para todo o grupo. Assim, *Buccinanops* spp. serviu como *proxy* para os gastrópodes, *Loxopagurus loxochelis* para os crustáceos decápodos, *Trichiurus lepturus* para os peixes teleósteos, Salpidae para as salpas, e *Lychnorhiza lucerna* foi selecionada como representante dos cnidários devido à sua alta abundância na área de estudo (Morandini et al. 2005, Schiariti et al. 2018). Os valores isotópicos dessas presas foram obtidos na literatura e referem-se às zonas costeira (*Buccinanops spp.*, *L. loxochelis*, *T. lepturus* e *L. lucerna*) e oceânica (salpas) do sul do Brasil e Uruguai (Medeiros et al. 2019, Leoni et al. 2024).

Polígonos de mistura isotópica (Smith et al. 2013) foram utilizados para avaliar qual o fator de discriminação trófica (TDF ou *Trophic Discrimination Factor*) entre presa e consumidor que melhor se adapta aos valores isotópicos de cada grupo de indivíduos e das suas potenciais presas. A seleção dos valores adequados de TDF é crucial, uma vez que estes influenciam fortemente os resultados dos modelos de mistura isotópica utilizados para estimar as contribuições das presas para as dietas dos predadores. Os únicos TDFs disponíveis calculados especificamente para os escudos da tartaruga-cabeçuda são os de Reich e colaboradores (2008), que incluem valores tanto para os recém-nascidos como para os juvenis. Como o conjunto de dados analisados não inclui filhotes, foram testados os valores referentes a juvenis (1,77 ± 0,58‰ para $\delta^{13}C$ e -0,64 ± 0,09‰ para $\delta^{15}N$). Entretanto, não há TDFs publicados para indivíduos adultos. Diante

disso, testamos também um conjunto alternativo de valores obtidos para a pele de juvenis de tartaruga-cabeçuda (1,11 ± 0,17‰ para $\delta^{13}C$ e 1,6 ± 0,07‰ para $\delta^{15}N$) (Reich et al. 2008), por se tratar também de um tecido queratinizado. Todas as análises estatísticas foram realizadas no software R versão 4.3.1 com α=0,05 (R Core Team 2023).

2.5. Análise dos dados (Artigo 2)

Para as análises realizadas no Artigo 2, foram incluídos apenas os indivíduos cuja classificação ontogenética foi claramente definida no Artigo 1 (apresentados na seção 3.1). Dessa forma, foram desconsiderados os indivíduos que apresentaram recrutamento do ambiente oceânico para o nerítico (n = 6), bem como aqueles com valores de $\delta^{15}N$ oscilando em torno do ponto de corte identificado na análise de agrupamento (n = 4), o que impossibilitou uma categorização segura entre os estágios de vida. Essa medida foi adotada para garantir maior robustez nas comparações entre grupos. Além disso, foram desconsiderados os indivíduos neríticos com sexo indeterminado (n = 5), uma vez que este grupo foi subdividido por sexo nas análises.

Após a seleção de dados, elipses isotópicas computadas com o pacote SIBER (*Stable Isotope Bayesian Ellipses in R*) (Jackson et al. 2023) foram utilizadas para estimar a largura de nicho isotópico de dois grupos principais: oceânicos e neríticos, baseado na análise de agrupamento descrita na seção anterior. O grupo dos neríticos incluiu tanto juvenis neríticos quanto adultos, uma vez que análises estatísticas prévias (seção 3.1) não indicaram diferenças significativas entre esses estágios de vida, para $\delta^{13}C$ e $\delta^{15}N$. Os indivíduos neríticos foram subdivididos por sexo, considerando que a análise estatística revelou diferenças nos valores de $\delta^{13}C$ entre machos e fêmeas (seção 3.1). Os indivíduos oceânicos, por sua vez, não foram subdivididos devido ao reduzido número amostral. As métricas de nicho isotópico foram calculadas com base em todos os dados provenientes da subamostragem das camadas do escudo. Foi adotada a área da elipse padrão ajustada a pequenos tamanhos amostrais (*Standard Elipse Area*, SEAc) como medida do nicho isotópico contendo aproximadamente 40% dos dados. A sobreposição de nicho isotópico entre os grupos foi calculada como a área compartilhada de SEAc, expressa em percentual relativo a cada grupo. Para isso, a área de interseção foi dividida pela área de cada elipse individual, permitindo avaliar a proporção de nicho compartilhado em relação ao nicho total de cada grupo.

O grau de especialização individual e consistência temporal foram medidos para $\delta^{13}C$ e $\delta^{15}N$, para os mesmos grupos (neríticos e oceânicos). A especialização individual foi quantificada através do índice WIC/TNW para dados contínuos, que compara a amplitude do nicho do indivíduo com o da sua população como um todo, variando de 0, quando a população é composta por especialistas que utilizam apenas uma parte do utilizado pela população geral, a 1, quando os indivíduos são generalistas e utilizam todo esse recurso. A análise de variância (ANOVA) foi utilizada como uma aproximação para comparar estes valores dentro e entre os indivíduos, seguindo a metodologia proposta por Vander Zanden e colaboradores (2013). A soma média dos quadrados dentro dos indivíduos (MSW ou *mean sum-of-squares within individuals*) mede a variabilidade dentro dos indivíduos, que utilizamos como *proxy* para WIC, e foi calculada por meio da equação:

$$MSW = \frac{\Sigma_i \Sigma_j (x_{ij} - \bar{x_i})^2}{(N - k)}$$

E a soma média dos quadrados entre indivíduos (MSB ou *mean sum-of-squares between individuals*) mede a variabilidade entre indivíduos e foi o *proxy* para o BIC, sendo calculado como:

$$MSB = \frac{\Sigma_i \Sigma_j (x_{ij} - \bar{x_i})^2}{(k - 1)}$$

Onde *i* representa um indivíduo, *j* representa uma única camada do escudo, *N* é o número total de observações e *k* é o número de indivíduos. A soma MSB + MSW foi *proxy* para TNW (Vander Zanden et al., 2013).

O WIC também foi utilizado para avaliar a consistência temporal, isto é, a variação dentro dos indivíduos ao longo do tempo. Valores baixos de WIC indicam que os indivíduos são consistentes no uso de recursos ao longo do tempo (Vander Zanden et al. 2013).

Foi assumido que todos os indivíduos amostrados no sul do Brasil e Uruguai pertencem à população brasileira, baseado em dados moleculares já publicados, que revelam que a maioria dos indivíduos encalhados nas praias ou capturados em pescarias costeiras pertencem às áreas de desova do Brasil (Caraccio et al. 2008, Prosdocimi et al.

2015, Medeiros 2019). Porém, sabe-se que no ambiente oceânico também é observada a presença de estoques mistos de *C. caretta*, compostos principalmente por indivíduos de colônias brasileiras, mas incluindo juvenis provenientes do Atlântico Norte, Mediterrâneo, Pacífico e Índico em menores proporções (Reis et al. 2010, Shamblin et al. 2014).

3. RESULTADOS

3.1. Artigo 1

As tartarugas-cabeçuda amostradas (n = 42) variaram em tamanho de 24 a 114 cm de CCC (média = 77,7 cm, mediana = 77,5 cm). Até 45 camadas de cada escudo foram subamostradas, resultando em 611 camadas amostradas para AIE, com uma média de 22,4 camadas por indivíduo (mediana = 21,5, intervalo = 6 a 45 camadas por indivíduo). Entre os indivíduos amostrados, 20 foram determinados como fêmeas, 16 como machos e 6 não tiveram seu sexo determinado (Fig. 9). Os valores das camadas de 50 μm do escudo dos indivíduos variaram para o $\delta^{13}C$ de -19,8 a -12,4‰ (média ± DP = -16,1‰ ± 1,6‰) e para $\delta^{15}N$ de 4,4 a 17,7‰ (média ± DP = 12,8‰ ± 3‰).

Não foram observadas diferenças significativas nos valores de $\delta^{13}C$ (t_9 = -2,10; p = 0,07) e $\delta^{15}N$ (t_9 = -1,25; p = 0,24) entre as amostras submetidas ou não à extração lipídica.

Dois agrupamentos (clusters) baseados em $\delta^{15}N$ se ajustam melhor à distribuição da composição de isótopos estáveis para tartarugas-cabeçuda. A silhueta média de 0,74 é indicativa de uma estrutura forte dentro do conjunto de dados (Tabela 1). O agrupamento com valores de $\delta^{15}N$ maiores (média ± DP $\delta^{15}N$ = 14,30‰ ± 1,27; média ± DP $\delta^{13}C$ = -15,52‰ ± 1,16‰; n = 474) foi separado aproximadamente em $\delta^{15}N$ = 10,97‰ do agrupamento com valores de $\delta^{15}N$ menores (média ± DP $\delta^{15}N$ = 7,78‰ ± 1,69‰; média ± DP $\delta^{13}C$ = -18,31‰ ± 0,72; n=137), estabelecido como ponto de corte entre os dois agrupamentos (Fig. 9b). O limite superior de $\delta^{15}N$ do grupo oceânico foi de 10,93‰ e o limite inferior do grupo nerítico foi de 11,02‰.

Tabela 1: Determinação do número de clusters com base nas larguras médias das silhuetas usando o algoritmo de particionamento *pam*. O valor em negrito indica o melhor ajuste.

Número de clusters	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$ e $\delta^{15}N$
2	0,62	**0,74**	0,68
3	0,56	0,61	0,43
4	0,55	0,54	0,40

Valores de $\delta^{15}N$ inferiores a 10,97‰ foram classificados como pertencentes ao estágio oceânico, enquanto valores superiores foram indicativos do estágio nerítico. Os indivíduos cujos valores de $\delta^{15}N$ ao longo das camadas do escudo oscilaram em torno de 10,97‰ (n = 4) e não apresentaram um padrão claro que permitisse sua classificação em um dos três grupos foram excluídos das análises, assim como os indivíduos que apresentaram recrutamento (n = 6). Os valores médios (±DP), bem como os máximos e mínimos, das razões isotópicas para cada estágio de vida estão apresentados nas Tabelas 2 e 3.

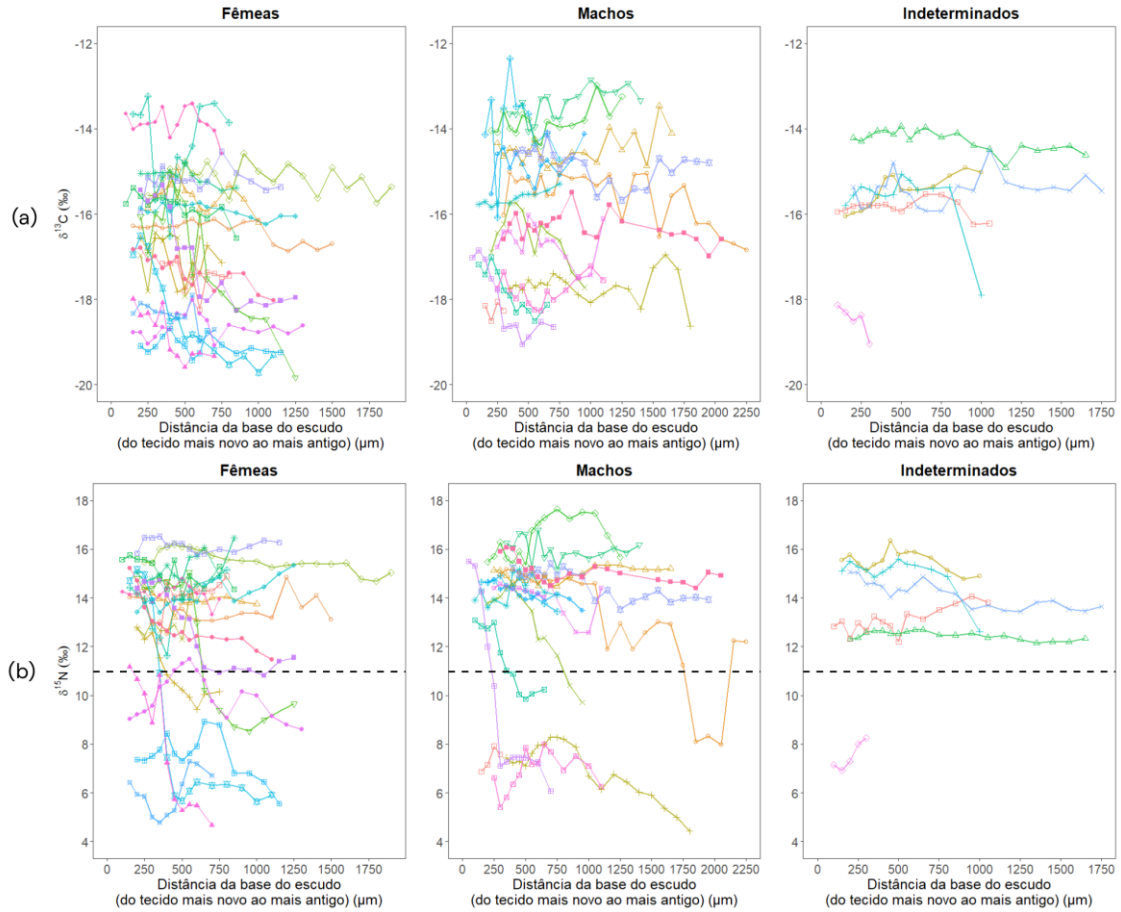


Figura 9: Variação nos valores de $\delta^{13}C$ e $\delta^{15}N$ ao longo das camadas sucessivas dos escudos da carapaça de tartarugas-cabeçuda (*Caretta caretta*) do Atlântico Sul Ocidental (ASO). (a) Valores de $\delta^{13}C$ para cada indivíduo, representados por um símbolo e linha únicos ao longo de todas as camadas amostradas. (b) Valores de $\delta^{15}N$ com o mesmo formato e os mesmos símbolos

individuais. A linha tracejada representa o valor de $\delta^{15}N = 10,97‰$, utilizado como ponto de corte para distinguir entre os agrupamentos oceânico ($\delta^{15}N < 10,97‰$) e nerítico ($\delta^{15}N > 10,97‰$). O número de camadas reflete a espessura da amostra.

Tabela 2: Valores mínimos, máximos e médios (± DP) de $\delta^{13}C$ (‰) e $\delta^{15}N$ (‰) para os grupos definidos por estágio de vida: juvenis oceânicos (JO), juvenis neríticos (JN) e adultos (Ad).

Grupo	$\delta^{13}C$ (min / max)	$\delta^{13}C$ (média ± DP)	$\delta^{15}N$ (min / max)	$\delta^{15}N$ (média ± DP)
JO	-19,42 / -16,96	-18,19 ± 0,63	4,43 / 8,93	6,91 ± 1,03
JN	-18,24 / -12,35	-15,70 ± 1,21	11,47 / 16,46	14,43 ± 1,07
Ad	-16,33 / -12,98	-14,76 ± 0,89	12,52 / 17,65	14,95 ± 1,08

Tabela 3: Médias e desvios padrões (DP) dos valores de $\delta^{13}C$ e $\delta^{15}N$.

Estágio de vida	Sexo	*N*	$\delta^{13}C$ (média ± DP)	$\delta^{15}N$ (média ± DP)
Juvenil oceânico	F	2	-18,78 ± 0,44	6,85 ± 1,14
Juvenil oceânico	M	3	-17,78 ± 0,36	6,95 ± 0,95
Juvenil nerítico	F	11	-16,03 ± 1,07	14,21 ± 1,23
Juvenil nerítico	M	7	-15,25 ± 1,25	14,72 ± 0,73
Adulto	F	7	-15,12 ± 0,90	14,66 ± 0,99
Adulto	M	7	-14,41 ± 0,73	15,25 ± 1,10

Ao avaliar e comparar os modelos lineares, verificou-se que, para o $\delta^{13}C$, o modelo com melhor ajuste, com base no Critério de Informação de Akaike de segunda ordem (AICc), foi aquele que incluiu os termos estágio de vida e sexo, além do indivíduo como efeito aleatório (Tabela 4). Para o $\delta^{15}N$, o modelo mais adequado foi o que considerou apenas o estágio de vida como efeito fixo, também incluindo o indivíduo como efeito aleatório (Tabela 4).

Tabela 4: Variáveis explicativas incluídas nos modelos lineares (ML) e modelos lineares mistos (MLM) para $\delta^{13}C$ e $\delta^{15}N$. O modelo com melhor ajuste para cada isótopo está em negrito, com base no Critério de Informação de Akaike de segunda ordem (AICc) e na diferença de AICc entre cada modelo e o modelo com o menor AICc (ΔAICc).

Isótopo	Modelo	Variáveis explicativas	Efeito aleatório	AICc	ΔAICc
$\delta^{13}C$	1	Estágio de vida	-	1101,79	586,63
	2	Estágio de vida e sexo	-	1044,69	529,53
	3	Estágio de vida, sexo e sua interação	-	1047,85	532,69
	4	Estágio de vida	Indivíduo	518,98	3,82
	5	**Estágio de vida e sexo**	**Indivíduo**	**515,16**	**0**
	6	Estágio de vida, sexo e sua interação	Indivíduo	516,15	0,99
$\delta^{15}N$	1	Estágio de vida	-	1124,82	278,18
	2	Estágio de vida e sexo	-	1108,46	261,83
	3	Estágio de vida, sexo e sua interação	-	1110,18	263,54

4	**Estágio de vida**	**Indivíduo**	**846,64**	**0**
5	Estágio de vida e sexo	Indivíduo	847,52	0,88
6	Estágio de vida, sexo e sua interação	Indivíduo	849,08	2,44

Os MLMs revelaram que, em relação ao estágio de vida, tanto para o $\delta^{13}C$ quanto para $\delta^{15}N$, indivíduos adultos (Ad) e juvenis neríticos (JN) não diferiram entre si, mas ambos exibiram valores significativamente superiores aos juvenis oceânicos (JO) (Ad = JN > JO) (Tabela 5). Em relação ao sexo, diferenças significativas foram observadas apenas em $\delta^{13}C$ (Tabela 5), com machos apresentando valores mais elevados que as fêmeas (Tabela 3).

Tabela 5: Comparações entre os estágios de vida (Ad = adulto, JN = juvenil nerítico, JO = juvenil oceânico) ou entre os sexos (F = fêmea, M = macho) para os valores de $\delta^{13}C$, com base no modelo linear misto. A estimativa representa a diferença média entre os grupos, acompanhada do erro padrão, graus de liberdade (GL), valor t e p-valor. Diferenças estatisticamente significativas ($p < 0,05$) estão indicadas em negrito.

Isótopo	Comparação	Estimativa	Erro padrão	GL	t	p-valor
$\delta^{13}C$	Ad - JN	0,726	0,334	33,1	2,171	0,0912
	Ad - JO	3,507	0,486	32,8	7,210	**<0,0001**
	JN - JO	2,781	0,475	32,7	5,855	**<0,0001**
	F - M	-0,814	0,311	32,9	-2,616	**0,0133**
$\delta^{15}N$	Ad - JN	0,376	0,324	34,3	1,161	0,4840
	Ad - JO	7,917	0,470	33,5	16,831	**<0,0001**
	JN - JO	7,541	0,455	33,1	16,577	**<0,0001**

Portanto, as análises sequenciais dos isótopos estáveis de carbono e nitrogênio nas camadas do escudo da carapaça de indivíduos de tartarugas-cabeçuda evidenciaram um aumento significativo nos valores de $\delta^{13}C$ e $\delta^{15}N$ entre os indivíduos oceânicos e neríticos (juvenis e adultos). Esse padrão é indicativo de mudanças ontogenética, tanto em habitat quanto em relação à dieta.

Para estimar a contribuição das presas na dieta da tartaruga-cabeçuda utilizando o pacote MixSIAR, os indivíduos foram agrupados com base no padrão de variação ontogenética observado no seu transecto de $\delta^{15}N$ (Fig. 10). Indivíduos cujos valores de $\delta^{15}N$ oscilaram em torno do ponto de corte identificado na análise de agrupamento (n = 4), sem apresentar um padrão definido, foram excluídos da análise. Dessa forma, os modelos de mistura isotópica foram gerados para três grupos: oceânicos, neríticos e

recrutas. Os intervalos de variação dos valores de $\delta^{13}C$, $\delta^{15}N$ e do comprimento curvilíneo da carapaça (CCC) para cada grupo estão apresentados na Tabela 6.

