

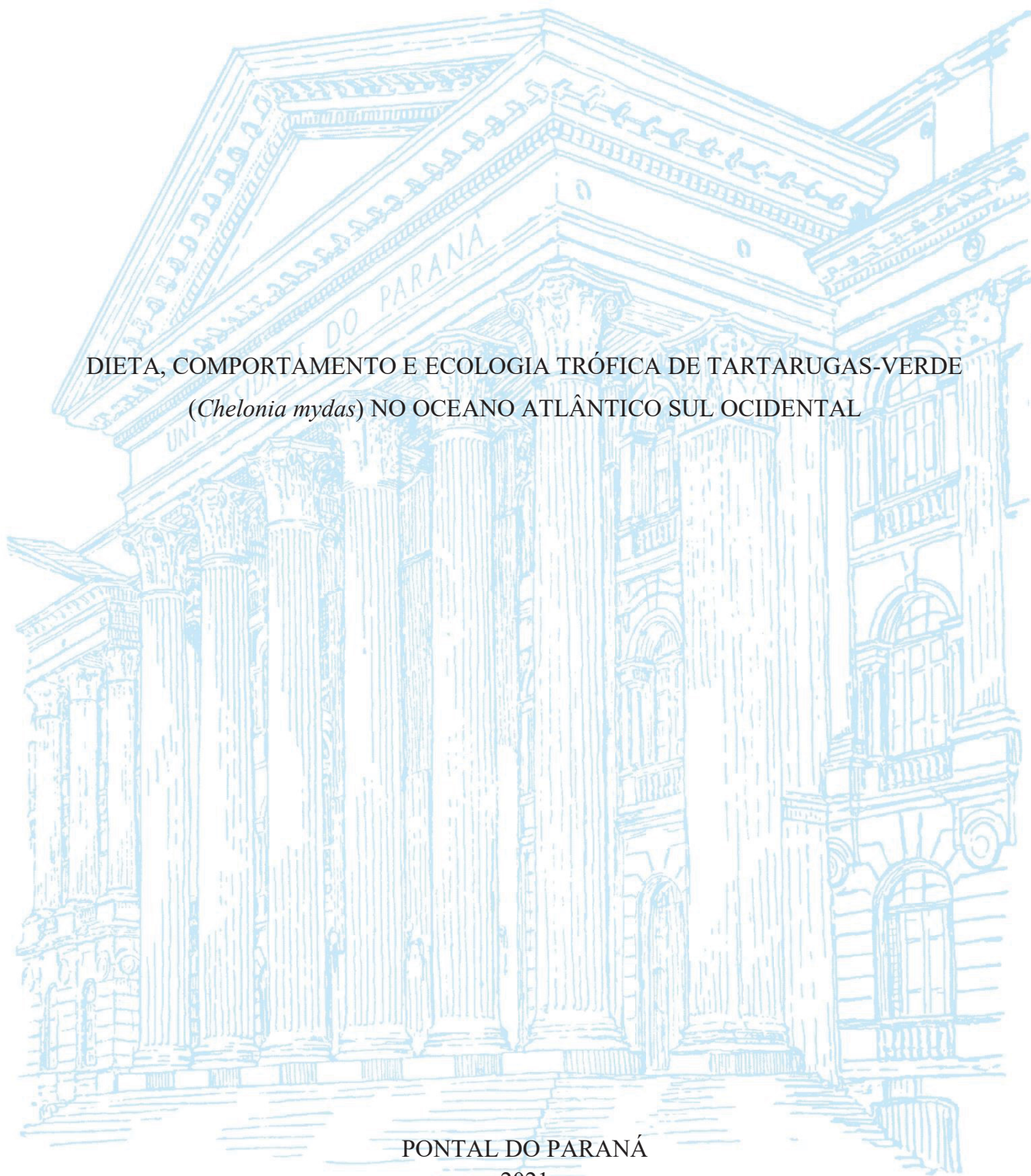
UNIVERSIDADE FEDERAL DO PARANÁ

LUCIANA ROLINSKI GAMA

DIETA, COMPORTAMENTO E ECOLOGIA TRÓFICA DE TARTARUGAS-VERDE
(*Chelonia mydas*) NO OCEANO ATLÂNTICO SUL OCIDENTAL

PONTAL DO PARANÁ

2021



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DIETA, COMPORTAMENTO E ECOLOGIA TRÓFICA DE TARTARUGAS-VERDE
(*Chelonia mydas*) NO OCEANO ATLÂNTICO SUL OCIDENTAL

Tese apresentada como requisito parcial à obtenção do grau de Doutora, Programa de Pós-graduação em Sistemas Costeiros e Oceânicos, Centro de Estudos do Mar, Setor de Ciências da Terra, Universidade Federal do Paraná.

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“I also could not fathom a world without them. These are fascinating creatures, and I am wagering that the more you know about them, the more you will want to make sure that they are here for generations of us yet unborn.”

RESUMO

A tartaruga-verde (*Chelonia mydas*) é uma das espécies mais frequentes de tartaruga marinha no Oceano Atlântico Sul Ocidental (ASO), área esta que compreende as costas do Brasil, Argentina e Uruguai. No sul do Brasil, o litoral do Paraná é um importante corredor migratório para as tartarugas-verde, além de ser habitat de forrageamento e desenvolvimento para os juvenis da espécie. A cada ano mais de 1000 indivíduos são encontrados encalhados mortos nesta área devido a diversos fatores como mortalidade natural e interações diretas e indiretas com atividades antrópicas negativas. Este alto número de encalhes permite o estudo da ecologia trófica da espécie, a qual tem sido realizada no Paraná desde 2004. Duas metodologias de análise da dieta foram realizadas, incluindo a análise do trato digestório de espécimes mortos e a análise de isótopos estáveis. Ambas podem auxiliar na compreensão da ecologia trófica e da dinâmica do habitat ao longo do tempo. Esta informação é crítica para identificar áreas prioritárias para conservação e planos de manejo. Por meio da análise de tratos digestórios de tartarugas-verde juvenis encontradas encalhadas mortas ao longo de 12 anos e da análise de isótopos estáveis da epiderme de indivíduos capturados vivos e dos espécimes mortos, esta tese é formada por dois capítulos com os objetivos de: 1) identificar o habitat de forrageamento das tartarugas-verde juvenis que utilizam o litoral do Paraná; 2) avaliar a variação da dieta entre os anos e como ela se relaciona com a disponibilidade de alimento; 3) caracterizar a dieta da agregação de tartarugas-verde que forrageia no litoral paranaense e investigar as variações intra anuais da dieta. Como resultados, encontrou-se diferentes tamanhos de nichos tróficos para as tartarugas-verde que utilizam a área, bem como diferentes contribuições dos itens alimentares para a dieta, com indivíduos maiores sendo onívoros. As fanerógamas marinhas e propágulos de mangue (Magnoliophyta), macroalgas vermelhas (Rhodophyta) e Mollusca foram os itens mais consumidos, totalizando 49 diferentes espécies de macroalgas, 1 espécie de cianobactéria, além de 5 filos de invertebrados, compreendendo, entre outros, 36 espécies de Mollusca. Houve variação interanual e intra-anual dos itens alimentares consumidos, bem como maior diversidade de macroalgas consumidas durante as estações de outono e de inverno, e alta frequência de ocorrência de lixo marinho nos tratos digestórios analisados, o qual esteve presente ao longo de todas as estações de todos os anos, com destaque durante os eventos de La Niña. Juntos, estes dados podem auxiliar na compreensão de lacunas existentes na ecologia trófica da espécie no ASO, contribuindo para a conservação da mesma e de seu habitat.

Palavras-chave: *Chelonia mydas*, forrageamento, diversidade ecológica, plasticidade alimentar

ABSTRACT

The green turtle (*Chelonia mydas*) is one of the most common species of sea turtle in the Southwestern Atlantic Ocean (SWAO), an area which includes coastal Brazil, Argentina, and Uruguay. In south Brazil, the Paraná coast is an important migratory corridor for green turtles and provides foraging and development habitat for juvenile green turtles. Every year more than 1000 individuals are found dead-stranded in this area because of several factors such as natural mortality and direct and indirect interactions with anthropogenic activities. This high number of strandings allows opportunities to study green turtle trophic ecology, which have been conducted in Paraná since 2004. Two established methodologies used to investigate trophic ecology include digestive tract analysis and stable isotope analysis. Both can generate insights into green turtle foraging and critical habitat dynamics over time. This information is critical to identifying conservation priorities areas and informing management plans. Using digestive tract analysis of dead-stranded juvenile green turtles that spanned many years and stable isotope analysis of live-captured and dead-stranded sea turtle tissue, this thesis is comprised of two chapters and aims to: 1) identify critical habitat for green turtles off the Paraná coast; 2) evaluate variation of diet within years and how it relates to the food resources availability and 3) characterize the diet of the foraging aggregation of green turtles and investigate interannual variations in diet. This study found that green turtles off the Paraná coast present different trophic niche widths and diet items contributions, with larger individual being omnivorous. The seagrass and the mangrove (Magnoliophyta), red macroalgae (Rhodophyta) and Mollusca were the most consumed items, comprising 49 different species of macroalgae, one species of cyanobacteria, besides 5 invertebrate phyla, which were composed by 36 species of Mollusca, among others. There was interannual and intra-annual variations of the consumed items, as well as higher macroalgae diversity during autumn and winter seasons, and high frequency of occurrence of marine debris, which was found along every season of all the sampling years, highlighting the La Niña event years. Together, results from this thesis will help fill ecological knowledge gaps for foraging juvenile green turtles and their habitat off the Paraná coast, informing continuing conservation priorities for this species in the SWAO.

Key words: *Chelonia mydas*, foraging, ecological diversity, foraging plasticity

PREFÁCIO

Este trabalho foi dividido em capítulos, conforme as hipóteses testadas e temática foco, no entanto, considerando a contribuição coletiva, apresentamos uma integração desta estrutura, incluindo uma introdução geral, objetivo geral do trabalho e os específicos de cada capítulo, e metodologia geral, a qual foi escrita em subtópicos referentes aos capítulos apresentados. Na sequência apresentamos os dois capítulos, cada um deles estruturado em formato de artigos científicos, elaborados seguindo as normas das respectivas revistas científicas. A última parte desta tese traz as considerações finais, compilando os principais resultados encontrados de forma a destacar a contribuição científica deste estudo.

O primeiro capítulo, '*Trophic ecology of juvenile green turtles in the Southwestern Atlantic Ocean: insights from stable isotope analysis and niche modelling*', teve como objetivo analisar a composição isotópica dos tecidos das tartarugas-verde que utilizam o litoral paranaense para se alimentar. Como resultados, verificou-se que indivíduos maiores apresentam uma dieta onívora, ao contrário do registrado para os juvenis de mesmo tamanho que forrageiam no Oceano Atlântico Sul Ocidental, e que a população é composta tanto por indivíduos residentes quanto por recém recrutados da zona oceânica, sendo possível melhor compreender a diversidade de relações ecológicas entre os juvenis que transitam e se alimentam na região do ASO, assim como avançar no entendimento da região do Paraná como uma importante área de agregação da espécie ao longo de seus deslocamentos quando juvenis. Este capítulo está publicado no periódico *Marine Ecology Progress Series*, (ISSN: 0171-8630; IF = 2.32, Qualis A1 biodiversidade) que aborda pesquisas relacionadas à ecologia no ambiente marinho.

O segundo capítulo, '*Long-term dietary shifts of immature green turtles *Chelonia mydas* in the Southwestern Atlantic Ocean*', apresenta dados da variação sazonal na dieta de *C. mydas* ao longo de 12 anos, destacando a influência dos eventos climáticos de El Niño e de La Niña e outros fatores ambientais de escala regional. Neste capítulo é apresentada a identificação em nível específico das macroalgas, em caráter inédito, e dos invertebrados (no menor nível taxonômico possível) consumidos pela tartaruga-verde, permitindo um refinamento das relações tróficas e trazendo base para avaliações de alterações na dieta ao longo do tempo. Verificou-se que angiospermas (Magnoliophyta), incluindo a grama marinha e o propágulo de mangue; as algas vermelhas (Rhodophyta); e moluscos foram os itens mais frequentemente consumidos. Houve variação interanual da dieta, além de variação dos itens consumidos relacionada aos eventos climáticos avaliados. Considerando a ingestão de itens que causam

impactos à saúde dos juvenis de *C. mydas*, houve maior consumo de lixo marinho durante a La Niña. Quanto à sazonalidade em escala regional, durante o outono (meses de abril, maio e junho) e inverno (meses de julho, agosto e setembro), houve maior riqueza de itens consumidos, bem como variação no consumo de invertebrados. Ao longo dos anos as principais variações foram entre os períodos de 2008, 2011, e de 2015 a 2020. Este capítulo será submetido ao periódico *Marine Biology* (0025-3162; IF = 2.57, Qualis A1 biodiversidade), a qual aborda estudos relacionados à ecologia de espécies ameaçadas.

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1. INTRODUÇÃO GERAL

Estudos de dieta de espécies marinhas ameaçadas, como é o caso de *Chelonia mydas* Linnaeus 1758, são importantes para determinar as áreas de alimentação e principais recursos utilizadas pelas mesmas, além de possibilitar uma maior compreensão das relações ecológicas da espécie (James et al. 2005; Nagaoka et al. 2012). Alguns indivíduos apresentam comportamento alimentar generalista, consumindo uma maior diversidade de itens alimentares; enquanto os de comportamento especialista apresentam uma dieta mais restrita, especializada em determinados itens, consumindo-os de acordo com a preferência e disponibilidade no habitat (Bernays & Funk 1999; Petrov et al. 2020). A teoria do “forrageamento ótimo”, proposta por MacArthur & Pianka (1996), explica que, em geral, o forrageamento realizado pelos animais é uma consequência da estratégia com menor gasto energético para esta atividade. A dieta é, portanto, um fator chave para a sobrevivência da espécie, bem como está intimamente relacionada com a taxa de crescimento, com o sucesso reprodutivo e a condição de saúde e resiliência dos organismos (Bjorndal 1980; Brown et al. 1994; Birnie-Gauvin et al., 2017).

A tartaruga-verde (*C. mydas*) é uma espécie mundialmente ameaçada (IUCN 2020 - *International Union for Conservation of Nature and Natural Resources*), sobre a qual diversos impactos antrópicos incidem, tais como a poluição e consumo de lixo marinho, captura acidental, contaminação (Bugoni et al. 2003; Wallace et al. 2010; Schuyler et al. 2012; Wildermann et al., 2018; Domiciano et al. 2019). A dieta e as relações ecológicas da espécie vêm sendo amplamente estudadas, mas diversos desafios ainda precisam ser alcançados. A espécie é a única tartaruga marinha primariamente herbívora (Bjorndal & Bolten 1988), mas com amplas variações regionais quanto ao potencial de onivoria dos juvenis (Esteban et al. 2020). *C. mydas* ocorre com frequência na região costeira do Oceano Atlântico Sul Ocidental (ASO), utilizando a região para alimentação, recrutamento e desenvolvimento (González Carman et al. 2011; Marcovaldi & Santos 2011; Andrade et al. 2016; Gama et al. 2016; Coelho et al. 2018; Vélez-Rubio et al. 2018).

Durante o desenvolvimento ontogenético, os juvenis de *C. mydas* são recrutados da zona oceânica para a costeira, e em algumas regiões alteram a dieta de filhotes do padrão onívoro para o herbívoro durante a juventude e vida adulta. No entanto, este processo pode variar entre indivíduos de mesma classe de tamanho e idade, e entre áreas geográficas (Lutz et al. 1996; Cardona et al. 2009; González Carman et al. 2012; Andrade et al. 2016; Gama et al. 2016; Vélez-Rubio et al. 2016; Turner Tomaszewicz et al. 2018; Esteban et al. 2020). Em zonas

temperadas e subtropicais do ASO, após o recrutamento costeiro, juvenis de *C. mydas* ainda deslocam entre áreas oceânicas e costeiras para se alimentar (González Carman et al. 2012), o que possivelmente resulta em uma dieta mais diversificada (Reisser et al. 2013; González Carman et al. 2014; Vélez-Rubio et al. 2018).

Além disso, a temperatura da superfície da água do mar (SST) também é um fator que influencia na composição da dieta, como observado por Esteban et al. (2020). Em regiões de alta latitude, mais frias, o consumo de itens de origem animal é maior quando comparado a regiões mais quentes, onde a predominância é da herbivoria. Em uma mesma área de alimentação no ASO, fatores intrínsecos (ex. idade e origem genética) e extrínsecos (disponibilidade de alimento, variação ambiental temporal e espacial) interagem e atuam na variação comportamental, uso de área e dinâmica alimentar dos juvenis (Santos et al. 2015; Andrade et al. 2016; Gama et al. 2016; Vélez-Rubio et al. 2016; Coelho et al. 2018; Vélez-Rubio et al. 2018).