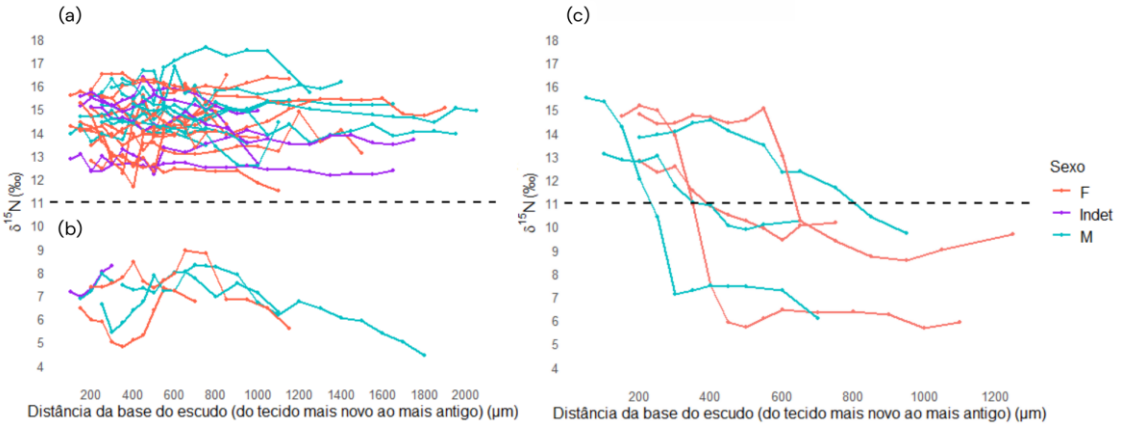


Figura 10: Transectos de isótopos estáveis de nitrogênio por padrão de história de vida em tartarugas-cabeçuda (*Caretta caretta*) do Atlântico Sul Ocidental (ASO). (a) Indivíduos neríticos, (b) juvenis oceânicos e (c) recrutas. A linha tracejada indica o ponto de corte de $\delta^{15}N$ (10,97‰) que separa os grupos oceânicos e neríticos. As cores representam o sexo: F = fêmeas (laranja), M = machos (ciano) e Indet = indeterminado (roxo).

Tabela 6: Valores mínimos e máximos de comprimento curvilíneo da carapaça (CCC), $\delta^{13}C$ e $\delta^{15}N$ de tartarugas-cabeçuda agrupadas por padrão de história de vida.

Grupo	*N*	CCC min-max (cm)	$\delta^{13}C$ min-max (‰)	$\delta^{15}N$ min-max (‰)
Oceânicos	6	24,0 a 66,5	-19,42 a -16,96	4,43 a 8,93
Neríticos	26	62,4 a 114	-18,24 a -12,35	11,47 a 17,65
Recrutas	6	59,5 a 70,1	-19,83 a -15,07	5,64 a 15,50

Foram gerados polígonos de mistura para os mesmos grupos. Para os oceânicos, o TDF específico dos escudos de tartaruga-cabeçuda apresentou o melhor ajuste (Fig. 11a), enquanto que para os recrutas e neríticos, o TDF específico da pele de tartaruga-cabeçuda ficou melhor ajustado (Fig. 11, d, f).

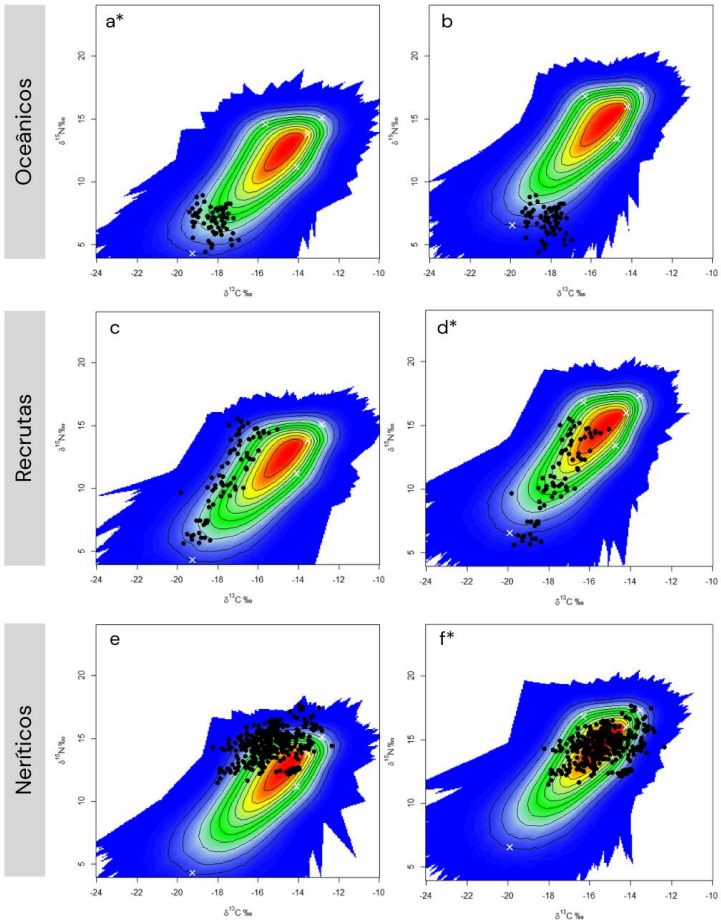


Figura 11: Polígonos de mistura isotópica utilizando dois conjuntos diferentes de TDFs para a correção dos valores dos tecidos de presas. Nos polígonos à esquerda (a, c, e) foram utilizados TDFs específicos dos escudos de tartaruga-cabeçuda (1,77‰ para $\delta^{13}C$ e -0,64‰ para $\delta^{15}N$; Reich et al. 2008), enquanto nos polígonos à direita (b, d, f) foram utilizados TDFs específicos da pele de tartaruga-cabeçuda (1,11 ± 0,17‰ para $\delta^{13}C$ e 1,6 ± 0,07‰ para $\delta^{15}N$; Reich et al. 2008). Asteriscos (*) indicam o conjunto TDF que forneceu o melhor ajuste para cada grupo.

Modelos iniciais indicaram que os cnidários contribuíram com <10% para a dieta de cada grupo e, por isso, foram excluídos das análises finais para reduzir incertezas, mantendo-se apenas os quatro grupos de presas mais representativos. Com essa configuração, os resultados revelaram padrões distintos de contribuição das presas entre os grupos analisados (Fig. 12). Para os oceânicos, a dieta foi dominada por salpas, com 72,7% (64,5 – 81,4% no IC 95%, conforme resultados do modelo), e menor contribuição de peixes (12,8% (0,3 – 26,3%), que se manteve constante ao longo da ontogenia) (Fig. 12a). Entre os recrutas, as contribuições médias iniciaram em 57,9% (46,1 – 68,5%) para salpas, seguidas por 16,7% (0,2 – 34,6%) para gastrópodes e 16,9% (0,3 – 44,7%) para

crustáceos. Para esse grupo, mudanças ontogenéticas foram evidentes: as salpas predominaram durante o estágio pré-recrutamento (camadas mais antigas do escudo), com menor contribuição de gastrópodes e crustáceos; enquanto no estágio pós-recrutamento, a contribuição dos peixes aumentou de forma acentuada, enquanto a das demais presas diminuiu (Fig. 12b). Nos neríticos, os crustáceos foram o grupo mais representativo, com média de 49,2% (1,1 – 78,4%), seguidos por peixes, com 23,9% (0,7 – 42%), e gastrópodes, com 19,3% (0,1 – 68,4%), sem mudanças ontogenéticas evidentes (Fig. 12c). Entretanto, a ampla sobreposição entre os intervalos de credibilidade não permite visualizar claramente qual presa foi mais importante ao longo da ontogenia.

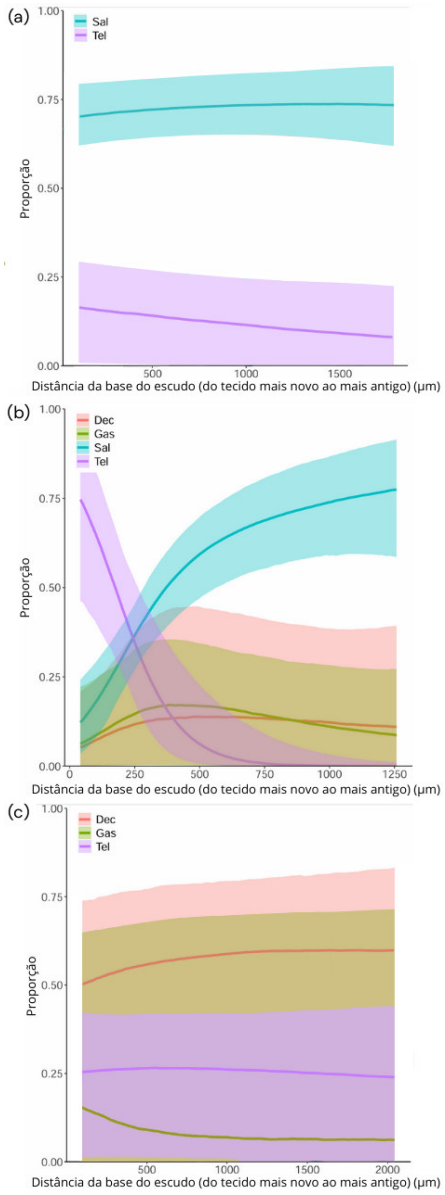


Figura 12: Gráficos de densidade (linhas = médias, sombras = intervalos de credibilidade de 95%) representando as proporções estimadas das contribuições de presas na dieta de tartarugas-cabeçuda (*Caretta caretta*) do Atlântico Sul Ocidental (ASO) ao longo das camadas sucessivas dos escudos da carapaça. (a) oceânicos, (b) recrutas e (c) neríticos. Sal – Salpida; Tel – Teleostei (*Trichiurus lepturus*); Dec – Decapoda (*Loxopagurus loxochelis*); Gas – Gastropoda (*Buccinanops* spp.). Presas com contribuição estimada inferior a 10% foram omitidas dos gráficos.

3.2. Artigo 2

Foram selecionadas 27 tartarugas-cabeçuda, com comprimento curvilíneo de carapaça variando entre 24 e 114 cm (média = 80,8 cm, mediana = 88 cm). A subamostragem dos escudos resultou em um total de 383 camadas para a AIE, com até 41 camadas por indivíduo (média = 22; mediana = 22; intervalo = 6–41). Entre os indivíduos analisados, 14 eram fêmeas, 12 machos e apenas um não teve seu sexo determinado (Fig. 13). Os valores isotópicos nas camadas de 50 µm do escudo variaram de -19,4‰ a -12,4‰ para $\delta^{13}C$ (média ± DP = -15,9 ± 1,6‰) e de 4,4‰ a 17,7‰ para $\delta^{15}N$ (média ± DP = 13,2 ± 3,1‰).

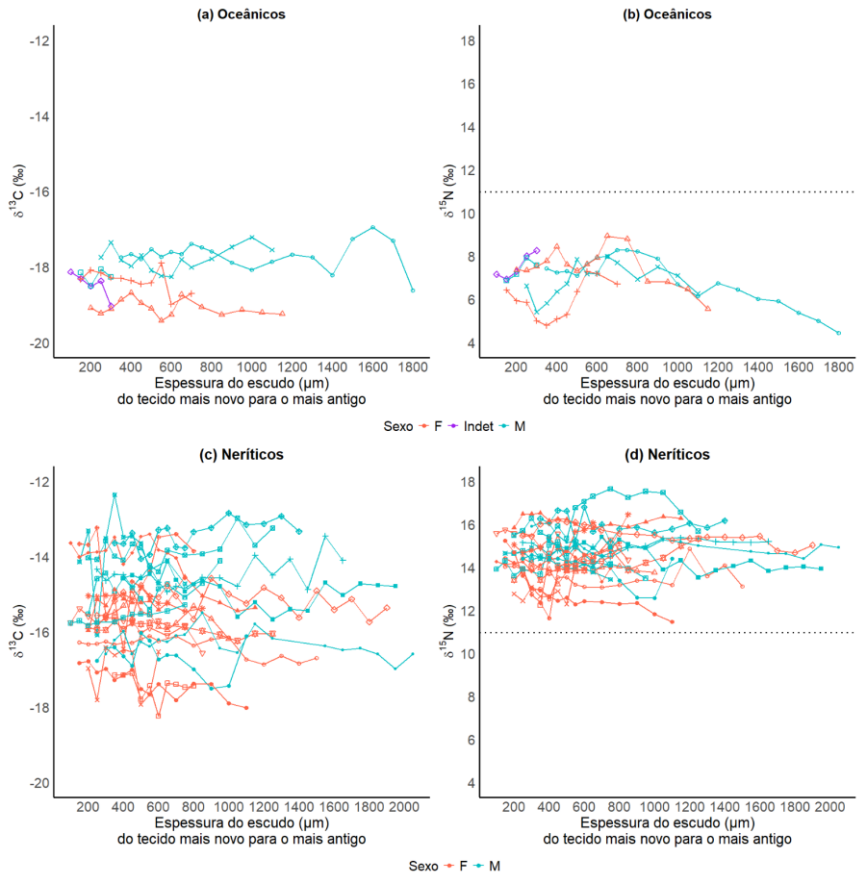


Figura 13: Variação dos valores de $\delta^{13}C$ (à esquerda) e $\delta^{15}N$ (à direita) ao longo de camadas sucessivas de 50 µm do escudo da carapaça de tartarugas-cabeçuda (*Caretta caretta*) do Atlântico Sul Ocidental (ASO), em: **(a), (b)** indivíduos oceânicos; **(c), (d)** indivíduos neríticos. As cores representam o sexo: F = fêmeas (laranja), M = machos (ciano) e Indet = indeterminado (roxo).

Em relação ao nicho isotópico (SEAc), observou-se que os indivíduos neríticos ocupam nichos com valores isotópicos mais elevados em comparação aos indivíduos oceânicos (Fig. 14). Além disso, houve uma sobreposição entre os nichos de fêmeas e machos neríticos de 47% e 58% nas elipses desses grupos, respectivamente. O grupo com nicho mais amplo foi o das fêmeas neríticas (SEAc = 3,66‰^{2}), seguido pelo grupo dos machos neríticos (SEAc = 2,96‰^{2}), enquanto o menor nicho foi observado nos indivíduos oceânicos (SEAc = 2,01‰^{2}).

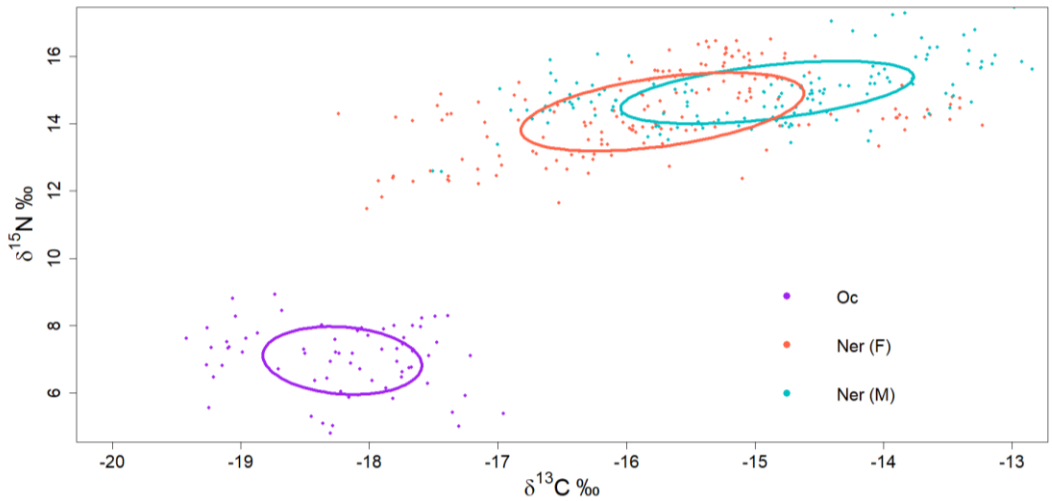


Figura 14: Elipses representando os nichos isotópicos (SEAc) de tartarugas-cabeçuda (*Caretta caretta)* do Atlântico Sul Ocidental (ASO) em diferentes grupos. Oc: oceânicos (roxo); Ner (F): neríticas (fêmeas) (laranja); Ner (M): neríticos (machos) (ciano).

A relação WIC/TNW, *proxy* para especialização individual, foi baixa para todos os grupos (≤ 0,2), indicando um alto grau de especialização individual nos diferentes estágios ontogenéticos (Tabela 7). Os indivíduos neríticos (machos e fêmeas) apresentaram valores de WIC/TNW semelhantes para $\delta^{13}C$ e $\delta^{15}N$, sugerindo níveis comparáveis de especialização individual entre os dois sexos (Tabela 7). Os indivíduos oceânicos também apresentaram valores de WIC/TNW para $\delta^{13}C$ semelhantes aos observados nos grupos dos indivíduos neríticos, porém exibiram um valor relativamente

mais elevado para $\delta^{15}N$, o que indica um grau ligeiramente menor de especialização individual (Tabela 7).

Como indicador de consistência temporal, os valores de WIC foram baixos em todos os grupos (WIC < 0,20 para $\delta^{13}C$ e < 0,85 para $\delta^{15}N$), reforçando a ideia de que os indivíduos mantêm padrões alimentares estáveis ao longo do tempo (Tabela 7). Em relação ao $\delta^{13}C$, os indivíduos oceânicos apresentaram o menor valor de WIC, enquanto fêmeas e machos neríticos exibiram valores mais elevados e similares entre si. Para o $\delta^{15}N$, os valores de WIC dos grupos neríticos foram menores e próximos entre si em comparação ao grupo oceânico, sugerindo que ambos os sexos apresentam níveis semelhantes de consistência temporal no estágio nerítico, sendo mais consistentes do que os indivíduos oceânicos (Tabela 7).

Esses resultados sugerem que as tartarugas-cabeçuda do ASO podem ser caracterizadas como uma população generalista composta por indivíduos especialistas. Assim, mesmo em diferentes fases do ciclo de vida, as tartarugas tendem a se alimentar de presas específicas ou com composições isotópicas similares.

Tabela 7: Variação intraindividual (WIC), variação entre indivíduos (BIC) e largura total do nicho (TNW) para $\delta^{13}C$ e $\delta^{15}N$ de camadas do escudo da carapaça de tartarugas-cabeçuda.

Grupo	*N*	$\delta^{13}C$				$\delta^{15}N$			
		WIC	BIC	TNW	WIC/TNW	WIC	BIC	TNW	WIC/TNW
Oceânicos	6	0,09	4,04	4,13	**0,02**	0,83	3,37	4,20	**0,20**
Fêmeas neríticas	12	0,17	16,18	16,35	**0,01**	0,38	15,53	15,91	**0,02**
Machos neríticos	9	0,19	19,88	20,06	**0,01**	0,30	10,43	10,73	**0,03**

4. CONCLUSÕES PRINCIPAIS

No presente estudo, foi realizada uma ampla análise isotópica a fim de caracterizar os padrões de uso do habitat e de recursos alimentares por *Caretta caretta* no Oceano Atlântico Sul Ocidental. Com base nos resultados obtidos nesta dissertação, conclui-se que:

- Os indivíduos de tartaruga-cabeçuda apresentaram padrões distintos de uso do habitat e de recursos alimentares entre estágios de vida;

- Os indivíduos de tartaruga-cabeçuda apresentaram padrões semelhantes de uso do habitat e de recursos alimentares entre sexos, porém as fêmeas apresentam valores de $\delta^{13}C$ mais deplecionados em comparação aos machos;

- Os indivíduos de tartaruga-cabeçuda apresentaram dois padrões principais de recrutamento ontogenético (discreto e facultativo);

- Os indivíduos de tartaruga-cabeçuda apresentaram consistência temporal no uso do habitat e de recursos alimentares em todos os estágios de vida;

- A população de tartarugas-cabeçuda do ASO é generalista, composta por indivíduos especialistas em todos os estágios de vida.

Essas conclusões trazem informações relevantes para a biologia e a conservação da tartaruga-cabeçuda no ASO, ao evidenciar como diferentes estágios de vida utilizam o habitat e exploram recursos alimentares de forma distinta. A dicotomia observada entre as fases oceânica e nerítica indica que indivíduos oceânicos, por exemplo, são vulneráveis à captura incidental em pescarias de espinhel pelágico (Sales et al. 2008, Jimenez et al. 2009), enquanto indivíduos neríticos estão sujeitos à captura incidental no arrasto de parelha (Monteiro et al. 2016), o que ameaça a estrutura e a viabilidade da população a longo prazo. O reconhecimento de que a população é generalista, mas composta por indivíduos especialistas, reforça a necessidade de considerar múltiplos cenários de vulnerabilidade. A compreensão dessas diferenças no uso do habitat e de recursos alimentares é fundamental para subsidiar medidas de mitigação das ameaças, como a delimitação de áreas prioritárias de proteção, o ordenamento do esforço pesqueiro em regiões críticas e o desenvolvimento de estratégias de conservação mais eficazes ao longo do ciclo de vida da espécie.

Além disso, este estudo abre caminho para novas investigações que podem aprofundar o entendimento sobre os padrões de uso de recursos por *C. caretta*. Recomenda-se a integração de diferentes tecidos com taxas de renovação variadas e o refinamento dos fatores de discriminação trófica específicos para a espécie em diferentes

estágios de vida. Sugere-se também investir na determinação sexual dos indivíduos para possibilitar comparações mais robustas entre machos e fêmeas, além de associar as informações de análises de isótopos estáveis a outras ferramentas complementares, como telemetria satelital e/ou análise de conteúdo estomacal. Esses esforços futuros permitirão aprimorar a resolução temporal e espacial das análises, ampliando a capacidade de avaliar a resposta das tartarugas frente às pressões antrópicas e às mudanças ambientais.