Estudos relacionados ao comportamento alimentar de *C. mydas* foram realizados no ASO utilizando metodologias distintas: i. telemetria (González Carman et al. 2012; Vélez-Rubio et al. 2018); ii. análise do trato digestório de espécimes mortos (Bugoni et al. 2003; Guebert-Bartholo et al. 2011; Marcovaldi & Santos 2011; Nagaoka et al. 2012; Awabdi et al. 2013; Santos et al. 2015; Gama et al. 2016; Vélez-Rubio et al. 2016); e iii. análise de isótopos estáveis (González Carman et al. 2014; Bezerra et al. 2015; Vélez-Rubio et al. 2016; Di Benedetto et al. 2017; Vélez-Rubio et al. 2018; Campos & Cardona 2019).

Especificamente sobre as técnicas utilizadas neste estudo (ii e iii), a análise dos tratos digestórios possibilita a identificação e mensuração dos itens recém consumidos, bem como a inferência sobre a possível área de alimentação dos espécimes, quando é conhecida a diversidade e a riqueza de organismos consumidos e das distintas localidades ao longo da distribuição. Por sua vez, a técnica de isótopos estáveis (IE) de carbono (C) e nitrogênio (N), associada às análises de dieta, permite avaliar os itens consumidos a longo prazo (entre meses e anos, dependendo da matriz analisada, pois provê informações quanto à posição ocupada pelos animais na teia trófica, em um gradiente latitudinal (delta de isótopos de nitrogênio, $\delta^{15}\text{N}$), e quanto ao habitat costeiro e/ou oceânico de forrageio (delta de isótopos de carbono, $\delta^{13}\text{C}$) (Seminoff et al. 2006; Reich et al. 2007; Bisi et al. 2013; Vélez-Rubio et al. 2018).

Adicionalmente, a análise comparativa entre a composição isotópica de animais de uma mesma área encontrados encalhados mortos, e de animais capturados vivos, permite uma maior compreensão quanto à diversidade ecológica entre ambos os grupos, bem como dentro de cada grupo de indivíduos, uma vez que diferenças na dieta, fase ontogenética e nos padrões de

migração podem ser observadas (Newsome et al. 2010; Vélez-Rubio et al. 2013; 2018; Turner Tomaszewicz et al. 2018). Resultados de estudos sobre a dieta de *C. mydas* utilizando isótopos estáveis já realizados no ASO indicaram predominância tanto de itens de origem animal (González Carman et al. 2014), como de macroalgas (Di Benedetto et al. 2017); além do aumento na frequência de consumo de macroalgas por tartarugas-verde com maiores comprimento curvilíneo de carapaça (Vélez-Rubio et al. 2016). A diversidade encontrada evidencia uma variação individual, regional, ou mesmo sazonal na dieta de *C. mydas* na região do ASO, influenciada pelas mudanças climáticas e suscetível a mudanças futuras.

Ao longo do ASO e especificamente no litoral sul e sudeste brasileiro, estoques genéticos mistos (originários de diferentes sítios reprodutivos) de juvenis de *C. mydas* se agregam para alimentação e utilizam a plataforma continental como corredor migratório, movimentando-se entre diferentes áreas de alimentação, incluindo a zona costeira e áreas oceânicas (González Carman et al. 2012; Jordão et al. 2015; Vélez-Rubio et al. 2018; Fuentes et al. 2020). Dados de monitoramento por satélite sugerem variação no comportamento migratório e no tempo de residência das tartarugas-verde em diferentes áreas, relacionada principalmente à influência das condições ambientais em regiões temperadas, as quais induzem a migração dos animais quando sob temperaturas mais baixas (González Carman et al. 2012; Godley et al. 2003; Vélez-Rubio et al. 2018). Entretanto, as áreas costeiras compreendem regiões onde diversos tipos e intensidades de atividades antrópicas impactantes podem ameaçar a espécie (IUCN, 2020; Fuentes et al., 2020).

Na região sul do Brasil, o litoral do Paraná, apesar de seus reduzidos ~90 km de costa, é parte da zona climática subtropical e do corredor migratório das cinco espécies de tartarugas marinhas que ocorrem no Brasil (Marcovaldi & Santos 2011). Esta é uma importante área de forrageio e desenvolvimento para *C. mydas* juvenis, devido às pradarias de fanerógamas marinhas, densos manguezais, costões rochosos repletos de macroalgas e diversos invertebrados, baías permeadas por substratos consolidados naturais e artificiais, assim como de ilhas costeiras (Guebert-Bartholo et al. 2011; Pellizzari et al. 2014; Andrade et al. 2016; Gama et al. 2016). No entanto, há diversas atividades humanas que causam impactos negativos aos animais, tais como a urbanização desordenada, atividades pesqueiras responsáveis pelas capturas acidentais, a poluição e a degradação do habitat (Domiciano et al. 2019).

Para a proteção da espécie, desde 2011 foi estabelecido um plano de ação nacional para conservação das tartarugas marinhas, o qual é uma importante política pública e instrumento de gestão (Plano de Ação Nacional para Conservação das Tartarugas Marinhas). Além deste, outros processos legais de conservação atuam como ferramentas de conservação para a espécie,

no entanto, o registro de indivíduos mortos ao ano ultrapassa 1000 espécimes no Paraná e mais de 10000 para o sudeste e sul do Brasil (Cantor et al. 2020). Nesta região, entre os animais encalhados há predominância de indivíduos entre dois e 16 anos de idade, ou seja, incluindo os recém-recrutados de zona oceânica e os em deslocamento entre áreas de alimentação costeiras adjacentes (Andrade et al. 2016; dados PMP-BS¹). Os indivíduos são geralmente originários de sítios reprodutivos do Atlântico e Caribe, tais como Ilha de Ascensão, República Africana de Guiné-Bissau, e Ilha das Aves, ao norte da Venezuela (Jordão et al. 2015; Coelho et al. 2018; Savada et al. 2021).

Desta forma, delimitar as variações existentes na dieta da espécie é importante para a compreensão do comportamento alimentar das tartarugas-verde juvenis no ASO e sua capacidade adaptativa às alterações ambientais. Além disso, a partir de dados de diversidade de macroalgas no litoral do Paraná (Pellizzari et al. 2014), identificar as espécies consumidas pelas tartarugas-verde, sua distribuição no habitat e se o consumo é sazonal, traz uma contribuição essencial e inédita para melhor compreender o uso do espaço e habitat pela espécie, e os possíveis impactos aos animais e ecossistema associado.

Portanto, considerando os fatores de variações relatados na literatura, para a primeira parte deste estudo a análise da dieta é feita em razão do fator intrínseco tamanho corpóreo (CCC em cm). A partir da análise de isótopos estáveis de indivíduos mortos e vivos que utilizam o litoral do Paraná para alimentação, buscou-se inferir sobre a ecologia trófica de *C. mydas* no Atlântico Sul. Além disso, a abordagem permitiu avaliar a diversidade ecológica, em termos de comportamento alimentar, existente entre os espécimes, e verificar a tendência à herbivoria ao longo do desenvolvimento dos juvenis. Na segunda parte do estudo, a análise foi feita em razão dos fatores extrínsecos (anos, eventos climáticos e estações do ano). A análise da dieta em longo prazo (doze anos) visou evidenciar as flutuações temporal e o potencial efeito de eventos climáticos, e as mudanças na forma de utilização das áreas de alimentação, além da análise taxonômica específica de macroalgas e de invertebrados consumidos pelos indivíduos, possibilitando o rastreamento de habitats-chave para a conservação da espécie.

1.2. OBJETIVOS E HIPÓTESES

Este estudo visa explorar aspectos da ecologia trófica dos juvenis de tartaruga-verde em uma de suas áreas de alimentação no ASO - o litoral do Paraná -, a fim de compreender os

¹ <https://simba.petrobras.com.br/simba/web/>

fatores de influência locais e regionais que determinam as relações ecológicas da espécie, além de estabelecer uma linha de base para futuros estudos sobre avaliação dos efeitos da degradação dos habitats e mudanças climáticas na alimentação das tartarugas marinhas. Considerando os trabalhos com enfoque em análise da dieta e utilização de análise de isótopos estáveis realizados com *C. mydas* no Oceano Atlântico Sul Ocidental, as hipóteses testadas neste estudo foram:

- Há variação isotópica entre os indivíduos de acordo com seu tamanho, sendo que indivíduos maiores apresentam valores isotópicos correspondentes a uma dieta herbívora, enquanto os indivíduos menores, valores isotópicos correspondentes a uma dieta onívora (Capítulo 1);

- Há variação interanual na dieta de *C. mydas* influenciada pelas variações ambientais, com ênfase na variação climática (eventos de El Niño e La Niña); e há variações sazonais quando analisados itens alimentares em nível específico (Capítulo 2).

Sendo assim, os objetivos deste estudo foram:

1. Definir as razões de isótopos estáveis de Carbono ($\delta^{13}\text{C}$) e de Nitrogênio ($\delta^{15}\text{N}$) para os juvenis de *C. mydas* encontrados encalhados mortos, ou intencionalmente capturados-marcados-soltos vivos na costa do Paraná, além de definir o tamanho do nicho trófico e identificar os itens alimentares de maior contribuição na dieta da espécie (Capítulo 1);
2. Caracterizar a dieta dos juvenis de *C. mydas* ao longo de 12 anos de estudos no litoral do Paraná e investigar a variação interanual na dieta de *C. mydas* que se agregam no litoral do Paraná, além de avaliar a variação sazonal da composição e riqueza de espécies de macroalgas, e de espécies de invertebrados consumidos pelos indivíduos, com ênfase nas variações climáticas extremas, nas áreas de alimentação (Capítulo 2).

2. MATERIAL E MÉTODOS GERAIS

2.1. ÁREA DE ESTUDO

O litoral do Paraná, apesar de apresentar apenas ~90 km de linha de costa, é composto por várias baías e estuários que representam, no total, mais de 1000 km de extensão (Lana et al. 2001) (Fig. 1). Situado na zona climática subtropical, tem influência de correntes de águas frias do sul (ex. Malvinas) e quentes do norte (ex. Corrente do Brasil) (Noernberg & Alberti 2014),

além de uma diversidade de habitats como costões rochosos costeiros, planícies de maré com gramíneas marinhas, manguezais e ilhas (Lana et al. 2001), os quais provêm recurso alimentar animal e vegetal, tornando esta área importante para alimentação e desenvolvimento dos espécimes de *C. mydas* (Guebert-Bartholo et al. 2011; Gama et al. 2016).

2.2. COLETA DE EXEMPLARES ENCALHADOS MORTOS DE *C. mydas*

As coletas dos juvenis de *C. mydas* encalhados mortos foram realizadas no Complexo Estuarino de Paranaguá (CEP) e na área costeira do estado do Paraná (Fig. 1). Todos os espécimes foram classificados quanto ao estágio de decomposição da carcaça e tiveram sua biometria mensurada (cm). Apenas carcaças nos estágios iniciais de decomposição (com perda parcial de tecidos; carapaça, plastrão e nadadeiras íntegras; inchaço ausente a moderado; órgãos intactos) foram consideradas para avaliação. A escolha de coleta dos espécimes do Paraná se justifica pelo acesso às carcaças e a estudos anteriores que evidenciam a conexão desta região com áreas mais ao sul (ex. Uruguai, Vélez-Rubio et al. 2018) e ao norte (Fuentes et al. 2020).

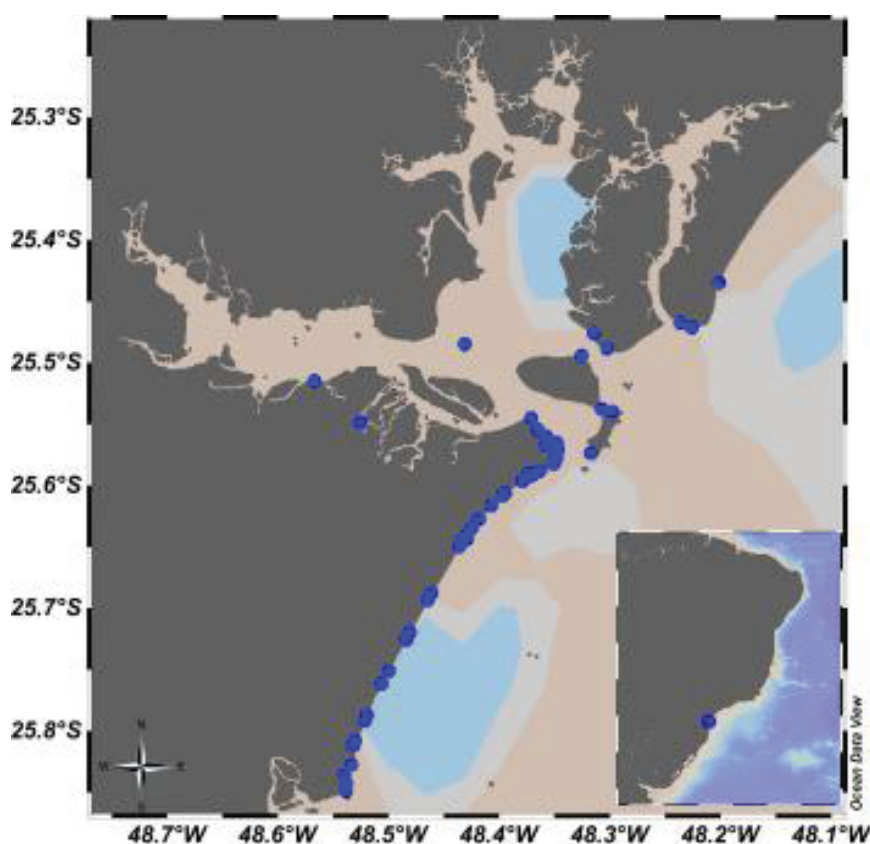


Figure 1. Mapa do litoral paranaense, com detalhe do Complexo Estuarino de Paranaguá (CEP), e dos locais onde foram realizadas as coletas dos espécimes de tartarugas-verde juvenis (pontos azuis).

As carcaças de *C. mydas* foram coletadas por meio de monitoramentos de praia diários, entre 2015 e 2020, pela equipe do Laboratório de Ecologia e Conservação do Centro de Estudos do Mar (LEC) (CEM/UFPR), via Projeto de Monitoramento de Praias da Bacia de Santos (PMP-BS). Os espécimes foram mensurados quanto ao comprimento curvilíneo de carapaça (CCC, cm) e submetidos à necropsia (*c.f.* Wyneken 2001), na qual os tratos digestórios foram coletados e congelados para posterior dissecação e análise da dieta. Para as análises de isótopos estáveis, tecidos epiteliais da região posterior da nuca foram coletados com bisturi estéril e armazenados congelados. A escolha dos tecidos epiteliais foi devido ao fato de serem metabolicamente menos ativos e refletirem a dieta a curto-médio prazo, além da viabilidade de coleta tanto nos espécimes vivos quanto nos mortos. Para determinação sexual, foi utilizada a metodologia de histologia gonadal (Duarte et al. 2011), a partir de dados obtidos pelo PMP-BS.

2.3. COLETA DE EXEMPLARES VIVOS DE *C. mydas*

As capturas intencionais de tartarugas-verde juvenis foram realizadas no litoral do Paraná, com o objetivo de marcação e soltura dos animais. A captura foi realizada por meio de uma rede de emalhe modificada de 50 metros de comprimento, com 3 metros de altura e 30 cm de malha entrenós, nos meses de maio, junho, setembro e outubro de 2016; fevereiro e março de 2017; março e junho de 2018, totalizando 58 dias de esforço de capturas. Durante as capturas, a rede foi checada continuamente e as tartarugas emalhadas foram removidas rapidamente e levadas à embarcação de pesquisa para biometria (comprimento curvilíneo de carapaça; CCC) e estimativa de massa corporal (em kg), assim como para a coleta de amostras. Todas as tartarugas vivas foram anilhadas e soltas na área dentro do prazo máximo de duas horas após a captura. Alguns animais foram marcados para rastreamento via satélite e, com base nestes, não foram observadas alterações comportamentais após a soltura dos indivíduos.

2.4. COLETAS DE MACROALGAS EM ÁREAS DE ALIMENTAÇÃO

A coleta de macroalgas foi realizada nos litorais do Paraná, Santa Catarina e São Paulo, totalizando uma extensão de 1511.4 km. Estas áreas foram selecionadas com base em estudos prévios de telemetria realizados no ASO (González Carman et al. 2012; Vélez-Rubio et al. 2018), nos quais foi verificado que os espécimes marcados com transmissores por satélite (TAGs) migraram ao longo da costa brasileira (desde a costa do Uruguai até o Estado do Paraná,

assim como do Paraná até a Bahia – Fuentes et al. 2020). As macroalgas foram coletadas nestas áreas visando verificar a conectividade entre elas no ASO com base nas assinaturas isotópicas das mesmas.