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ANEXO I

Sex- and life stage-related patterns of resource use in Loggerhead turtle (*Caretta caretta*) from the Southwestern Atlantic Ocean

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(Manuscrito submetido ao periódico *Marine Biology*)

Sex- and life stage-related patterns of resource use in Loggerhead turtle (*Caretta caretta*) from the Southwestern Atlantic Ocean

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Abstract

The Southwestern Atlantic Ocean (SWAO) is an important feeding and developmental area for Loggerhead turtle (*Caretta caretta*). In this study, we used stable isotope analysis (SIA) of sequential layers of carapace scutes to investigate patterns of resource use in this species from the SWAO, considering individuals from different life stages and sexes. Samples were collected from 42 individuals stranded or incidentally caught by pelagic longline and bottom pair trawl fishery in southern Brazil and Uruguay (from 31º21′S–51º05′W to 34º55′S–56º09′W), between 2013 and 2024. Cluster analysis based on $\delta^{15}N$ values revealed two distinct groups, corresponding to oceanic and neritic foraging habitats, with a threshold at 10.97‰. Linear mixed models indicated a significant increase in $\delta^{13}C$ and $\delta^{15}N$ values with ontogenetic stage, reflecting the shift from oceanic to neritic habitats. Significant differences between sexes were observed only for $\delta^{13}C$ values. Bayesian mixing models (MixSIAR) were used to estimate prey contributions to the diet, based on isotopic values from the literature, revealing a dominance of pelagic prey in oceanic non-shifters and of benthic invertebrates in neritic non-shifters. Shifters showed a transition from oceanic to neritic habitats, with a dietary shift from pelagic to benthic prey. This transition varied among individuals, indicating two main ontogenetic shift patterns: discrete and facultative. Our results enhance the understanding of life-history variation in loggerhead turtles and highlight that sequential analysis of carapace scutes is a valuable tool for reconstructing long-term resource use patterns, providing a broader view of the ecology of this long-lived and endangered species.

Keywords: trophic ecology, stable isotopes, *Caretta caretta,* ontogenetic shift, SWAO

Introduction

Studies on feeding ecology of sea turtles can provide valuable information on the use of trophic resources, the quality of feeding areas, and how human activities may interfere with the use of habitat by these animals (Bjorndal 1997). This information is essential to guide conservation actions for threatened species, as it allows the identification of critical habitats (Bjorndal 1997; Cameron et al. 2019) and the assessment of the population's vulnerability to different threats (Plotkin et al. 1993; Seney and Musick 2007). Among sea turtles, the loggerhead turtle (*Caretta caretta*) represents a particularly relevant model for such studies, given its wide distribution and complex life cycle, which involves the use of multiple habitats throughout development.

The species occurs in tropical and subtropical waters worldwide (Márquez 1990). Similar to other sea turtle species, it has a long and complex life cycle. Following hatching, juveniles spend an extended period in the oceanic habitat — approximately 12 years for populations in the southwestern Atlantic — before recruiting to coastal areas (Petitet et al. 2012). When they become large juveniles, they recruit to the neritic habitat to complete their development, making migrations throughout adulthood between foraging and nesting grounds (Musick and Limpus 1997; Bolten 2003). However, they may undergo a complex transitional period of variable duration, using both oceanic and coastal environments for feeding and development (Bolten 2003; Casale et al. 2008), which is supported by satellite telemetry studies (McClellan and Read 2007; Barceló et al. 2013; González Carman et al. 2016). Thus, individuals may exhibit different ontogenetic shifts patterns, including discrete ontogenetic shift (single-year, one-way transition from the oceanic to the neritic habitat); facultative ontogenetic shift (gradual transition over multiple years, characterized by utilization of both oceanic and neritic resources); or continual ontogenetic shift (multiple, discrete transitions over time), reflecting different recruitment strategies during development (Ramirez et al. 2015).

Therefore, in loggerhead turtles, ontogenetic shifts in habitat are accompanied by corresponding changes in diet. The species is generally considered a carnivore generalist (Márquez 1990), feeding mainly on mollusks and crustaceans, although diet composition varies with foraging habitat and life stage (Bolten 2003; McClellan et al. 2010; Medeiros et al. 2019). During the oceanic phase, small juveniles act as opportunistic feeders,

consuming pelagic prey – primarily gelatinous organisms such as salps and pyrosomes. As they recruit to neritic habitats, large juveniles begin to specialize in benthic prey, particularly crustaceans, mollusks and fish, which remain the dominant components of their diet throughout life (Jones and Seminoff 2013).

Stable isotope analysis (SIA) of carbon and nitrogen has been widely used in ecological research to discriminate food and habitat use (via $\delta^{13}C$) and trophic level (via $\delta^{15}N$) of a consumer (Post 2002; Fry 2006). The time required for the isotopic values of the sources (diet) to be reflected in the tissues of consumers is called isotopic turnover rate, which vary among tissue types (Newsome et al. 2010). Tissues such as skin and muscle, for example, have a rapid renewal and reflect the diet values of the last few weeks or months (Seminoff et al. 2007; Reich et al. 2008). On the other hand, tissues considered metabolically inert, such as carapace scutes, in the case of sea turtles (Vélez-Rubio et al. 2018), offer an alternative approach to reconstruct ontogenetic changes in diet and habitat. The scute is a keratinized epidermis that covers the bony shell of most chelonians and grows continuously, with new tissue forming beneath the older layers (Alibardi 2005).

Studies using SIA and satellite telemetry have revealed variability in habitat use and foraging strategies among loggerhead turtles, often associated with life stage (McClellan and Read 2007; Schofield et al. 2010; Hawkes et al. 2011; Medeiros et al. 2019). Some studies indicate that the species may exhibit a dichotomy in habitat use, in some cases linked to body size (Hatase et al. 2002; Hawkes et al. 2006; Medeiros et al. 2019), whereas others have found no size-related dichotomy (McClellan and Read 2007; Schofield et al. 2010; Monteiro 2017). However, sex-based differences have been less explored, and males remain underrepresented in the literature due to the difficulty of accessing this portion of the population, with most studies focusing on adult females (Haywood et al. 2019). Nonetheless, some studies have investigated sex differences in movement and foraging behavior. In the Northwest Atlantic, for example, adult males exhibited variation in $\delta^{13}C$ and $\delta^{15}N$ values similar to that observed in adult females, suggesting that both sexes may adopt similar foraging strategies (Reich et al. 2010; Pajuelo et al. 2012). In the Southwestern Atlantic Ocean (SWAO), evidence from southern Brazil indicates that while adult males tend to remain in coastal areas, juveniles exhibit more variable habitat and resource use (Medeiros et al. 2019).

The SWAO is an important nesting, feeding and development area for loggerhead turtles (Marcovaldi and Marcovaldi 1999; Vélez-Rubio et al. 2013; González Carman et al. 2016; Monteiro et al. 2016). In Brazil, the loggerhead turtle is the most abundant species of sea turtle, with regular nesting recorded between Sergipe and Rio de Janeiro (Marcovaldi and Chaloupka 2007). In addition, the coast of Ceará has been identified as the main foraging area for females that nest in Bahia (Marcovaldi et al. 2010). Coastal and oceanic waters in southern Brazil, Uruguay and Argentina have also been identified as important feeding areas for loggerhead turtles, particularly for juveniles and adults (Bugoni et al. 2003; Barceló et al. 2013; González Carman et al. 2016; Monteiro et al. 2016), which is suggested by the high stranding rates observed annually in southern Brazil and Uruguay (Vélez-Rubio et al. 2013; Monteiro et al. 2016).

In this study, we investigate for the first time differences in resource use — encompassing both habitat and diet — between sex and life stages of the loggerhead turtle in the SWAO. We hypothesize that juvenile individuals utilize both neritic and oceanic habitats, whereas adults primarily use neritic habitats; that males and females exhibit similar resource use patterns; and that juveniles display an ontogenetic shift pattern with a facultative transition in their resource use.

Materials and methods

Study area

The study area comprises the southwestern Atlantic coast, from the Lagoa do Peixe in Rio Grande do Sul (31º21′S–51º05′W, Brazil) to the Department of Montevideo (34º55′S–56º09′W, Uruguay) (Fig. 1). This approximately 700 km stretch of coastline is characterized, in southern Brazil, by a straightened shoreline with fully exposed sandy beaches, whereas in Uruguay, it consists of a succession of sandy beach arcs separated by rocky outcrops (Muehe 2006; Vélez-Rubio et al. 2021). This region is directly influenced by the Subtropical Convergence, which results from the convergence between Brazil and Malvinas Currents, as well as by freshwater inputs from the Río de la Plata and Lagoa dos Patos, processes that contribute to high productivity in the region (Odebrecht and Castello 2001; Piola et al. 2008), making the area an important foraging and developmental habitat for some species of sea turtles (Bugoni et al. 2003).

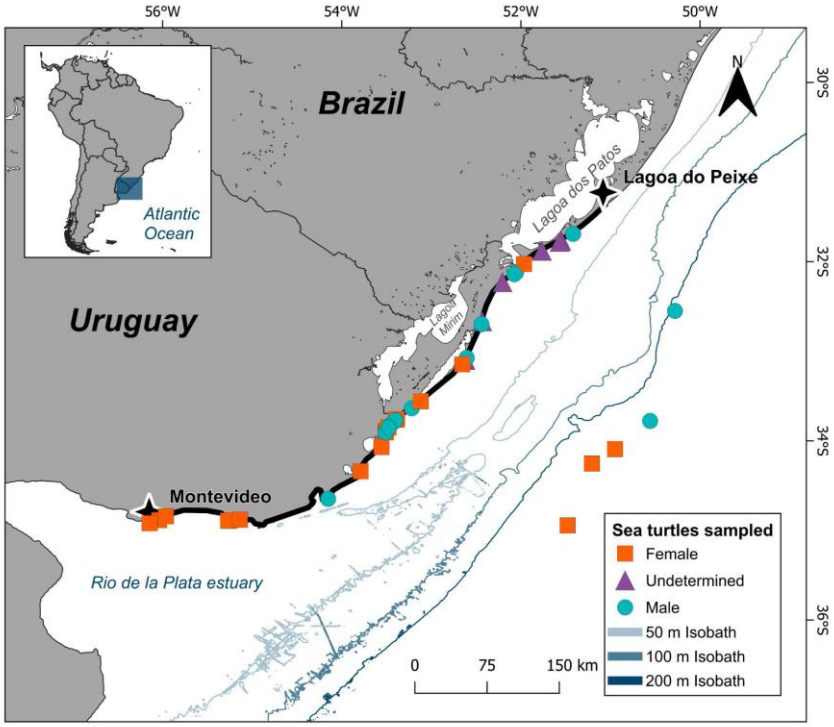


Fig. 1 Map of the study area in southern Brazil and Uruguay, showing the sampling locations of loggerhead turtles (*Caretta caretta*) obtained from stranded and incidentally caught individuals. Colors and symbols indicate sex

Sampling

Scute samples of loggerhead turtles were obtained from specimens stranded dead along the the Southernmost Brazilian state, Rio Grande do Sul (n = 13) and the Uruguayan coast (n = 22) between 2013 and 2024, during beach monitoring trips carried out by the Núcleo de Educação e Monitoramento Ambiental - NEMA (from 2013 to 2023) and the Asociación Civil Karumbé (from 2015 to 2024), respectively (see Vélez-Rubio et al. 2013 and Monteiro et al. 2016 for more information on beach monitoring). Samples were also obtained from specimens caught incidentally in the pelagic longline (n=5) and trawl (n=2) fisheries in southern Brazil, between 2014 and 2022, from fishing and incidental catch monitoring programs carried out by NEMA.

All turtles sampled had curved carapace length (CCL) recorded, measured from the nuchal notch to the anterior midpoint of the nuchal scute to the tip of the posterior marginal scute (Pritchard and Mortimer 1999). Sex was determined by macroscopic

152 analysis of the gonads during necropsy (Wyneken 2001) and/or by tail length, for adults
153 > 83 cm CCL, the minimum size for females that nests in Brazil (Baptistotte et al. 2003).

154 The third lateral scutes were entirely removed from each turtle, and the samples
155 were then stored frozen at -4ºC without any preservatives until processing. In the
156 laboratory, subsamples were collected from the posterior medial region of the scute using
157 a 6-mm diameter Golgran biopsy punch, following Reich et al. (2007). Only biopsy
158 samples that reached the innermost layer of the scute were used.

159 **Stable isotope analysis**

160 Following the methodology proposed by Vélez-Rubio et al. (2018), all scute
161 samples were embedded in O.C.T. (Optimal Cutting Temperature compound, Tissue-
162 Teck®) with the dorsal (oldest) side facing down, frozen at -20ºC and sectioned into
163 sequential 50-µm layers using a sliding microtome (Leica SM2000 R). Each layer was
164 individually rinsed with distilled water for 24 h and then dried for 24 h at 60ºC.

165 The number of layers obtained varied among individuals and was proportional to
166 the thickness of each scute. According to Vander Zanden et al. (2010), we assume that
167 each 50-µm-thick layer corresponds to a period of approximately 0.6 years for adult
168 individuals. Each layer was analyzed independently for the stable isotope ratios of carbon
169 and nitrogen. Samples were weighed into tin capsules with a microbalance (approximately
170 0.3 mg of sample) and analyzed in continuous flow isotope ratio mass spectrometer (EA
171 Flash 2000 Delta V Advantage and TC/EA; ThermoFisher Scientific™) at the Centro
172 Integrado de Análises (CIA) - FURG. When individual scute layers did not yield sufficient
173 material for stable isotope analysis, these layers were excluded from sampling. This
174 approach was adopted to avoid merging adjacent layers, thereby preserving the temporal
175 resolution of the dataset (i.e., treating each layer as a ~0.6-year time unit).

176 Stable isotope abundances were expressed in δ notation according to the following
177 expression:

178 $$\delta X(‰) = (Rsample/Rstandard) - 1$$

where X is ^{13}C or ^{15}N, Rsample is the heavy to light isotope ratio of the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) respectively, and Rstandard is the heavy to light isotope ratio of the reference standard. The CIA/FURG uses caffeine, glutamic acid, acetanilide, NBS22, cane sugar, beet sugar, N_1 and N_2 as international standards, all of which are certified by the International Atomic Energy Agency. Analytical precision, determined from analyses of glutamic acid and caffeine interspersed with the samples, was 0.07‰ for $\delta^{13}C$ and 0.28‰ for $\delta^{15}N$.

Given that the presence of lipids can alter $\delta^{13}C$ values (Post et al. 2007), an experiment was conducted to evaluate the effect of lipid extraction on $\delta^{13}C$ and $\delta^{15}N$ values of the samples. For the experiment, two subsamples of 10 specimens were used, separated into two groups. To ensure comparability between groups, the central scute layers corresponding to the same position in the sequence of sections obtained with the microtome were selected (Fig. S1). In the first group, the lipids were extracted with a chloroform/methanol solution (2:1) (~1.5 mL) (Medeiros et al. 2019); the second group, the control group, did not undergo any extraction process. The extractions were performed using eppendorfs, changing the Chl:Met solution three times a day. After the last extraction, the samples were dried at 60°C for 24 h, followed by independent analysis of the C and N stable isotope ratios.

Statistical analysis

A paired Student's t-test was conducted to verify significant differences between lipid-extracted and non-extracted scute samples, separately for $\delta^{13}C$ and $\delta^{15}N$ values, after checking the assumptions of normality and homoscedasticity using the Shapiro-Wilk and Levene tests, respectively.

To identify the number of groups that best fit the data, a cluster analysis was carried out. This analysis considered the $\delta^{13}C$ and $\delta^{15}N$ values separately and together, using the pam function from the cluster package in R (Maechler et al. 2025). Dissimilarities between individuals were calculated based on the Euclidean distance, and the best fit for the number of clusters was determined from the average width of the silhouette. This measure is important in clustering validity, as it reflects the strength of

208 association of each observation with its respective group (Kaufman and Rousseeuw
209 1990). Silhouette values between 0.7 and 1 indicate a strong structure within the dataset.

210 The classification of adult and juvenile life stages was based on the curved
211 carapace length: individuals with CCL > 83 cm, corresponding to the minimum size of
212 nesting females in Brazil (Baptistotte et al. 2003), were classified as adults. However,
213 considering that the scute retains chronological dietary information spanning several
214 years, a retrospective growth analysis was performed to estimate the approximate layer
215 within each adult individual corresponding to the time at which it likely reached 83 cm.
216 For this, average growth rates by size class described by Petitet et al. (2012) were applied
217 retrospectively, estimating body size for each layer based on the assumption that each
218 represents approximately 0.6 years (Vander Zanden et al. 2010). Based on these estimates,
219 outer layers (formed before reaching 83 cm CCL) were categorized as belonging to the
220 neritic juvenile stage, while inner layers (formed after surpassing 83 cm CCL) were
221 considered adult. This estimate minimized, but did not eliminate, the chance of incorrectly
222 classifying life stages within individuals. Individuals with a CCL < 83 cm were considered
223 juveniles, and their classification as oceanic or neritic was based on the cluster analysis
224 of the $\delta^{15}N$ values of the scute layers. The recruitment point was defined as the first layer
225 in which the $\delta^{15}N$ value was higher than the threshold value of the established cut-off
226 point.

227 To assess the influence of life stage, sex and their interaction on the $\delta^{13}C$ and $\delta^{15}N$
228 values of *C. caretta* individuals, we used Linear Models (LM) and Linear Mixed Models
229 (LMM). To deal with repeated sampling of the same scute or individual, the individual
230 was treated as a random term, while sex, life stage and their interaction were treated as
231 fixed terms. Individuals with undetermined sex were excluded from the analyses to allow
232 for an appropriate evaluation of the effect of sex and its interaction with life stage. Starting
233 from a simple initial model including only one fixed term (life stage), subsequent models
234 were generated by progressively including the other terms. The most appropriate model,
235 which includes the individual as a random term and the other factors and their interaction
236 as fixed terms, was selected based on the lowest values of the second-order Akaike
237 Information Criterion (AICc) (Burnham and Anderson 2002). Finally, pairwise multiple

comparisons were carried out with Tukey's adjustment, using the emmeans package in R (Lenth 2025).

We used Bayesian stable isotope mixing models (package MixSIAR, Stock et al. 2018) to estimate dietary composition based on $\delta^{13}C$ and $\delta^{15}N$ values, with a 95% credible interval. This package allowed for the inclusion of a continuous covariate (scute thickness), thereby representing ontogenetic variation in resource use. Prey selection was based on previous studies of *C. caretta* diet in southern Brazil and Uruguay (Martinez Souza 2009; Barros 2010), prioritizing the four most representative prey groups: crustaceans, mollusks, fishes, and salps. In addition, cnidarians were included in the analyses because stomach content studies often underestimate their presence as prey for sea turtles, as jellyfish are mostly composed of water and are rapidly digested, limiting their detection with traditional methods (Van Nierop and Den Hartog 1984). Although they are generally recorded in low or negligible proportions in stomach content studies in the study area (Bugoni et al. 2003; Martinez Souza 2009; Barros 2010), there are records of their consumption in other regions, such as the North Atlantic coast, the Mediterranean Sea, and Australia (Jones and Seminoff 2013).

After defining the prey groups, the lowest available taxonomic level (species, genus, or family) with the highest contribution to the diet according to the Index of Relative Importance (IRI) reported in the literature was selected, serving as a proxy for the entire group. Accordingly, *Buccinanops* spp. served as a proxy for gastropods, *Loxopagurus loxochelis* for decapod crustaceans, *Trichiurus lepturus* for teleost fishes, Salpidae for salps, and *Lychnorhiza lucerna* was selected as the representative of cnidarians due to its high abundance in the study area (Morandini et al. 2005; Schiariti et al. 2018). The isotopic values of these prey species were obtained from the literature and correspond to the coastal (*Buccinanops spp.*, *L. loxochelis*, *T. lepturus*, and *L. lucerna*) and oceanic (salps) zones off southern Brazil and Uruguay (Medeiros et al. 2019; Leoni et al. 2024).

Isotopic mixing polygons (Smith et al. 2013) were used to assess the fitness distinct of prey-to-consumer trophic discrimination factors (TDF). The selection of appropriate TDF values is crucial, as they strongly influence the output of isotopic mixing models used to estimate prey contributions to predator diets. The only available TDFs

specifically calculated for loggerhead turtle scutes are from Reich et al (2008), which include values for both hatchlings and juveniles. Since our dataset does not include hatchlings, we tested the juvenile-specific values (1.77 ± 0.58‰ for $\delta^{13}C$ and -0.64 ± 0.09‰ for $\delta^{15}N$). However, no TDFs have been published for adult individuals. Therefore, we also tested an alternative set of values estimated for the skin of juvenile loggerheads (1.11 ± 0.17‰ for $\delta^{13}C$ and 1.6 ± 0.07‰ for $\delta^{15}N$) (Reich et al. 2008), since this tissue is also keratinized. All statistical analyses were performed in R software version 4.3.1 with α=0.05 (R Core Team 2023).

Results

The loggerhead turtles sampled (n = 42) ranged in size from 24 to 114 cm CCL (mean = 77.7 cm, median = 76.9 cm). Up to 45 layers were subsampled from each scute, resulting in a total of 611 layers analyzed for SIA, with an average of 22.4 layers per individual (ranging from 6 layers, representing approximately the last 3.6 years, to 45 layers, representing ~27 years). Among the individuals sampled, 20 were determined to be females, 16 were males and 6 had no sex determined. The $\delta^{13}C$ and $\delta^{15}N$ values of the 50-µm layers of the individuals' scute ranged from -19.8 to -12.4‰ (mean ± SD = -16.1‰ ± 1.6‰) and from 4.4 to 17.7‰ (mean ± SD = 12.8‰ ± 3‰), respectively.

Statistical comparisons revealed no changes on $\delta^{13}C$ (Paired *t* test, t_9 = -2.10, p = 0.07) and $\delta^{15}N$ (Paired *t* test, t_9 = -1.25, p = 0.24) values between extracted and non-extracted subsamples (Table S1).