Especificamente, o litoral de Santa Catarina apresenta 561,4 km de extensão, situado na zona climática subtropical (Nimer 1979), limitando os litorais sudeste (ao norte) e sul (ao sul). Apresenta uma diversidade de habitats como as praias arenosas, pequenas baías e enseadas, costões rochosos, lagoas costeiras e os sambaquis (Horn Filho et al. 2017). Representa o maior polo pesqueiro do país, contendo alta diversidade de ambientes, como a presença de vários costões rochosos (Rodrigues et al. 2004), os quais servem de substrato para macroalgas e outros invertebrados.

O litoral de São Paulo apresenta aproximadamente 860 km de extensão, sendo o clima um dos mais diversificados do Brasil, considerado como de transição entre o subtropical e tropical (Nilmer 1979). Formado por uma linha de costa recortada por baías e enseadas, é dividido em litorais norte, central e sul, os quais contam com uma alta diversidade biológica (Braga et al. 2005; Souza & Luna 2008) e consequente presença e alta riqueza e biomassa de macroalgas em ilhas e costões rochosos (Junior et al. 1991; Tavares et al. 2013).

As coletas das macroalgas foram realizadas em seis áreas: 1. Ilha das Cabras (23°49'42''; 45°23'32'') e 2. Portinho (23°51'51''; 45°25'48''), em Ilha de São Sebastião, 3. Praia dos Sonhos (24°11'38''; 46°47'40'') e Cama de Anchieta (24°11'53''; 46°48'14''), em Itanhaém – todas no litoral de São Paulo; 4. Arquipélago de Currais (25°44'09''; 48°21'55''), no Paraná; e 5. Armação do Itapocaroí (26°46'01''; 48°38'25''), Santa Catarina (Fig. 2). Em todas as áreas há registro de *C. mydas*, bem como de macroalgas ingeridas por elas (Amado Filho et al. 2004; Gallo et al. 2006; Guebert-Bartholo et al. 2011; Reisser et al. 2013; Pellizzari et al. 2014; Bumbeer et al. 2016; Gama et al. 2016).

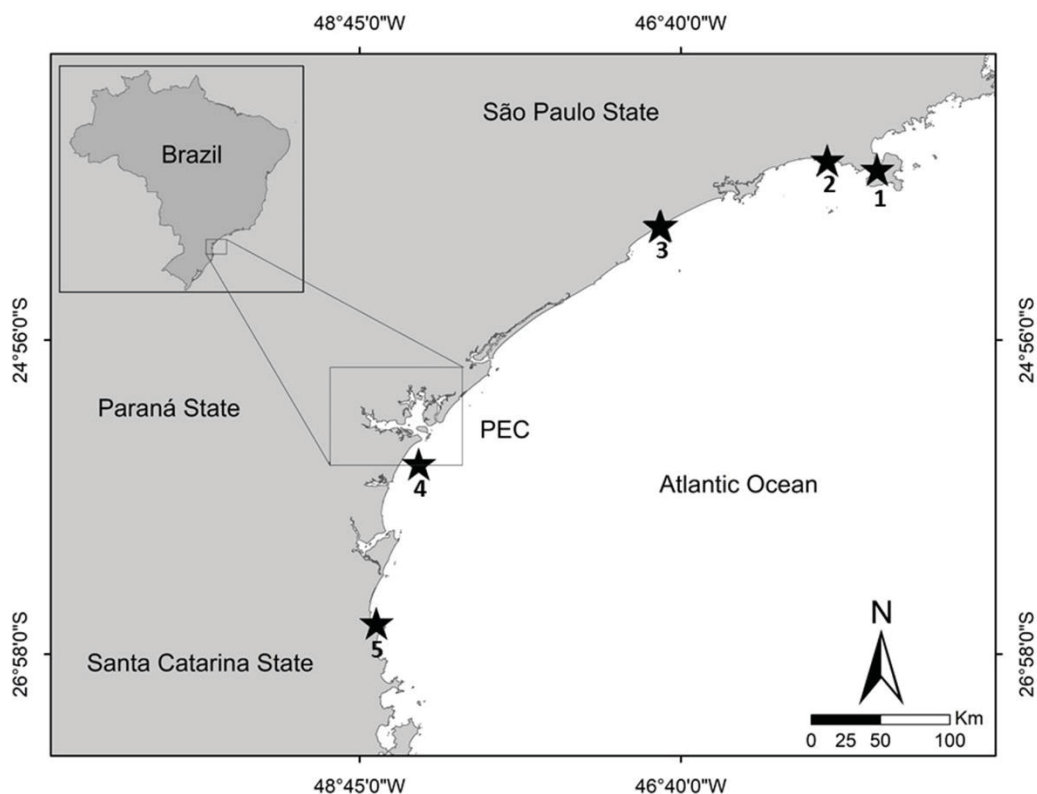


Figura 2: Mapa das áreas de coletas de macroalgas, incluindo (no sentido sul-norte): 1. Ilha das Cabras, em Ilha de São Sebastião; 2. Portinho; 3. Praia dos Sonhos e Cama de Anchietá, em Itanhaém, São Paulo; 4. Arquipélago de Currais, no Paraná; e 5. Armação do Itapocaroí, em Santa Catarina.

As macroalgas foram coletadas manualmente entre os meses de dezembro a fevereiro (2017-2018), e de junho a agosto (2018), no litoral de São Paulo, Paraná e Santa Catarina, por meio de mergulhos autônomos em áreas de substrato não consolidado ou em costões rochosos (Fig. 3). As coletas foram realizadas durante primavera e verão (de outubro a março), período mais chuvoso; e durante outono e inverno (de abril a setembro) período mais seco; visando avaliar possíveis variações sazonais na disponibilidade de recursos alimentares entre as áreas de alimentação.

As macroalgas que compõem a dieta das tartarugas-verde, conforme dados de literatura (Nagaoka et al. 2012; Gama et al. 2016; Corbisier et al. 2014; Vinagre et al. 2018), foram coletadas e armazenadas em sacos plásticos “zip lock” contendo água do mar, sendo posteriormente congeladas para preservação do material.



Figura 3: Coleta de macroalgas com mergulho autônomo na Ilha das Palmas, em Ilha de São Sebastião (esquerda), e em costão rochoso na Praia dos Sonhos, Itanhaém (direita), ambas no Estado de São Paulo.

Considerando que a cada coleta, múltiplas espécies estavam associadas (em *turf*), a identificação das macroalgas até o menor nível taxonômico possível foi realizada em parceria com a professora Dra. Franciane Pellizzari, coordenadora do Laboratório de Ficologia e Qualidade de Água Marinha da UNESPAR, campus Paranaguá. Uma alíquota de cada amostra congelada foi retirada, pré-triada e armazenada em formaldeído 4% diluído em água do mar filtrada, para posterior identificação, mantendo o restante da amostra congelada.

2.5. ANÁLISE DE ISÓTOPOS ESTÁVEIS

Apenas as amostras de tecido epidérmico foram utilizadas para serem analisadas isotopicamente. Para estas, a extração de lipídeos não foi realizada, visto que estudos prévios indicaram que ela é desnecessária quando o conteúdo lipídico da amostra é $\leq 5\%$ e/ou quando $C:N < 3.5$ (Post et al. 2007, Turner Tomaszewicz et al. 2017), o qual foi verificado em nosso estudo. As amostras foram secadas em estufas a 60°C por 48h e acondicionadas em cápsulas de estanho para posterior análise das razões isotópicas no espectrômetro de massa de razão isotópica EA-IRMS (*Elemental analyser – Isotope Ratio Mass Spectrometer*) (Hobson & Welch 1992). Foram injetados dois materiais de referência certificados, para avaliar a calibração do equipamento, o USGS-40, que apresentou recuperação de 96% para $\delta^{15}\text{N}$ e 100% para $\delta^{13}\text{C}$, e o IAEA-600, com recuperação de 97% para $\delta^{15}\text{N}$ e 100% para $\delta^{13}\text{C}$.

As amostras de macroalgas presentes nas seis áreas de coleta, e já descritas na dieta de *C. mydas* (Nagaoka et al. 2012; Gama et al. 2016; Corbisier et al. 2014; Vinagre et al. 2018), foram analisadas após secagem em estufa a 60°C por 24h. Os isótopos de C e de N das tartarugas-verde e das macroalgas foram analisados e expressos na razão delta (δ). A razão delta (δ) é a diferença em partes por mil entre a razão de isótopos estáveis encontrados na amostra e no padrão (Peterson & Fry 1987).