Two clusters, based only on $\delta^{15}N$, best fit the distribution of stable isotope composition for loggerhead turtles. The average silhouette of 0.74 is indicative of a strong structure within the data set (Table 1). The most enriched cluster (mean ± SD $\delta^{15}N$ = 14.30‰ ± 1.27; mean ± SD $\delta^{13}C$ = -15.52‰ ± 1.16‰; n = 474) was separated by approximately $\delta^{15}N$ = 10.97‰ from the most depleted cluster (mean ± SD $\delta^{15}N$ = 7.78‰ ± 1.69‰; mean ± SD $\delta^{13}C$ = -18.31‰ ± 0.72; n=137), established as the cut-off point between the two groupings (Fig. 2b). The upper limit of $\delta^{15}N$ for the oceanic group was 10.93‰ and the lower limit for the neritic group was 11.02‰.

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

Number of clusters	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$ and $\delta^{15}N$
2	0.62	**0.74**	0.68
3	0.56	0.61	0.43
4	0.55	0.54	0.40

The $\delta^{15}N$ values below 10.97‰ were classified as belonging to the oceanic stage, while higher values were indicative of the neritic stage. Individuals whose $\delta^{15}N$ values across scute layers fluctuated around 10.97‰ and did not show a clear pattern allowing classification into one of the three groups were considered "indeterminate shifters" (n=4, Fig. S5) and were excluded from the analyses. A summary of the isotopic values for each life stage is presented in Tables 2 and 3.

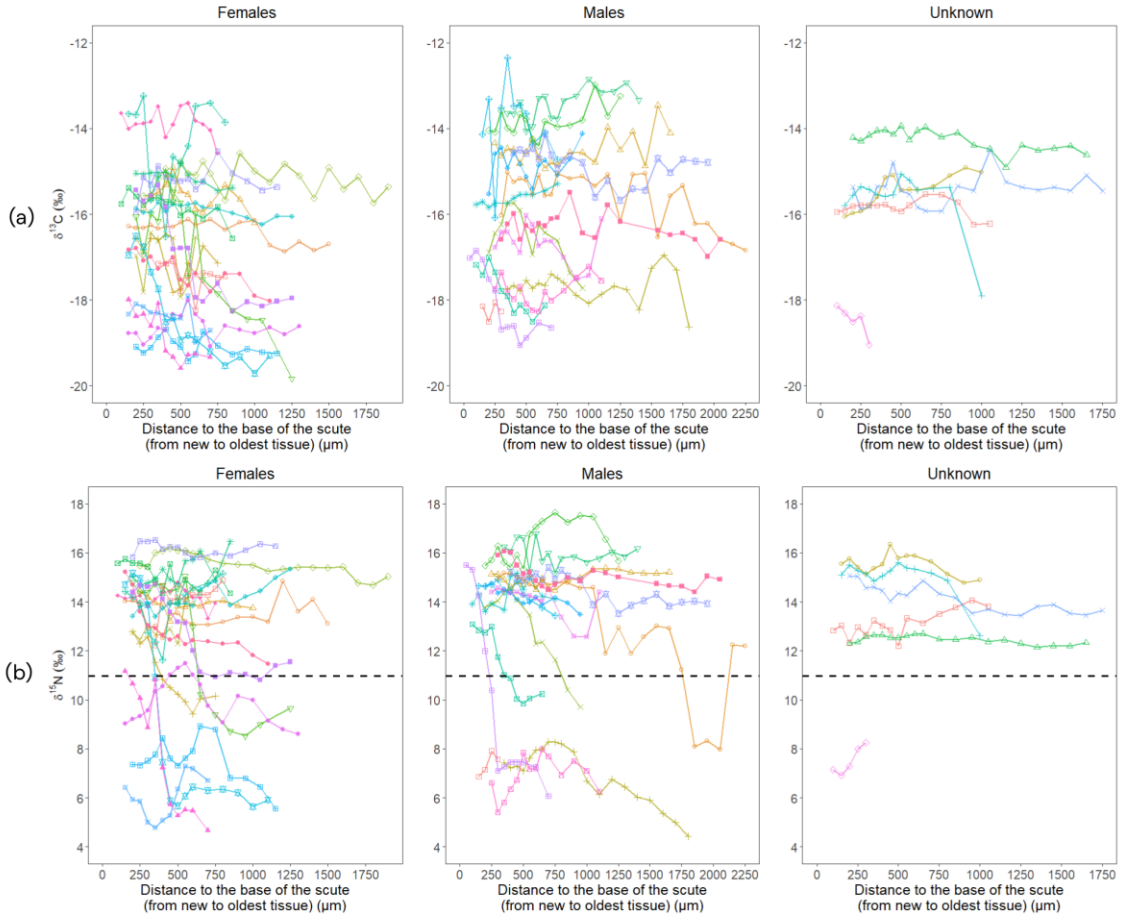


Fig. 2 Variation in $\delta^{13}C$ and $\delta^{15}N$ values across successive layers of the carapace scutes of loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). **(a)** $\delta^{13}C$ values for each individual, represented by a unique symbol and colour line across all sampled layers. **(b)** $\delta^{15}N$ values shown in the same format and with the same individual symbols. The

dashed line represents the $\delta^{15}N$ value of 10.97‰, used as a threshold to distinguish between oceanic ($\delta^{15}N$ < 10,97‰) and neritic ($\delta^{15}N$ > 10,97‰) groupings. The number of layers reflects the scute thickness

Table 2 Minimum, maximum, and mean (± SD) values of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) for groups defined by life stage of loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean: oceanic juveniles (OJ), neritic juveniles (NJ), and adults (Ad)

Group	$\delta^{13}C$ (min : max)	$\delta^{13}C$ (mean ± SD)	$\delta^{15}N$ (min : max)	$\delta^{15}N$ (mean ± SD)
OJ	-19.42 / -16.96	-18.19 ± 0.63	4.43 / 8.93	6.91 ± 1.03
NJ	-18.24 / -12.35	-15.70 ± 1.21	11.47 / 16.46	14.43 ± 1.07
Ad	-16.33 / -12.98	-14.76 ± 0.89	12.52 / 17.65	14.95 ± 1.08

Table 3 Means and standard deviations (SD) of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values for life stages (Ad = adult, NJ = neritic juvenile, OJ = oceanic juvenile) and sexes (F= female, M= male) of loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean

Stage	Sex	*N*	$\delta^{13}C$ (mean±SD)	$\delta^{15}N$ (mean±SD)
OJ	F	2	-18.78 ± 0.44	6.85 ± 1.14
OJ	M	3	-17.78 ± 0.36	6.95 ± 0.95
NJ	F	11	-16.03 ± 1.07	14.21 ± 1.23
NJ	M	7	-15.25 ± 1.25	14.72 ± 0.73
Ad	F	7	-15.12 ± 0.90	14.66 ± 0.99
Ad	M	7	-14.41 ± 0.73	15.25 ± 1.10

When evaluating and comparing the linear mixing models, it was found that, for $\delta^{13}C$, the best-fitting model based on the second-order Akaike Information Criterion (AICc) included life stage and sex as fixed effects, in addition to individual as a random effect (Table 4). For $\delta^{15}N$, the most appropriate model included only life stage as a fixed effect, also accounting for individual as a random effect (Table 4).

Table 4 Explanatory variables included in the linear models (LM) and linear mixed models (LMM) for $\delta^{13}C$ and $\delta^{15}N$. The best-fit model for each isotope is shown in bold, based on the second-order Akaike Information Criterion (AICc) and the difference in AICc between each model and the model with the lowest AICc (ΔAICc)

Isotope	Model	Explanatory variables	Random effect	AICc	ΔAICc
$\delta^{13}C$	1	Life stage	-	1101.79	586.63
	2	Life stage and sex	-	1044.69	529.53
	3	Life stage, sex and their interaction	-	1047.85	532.69
	4	Life stage	Individual	518.98	3.82

	5	**Life stage and sex**	**Individual**	**515.16**	**0**
	6	Life stage, sex and their interaction	Individual	516.15	0.99
$\delta^{15}N$	1	Life stage	-	1124.82	278.18
	2	Life stage and sex	-	1108.46	261.83
	3	Life stage, sex and their interaction	-	1110.18	263.54
	4	**Life stage**	**Individual**	**846.64**	**0**
	5	Life stage and sex	Individual	847.52	0.88
	6	Life stage, sex and their interaction	Individual	849.08	2.44

The linear mixed models (LMMs) revealed that, regarding life stage, both $\delta^{13}C$ and $\delta^{15}N$ values did not differ between adult (Ad) and neritic juvenile (NJ) individuals, but both showed significantly higher values than oceanic juveniles (OJ) (Ad = NJ > OJ) (Table 5). Regarding sex, significant differences were observed only for $\delta^{13}C$ (Table 5), with males showing higher values than females (Table 3).

Table 5 Comparisons between life stages (Ad = adult, NJ = neritic juvenile, OJ = oceanic juvenile) or sex (F = female, M = male) for $\delta^{13}C$ and $\delta^{15}N$ values, based on the LMM. The estimate represents the mean difference between the groups, accompanied by the standard error (SE), degrees of freedom (df), t-value and p-value. Statistically significant differences ($p < 0.05$) are indicated in bold

Isotope	Comparison	Estimate	SE	df	t-ratio	p-value
$\delta^{13}C$	Ad - NJ	0.726	0.334	33.1	2.171	0.0912
	Ad - OJ	3.507	0.486	32.8	7.210	**<0.0001**
	NJ - OJ	2.781	0.475	32.7	5.855	**<0.0001**
	F - M	-0.814	0.311	32.9	-2.616	**0.0133**
$\delta^{15}N$	Ad - NJ	0.376	0.324	34.3	1.161	0.4840
	Ad - OJ	7.917	0.470	33.5	16.831	**<0.0001**
	NJ - OJ	7.541	0.455	33.1	16.577	**<0.0001**

Therefore, the sequential analysis of stable carbon and nitrogen isotopes in the scute layers of loggerhead turtles showed a significant increase in $\delta^{13}C$ and $\delta^{15}N$ values between oceanic (only juveniles) and neritic individuals (juveniles and adults). This pattern is indicative of ontogenetic changes, both in terms of habitat and diet.

To estimate the contribution of prey to the loggerhead turtles diet using the MixSIAR package, individuals were regrouped based on the pattern of ontogenetic variation observed in their $\delta^{15}N$ transect (Fig. 3). Thus, the isotopic mixing models were

generated for three groups: oceanic non-shifters (oceanic juveniles), neritic non-shifters (both neritic juveniles and adults), and shifters. The variation ranges of $\delta^{13}C$, $\delta^{15}N$ and CCL values for each group are presented in Table 6.

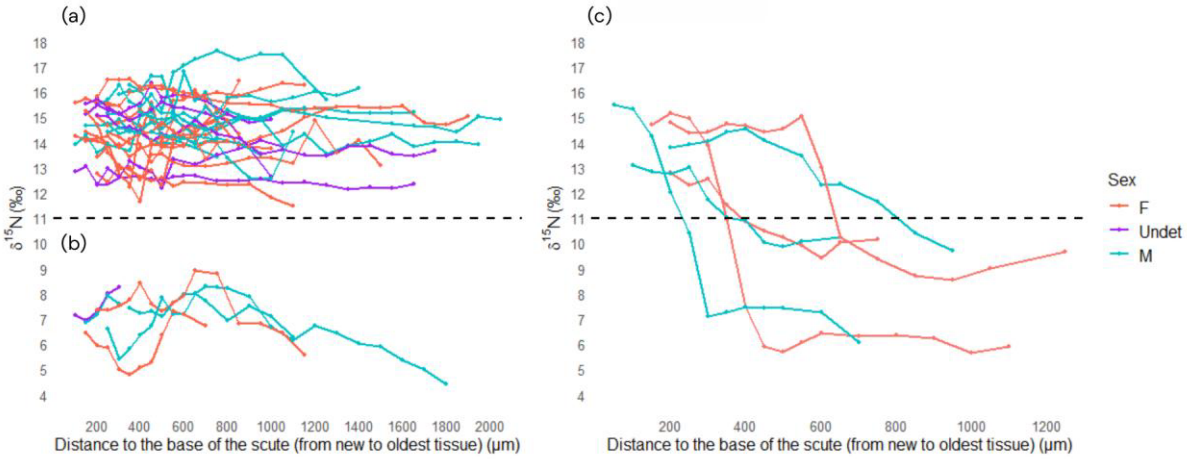


Fig. 3 Turtle-specific nitrogen stable isotope transects by life history pattern in loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). **(a)** Neritic non-shifters individuals, **(b)** oceanic non-shifters individuals, and **(c)** shifters. The dashed line indicates the $\delta^{15}N$ threshold (10.97‰) separating oceanic and neritic groups. Colors represent sex: F = females (orange), M = males (cyan) and U = undetermined (purple)

Table 6 Minimum and maximum values of curved carapace length (CCL), $\delta^{13}C$ (‰), and $\delta^{15}N$ (‰) for loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO) grouped by life history pattern

Group	*N*	CCL min-max (cm)	$\delta^{13}C$ min-max, range	$\delta^{15}N$ min-max, range
Oceanic non-shifters	6	24 to 66.5	-19.42 to -16.96	4.43 to 8.93
Neritic non-shifters	26	62.4 to 114	-18.24 to -12.35	11.47 to 17.65
Shifters	6	59.5 to 70.1	-19.83 to -15.07	5.64 to 15.50

Mixing polygons were generated for the same groups. For oceanic non-shifters, the loggerhead scute TDFs provided the best fit (Fig. 4, a), while for shifters and neritic non-shifters, the loggerhead skin TDFs showed a better match (Fig. 4, d, f).

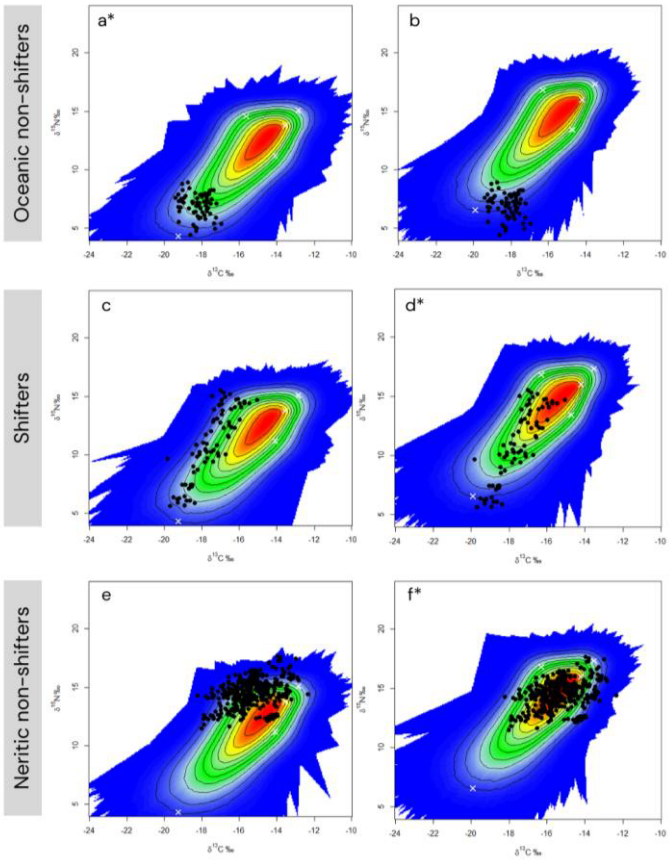


Fig. 4 Isotopic mixing polygons using three different sets of TDFs for the correction of prey tissue values. Polygons on the left (a, c, e) use loggerhead scute TDFs (1.77‰ for $\delta^{13}C$ and –0.64‰ for $\delta^{15}N$; Reich et al. 2008), while polygons on the right (b, d, f) use loggerhead skin TDFs (1.11‰ for $\delta^{13}C$ and 1.60‰ for $\delta^{15}N$; Reich et al. 2008). Asterisks (*) indicate the TDF set that provided the best fit for each group

Initial models showed that cnidarians contributed <10% to the diet of any group and were therefore excluded from the final models to avoid adding uncertainty to the model, retaining only the four main prey groups. Under this configuration, the results revealed distinct patterns of prey contribution among the analyzed groups (Fig. 5). For oceanic non-shifters, the diet was dominated by salps, with 72.7% (64.5 – 81.4% at 95% C.I., as the following model results) with a smaller contribution of fishes (12.8% (0.3 – 26.3%), which remained constant all along ontogeny) (Fig. 5a). Among shifters, average contributions started from 57.9% (46.1 – 68.5%) for salps, following by 16.7% (0.2 – 34.6%) for gastropods and by 16.9% (0.3 – 44.7%) for crustaceans. For this group, ontogenetic changes were clear, with salps predominating during the pre-shift life stage (oldest scute layers), with minor contributions from gastropods and crustaceans; while

during the post-shift life stage, fish contributions increased markedly, while contributions of other prey decreased (Fig. 5b). For neritic non-shifters, crustaceans contributed most, with 49.2% in average (1.1 – 78.4%) followed by fishes, with 23.9% (0.7 – 42%), and gastropods, with 19.3% (0.1 – 68.4%), with no clear ontogenetic changes (Fig. 5c).

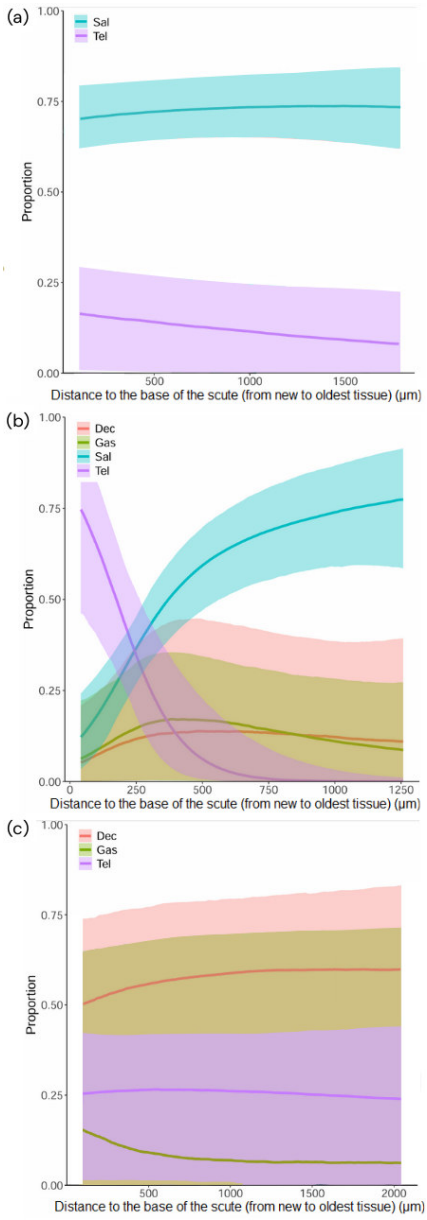


Fig. 5 Density plots (lines = means, shaded areas = 95% credibility intervals) representing the estimated proportions of prey contributions to the diet of loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO) across successive carapace scute layers. (a) oceanic non-shifters, (b) shifters, and (c) neritic non-shifters. Sal – Salpida; Tel – Teleostei (*Trichiurus lepturus*); Dec – Decapoda (*Loxopagurus loxochelis*); Gas – Gastropoda (*Buccinanops* spp.). Prey items with estimated contributions below 10% were omitted from the plots

Discussion

Archives of individual foraging history derived from retrospectively ordered isotopic data in scute layers of oceanic and neritic loggerhead turtles provided novel insights into the resource use of this species. By analyzing these sequential layers, we were able to reconstruct individual foraging and habitat-use histories, beginning in early life stages in oceanic waters, the transitional period and the shift to neritic habitats. To our knowledge, this is the first study to investigate sex-based differences across life stages in loggerhead turtles from the Southwestern Atlantic Ocean.

Our results showed clear differences across life stages of loggerheads in SWAO: both neritic juveniles and adults exhibited higher $\delta^{13}C$ and $\delta^{15}N$ values compared to oceanic juveniles, reflecting the habitat and dietary changes associated with the ontogenetic shift. These findings are consistent with the well-documented dichotomy in foraging strategies between oceanic and neritic habitats in loggerhead turtles (Hatase et al. 2002; Hawkes et al. 2006; McClellan et al. 2010; Saito et al. 2015; Medeiros et al. 2019).

Mixing model outputs indicated that oceanic non-shifters showed a dominant contribution of oceanic species such as salps. This pattern is consistent with diet studies that have already indicated a predominant presence of salps and pyrosomes in the diet of oceanic juveniles (Martinez Souza 2009; Barros 2010). However, the mixing model results also revealed smaller contributions of neritic prey, such as fish. The presence of coastal prey may reflect a transitional phase between the oceanic and neritic stages for at least one individual in the group. The largest individual (66.5 cm CCL) classified within this group was found stranded on the beach (turtle CCR; Table S2). The sampling location, combined with its size — closely matching the average recruitment size estimated for loggerhead turtles in southern Brazil (~65 cm CCL, ranging from 55.7 to 77.9 cm; Monteiro 2017) — and its $\delta^{15}N$ trajectory (showing marked $\delta^{15}N$ fluctuations over time, with an increasing trend) (turtle CCR; Fig. S2), suggests that this turtle may have recently initiated recruitment into neritic habitats. This individual also exhibited the highest $\delta^{15}N$ values among all oceanic non-shifters, further supporting this interpretation. Additionally, due to a methodological limitation, the three outermost scute layers of this individual, which represents the most recent portion of the turtle's life, could not be

analyzed. Together, these findings indicate that we may be observing the beginning of the recruitment process, which could explain the inclusion of neritic prey in the mixing model.