2.6. ANÁLISE DA DIETA

Os tratos digestórios das tartarugas-verdes coletadas encalhadas mortas de 2015 a 2020 foram removidos e o respectivo conteúdo alimentar foi triado e analisado. Os itens foram congelados para identificação taxonômica do conteúdo dos tratos, e para análises de isótopos estáveis. Os itens alimentares foram identificados sob microscópios e estereomicroscópios via cortes histológicos e análises de estruturas vegetativas e reprodutivas das macroalgas (quando possível devido ao grau de degradação do material). As imagens foram comparadas em base de dados taxonômicos, como dissertações e teses, guias, livros e pranchas de identificação macroficológica marinha do Atlântico Sul Ocidental.

Informações secundárias incluídas no estudo pretérito realizado entre 2008-2014 no Paraná (Gama et al. 2016) foram agregadas aos resultados de 2015-2020 obtidos nesta tese, visando identificar e avaliar as variações em escala temporal na dieta e na forma de uso dos ambientes costeiros pelas tartarugas-verde.

2.7. ANÁLISES ESTATÍSTICAS

O comprimento curvilíneo de carapaça (CCC, em cm) dos espécimes, o ano do encalhe e as estações do ano (outono e inverno correspondentes à seca - abril a setembro; primavera e verão correspondentes à chuvosa - outubro a março) em que os espécimes foram coletados foram conjuntamente analisados e comparados com estudos prévios (Gama et al. 2016) visando analisar a variação temporal da dieta e a caracterização populacional ao longo de 12 anos (2008-2020).

De maneira detalhada, os métodos analíticos são descritos nos capítulos que seguem, sendo que, para o primeiro capítulo, as elipses isotópicas foram feitas para espécimes vivos e

mortos de tartarugas-verde, com base em seus valores de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$. Um modelo misto Bayesiano (MixSIAR) foi aplicado para determinar as contribuições dos itens alimentares dos espécimes residentes na área. No segundo capítulo, com enfoque na variação temporal dos recursos alimentares consumidos e sua relação com disponibilidade no habitat de forrageamento, uma análise de variância multivariada permutacional (PERMANOVA) e uma análise de componentes principais (PCA) foram aplicadas.

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3. CAPÍTULO 1

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Trophic ecology of juvenile green turtles in the Southwestern Atlantic Ocean: insights from stable isotope analysis and niche modelling

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Abstract

Determining the diet and trophic status of endangered species can provide insights into their key habitats and predator-prey relationships, both essential for conservation. Integrating dietary information from live-captured and dead-stranded turtles from the same area can also shed light on their ecological diversity. Here, diet intake and prey diversity are determined for juvenile green turtles (*Chelonia mydas*) from a mixed stock foraging aggregation in the Southwestern Atlantic Ocean (SWAO) using stable-carbon ($\delta^{13}\text{C}$) and -nitrogen ($\delta^{15}\text{N}$) isotope analysis. Skin samples were collected from 117 live-captured (LC) turtles and 66 dead-stranded (DS)

individuals in Paraná coast, southern Brazil. Bayesian isotope ellipse space was determined using the program SIBER. A larger isotopic niche space was found among DS turtles, probably because it included long-term resident turtles and recently settled individuals, the latter of which presented low $\delta^{15}\text{N}$ values compared to larger putative local turtles. The Bayesian stable isotope mixing model MixSIAR was used to determine dietary contributions, using isotopic values of putative prey. MixSIAR results indicated invertebrates and macroalgae as primary prey groups, showing green turtles' omnivorous strategy in the SWAO. Moreover, many of the smallest DS turtles had $\delta^{15}\text{N}$ values suggestive of seagrass consumption, which may reflect individual- and/or life-stage-based diet variability. These findings underscore the value of integrating stranding monitoring protocols with research on live green turtles to evaluate habitat use and diet intake assembled in a neritic foraging area. The data also establish knowledge about green turtle foraging ecology and are relevant for species and habitat conservation throughout the SWAO.

Keywords: *Chelonia mydas*, foraging ecology, SW Atlantic, isotopic ratio, mixing model, Bayesian inference

1. INTRODUCTION

Understanding diet composition and predator-prey relationships of endangered species can inform the identification of key feeding areas and provide insights into species' foraging ecology (James et al. 2005, McClellan & Read 2007, Nagaoka et al. 2012). This information is crucial to determine priority habitat for conservation and management plans, and to provide insights into areas that offer the greatest resources for consumers (Fuentes et al. 2006). When implemented in management frameworks, knowledge about dietary needs and habitat use may

support better decisions during the development of marine protected areas, fisheries, management practices, and mitigation strategies for habitat stressors such as marine debris (Schuyler et al. 2013, Hays et al. 2019, Haywood 2019). However, despite the value of this information for wildlife conservation, the elusive and cryptic nature of many animals, particularly marine species, makes it difficult to study them in the wild and obtain direct information on their foraging ecology (Reich et al. 2007).

Stable isotope analysis (SIA) of bulk animal tissue is a useful tool to study the diet and habitat use of elusive species (Haak et al. 2019, Hobson et al. 2019, Roswag et al. 2019). This is because stable isotope values of animal tissues reflect their diet and the ecosystem within which they forage (Hobson 1999). Body tissue such as skin or blood can provide insights about consumer's assimilated nutrients and trophic status that are otherwise not attainable with conventional diet analysis techniques such as oesophageal lavage or digestive tract inspection (Knoff et al. 2008, Litz et al. 2017). Stable carbon isotope ($\delta^{13}\text{C}$) values of consumer tissues are generally used to determine the origins of nutrients, with a continuum of progressive ^{13}C -depletion in tissues of marine species as they forage farther from the coast (Gannes et al. 1998, Jones & Seminoff, 2013). The $\delta^{13}\text{C}$ values in consumer tissues may also be influenced by the photosynthetic pathways and glucose synthesis of plant species, as well as the carbon sources for these consumed foods (Hobbie & Werner, 2004). For example, in coastal estuarine habitats, mangroves (e.g., *Avicennia schaueriana*), which are marine angiosperms that derive carbon from terrestrial-based systems, will have substantially lower $\delta^{13}\text{C}$ values relative to seagrass and marine macroalgae located only a few meters away (Lepoint et al. 2004). Conversely, stable nitrogen isotope ($\delta^{15}\text{N}$) analysis of body tissues provides information on the trophic level of a consumer due to the preferential retention of the heavier ^{15}N during nutrient assimilation, which results in a stepwise increase in $\delta^{15}\text{N}$ from prey to consumer (Seminoff et al. 2006, Reich et al. 2007, Bisi et al. 2013).

Sea turtles are among the taxa for which SIA has proven useful for elucidating foraging ecology of individuals and populations (Godley et al. 1998, Arthur et al. 2008, Burkholder et al. 2011, Gillis et al. 2018; Vélez-Rubio et al. 2018). All sea turtles are migratory and have complex life histories during which they occupy distinct habitats and consume different diets depending on their life stage (i.e., ontogenetic habitat and diet shifts observed for green turtles; Cardona et al. 2009, González Carman et al. 2012, Gama et al. 2016, Vélez-Rubio et al. 2018). As dietary nutrients are assimilated, the isotopic values of these foods are reflected in consumer body tissues (Seminoff et al. 2006). Thus, stable isotope values can provide information about individual diet differences as well as the previous location of organisms that move among spatially discrete food webs that are isotopically distinct (often termed ‘isoscapes’) (Seminoff et al. 2002, Vander Zanden et al. 2012, Turner Tomaszewicz et al. 2016; 2018). Stable isotope data from individuals of differing size and from multiple years in the same area can provide insights about ecological diversity (e.g., behaviour, habitat use) across life stages, and when examined in the context of baseline isotope values, these data can provide information about residency patterns among studied turtles (Vélez-Rubio et al. 2014; 2018, Newsome et al. 2010, Turner Tomaszewicz et al. 2018).