The pattern of juvenile loggerheads primarily occupying oceanic waters aligns with previous satellite telemetry data. For example, Mansfield et al. (2017) deployed satellite tags on laboratory-reared, one-year-old loggerheads from nesting beaches in Bahia, Brazil, and observed that trajectories along the South Atlantic were mostly parallel to the coast, with turtles travelling along the outer edge of the continental shelf. Similarly, Barceló et al. (2013) tracked juvenile loggerheads captured as bycatch in pelagic longline fisheries off Uruguay and Brazil. While most turtles remained in oceanic waters, a few migrated toward neritic zones. Although the study could not compare the sizes of turtles that spent significant time on the continental shelf with those tracked primarily in deeper waters due to small sample size, the mean CCL of individuals in the study was 61.8 ± 6.9 cm. This suggests that those turtles moving into neritic areas may have been undergoing the oceanic-to-neritic transition.

Through the sequential analysis of carapace scute layers, we were able to detect the recruitment to neritic habitats and a dietary shift from lower to higher trophic levels, as evidenced by increases in $\delta^{13}C$ and $\delta^{15}N$ values over time (Post 2002) (Table S3). As expected, shifters exhibited a transition: prior to recruitment, they relied heavily on oceanic prey like salps but also showed more diverse feeding patterns, including smaller contributions from neritic prey; after recruitment, their diet shifted towards coastal resources, with fish as the main contributor. This prey variation may reflect two distinct recruitment patterns into neritic habitats previously described for juvenile loggerheads in the North Atlantic (Ramirez et al. 2015).

In our study, these patterns were described through individual isotopic trajectories. Although both isotopes showed convergent patterns across individuals, $\delta^{15}N$ was more effective in detecting ontogenetic shifts, as previously reported for loggerhead turtles in the northwestern Atlantic (Ramirez et al. 2015), the North Pacific (Turner Tomaszewicz et al. 2016), and southern Brazil (Monteiro 2017). Our results showed that three individuals exhibited a gradual increase in $\delta^{15}N$ values over multiple years, consistent with the *facultative shifter* pattern described by Ramirez et al. (2015) (Fig. S3). These turtles displayed gradual increase in $\delta^{15}N$ values over multiple years, exceeding the

461 10.97‰ threshold, which may reflect the consumption of mixed oceanic and neritic prey
462 or the use of isotopically distinct transitional habitats. In contrast, the remaining three
463 individuals exhibited sharp $\delta^{15}N$ increases greater than 3‰ within a one-year interval,
464 aligning with the *discrete shifter* profile — a pattern characteristic of a one-way
465 ontogenetic shift (Fig. S3). Notably, two of these turtles had very low $\delta^{15}N$ values prior
466 to the shift (~6-7‰), while the third individual already showed intermediate $\delta^{15}N$ values
467 (~9-10‰) (Fig. S3). This suggests that this individual was likely already incorporating a
468 mixed diet prior to undergoing the discrete isotopic shift. Together, the presence of both
469 facultative and discrete shifters in our dataset highlights the plasticity of foraging
470 behavior during the juvenile stage and underscores the importance of individual-level
471 approaches to better understand life-history strategies in the loggerhead turtle.

472 The neritic non-shifters (Fig. S4) primarily use coastal waters and feed on benthic
473 organisms, particularly crustaceans, fish, and gastropods. Although the broad and
474 overlapping credible intervals produced by the mixing model prevent detailed discussion
475 of the main dietary contributor throughout ontogeny, the results still allow inferences on
476 the use of the neritic habitat by these individuals. To better understand these results, the
477 representatives of crustacean and gastropod groups were the hermit crab *Loxopagurus*
478 *loxochelis* and the gastropod *Buccinanops* spp., low-mobility prey commonly found up to
479 the 45 m isobath (Capitoli and Bemvenuti 2004), highlighting the species' preference for
480 the inner continental shelf as a foraging ground. In Brazil, satellite tracking of adult
481 females nesting in Bahia has also shown high site fidelity to neritic foraging areas along
482 the northern and northeastern coasts (Marcovaldi et al. 2010). In addition to benthic prey,
483 fish also contributed to the diet of this group, suggesting opportunistic feeding on fishery
484 discards over ontogeny. This interpretation is supported by the improbability of
485 loggerhead turtles actively preying on live fish (Plotkin et al. 1993), and by the fact that
486 the representative species, the cutlassfish (*Trichiurus lepturus*), are not targeted by
487 directed fisheries in the region and are frequently discarded as bycatch, particularly in
488 coastal bottom pair trawl fisheries (Cardoso et al. 2021).

489 Similar patterns of high teleost contributions have also been reported in the
490 Mediterranean Sea (Tomas et al. 2001) and the United States (Seney and Musick 2007),
491 likely due to consumption of discarded bycatch. Thus, the importance of teleost fish in

492 the present study may be driven by the high intensity of bottom trawl fisheries (Haimovici
493 1997), providing an easily accessible food source, reducing the energetic cost of foraging.
494 This interpretation is further supported by the fact that trawling is the leading cause of
495 loggerhead mortality in the region (Maruyama et al. 2024), indicating strong interaction
496 between fisheries and turtle foraging areas.

497 Although four individuals could not be assigned to any of the three main
498 categories (neritic non-shifters, oceanic non-shifters, or shifters) and were classified as
499 *indeterminate shifters* (Fig. S5), their isotopic profiles suggest that they were likely either
500 undergoing or had undergone recruitment. However, rather than following a one-way
501 transition from oceanic to neritic habitats, these turtles exhibited more variable $\delta^{15}N$
502 trajectories, characterized by alternating increases and decreases that do not fit neatly into
503 discrete or facultative patterns. One individual in particular (turtle CCBBUYA, Fig. S5)
504 initially presented $\delta^{15}N$ values consistent with neritic foraging, followed by ~1.8 years
505 with markedly lower $\delta^{15}N$ values, indicative of a return to oceanic conditions.
506 Subsequently, the $\delta^{15}N$ values increased again and stabilized within the neritic range,
507 suggesting that the individual ultimately completed recruitment. This pattern resembles
508 the *continual shifter* profile described by Ramirez et al. (2015), in which turtles exhibited
509 multiple sharp increases and decreases in $\delta^{15}N$ values over multiple years. This further
510 highlights the complexity and individual variation in resource use during the juvenile
511 stage.

512 The classification of individuals as oceanic, neritic, or shifters in this study was
513 based on $\delta^{15}N$ isotopic profiles, but these categories also reflect the context in which
514 individuals were sampled or recovered. Among the oceanic individuals, three turtles were
515 incidentally captured by the pelagic longline fishery off southern Brazil, while three were
516 found stranded along the coast of southern Brazil (Table S2). Of the three stranded turtles,
517 two of the smaller individuals (turtles CCAA, CCZ; Table S2, Fig. S2) were likely
518 debilitated and moved toward the coast, ultimately stranding there, while the larger
519 individual may have recently initiated recruitment into neritic habitats (turtle CCR), as
520 discussed previously. Among the shifters, five individuals were found stranded along the
521 Uruguayan coast, and one was incidentally captured by the pelagic longline fishery off
522 southern Brazil (Table S2). Among neritic individuals, most were found stranded along

523 the coasts of southern Brazil and Uruguay (n = 24), and two were incidentally captured in
524 bottom pair trawl fisheries (Table S2). According to Maruyama et al. (2024), interactions
525 with bottom pair trawl fisheries are the main cause of loggerhead mortality in the region,
526 which is reflected in the high number of strandings observed. These insights are crucial
527 for identifying the main threats faced by loggerhead turtles at different life stages.

528 We found that the isotopic values of male and female loggerhead turtles in the
529 SWAO were similar, but females generally exhibited more depleted $\delta^{13}C$ values compared
530 to males. While this difference could reflect variations in resource use or baseline isotopic
531 values, it is important to note that the study area is strongly influenced by freshwater
532 discharge from the Río de la Plata and Lagoa dos Patos. This influence leads to high
533 temporal and spatial variability in $\delta^{13}C$ values, due to fluctuating contributions of
534 terrestrial versus marine sources (Botto et al. 2011; Troina et al. 2020; Cani et al. 2023).
535 Therefore, based solely on $\delta^{13}C$ values, it is not possible to definitively conclude that
536 males and females differ in their resource use within this region. Moreover, substantial
537 differences are unlikely, as previous studies have found no significant differences between
538 the sexes. In the Northwest Atlantic, stable isotope values in red blood cells and skin of
539 adult loggerhead turtles showed similar variation in $\delta^{13}C$ and $\delta^{15}N$ between males and
540 females, suggesting that both sexes adopt similar foraging strategies (Reich et al. 2010;
541 Pajuelo et al. 2012). In West Africa, satellite telemetry of adult males suggested a
542 dichotomy in migratory behavior that appears to be linked to body size, as previously
543 observed in adult females from the same population (Hawkes et al. 2006; Varo-Cruz et
544 al. 2013). In southwestern Japan, satellite tracking showed that larger males remained in
545 coastal waters, but made excursions around the open ocean of the East China Sea (Saito
546 et al. 2015), displaying a post-nesting dispersal pattern similar to that reported for females
547 in the region (Kamezaki et al. 1997).

548 In this study, we used the trophic discrimination factor (TDF) estimated for scutes
549 and skin of juvenile loggerhead turtles from the North Atlantic (Reich et al. 2008), due to
550 the lack of specific values for loggerhead turtles in the South Atlantic. Although the TDF
551 used for oceanic non-shifters was derived from scutes of juvenile *C. caretta*, the oceanic
552 environment of the North Atlantic differs substantially from our study area. The TDF
553 estimated from the skin of juvenile loggerheads provided a better fit for the neritic non-

554 shifters and shifters, despite being specific to another tissue. Therefore, a study is needed
555 to estimate appropriate TDFs for South Atlantic loggerheads across different life stages,
556 including adults, to increase the accuracy of dietary inferences. This is particularly
557 important since variations in TDF values can significantly influence the model outputs.
558 Additionally, it is important to note that not all prey items commonly consumed by
559 loggerheads in the study area were included in the model. Instead, we selected
560 representative taxa from the main prey groups reported in diet studies for the study area
561 (Martinez Souza 2009; Barros 2010). Furthermore, the isotopic values obtained from the
562 literature also show temporal and spatial variability, albeit small, which is another factor
563 that should be considered. In light of these limitations, the resulting interpretations should
564 be considered with caution.

565 In our analyses of loggerhead turtle scutes, we found no evidence that lipids
566 influenced $\delta^{13}C$ values, based on the lipid extraction test performed. Although earlier
567 studies have often used the C:N ratio as an indicator of tissue lipid content, with values
568 <3.5 generally considered not to require lipid removal or mathematical correction (Post
569 et al. 2007), several studies have found no consistent relationship between bulk C:N ratios
570 and lipid percentages in various organisms, including sea turtles (Medeiros et al. 2015).
571 Therefore, even though the C:N ratio of our dataset was 3.3 (n = 626, personal
572 observation), we chose to empirically test the need for lipid extraction. Based on these
573 results, we conclude that, although several previous studies have performed lipid
574 extraction on this tissue in sea turtles as a standard protocol (e.g., Cardona et al. 2009;
575 Vander Zanden et al. 2010; Vélez-Rubio et al. 2018; Silver-Gorges et al. 2023), our
576 findings suggest that this procedure may not be necessary for this tissue. Therefore,
577 excluding this step from the analytical protocol may optimize methodological efficiency
578 by reducing sample handling and processing time without compromising data quality.

579 The SWAO represents critical foraging and developmental ground for loggerhead
580 sea turtles across different life stages. However, this region also supports extensive
581 commercial fisheries, and bycatch remains the main threat to loggerhead turtles. During
582 the oceanic phase, loggerheads are highly vulnerable to pelagic longline fisheries (Sales
583 et al. 2008; Jimenez et al. 2009; López-Mendilaharsu et al. 2020), while in the neritic
584 phase mortality is primarily associated with incidental capture in trawl fisheries along the

continental shelf (Laporta et al. 2012; Monteiro et al. 2016; López-Mendilaharsu et al. 2020). Individuals that shift between these two habitats are thus exposed to both sources of mortality, to varying degrees depending on their residence time in each area. This oceanic-neritic dichotomy highlights a threat to population structure and long-term viability. To ensure the conservation of loggerhead turtles in the SWAO, mitigation actions should include the delineation of priority protection areas, the regulation of fishing effort in critical regions, and the development and continuous refinement of conservation strategies throughout the species' life cycle.

Conclusions

The present study revealed differences in how carbon and nitrogen are integrated across life stages in loggerhead turtles and highlighted a clear foraging dichotomy between oceanic and neritic phases. We found that adults use coastal habitats, while juveniles show greater variability in resource use, with larger individuals occupying neritic habitats and smaller ones foraging in oceanic habitats. Furthermore, although males and females differed in $\delta^{13}C$ values, it is unlikely that they use distinct habitats. These insights provide critical information for identifying conservation priorities throughout the turtle's ontogeny and emphasize the need for targeted mitigation measures to safeguard essential foraging grounds.

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615 **Author contributions**

616 CCA, DSM and GMV conceived the ideas and design methodology. SCE, APS,
617 DSM and GMV collected the data. CCA prepared scute samples and performed stable
618 isotope analysis. CCA and RFB realized data analysis. CCA wrote the first version with
619 support of DSM and GMV. All the authors reviewed and gave the approval of the final
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629 **Data availability**

630 Data are available upon request.

631 **Compliance with ethical standards**

632 **Conflict of interest**

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

634 **Ethical approval**

635 This study does not involve any human participants. No live animals were used
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SUPPLEMENTARY MATERIAL

Sex- and life stage-related patterns of resource use in Loggerhead turtle (*Caretta caretta*) from the Southwestern Atlantic Ocean

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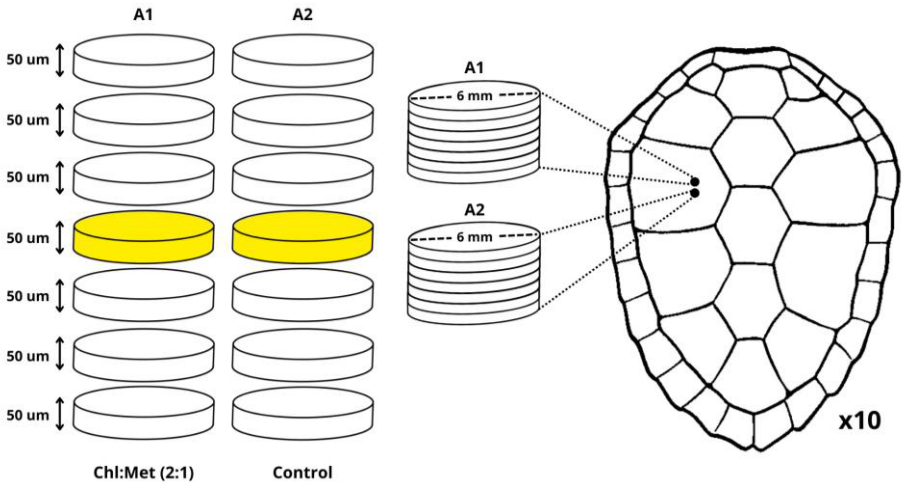


Figure S1. Schematic representation of the lipid extraction test. Two samples (A1 and A2) were obtained from the carapace scutes of 10 adult individuals. Each sample was sectioned into successive 50-µm layers, and the corresponding central layers (highlighted in yellow) were selected for stable isotope analysis (SIA), ensuring that they represented the same position within the sequence of layers. The layers of the test group were subjected to lipid extraction using a chloroform/methanol (Chl:Met) (2:1) solution, while the control group layers were not subjected to any treatment.

Table S1. Curved carapace length (CCL), C:N ratio, isotopic values of $\delta^{13}C$ and $\delta^{15}N$ of adult individuals of loggerhead turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean (SWAO).

CCL (cm)	C:N non-extracted	C:N extracted	$\delta^{13}C$ (‰) non-extracted	$\delta^{13}C$ (‰) extracted	$\delta^{15}N$ (‰) non-extracted	$\delta^{15}N$ (‰) extracted
94	3.52	3.30	-15.72	-15.25	13.41	13.29
97	3.32	3.32	-14.89	-14.81	15.86	16.60
97	3.31	3.37	-15.64	-16.02	14.78	15.81
98	3.40	3.41	-14.88	-15.10	15.07	15.09
98	3.38	3.40	-15.34	-15.09	12.44	12.93
99	3.42	3.38	-15.56	-15.44	13.80	13.82
99	3.60	3.39	-18.78	-18.30	10.62	11.12
101	3.48	3.33	-14.85	-14.38	16.46	15.38
101	3.54	3.34	-15.24	-14.47	15.38	15.78
101	3.35	3.35	-15.94	-15.70	13.81	14.10

Table S2. Summary table with information of 42 loggerhead turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean (SWAO) between 2013 and 2024. Dates given as yyyy/mm/dd. CCL: curved carapace length. Sex: F = female, M = male, U = unknown. Life stage: Juv = juvenile, Ad = adult. Asterisks (*) indicate recruitment to neritic habitats.

Turtle ID	Country	Date	CCL (cm)	Sex	Life stage	Shift pattern	Layers	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		Source
								first layer	last layer	first layer	last layer	
CCFFA	Brazil	2013/10/11	77.5	U	Juv	Neritic	21	-15.94	-16.22	12.84	13.82	Beach
CCII	Brazil	2013/12/19	86	U	Ad	Neritic	20	-16.05	-15.02	15.55	14.89	Beach
CCHHB	Brazil	2014/02/05	114	M	Ad	Neritic	25	-14.04	-13.24	15.49	15.68	Beach
CCKK	Brazil	2014/02/21	88	F	Ad	Neritic	16	-13.66	-13.85	14.42	15.15	Trawl
CCAA	Brazil	2014/03/06	24	M	Juv	Oceanic	6	-18.15	-18.26	6.87	7.58	Beach
CCMUYA	Uruguay	2015/02/02	68.5	M	Juv*	Shifter	13	-17.18	-18.13	13.09*	10.24*	Beach
CCJJA	Brazil	2015/03/13	82	U	Juv	Neritic	33	-14.21	-14.61	12.31	12.34	Beach
CCJUY	Uruguay	2015/03/29	99.6	M	Ad	Neritic	28	-13.64	-13.33	16.26	16.17	Beach
CCP	Brazil	2015/04/07	107.5	M	Ad	Neritic	19	-15.52	-14.12	14.65	13.49	Beach
CCLL	Brazil	2015/05/22	79	U	Juv	Neritic	20	-15.79	-17.90	15.11	12.63	Trawl
CCBUY	Uruguay	2016/01/04	70.4	F	Juv	Neritic	20	-15.57	-16.19	14.19	13.75	Beach
CCHUY	Uruguay	2016/02/04	93.2	F	Ad	Neritic	17	-15.04	-15.38	15.05	16.46	Beach
CCRR	Brazil	2016/12/28	85	U	Ad	Neritic	35	-15.37	-15.45	15.07	13.66	Beach
CCQQ	Brazil	2016/12/28	105	M	Ad	Neritic	39	-14.56	-14.79	15.22	13.94	Beach
CCFUY	Uruguay	2017/01/20	95	F	Ad	Neritic	17	-15.75	-16.56	15.58	14.35	Beach
CCAUY	Uruguay	2017/03/11	93.6	F	Ad	Neritic	30	-16.28	-16.70	14.03	13.11	Beach
CCKUY	Uruguay	2017/03/11	105	F	Ad	Neritic	25	-15.86	-16.05	13.42	15.34	Beach
CCUUY	Uruguay	2017/12/06	75	F	Juv	Indeterminate	25	-15.44	-17.96	14.39	11.55	Beach
CCFFUY	Uruguay	2017/12/12	70.1	F	Juv*	Shifter	25	-16.06	-19.83	14.79*	9.66*	Beach
CCCCUY	Uruguay	2017/12/20	71.9	F	Juv	Neritic	12	-16.97	-16.53	12.77	14.56	Beach
CCCAUY	Uruguay	2018/01/21	92.7	M	Ad	Neritic	33	-14.49	-14.10	14.60	15.20	Beach
CCDDUY	Uruguay	2018/01/30	63.2	M	Juv*	Shifter	19	-16.89	-17.72	13.79*	9.71*	Beach
CCXUY	Uruguay	2019/01/16	75.2	F	Juv	Neritic	22	-16.83	-18.02	15.23	11.47	Beach

CCNA	Brazil	2019/03/07	91.5	M	Ad	Neritic	15	-15.77	-15.28	13.91	14.11	Beach
CCYA	Brazil	2019/03/21	51.5	M	Juv	Oceanic	22	-17.74	-17.55	6.62	6.27	Longline
CCV	Brazil	2019/03/21	69	F	Juv	Indeterminate	26	-18.77	-18.61	9.04	8.62	Longline
CCWUYB	Uruguay	2019/04/21	57.4	F	Juv	Indeterminate	14	-17.99	-19.33	11.18	4.68	Beach
CCTUYA	Uruguay	2019/06/04	103	F	Ad	Neritic	23	-15.96	-15.36	15.84	16.28	Beach
CCRUY	Uruguay	2019/11/23	66.1	M	Juv*	Shifter	14	-17.02	-18.65	15.51*	6.07*	Beach
CCQUY	Uruguay	2020/01/04	66.9	F	Juv*	Shifter	22	-16.95	-19.29	14.71*	5.92*	Beach
CCEEUY	Uruguay	2020/01/17	78	F	Juv	Neritic	38	-15.57	-15.36	15.48	15.03	Beach
CCBBUYA	Uruguay	2020/05/24	76.2	M	Juv	Indeterminate	45	-16.03	-16.84	14.95	12.20	Beach
CCSUYA	Uruguay	2021/03/04	73.4	M	Juv	Neritic	22	-16.77	-16.11	14.40	14.40	Beach
CCZ	Brazil	2021/06/16	29	U	Juv	Oceanic	6	-18.13	-19.04	7.16	8.26	Beach
CCDD	Brazil	2021/06/18	52	M	Juv	Oceanic	36	-17.74	-18.62	7.44	4.43	Longline
CCR	Brazil	2021/06/21	66.5	F	Juv	Oceanic	23	-19.09	-19.25	7.36	5.55	Beach
CCT	Brazil	2021/06/25	65	F	Juv	Oceanic	14	-18.33	-18.71	6.42	6.71	Longline
CCX	Brazil	2022/04/07	102	F	Ad	Neritic	15	-13.64	-14.58	14.27	13.97	Beach
CCCCA	Brazil	2022/08/09	59.5	F	Juv*	Shifter	15	-16.56	-17.14	12.79*	10.16*	Longline
CCO	Brazil	2023/01/17	89	M	Ad	Neritic	15	-14.14	-14.72	14.65	13.44	Beach
CCZUY	Uruguay	2024/02/19	82.1	M	Juv	Neritic	41	-16.59	-16.59	15.90	14.92	Beach
CCAAUY	Uruguay	2024/03/14	62.4	F	Juv	Neritic	16	-17.15	-17.44	12.22	14.89	Beach

Table S3. Values of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) pre and post-shift to the neritic habitat of shifter individuals of loggerhead turtles (*Caretta caretta*) from the southwestern Atlantic Ocean (SWAO). ID = individual identification code.

Turtle ID	$\delta^{13}C$ pre-shift	$\delta^{13}C$ post-shift	$\delta^{15}N$ pre-shift	$\delta^{15}N$ post-shift	Difference $\delta^{13}C$	Difference $\delta^{15}N$
CCCCA	-17.31	-16.64	10.16	12.29	0.67	2.13
CCMUYA	-18.26	-17.44	10.22	12.41	0.82	2.19
CCQUY	-18.94	-16.89	6.63	14.68	2.05	8.05
CCRUY	-18.60	-17.11	7.56	14.27	1.49	6.71
CCFFUY	-18.39	-16.10	9.26	14.44	2.29	5.19
CCDDUY	-17.54	-16.32	10.06	13.45	1.23	3.40
Mean	**-18.17**	**-16.75**	**8.98**	**13.59**	**1.43**	**4.61**

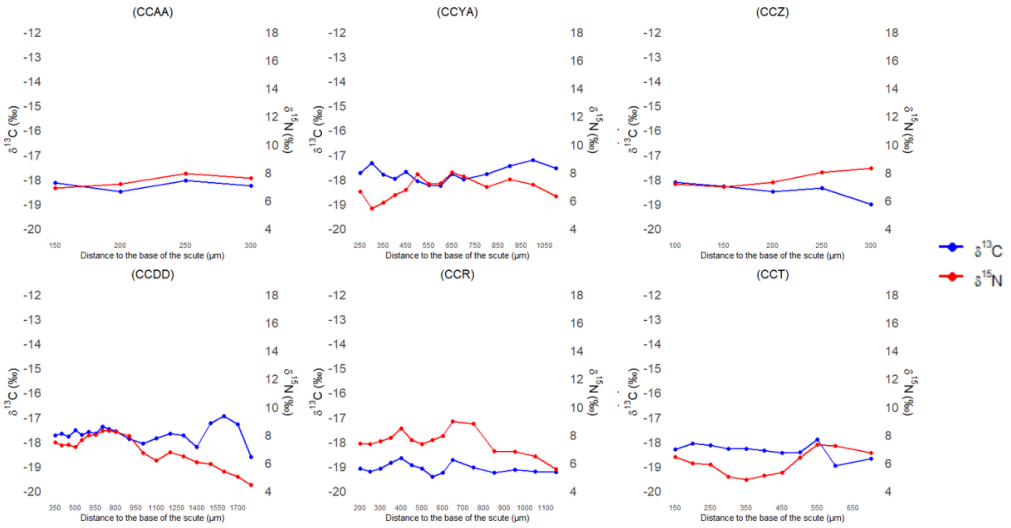


Figure S2. Individual $\delta^{13}C$ (blue) and $\delta^{15}N$ (red) values of oceanic non-shifters (n=6) loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). The x-axis represents the distance to the base of the scute (from new to oldest tissue, in µm).

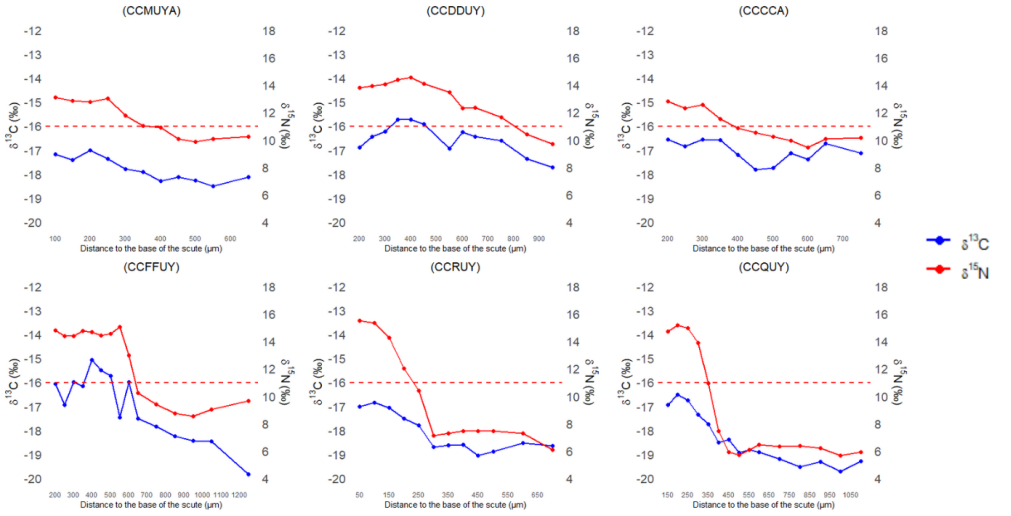


Figure S3. Individual $\delta^{13}C$ (blue) and $\delta^{15}N$ (red) values of shifters (n=6) loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). The x-axis represents the distance to the base of the scute (from new to oldest tissue, in µm). The dashed line indicates the $\delta^{15}N$ threshold (10.97‰) separating oceanic and neritic groups. "Facultative shifters" are shown in the top row, and "discrete shifters" in the bottom row.

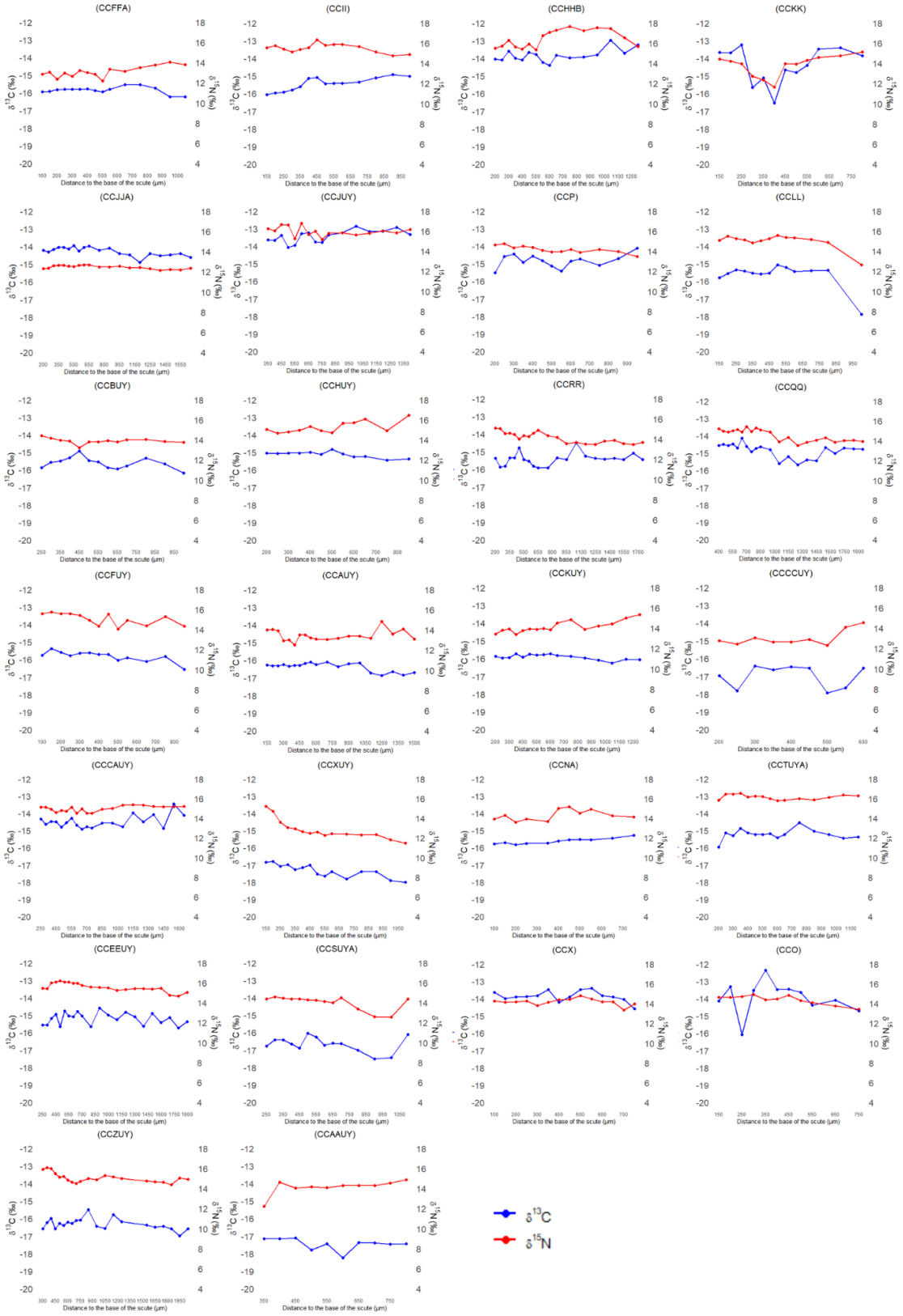


Figure S4. Individual $\delta^{13}C$ (blue) and $\delta^{15}N$ (red) values of neritic non-shifters (n=26) loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). The x-axis represents the distance to the base of the scute (from new to oldest tissue, in µm).

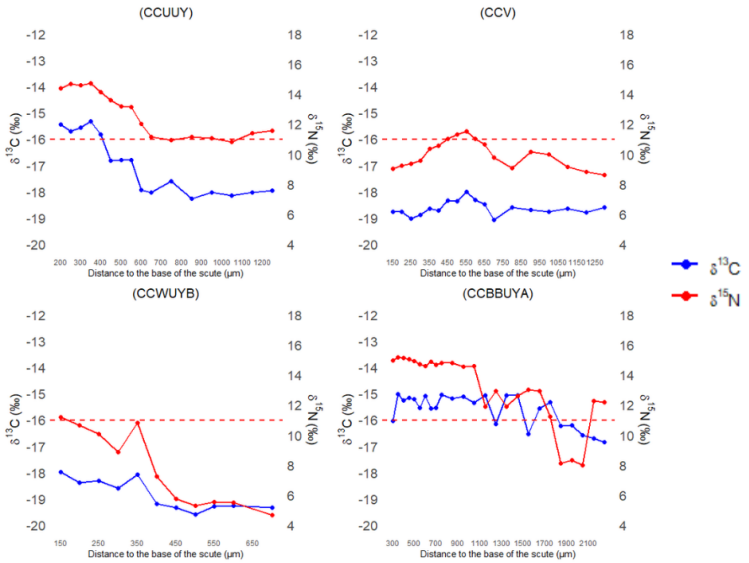


Figure S5. Individual $\delta^{13}C$ (blue) and $\delta^{15}N$ (red) values of indeterminate shifters (n=4) loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). The x-axis represents the distance to the base of the scute (from new to oldest tissue, in µm). The dashed line indicates the $\delta^{15}N$ threshold (10.97‰) separating oceanic and neritic groups.

ANEXO II

Individual specialization and temporal consistency in resource use by loggerhead turtles in successive life stages in the Southwestern Atlantic Ocean

Celina C. Almeida, Sérgio C. Estima, Andrine Paiva da Silva, Gabriela M. Vélez-Rubio e Danielle S. Monteiro

(Manuscrito a ser submetido ao periódico *Oecologia*)

Individual specialization and temporal consistency in resource use by Loggerhead turtle in successive life stages in the Southwestern Atlantic Ocean

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Author Contributions: CCA, DSM and GMV conceived and designed the methodology. SCE, APS, DSM and GMV collected the data. CCA prepared scute samples and performed stable isotope analysis. CCA realized data analysis under supervision of DSM and GMV. CCA wrote the first version with support of DSM and GMV. All the authors reviewed and gave the approval of the final manuscript.

Abstract

Individual sea turtles within a population may rely on different habitats or food sources, and accounting for such individual differences is essential for understanding their ecology and informing conservation efforts. In this study, we investigated the isotopic niche, temporal consistency and degree of individual specialization across two life stages (oceanic and neritic) of loggerhead turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean (SWAO), considering sex differences within the neritic stage. Sequential $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses were conducted on successive layers of carapace scutes from 27 individuals stranded dead or incidentally killed in pelagic longline or trawl fishery from southern Brazil and Uruguay, between 2014 and 2024. Isotopic values indicated an ontogenetic dietary shift, with oceanic individuals feeding at lower trophic levels than neritic individuals. Both life stages showed low within individual component/total niche width ratios, indicating strong individual specialization within a generalist population. Moreover, resource use by individual turtles remained consistent across years within life stages, with neritic males and females being equally specialized and temporally consistent. Our findings show that individuals specialize on isotopically distinct resources over long periods, suggesting strong site and prey fidelity throughout ontogeny. These results highlight the importance of incorporating individual-level ecological strategies into conservation planning, especially in regions where bycatch represents a major threat across multiple habitats.

Keywords: isotopic niche, foraging patterns, *Caretta caretta,* ontogeny, scute

Introduction

The ecological niche, formalized by Hutchinson (1957) as an abstract n-dimensional space composed of environmental variables (diet and habitat) that allow a species to exist, is a fundamental concept in ecology, particularly in population studies. This definition facilitates the understanding of resource use, geographical diversity, and other aspects of community structure (McGill et al. 2006). Conventionally, ecologists use niche theory to describe a species' ecology as a whole, treating conspecific individuals as ecologically equivalent (Bolnick et al. 2003). However, there is a well-developed literature on niche width variation, originated with Van Valen's niche variation hypothesis (1965), which first incorporated the idea of individual variation in resource use into niche theory.

Individual resource use within a population can be assessed through two complementary metrics: individual specialization (Roughgarden 1972) and temporal consistency (Vander Zanden et al. 2013). Individual specialization refers to the extent to which individuals utilize a restricted subset of the population's ecological niche, or resource base, for reasons not attributable to characteristics such as age, sex, or morphological variation (Bolnick et al. 2003; Araújo et al. 2011). According to Optimal Foraging Theory, individuals tend to prioritize high-value resources (MacArthur and Pianka 1966; Schoener 1974) and expand their niche only when these preferred resources become scarce. Ecological mechanisms that lead to individual specialization may be related to intra- and interspecific competition, ecological opportunity (e.g., resource abundance and diversity), and predation (Araújo et al. 2011). According to Vander Zanden et al. (2010), populations can be classified as generalists, which can be made up of generalist or specialist individuals; or specialists, made up of specialist individuals. Temporal consistency, on the other hand, measures intra-individual variance, providing the ability to determine how variable individuals are in their resource use over time (Vander Zanden et al. 2013).

Stable isotope analysis (SIA) is a tool that has been widely used in feeding ecology studies and can complement traditional methods such as stomach content analysis, which only identifies food items consumed shortly before the animal's death or capture (Burke

et al. 1993; Plotkin et al. 1993). The SIA approach makes it possible to investigate both the long- and short-term diet, since it is a measure of the diet assimilated and not just ingested (Peterson and Fry 1987), and helps to ensure that items that are difficult to digest are not overestimated to the detriment of those that are easily digested (Plotkin et al. 1993). This is possible because the isotopic composition of a predator is directly related to that of its prey, through a diet assimilated over time (Deniro and Epstein 1981). Carbon isotopes are widely used to differentiate food resources from distinct habitats (oceanic vs. neritic, pelagic vs. benthic), while nitrogen isotopes are commonly used to estimate trophic position (Post 2002).

Tissues that are formed over time and remain inert after synthesis, such as vibrissae (Newsome et al. 2009), feathers (Cherel et al. 2008), teeth (Botta et al. 2012), and carapace scutes in the case of sea turtles (Reich et al. 2007), retain the resource-use history from when they were formed (Reich et al. 2007), allowing the reconstruction of ontogenetic shifts in diet and habitat use – herein referred to as "resource use" (Reich et al. 2007; Cardona et al. 2009; Vander Zanden et al. 2010; Vander Zanden et al. 2013; Vélez-Rubio et al. 2018; Muñoz et al. 2021; Silver-Gorges et al. 2023). In the case of sea turtles, carapace scutes are composed of multiple layers of keratin, where new tissue layers form beneath older ones (Alibardi 2005).

The loggerhead turtle (*Caretta caretta*) is distributed across tropical and subtropical waters worldwide (Márquez 1990). Like other sea turtle species, they spend their early life stages in the open ocean and recruit to neritic habitats when they grow into larger juveniles, continuing their development and undertaking migrations between feeding and nesting grounds during adulthood (Musick and Limpus 1997; Bolten 2003; McClellan et al. 2010). As adults, the species often display alternative life histories with some individuals preferring oceanic and other neritic habitats (Hatase et al. 2002; Hawkes et al. 2006). Despite ontogenetic shifts in diet composition, loggerhead turtles maintain a primarily carnivorous diet throughout life (Márquez 1990), feeding on pelagic prey during the oceanic phase, and shifting to benthic invertebrates in neritic habitats (Jones and Seminoff 2013).

When investigating the foraging patterns of a population, it is essential to also consider the individual strategies within a population, since variations between individuals can significantly influence the evolutionary, ecological and conservation dynamics of a population (Roughgarden et al. 1972, 1974; Bolnick et al 2003). In sea turtles, temporal consistency and individual specialization over time have been assessed by using SIA in scutes of green (*Chelonia mydas*) and loggerhead turtles (Vander Zanden et al. 2010, 2013; Pajuelo et al. 2016; Cardona et al. 2017; Muñoz et al. 2021) and humeri of loggerhead and olive ridley (*Lepidochelys olivacea*) sea turtles (Monteiro 2017; Petitet et al. 2023). However, most studies have focused on adult females, and much less is known about males — mainly because, unlike females, they do not come ashore and are therefore more difficult to access. In addition, few studies on this phenomenon have addressed different life stages within the same population.

Loggerhead turtle individuals are commonly found stranded dead on beaches in southern Brazil and Uruguay (Vélez-Rubio et al. 2013; Monteiro et al. 2016). Throughout their life cycle, they are exposed to various threats, with incidental capture in artisanal and industrial fisheries being the primary threat to their survival (Hall et al. 2000; Wallace et al. 2013). In addition to the high mortality caused by bycatch, other significant threats include the loss of nesting beaches and foraging habitats, oil pollution, ingestion and entanglement in anthropogenic materials, and climate change (Lutcavage et al. 1997; Hamann et al. 2010). Due to these factors, the species is classified as “Vulnerable” on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Casale and Tucker 2017). Thus, recognizing patterns of individual specialization, variability within the population, and temporal consistency can provide insights into how differences among individuals may influence their vulnerability to fisheries bycatch across different areas and life stages.

Thus, the present study aims to characterize the isotopic niche and the existence and degree of individual specialization in resource use between different life stages and sexes of *C. caretta* in the Southwestern Atlantic Ocean (SWAO). We hypothesize that individuals are specialized in resource use, regardless of sex or life stage.