The Southwestern Atlantic Ocean (SWAO) hosts a regional management unit (RMU) of green turtles (*Chelonia mydas*, Wallace et al. 2011). This ocean region contains expansive neritic foraging areas for green turtles, especially juveniles, and stable isotope analysis has been used to evaluate diet composition at several sites (e.g. González Carman et al. 2014, Vélez-Rubio et al. 2018). Within the SWAO, in southern Brazil, the Paran  coast is used mainly by immature green turtles that are present year-round (Andrade et al. 2016, Gama et al. 2016, Coelho et al. 2018), but seasonally migrate within the region in search of warmer waters and areas with greater food availability (Marcovaldi & Santos 2011, Reisser et al. 2013, Gama et al. 2016, Vélez-Rubio et al. 2018). Throughout the SWAO and particularly along the Paran 

coast, many conservation challenges exist for this species. For example, more than 1,000 dead-stranded green turtles have been recorded per year since 2015, with bycatch in fisheries gear being a major cause of mortality (Cantor et al. 2020). Additional threats such as coastal habitat degradation, contamination, dredging, and urbanization are also present (Domiciano et al. 2017, Fuentes et al. 2020), which may affect diet, habitat use patterns and health condition of local green turtles.

In this study, the foraging ecology of juvenile green turtles along the Paraná coast of southern Brazil is examined via stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of both live-captured (LC) and dead-stranded (DS) green turtles, to test if this analysis can help us to understand i) the relationship between items consumptions and assimilation for regional green turtles; ii) if the latitudinal movement might be assessed by differences in the diet-intake and stable isotopes measures obtained in animals from the same foraging ground; iii) and if we can correlate diet and niche trophic with some specific development stages for juveniles. The main goal was to determine the recruitment histories of individual turtles and characterize the diet intake and isotopic niche (i.e., proxy for trophic niche) of the regional green turtle population. This was achieved by evaluating the stable isotope values of green turtle bulk skin tissue in the context of local and regional isoscape patterns. Diet composition of LC and DS turtles was determined using a Bayesian stable isotope mixing model that uses turtle and putative prey bulk tissue isotope values to model diet, and niche was determined with Bayesian isotope ellipse models that explored isotope variability among individuals in each group. Our results contribute to a better understanding of the foraging ecology and habitat use of green turtles, which is crucial to support marine habitat conservation efforts throughout the SWAO.

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted along the coastline of the state of Paraná, southern Brazil (25°20'S to 25°35'S, 48°17'W to 48°42'W, Figure 1). The study area includes numerous bays and the Paranaguá Estuarine Complex (PEC), a 612-km² semi-enclosed inlet characterized by mangroves, sandy beaches, seagrass meadows, and rocky shores, and classified as a World Heritage Site (Angulo 1992, Lana et al. 2001, UNESCO 2010). This is a subtropical region, influenced by the Brazil current (warm, summer currents) and the Falklands current (cold, winter currents), resulting in seasonal variation in sea surface temperature (18–30°C), local habitat conditions, and food resource availability (Matano et al. 2010). High marine productivity in the region provides rich food sources and promotes the presence of green turtles year-round (Guebert-Bartholo et al., 2011; Andrade et al. 2016, Gama et al. 2016, Coelho et al. 2018, Fuentes et al. 2020).

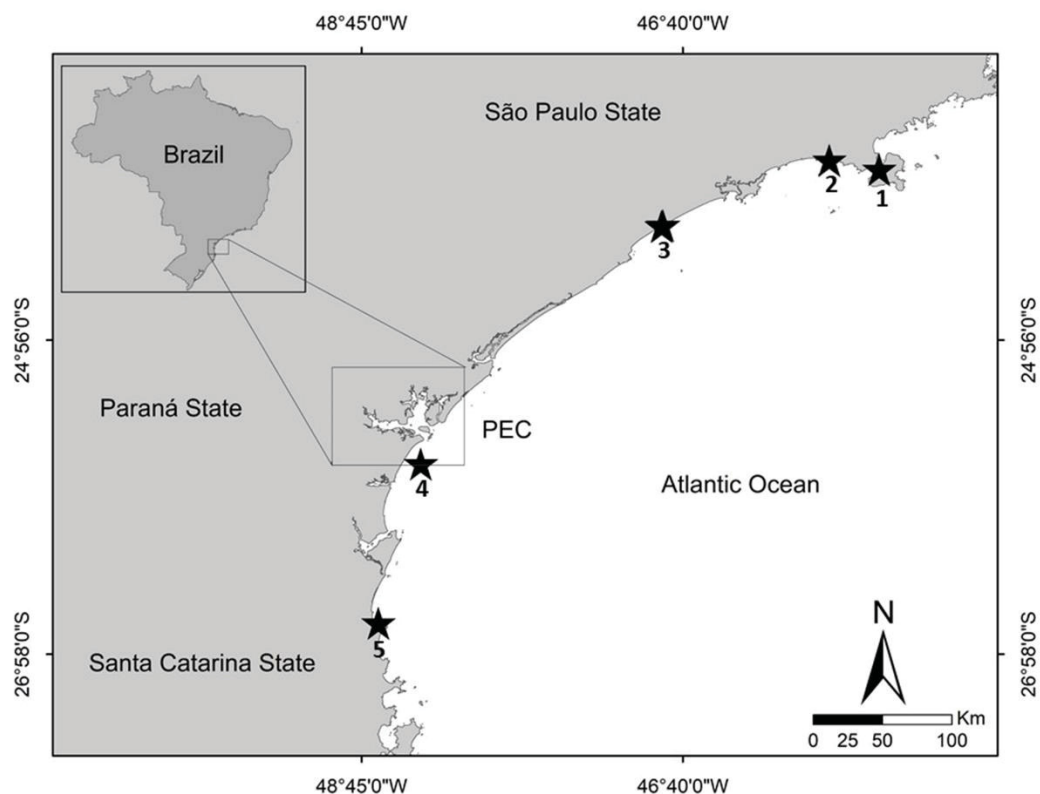


Figure 1. Map of the marine algae sampling areas along the coast of the Southwestern Atlantic Ocean, where site 1 is “Ilha das Cabras” and site 2 is “Portinho”, in Ilha Bela (São Paulo state); 3 is “Cama de Anchieta” and “Praia dos Sonhos”, in Itanhaém (São Paulo state); 4 is “Currais” in Paraná; and 5 is Penha, in Santa Catarina state. The zoomed square encompasses the Paraná coast of Brazil, including the Paranaguá Estuarine Complex, where the beach surveys were performed and dead-stranded green turtles were recovered, as well as the live-capture turtles were sampled.

2.2. Live-capture turtle sampling

A green turtle monitoring and health assessment program has been conducted in the PEC region since 2016 (Domiciano et al. 2019). As part of this program, intentional capture efforts were conducted during 58 field days in 2016 (May, June, September, October), 2017 (February, March), and 2018 (March, June). Turtle capture was conducted using a 50-m tangle net, with 3-m height and 0.30-m knot-to-knot mesh size. The net was checked continuously during the capture efforts and entangled green turtles were promptly removed and brought to the research boat (26-foot vessel with two 150-hp outboard motors). Onboard, body measurements such as curved carapace length (CCL; ± 0.1 cm) and body weight (W, ± 0.1 kg) were obtained using a flexible tape measure and hanging balance (Pesola AG, PHS100), respectively. All live-captured (LC) individuals were tagged with Inconel flipper tags (National Band and Tag Co., USA; Style 681) and released at the site of capture within two hours.

2.2. Dead-stranded turtles sampling

Dead-stranded (DS) green turtles were collected within the PEC and along the Paraná coast (~100 km) (Figure 1) during daily beach surveys conducted by personnel from the Ecology and Conservation Laboratory (Federal University of Paraná — UFPR) as part of the Project to Monitor the Beaches of Santos Bay (PMP-BS). The selected individuals to be sampled were obtained between July - September 2017 and April - June 2018, following the seasonal pattern. More than two thousand juvenile green turtles were found dead-stranded during this interval, but only a subset of 66 specimens was analysed due to financial and

logistical constraints. All the turtle specimens were identified to species and their decomposition stage was ranked (from 2 to 5; adapted from Geraci & Lounsbury, 2005); only carcasses classified as 2 and 3 (i.e., the freshest decomposition states) were sampled for this study. For each DS turtle, CCL (± 0.1 cm) was recorded.