Materials and methods

Sampling

Between 2014 to 2024, scute samples were collected from loggerhead turtles stranded dead along the Rio Grande do Sul (RS) State (Brazil) (n= 9) and Uruguayan coast (n= 14) by the local NGO Núcleo de Educação e Monitoramento Ambiental (NEMA) and Asociación Civil Karumbé, respectively, during beach monitoring trips. Additional samples were obtained from individuals incidentally captured by pelagic longline (n= 3) and bottom pair trawl (n= 1) fisheries operating off southern Brazil, between 2014 and 2021, through incidental catch monitoring programs conducted by NEMA. The southern coast of RS State and Uruguay are commonly used as feeding areas for individuals of loggerhead turtles throughout the year (Barceló et al. 2013; Monteiro 2017). It was assumed that all individuals sampled in southern Brazil and Uruguay belong to the Brazilian population, based on molecular data already published, which reveal that the majority of individuals stranded on beaches or caught in coastal fisheries belong to the nesting grounds of Brazil (Caraccio et al. 2008; Prosdocimi et al. 2015; Medeiros 2019). However, it is known that mixed stocks of *C. caretta* are also found in the oceanic environment, composed mainly of individuals from Brazilian rookeries, but also including juveniles from the North Atlantic, the Mediterranean, the Pacific and the Indian Ocean in smaller proportions (Reis et al. 2010; Shamblin et al. 2014).

Curved carapace length (CCL) was measured for all individuals, from the nuchal notch to the anterior midpoint of the nuchal scute to the tip of the posterior marginal scute (Pritchard and Mortimer 1999). Sex determination was based on gonadal inspection during necropsy procedures (Wyneken 2001) and/or by assessing tail length in adults exceeding 83 cm CCL, the minimum size for nesting females in Brazil (Baptistotte et al. 2003). Each individual was categorized as oceanic or neritic, based on a cluster analysis of the $\delta^{15}N$ values of the scute layers (see Almeida et al. Appendix I for details).

The third lateral scute was removed from each individual, and the samples were kept frozen at -4ºC without chemical preservatives until further analysis. Subsamples were obtained from the posterior medial portion of the scute using a 6-mm diameter

158 Golgran biopsy punch, according to Reich et al. (2007), and only those reaching the
159 innermost layer were selected for analysis.

160 **Stable isotope analysis**

161 All scute samples were rinsed with distilled water in the laboratory and each
162 sample was embedded in O.C.T. (Optimal Cutting Temperature Composite, Tissue-
163 Teck®) with the dorsal (oldest) side down, frozen at -20°C, and sectioned into successive
164 50-µm layers using Leica SM2000 R sliding microtome. Each layer was then rinsed for
165 24 h with distilled water and then dried at 60°C for 24 h (Following Vélez-Rubio et al.
166 2018).

167 The number of layers obtained depended on the total thickness of each scute.
168 According to Vander Zanden et al. (2010), we assume that each 50-µm-thick layer
169 corresponds to a period of approximately 0.6 years for adult individuals. Each layer was
170 independently analyzed for stable isotope ratios of carbon and nitrogen. Approximately
171 0.3 mg of each dried sample was weighed into tin capsules and analyzed via continuous
172 flow isotope ratio mass spectrometer (EA Flash 2000 Delta V Advantage and TC/EA;
173 ThermoFisher Scientific™) at the Centro Integrado de Análises (CIA) - FURG. In cases
174 for which single layers did not provide enough material for stable isotope analysis, those
175 layers were excluded from sampling to avoid combining adjacent layers and thereby
176 preserve the temporal resolution (i.e., maintain each layer as a time unit of ~0.6 years).
177 Since the carapace scutes have low lipid content (Almeida et al. Appendix I), sample
178 processing was performed without this step.

179 Stable isotopes values are expressed in δ notation as parts per thousand (‰), in
180 relation to international standards: caffeine, glutamic acid, acetanilide, NBS22, cane
181 sugar, beet sugar, N_1 and N_2, according to the following equation:

182 $$\delta X = (Rsample/Rstandard) - 1$$

183 where X is the ^{13}C or ^{15}N value and R is the corresponding sample and standard
184 ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Analytical precision for these data was determined using
185 glutamic acid and caffeine, and was 0.07‰ for $\delta^{13}C$ and 0.28‰ for $\delta^{15}N$.

Statistical analysis

Stable Isotope Bayesian Ellipses in R (SIBER package) (Jackson et al. 2023) was used to estimate the isotopic niche width of two main groups: oceanic and neritic. Neritic individuals (included both neritic juveniles and adults) were subdivided by sex, based on statistical evidence of $\delta^{13}C$ differences between males and females (see Almeida et al., Appendix I). Oceanic individuals, in contrast, were not subdivided due to the small sample size. The isotopic niche metrics were calculated based on all the data from the subsampling of the scute layers. The Standard Ellipse Area corrected for small sample sizes (SEAc) was adopted as the measure of the isotopic niche containing approximately 40% of the data. The isotopic niche overlap between the groups was calculated as the shared SEAc area, expressed as a percentage relative to each group. To do this, the intersection area was divided by the area of each individual ellipse, making it possible to assess the proportion of shared niche in relation to the total niche of each group.

The degree of individual specialization and temporal consistency was assessed for both $\delta^{13}C$ and $\delta^{15}N$ across the same groups. Based on a quantitative framework proposed by Roughgarden (1972), total niche width (TNW) of a population results from the sum of two components: the within-individual component (WIC) and the between-individual component (BIC), such that TNW = WIC + BIC. The WIC/TNW ratio is used as a metric to determine the degree of individual specialization, which compares the breadth of an individual's niche with that of its population as a whole, ranging from 0, when the population is made up of specialists who use only part of the resource used by the general population, to 1, when the individuals are generalists and use the entire resource. Analysis of variance (ANOVA) was used as an approximation to compare these values within and between individuals, following the methodology proposed by Vander Zanden et al. (2013). The mean sum-of-squares within individuals (MSW) measures the variability within individuals, which we used as a *proxy* for WIC, and was calculated using the equation:

$$MSW = \frac{\Sigma_i \Sigma_j (x_{ij} - \bar{x_i})^2}{(N - k)}$$

214 And the mean sum-of-squares between individuals (MSB) measures the
215 variability between individuals and was the *proxy* for the BIC, being calculated as:

216 $$MSB = \frac{\Sigma_i \Sigma_j (x_{ij} - \bar{x_i})^2}{(k - 1)}$$

217 Where *i* represents an individual, *j* represents a single layer of the scute, *N* is the
218 total number of observations and *k* is the number of individuals. The sum MSB + MSW
219 was proxied for TNW (Vander Zanden et al. 2013).

220 WIC was also used to assess temporal consistency, i.e. the variation within
221 individuals over time. Low WIC values indicate that individuals are consistent in their
222 use of resources over time (Vander Zanden et al. 2013).

223 **Results**

224 Loggerhead sea turtles sampled for scutes ranged in size from 24.0 to 114.0 cm
225 CCL (mean = 80.8 cm, median = 88 cm) (n = 27). The minimum number of 50-µM layers
226 obtained per individual was six, representing the last 4.2 years, and the maximum was 41,
227 representing the last 24.6 years, approximately (mean = 22 layers per individual). Among
228 the sampled individuals, 14 were females, 12 were males and one individual had
229 undetermined sex (Fig. 1). The $\delta^{13}C$ values ranged from -19.4‰ to -12.4‰ (mean ± SD
230 = -15.9 ± 1.6‰), and the $\delta^{15}N$ values ranged from 4.4 to 17.7‰ (13.2‰ ± 3.1‰).

231 Regarding isotopic niche width (SEAc), neritic individuals occupied niches with
232 higher isotopic values compared to oceanic individuals (Fig. 2). Additionally, there was
233 an overlap of 47% and 58% between the isotopic niches of neritic females and males,
234 respectively. The widest niche was observed in neritic females (SEAc = 3.66‰²),
235 followed by neritic males (SEAc = 2.96‰²), while the narrowest was found in oceanic
236 individuals (SEAc = 2.01‰²).

237 The WIC/TNW ratio, *proxy* for individual specialization, was low across all
238 groups (≤ 0.2), indicating a high degree of individual specialization across ontogenetic
239 stages (Table 1). Neritic individuals (males and females) had similar WIC/TNW values
240 for both $\delta^{13}C$ and $\delta^{15}N$, suggesting comparable levels of individual specialization between

241 sexes. Oceanic individuals showed WIC/TNW values for $\delta^{13}C$ similar to those of neritic
242 turtles but exhibited a relatively higher value for $\delta^{15}N$, indicating a slightly lower degree
243 of individual specialization based on this isotope (Table 1).

244 As an indicator of temporal consistency, WIC values were low across all groups
245 (WIC < 0.20 for $\delta^{13}C$ and < 0.85 for $\delta^{15}N$), reinforcing the idea that individuals maintain
246 stable foraging patterns over time (Table 1). For $\delta^{13}C$, oceanic individuals had the lowest
247 WIC value, while neritic males and females showed higher and similar values. For $\delta^{15}N$,
248 WIC values were lower and more similar between the neritic groups than in oceanic
249 individuals, suggesting that both sexes show comparable temporal consistency at the
250 neritic stage and greater consistency than oceanic turtles (Table 1).

251 **Discussion**

252 To our knowledge, this is the first study to assess individual specialization and
253 temporal consistency in resource use across sexes and life stages of loggerhead turtles
254 (*Caretta caretta*) in the Southwestern Atlantic Ocean (SWAO). The characterization of
255 resource use by individuals within a population depends heavily on the spatial and
256 temporal scale at which individuals are sampled (Layman et al. 2012). Although measures
257 of variation in resource use such as the WIC/TNW ratio are widely used to investigate
258 individual specialization, they are often based on single samples without considering the
259 time scale (Bolnick et al. 2003). In this context, stable isotopes make it possible to access
260 integrated information over time, reflecting dietary assimilation during the renewal period
261 of the analyzed tissue. In this study, we were able to exploit this advantage by using
262 multiple samples from the same individual, from successive layers of the scute of
263 loggerhead turtles, which allowed us to estimate both temporal consistency in resource
264 use and individual specialization. Each sample from the scute was considered to represent
265 an integration of information over approximately 0.6 years for adult individuals (Vander
266 Zanden et al. 2010), thus reflecting the average resource use for that specific time interval
267 based on stable isotope values. We estimate that scute samples from loggerhead turtles
268 can contain up to 24.6 years of resource use history, providing an extensive record for
269 investigating patterns in a long-lived species. The comparison of the long-term scute

records reveals that generalist populations of loggerhead turtles in the SWAO are composed of specialist individuals.

Differences in isotopic niche width were observed among groups, with neritic females displaying the broadest niche and oceanic individuals the narrowest. This pattern may indicate a lower diversity of resources or habitats used by oceanic individuals. However, these differences should be interpreted with caution, as they may also be influenced by the smaller number of oceanic individuals included in the analysis. Regarding sex, the broader niche observed in neritic females compared to males may suggest greater variability in resource use or habitat selection. In relation to isotopic values, neritic individuals exhibited higher $\delta^{13}C$ and $\delta^{15}N$ values than oceanic individuals, with no niche overlap between these life stages (Fig. 2). This pattern suggests a marked dietary difference, with oceanic individuals likely feeding on lower-trophic-level prey (e.g., gelatinous organisms), while neritic individuals consume prey with higher isotopic values, such as benthic invertebrates (Almeida et al. Appendix I). These findings align with previous studies on *C. caretta*, which describe oceanic-stage juveniles as opportunistic feeders of pelagic gelatinous organisms like salps and pyrosomes (Martinez Souza 2009; Barros 2010). Upon recruiting to neritic habitats, juveniles shift to feeding on benthic prey — such as crustaceans, mollusks, and fish — which dominate their adult diet (Bugoni et al. 2003; Martinez Souza 2009; Barros 2010; Jones and Seminoff 2013; Medeiros et al. 2019).

Our results showed that $\delta^{15}N$ values did not differ significantly between neritic females and males, which suggests that both sexes may forage at comparable trophic levels. However, neritic females generally exhibited more depleted $\delta^{13}C$ values than males, which may suggest differences in resource use or baseline isotopic values between sexes, despite the substantial isotopic niche overlap. However, it is unlikely that the sexes exhibit substantial differences in resource use, as previously observed in the Northwest Atlantic, where the variation in $\delta^{13}C$ and $\delta^{15}N$ values among males was similar to that of adult females (Reich et al. 2010; Pajuelo et al. 2012), suggesting that both sexes adopt comparable foraging strategies.

When assessing temporal consistency in resource use no clear ontogenetic pattern was observed for $\delta^{13}C$ WIC values. This lack of a clear pattern is unsurprising, as $\delta^{13}C$ in the study area is strongly influenced by inputs from the Río de la Plata and Lagoa dos Patos, as well as other water masses, which are affected by seasonal variability and local biogeochemical processes, resulting in high temporal and spatial fluctuations in $\delta^{13}C$ (Troina et al. 2020; Cani et al. 2023). Such variability limits the usefulness of $\delta^{13}C$ for detecting habitat differences among life stages, as well as precluding definitive conclusions about sex-based differences in resource use. $\delta^{15}N$ WIC values, in contrast, revealed a clearer ontogenetic pattern, allowing for more robust interpretations of dietary resource use. Oceanic individuals had the highest WIC $\delta^{15}N$ values, which may be attributed to opportunistic feeding behavior typical of oceanic environments (Bolten 2003). Neritic females and males showed lower WIC values, indicating more consistent resource use.

While nitrogen values displayed a clearer variation across life stages than carbon, the overall low WIC values for both $\delta^{13}C$ and $\delta^{15}N$ suggest high temporal fidelity to specific foraging areas throughout development. The higher WIC for $\delta^{15}N$ in oceanic juveniles, for instance, does not necessarily imply random feeding, but rather that these turtles may consume a mixture of pelagic prey within the same trophic level, or alternatively, pelagic prey from different trophic levels that, when averaged, result in consistent $\delta^{15}N$ values. High temporal consistency was also observed by Monteiro (2017) for both oceanic and neritic juvenile loggerhead turtles of southern Brazil.

The low WIC/TNW values observed across all groups indicate that individual specialization occurs throughout ontogeny, suggesting that these generalist populations are composed of individually specialized turtles. However, the degree of individual specialization varied with life stage, and the differences were more pronounced for $\delta^{15}N$. Both neritic groups showed similar WIC/TNW values, indicating the highest levels of individual specialization. In contrast, oceanic individuals exhibited higher WIC/TNW ratios, indicating more generalist foraging strategies compared to neritic individuals. These results are consistent with those of Monteiro (2017), who reported greater individual specialization in neritic turtles compared to oceanic ones in the same region.

The relatively lower degree of individual specialization observed among oceanic non-shifters may partly reflect the criteria used to classify between oceanic and neritic groups. Individuals were assigned to the oceanic category based on a cluster analysis of $\delta^{15}N$ values, in which turtles showing values consistently below the threshold across all analyzed scute layers were classified as oceanic (see Almeida et al. Appendix I for details). However, some individuals in this group may have already initiated the recruitment process, as indicated by their body sizes, which are consistent with the average size at recruitment reported for loggerhead turtles in southern Brazil (~65 cm CCL, range: 55.7–77.9 cm; Monteiro 2017). This is especially possible because the most superficial scute layers were not available for any of these individuals, preventing direct observation of their latest habitat use. Furthermore, $\delta^{15}N$ values in some turtles showed a tendency to increase over time, suggesting a gradual shift toward neritic foraging (Fig. S1). Alternatively, assuming that all life stages exhibit fidelity to their respective foraging grounds, we suggest that the observed variation in $\delta^{13}C$ and in $\delta^{15}N$ both within (WIC) and between individuals (BIC) likely reflects differences in resource use within those foraging grounds.

Another plausible explanation for the lower levels of individual specialization in the oceanic environment is the higher genetic variability found in these habitats. Although in this study we considered the individuals as belonging to Brazilian rookeries, it is important to note that oceanic foraging areas off Brazil and Uruguay are mainly occupied by smaller juveniles, which show greater genetic variability compared to neritic areas — although Brazilian haplotypes remain the most frequent. In these areas, haplotypes from the North Atlantic, Mediterranean Sea, Pacific and Indian Ocean have also been reported (Caraccio et al. 2008; Reis et al. 2010; Shamblin et al. 2014). Supporting this, the smallest individual in our dataset (turtle CCAA, 24 cm CCL; Table S1) was genetically identified as a hybrid of *Caretta caretta* × *Lepidochelys olivacea* (Medeiros et al. 2019). Therefore, the higher genetic variability in the oceanic environment may also contribute to the lower levels of individual specialization observed in this habitat.

High levels of individual specialization have also been observed in other sea turtle populations. In the North Atlantic, loggerhead turtles were classified as a generalist

population with specialist individuals based on SIA of scutes from adult males and females (Vander Zanden et al. 2010; Pajuelo et al. 2016), while similar patterns were found in adult loggerheads from Northwest Africa (Cardona et al. 2017) and in subadult and adult individuals from Japan (Muñoz et al. 2021). Among juvenile loggerheads in estuarine waters of North Carolina, USA, repeated SIA of plasma showed consistent resource use over time and strong individual specialization (Hall et al. 2015). For adult green turtles (*Chelonia mydas*) nesting in Costa Rica, individual specialization was higher in adults compared to juveniles (Vander Zanden et al. 2013). In olive ridley turtles (*Lepidochelys olivacea*), studies using epidermal tissue in the Pacific (Peavey et al. 2017) and dietary analysis along the Indian coast (Behera et al. 2014) have likewise characterized populations as generalists. Among adult olive ridley turtles from northeastern Brazil, older individuals exhibited a greater degree of specialization than younger ones (Petitet et al. 2023).

Loggerhead turtles are considered the most generalist among sea turtle species (Bjorndal 1997, 2003), but our findings suggest that in the SWAO this generalist population is composed of individually specialized turtles across different life stages. In the present study, individual specialization likely does not reflect reliance on a single prey item, but rather a consistent combination of prey types, habitat, and geographic location. The consumption of mixed prey is plausible, given that loggerhead stomach content analyses frequently reveal a variety of prey species within the same individual. Gut content analyses have documented high dietary diversity in loggerheads during both oceanic and neritic phases, with a total of 24 and 53 prey taxa identified in oceanic and neritic individuals, respectively, in southern Brazil (Barros 2010). In Uruguay, dietary analyses revealed 11 different taxa in stranded individuals found on the continental shelf, and 16 prey groups in individuals incidentally caught by pelagic longlines (Martínez Souza 2009). Stomach content analyses available for two neritic individuals from our study further illustrate this pattern, revealing a consistent benthic foraging behavior. One individual consumed the hermit crab *Loxopagurus loxochelis*, gastropods (*Buccinanops* spp., *Olivancillaria urceus*), the crab *Hepatus pudibundus*, as well as isopods and bivalves (NEMA unpublished data). The other individual fed on the crab *Libinia spinosa*

389 and the gastropod *Buccinanops* spp. (Karumbé unpublished data). These findings
390 emphasize the complexity of foraging strategies within the population and the importance
391 of considering individual variation when studying ecological niches.

392 Although several individuals exhibited consistent isotopic trajectories over time
393 (Fig. S2), reflecting long-term specialization in resource use (Vander Zanden et al. 2010),
394 one individual exhibited a distinct behavior from the others. Its $\delta^{15}N$ values decreased by
395 more than 2.3‰ between two consecutive layers, accompanied by a comparable decline
396 in $\delta^{13}C$ (1.87‰) (turtle CCKK; Fig. S2). Although $\delta^{13}C$ exhibited greater fluctuation
397 between layers, both isotopes remained at more negative levels for approximately 1.8
398 years before returning to values similar to those observed previously. This individual
399 variation in isotopic patterns may reflect temporary incursions into oceanic habitat, which
400 have been previously described for large juveniles and adult loggerhead turtles in
401 southern Brazil, where some turtles remained year-round in neritic waters while others
402 performed seasonal movements between neritic and oceanic environments (Monteiro
403 2017). These findings highlight the plasticity of the species, which exhibits high
404 individual variability in habitat use and foraging strategies (Monteiro 2017). Habitat use
405 plasticity has also been demonstrated for juvenile loggerhead turtles in North Carolina,
406 USA, where individuals return to coastal waters and then return to the open ocean,
407 sometimes for several years (McClellan and Read 2007). In the Northeastern Atlantic,
408 smaller adult female loggerheads have been found to forage in oceanic regions, whereas
409 larger individuals tend to forage in coastal habitats (Hawkes et al. 2006). Mansfield et al.
410 (2009) observed two movement patterns performed by immature loggerheads in foraging
411 areas in the Western North Atlantic: a seasonal north-south migratory pattern on the shelf
412 and a year-round oceanic dispersal strategy. In the Western North Pacific, post-nesting
413 adult female loggerheads have been reported to forage either in oceanic or neritic habitats,
414 with this divergence in feeding habitat use likely influenced by body size differences
415 (Hatase et al. 2002).

416 The reasons behind the variation in life-history strategies among loggerhead
417 turtles remain uncertain, but environmental factors such as sea surface temperatures
418 (SST), productivity, and prey availability are likely influential (Godley et al. 2008;

Howell et al. 2010; Mansfield and Putman 2013). In southern Brazil, seasonal movements may reflect an effort to avoid cold waters mainly during austral autumn and winter (Monteiro 2017). In Uruguay, satellite tracking revealed that turtles moved northward during the austral winter, likely in response to decreasing SST (Barceló et al. 2013). Similarly, juvenile loggerheads in the Río de la Plata estuary have been reported to migrate toward warmer Brazilian and Uruguayan waters during colder months (González Carman et al. 2016). A similar seasonal response could potentially explain the pattern observed for the individual in this study, particularly given the alternating $\delta^{13}C$ values over time. However, without precise seasonal resolution for each layer, this interpretation remains speculative.

While growing evidence highlights the ecological relevance of individual specialization across taxa (Araújo et al. 2011), variation in resource use within and among individuals remains poorly understood. It is believed that both intra- and interspecific competition can influence individual foraging decisions over time, and studies have shown that high intraspecific competition tends to increase individual specialization (Araújo et al. 2011), whereas interspecific competition can weaken individual specialization (Bolnick et al. 2010). Our results suggest that each life stage maintains consistent foraging strategies over time, with individuals repeatedly feeding on prey types or isotopically similar resources across multiple years, reflecting long-term fidelity to specific dietary resources.

The high degree of individual specialization and temporal consistency observed in both oceanic and neritic life stages brings advantages and disadvantages to the population. Populations composed of specialists exploiting different resources, as in the case of loggerhead turtles from the SWAO, can retain the benefits of specialization (such as efficiency in resource use) while the species as a whole can shift between different resources if one declines (Colles et al. 2009). Moreover, the consistent use of predictable foraging grounds may be more beneficial than exploring a new, uncharted habitat (Schofield et al. 2010). On the other hand, populations composed of long-term specialists may be less able to respond to rapid environmental changes (Bolnick et al. 2003). This vulnerability is particularly concerning for loggerheads in the SWAO, given the

significant overlap between fisheries and its distribution, which increases the risk of being caught as bycatch from both longline capture in oceanic areas and trawl fisheries along the continental shelf (Sales et al. 2008; Jimenez et al. 2009; Laporta et al. 2012; Monteiro et al. 2016; López-Mendilaharsu et al. 2020; Ríos et al. 2024). In this context, long-term individual specialization may increase the vulnerability of population structure and long-term viability in the face of anthropogenic threats, highlighting the need for adequate conservation measures that are regularly revised and adapted to dynamic environmental conditions.

While our results provide insights into individual specialization and temporal consistency in resource use, some methodological limitations should be considered when interpreting the findings. The temporal resolution of keratinized scute layers is based on estimates for adult individuals, with each 50-µm section corresponding to approximately 0.6 years. However, no specific deposition rate has been established for juvenile loggerheads, which introduces uncertainty in temporal interpretations for this life stage. Additionally, the absence of the most superficial layers in some samples implies a loss of recent dietary information. For instance, one turtle was incidentally captured in a pelagic longline fishery and likely had an oceanic isotopic composition in its most recent scute layer. However, usable material was only obtained from the fourth layer (~2.4 years prior to death), which had a neritic isotopic composition. As a result, this individual was classified as neritic, despite the probable oceanic origin of its final foraging activity. Another important point to consider is the broad temporal scale of the samples, which were collected between 2014 and 2024, with each individual providing multiple scute layers, covering several years of past resource use. This temporal span may have introduced additional variability into the results, as environmental conditions and prey availability likely fluctuated over the years. Although this temporal variability was not the focus of the present study, it represents an important aspect that could be further explored in future research. Despite these limitations, this study provides an important contribution as the first to investigate isotopic niche, temporal consistency in resource use and individual specialization across different sexes and life stages in *C. caretta* from the SWAO.

Conclusion

This study demonstrated that, in the SWAO, loggerhead turtles constitute a generalist population composed of individually specialized turtles, with varying degrees of specialization across ontogenetic stages, but not between sexes. The sequential analysis of carapace scutes allowed us to recover an extensive record of resource use, revealing consistent patterns of individual specialization and fidelity to foraging areas. By uncovering these long-term ecological traits, our findings expand the understanding of how loggerhead turtles interact with their habitats over time and highlight the importance of considering both individual and population scales in conservation planning. Moreover, this work reinforces the value of stable isotope analysis in inert tissues as a powerful tool to reconstruct life-history strategies in sea turtles (e.g. Vander Zanden et al. 2010; Vander Zanden et al. 2013; Pajuelo et al. 2016; Vélez-Rubio et al. 2018; Muñoz et al. 2021; Silver-Gorges et al. 2023), contributing to improved mitigation efforts aimed at reducing species mortality.

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Conflicts of interest: The authors declare that they have no conflict of interest.

Ethics 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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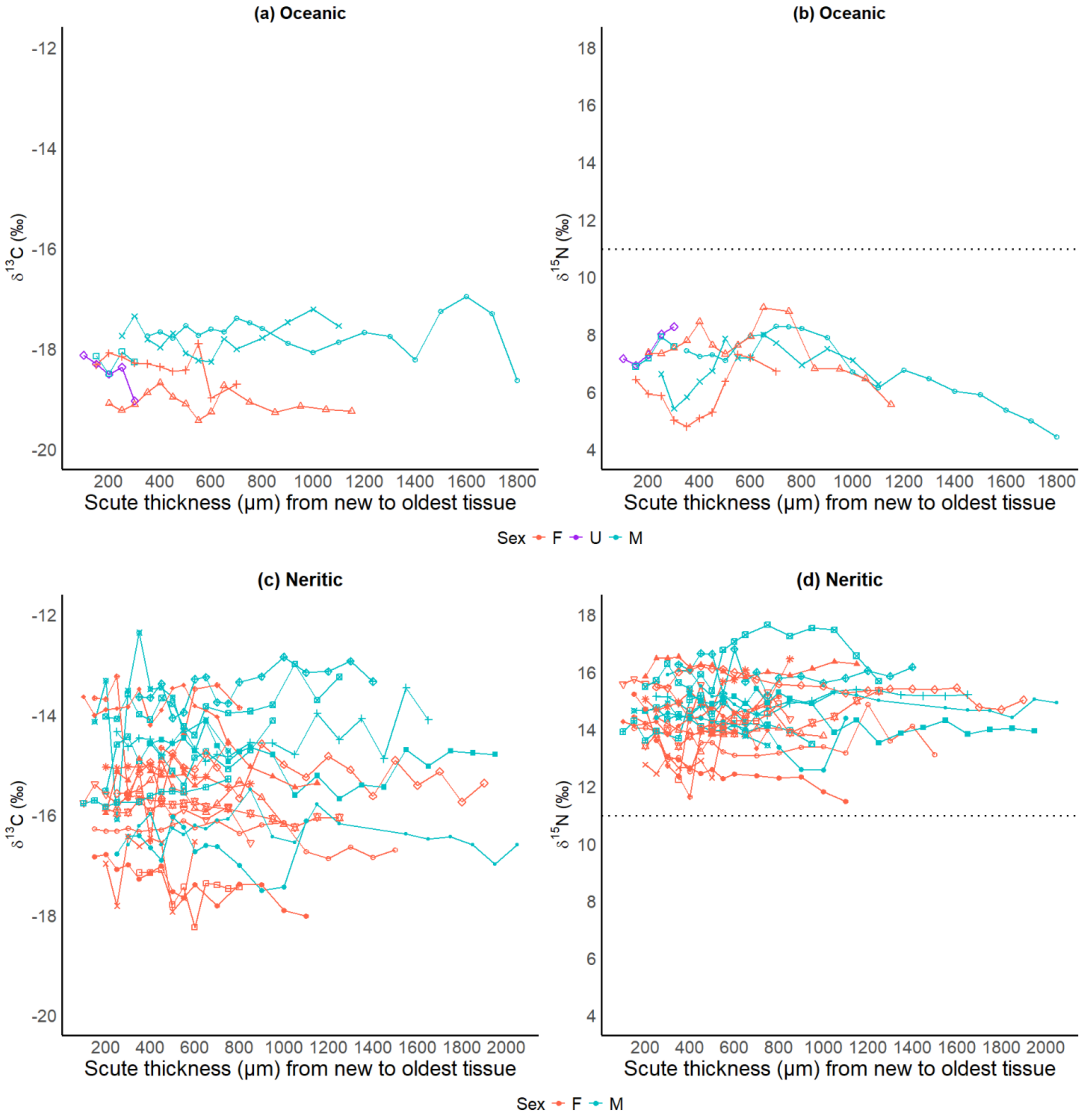
753 **Table 1**. Within Individual Component (WIC), Between Individual Component (BIC) and Total
754 Niche Width (TNW) for $\delta^{13}C$ and $\delta^{15}N$ of scute layers of loggerhead turtles (*Caretta caretta*) from
755 the Southwestern Atlantic Ocean (SWAO).

Group	*N*	$\delta^{13}C$				$\delta^{15}N$			
		WIC	BIC	TNW	WIC/TNW	WIC	BIC	TNW	WIC/TNW
Oceanic	6	0.09	4.04	4.13	**0.02**	0.83	3.37	4.2	**0.20**
Neritic females	12	0.17	16.18	16.35	**0.01**	0.38	15.53	15.91	**0.02**
Neritic males	9	0.19	19.88	20.06	**0.01**	0.30	10.43	10.73	**0.03**

FIGURE CAPTIONS

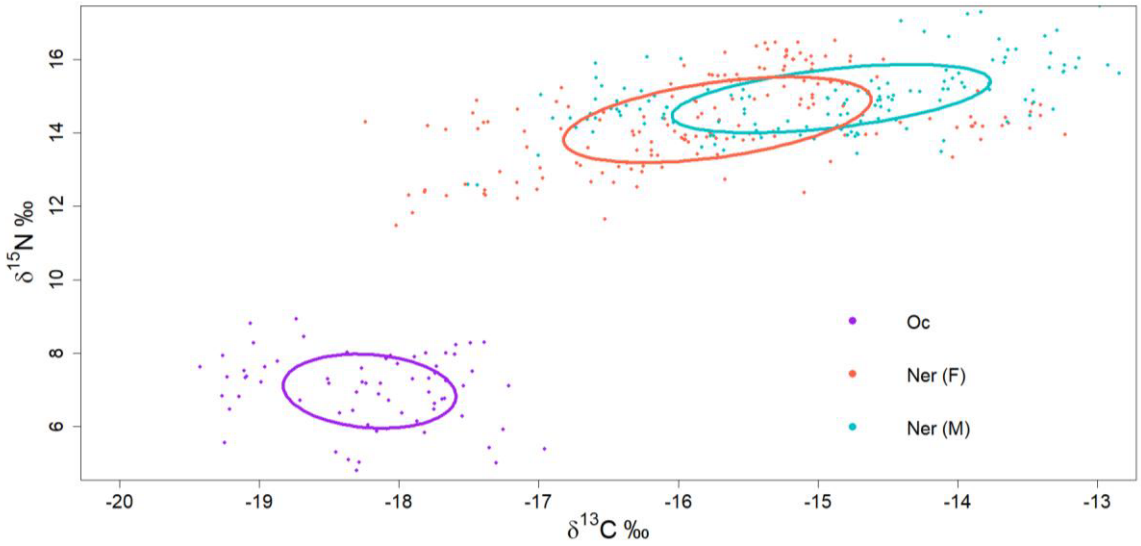
Figure 1. Variation in $\delta^{13}C$ (left column) and $\delta^{15}N$ (right column) values across successive 50 µm subsections of the carapace scutes of loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO) in **(a)**, **(b)** oceanic loggerhead turtles, **(c)**, **(d)** neritic loggerhead turtles. Colors represent sex: females (orange), males (cyan), and undetermined (purple).

Figure 2. Ellipses representing the isotopic niches (SEAc) of loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO) at different groups. Oc: oceanic (purple); Ner (F): neritic female (orange); Ner (M): neritic male (cyan).



766

767 **Figure 1.**



768

769 **Figure 2.**

SUPPLEMENTARY MATERIAL

Individual specialization and temporal consistency in resource use by Loggerhead turtle in successive life stages in the Southwestern Atlantic Ocean

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Table S1. Summary table with information of 27 loggerhead turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean (SWAO) between 2014 and 2024. Dates given as yyyy/mm/dd. CCL: curved carapace length. Sex: F = female, M = male, U = unknown. Life stage: Juv = juvenile, Ad = adult.

Turtle ID	Country	Date	CCL (cm)	Sex	Life stage	Habitat	Layers	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		Source
								first layer	last layer	first layer	last layer	
CCHHB	Brazil	2014/02/05	114	M	Ad	Neritic	25	-14.04	-13.24	15.49	15.68	Beach
CCKK	Brazil	2014/02/21	88	F	Ad	Neritic	16	-13.66	-13.85	14.42	15.15	Trawl
CCAA	Brazil	2014/03/06	24	M	Juv	Oceanic	6	-18.15	-18.26	6.87	7.58	Beach
CCJUY	Uruguay	2015/03/29	99.6	M	Ad	Neritic	28	-13.64	-13.33	16.26	16.17	Beach
CCP	Brazil	2015/04/07	107.5	M	Ad	Neritic	19	-15.52	-14.12	14.65	13.49	Beach
CCBUY	Uruguay	2016/01/04	70.4	F	Juv	Neritic	20	-15.57	-16.19	14.19	13.75	Beach
CCHUY	Uruguay	2016/02/04	93.2	F	Ad	Neritic	17	-15.04	-15.38	15.05	16.46	Beach
CCQQ	Brazil	2016/12/28	105	M	Ad	Neritic	39	-14.56	-14.79	15.22	13.94	Beach
CCFUY	Uruguay	2017/01/20	95	F	Ad	Neritic	17	-15.75	-16.56	15.58	14.35	Beach
CCAUY	Uruguay	2017/03/11	93.6	F	Ad	Neritic	30	-16.28	-16.70	14.03	13.11	Beach
CCKUY	Uruguay	2017/03/11	105	F	Ad	Neritic	25	-15.86	-16.05	13.42	15.34	Beach
CCCCUY	Uruguay	2017/12/20	71.9	F	Juv	Neritic	12	-16.97	-16.53	12.77	14.56	Beach
CCCAUY	Uruguay	2018/01/21	92.7	M	Ad	Neritic	33	-14.49	-14.10	14.60	15.20	Beach
CCXUY	Uruguay	2019/01/16	75.2	F	Juv	Neritic	22	-16.83	-18.02	15.23	11.47	Beach
CCNA	Brazil	2019/03/07	91.5	M	Ad	Neritic	15	-15.77	-15.28	13.91	14.11	Beach
CCYA	Brazil	2019/03/21	51.5	M	Juv	Oceanic	22	-17.74	-17.55	6.62	6.27	Longline
CCTUYA	Uruguay	2019/06/04	103	F	Ad	Neritic	23	-15.96	-15.36	15.84	16.28	Beach
CCEEUY	Uruguay	2020/01/17	78	F	Juv	Neritic	38	-15.57	-15.36	15.48	15.03	Beach
CCSUYA	Uruguay	2021/03/04	73.4	M	Juv	Neritic	22	-16.77	-16.11	14.40	14.40	Beach
CCZ	Brazil	2021/06/16	29	U	Juv	Oceanic	6	-18.13	-19.04	7.16	8.26	Beach
CCDD	Brazil	2021/06/18	52	M	Juv	Oceanic	36	-17.74	-18.62	7.44	4.43	Longline
CCR	Brazil	2021/06/21	66.5	F	Juv	Oceanic	23	-19.09	-19.25	7.36	5.55	Beach
CCT	Brazil	2021/06/25	65	F	Juv	Oceanic	14	-18.33	-18.71	6.42	6.71	Longline
CCX	Brazil	2022/04/07	102	F	Ad	Neritic	15	-13.64	-14.58	14.27	13.97	Beach

CCO	Brazil	2023/01/17	89	M	Ad	Neritic	15	-14.14	-14.72	14.65	13.44	Beach
CCZUY	Uruguay	2024/02/19	82.1	M	Juv	Neritic	41	-16.59	-16.59	15.90	14.92	Beach
CCAAUY	Uruguay	2024/03/14	62.4	F	Juv	Neritic	16	-17.15	-17.44	12.22	14.89	Beach

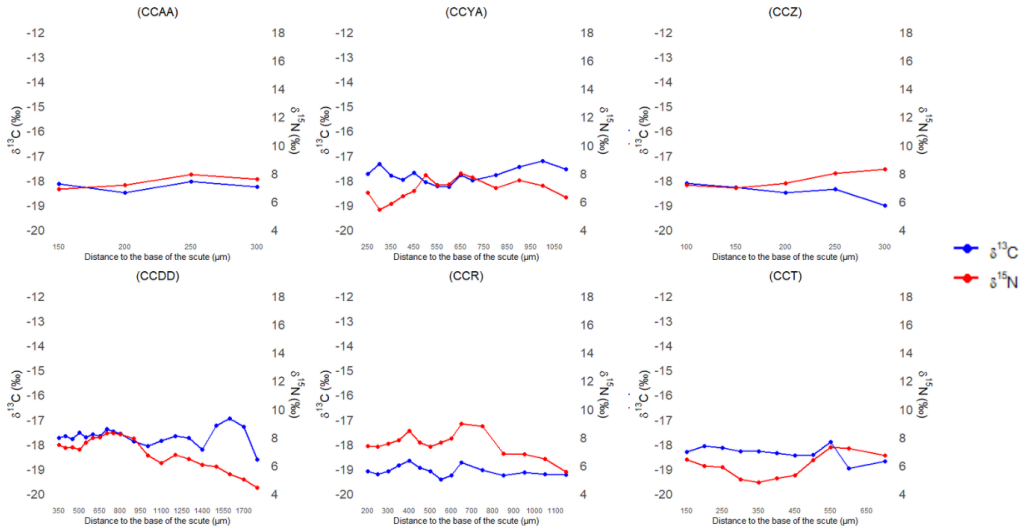


Figure S1. Individual $\delta^{13}C$ (blue) and $\delta^{15}N$ (red) values of oceanic (n=6) loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). The x-axis represents the distance to the base of the scute (from new to oldest tissue, in µm).

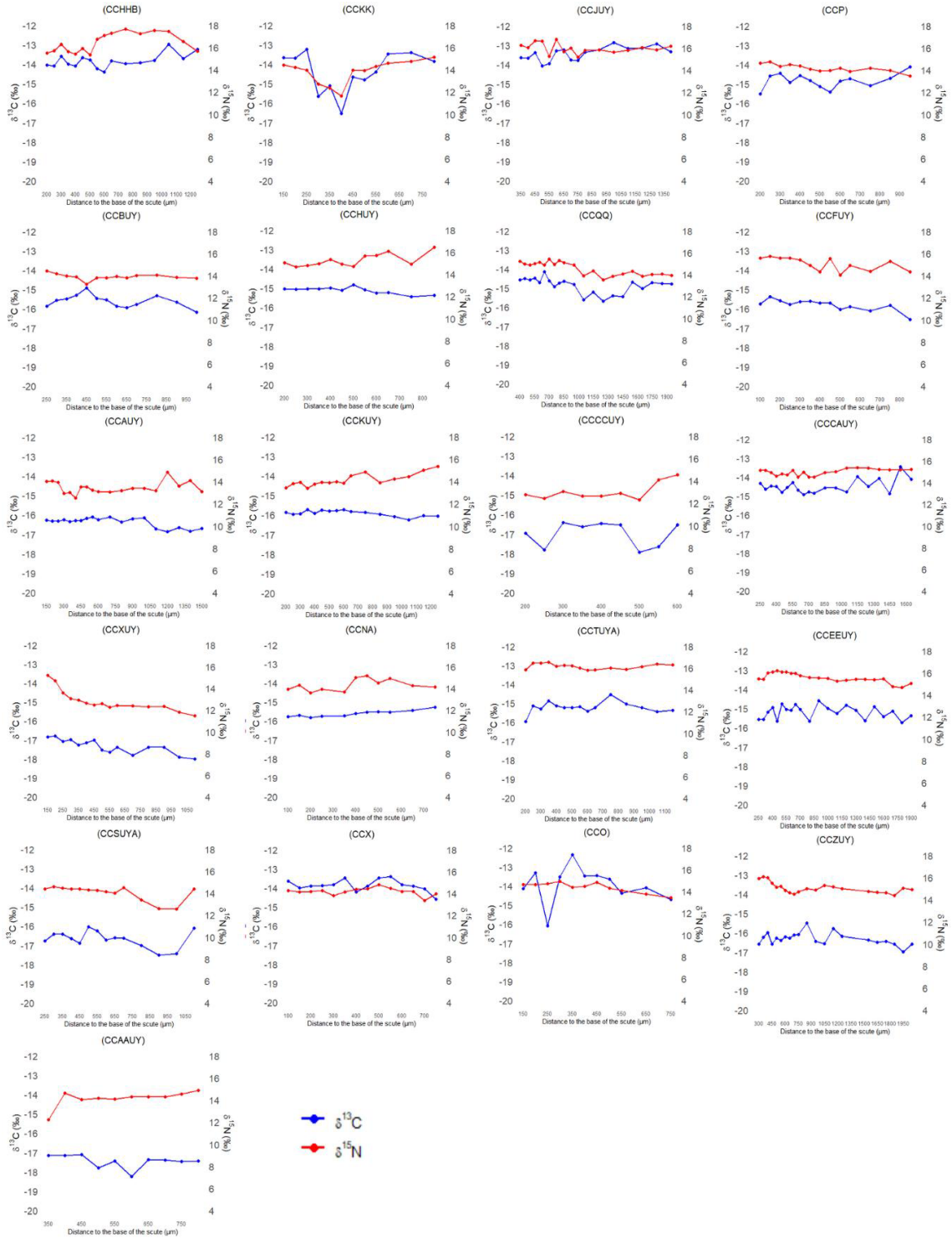


Figure S2. Individual $\delta^{13}C$ (blue) and $\delta^{15}N$ (red) values of neritic (n=21) loggerhead turtles (*Caretta caretta*) from the Southwestern Atlantic Ocean (SWAO). The x-axis represents the distance to the base of the scute (from new to oldest tissue, in µm).