2.3. Habitat sampling

Habitats were sampled to determine the isotope values of macroalgae that are potentially consumed by green turtles. Macroalgae were collected in six different areas along the SWAO coast from Ilha das Cabras (23°49'S, 45°23'W) in São Paulo state, to Praia da Armação (26°46'S, 48°38'W) in Santa Catarina state (Figure 1). These sites included the PEC, as well as other neritic habitats that have similar oceanographic influences and are part of this species migratory corridor (González Carman et al. 2012, Fuentes et al. 2020). Habitat sampling was conducted from December 2017 to February 2018, which corresponds with the austral summer; and from June to July 2018, which is during the austral winter. The most reported macroalgae in the diet of local green turtles (Nagaoka et al. 2012, Reisser et al. 2013, Gama et al. 2016) was collected at each site. All samples were stored in plastic “zip lock” bags with clean seawater, and frozen until analysis. Taxonomic identification was conducted at the Phycology and Marine Water Quality Laboratory (Paraná State University — UNESPAR) in Paranaguá, Brazil. Each sample was separated by histological sectioning, and morphological and reproductive features were examined via stereomicroscope when permissible based on sample quality. The most abundant samples were rinsed, lyophilized, and homogenized prior to isotopic analysis; these included Chlorophyta (*Caulerpa racemosa*, *Chaetomorpha antennina*, *Ulva fasciata*, *Ulva lactuca*, *Ulva intestinalis*), Rhodophyta (*Aglaothamnion felipponei*, *Amphiroa* sp., *Asparagopsis* sp., *Chondria* sp., *Hypnea spinella*, *Hypnea pseudomusciformis*, *Jania crassa*,

Laurencia sp., *Spyridia* sp.), Ochrophyta (*Chnoospora minima*, *Dictyota ciliolate*, *Sargassum cymosum*), and the cyanobacteria *Lyngbya majuscula*.

2.4. Tissues sampling and Stable isotope analysis

Epidermis samples (0.10–0.25 g; hereafter referred to as skin) were collected from both LC and DS turtles with a razor blade from the dorsal surface of the neck and frozen until analysis as per Gillis et al. (2018). Special care was taken to collect surface epidermal tissue without any underlying connective tissue.

Approximately 1.0 mg of skin from both LC and DS green turtles, and 0.5 mg of each forage item sample was loaded into tin capsules and analysed by an elemental analyser – isotope ratio mass spectrometer (EA-IRMS) at the São Paulo University Oceanographic Institute (IO-USP) in São Paulo, Brazil. Prior studies have indicated that lipid extraction is unnecessary when the sample lipid content is $\leq 5\%$ and/or when C:N < 3.5 (Post et al. 2007, Turner Tomaszewicz et al. 2017); therefore, we did not remove lipids from turtle tissues or food resource samples.

Analyses were undertaken for %C, %N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. Sample stable isotope ratios relative to an isotope standard are expressed in the following conventional delta (δ) notation, measured in parts per thousand (‰):

$$\delta = ([R_{\text{sample}}/R_{\text{standard}}] - 1) (1000)$$

where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in the sample and standard, respectively. All carbon isotopic results are expressed in standard delta notation relative to Vienna Pee Dee Belemnite (or “VPDB”). All nitrogen isotopic results are expressed in standard delta notation relative to the atmospheric air (or “AIR”). All analytical runs included the certificated USGS-40 (United States Geological

Survey) and IAEA-600 (International Atomic Energy Agency), which were inserted after every 40 samples to calibrate the isotopic results and to estimate the precision of the analysis. Replicate assays of standard materials indicated recoveries of the method of 96% to 100%, and analytical uncertainty of 0.18‰ and 0.05‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements, respectively.

2.5. Statistical analysis

The differences in the isotopic means for DS and LC turtles among the years were tested using a Tukey *post-hoc* test. To test for isotope differences between size classes (groupings made within 10-cm CCL size groups; Size Group 1: 26.0 – 36.0 cm; Size Group 2: 36.1 – 46.0 cm; Size Group 3: ≥ 46.1 cm; following Gama et al. [2016]) an ANOVA was performed for DS and LC turtles. Linear regression was conducted to detect correlation between turtles' CCL and isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). All statistical analyses were conducted using the software R 3.6.1, where $p < 0.05$ was used to define statistical significance. Only raw, corrected isotope data were used for analyses; no data transformation was conducted. The analysis of normality, homoscedasticity and standardized residuals showed the adequacy of the ANOVA assumptions (Sokal & Rohlf, 2012).

The Stable Isotope Bayesian Ellipses in package in R (SIBER) (Jackson et al. 2011) was used to generate and compare the bivariate ellipses for DS and LC juvenile green turtles based on their skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The convex hull total area (CHA) and the standard ellipse area (SEA) were calculated to determine the isotopic niche space for DS and LC (Jackson et al. 2011). The Bayesian mixing model MixSIAR (Stock & Semmens 2016) was used to determine the prey contributions to the diet of juvenile green turtles. Model input data included $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of live green turtles and putative prey species, as well as the values for dead green turtles and their prey species. Because of the limited dietary specificity revealed by MixSIAR when using numerous prey groups (Stock & Semmens 2016), here the analyses were limited to

five groups (“red algae”, “green algae”, “seagrass”, “mangrove”, “invertebrates”), with prey items grouped based on similarity in life-history traits and position in the food web (Lemons et al. 2011, Gillis et al. 2018). The “red algae” group was composed by *Hypnea spinella*, *Hypnea* sp., and *Hypnea pseudomusciformis*. The “green algae” group was composed by *Ulva fasciata*, *Ulva* sp., and *Ulva lactuca*. Both algae groups were composed by species collected in this study and in adjacent areas with similar values to the ones collected by us, to reduce the noise in our models (Table 1). For “seagrass”, the two isotope values for *Halodule wrightii* (which is the only species that occurs along the Paraná coast) are from sites with different environmental conditions along the Brazilian coast; however, they were used for model inputs because they were the only data available (Lazzari 2012, Corbisier et al. 2014). Furthermore, nitrogen isotope values of these seagrass were within the range of and cannot be distinguished in our model from other oceanic-type prey at a similar trophic level, including jellies and other similar prey items.

Table 1. Stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of the food items considered in our study for juvenile green turtles, which were included in the MixSIAR models. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are means followed by $\pm$ standard deviation (SD) (‰).

Prey group	N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	References
Green algae	10	-16.70 ± 0.77	7.40 ± 1.23	This study; Corbisier et al. 2006; Vélez-Rubio et al. 2016
Red algae	6	-17.20 ± 2.62	6.00 ± 1.06	This study; Corbisier et al. 2006; Vinagre et al. 2018
Seagrass	4	-13.80 ± 0.50	3.70 ± 0.70	Lazzari et al. 2012; Corbisier et al. 2014
Mangrove	3	-28.30 ± 0.20	3.10 ± 0.40	Larcher et al. 2016
Invertebrates	32	-15.40 ± 0.50	9.70 ± 1.40	Corbisier et al. 2006; Vinagre et al. 2018

The “mangrove” group consisted of *Avicennia schaueriana*, which is one of the most common mangrove species in the diets of green turtles from Paranaguá Estuarine Complex, Paraná state in southern Brazil (i.e., Guebert-Bartholo et al. 2011). Mangrove isotope values were obtained by values presented in the literature from Guaratuba Bay, also in the state of Paraná (Larcher et al. 2016). The “invertebrate” group reflected mean isotope values of 32 species from the region and obtained from the literature, including depositivorous (5), carnivorous (7) and suspensivorous (20) species (Supplementary Table 1; Corbisier et al. 2006, Vinagre et al. 2018).

We further explored green turtle diet characterization in MixSIAR by separating turtles into the three size groups (Size Group 1: 26.0 – 36.0 cm; Size Group 2: 36.1 – 46.0 cm; Size

2016	7	– 15.0 ± 1.8	– 17.0 to – 12.6	– 10.9 ± 0.9	9.7 to 12.1	50.7 ± 10.1	44.6 to 73.4	15.4 ± 2.9	12.7 to 21.7
2017	14	– 16.0 ± 0.9	– 17.9 to – 14.5	– 10.5 ± 1.0	9.1 to 12.5	44.4 ± 7.6	20.0 to 50.7	13.3 ± 2.3	5.5 to 14.8
2018	61	– 17.5 ± 1.2	– 20.2 to – 14.9	– 10.4 ± 1.0	8.3 to 12.8	40.2 ± 15.9	2.5 to 52.0	14.2 ± 0.7	12.5 to 16.9

Dead- stranded

2017	38	– 17.2 ± 1.0	– 19.7 to – 15.8	– 9.1 ± 1.8	4.9 to 13.0	42.0 ± 6.6	30.8 to 65.3	17.3 ± 5.0	9.6 to 38.7
2018	28	– 17.5 ± 1.8	– 25.2 to – 15.1	– 8.3 ± 1.7	4.9 to 12.0	41.9 ± 4.0	31.3 to 49.0	16.8 ± 2.8	13.9 to 28.3

Differences between the size groups were observed (ANOVA, $p \leq 0.05$), but there was no relationship between turtle size (CCL) and $\delta^{13}\text{C}$ for either group; however, there was a significant positive relationship between CCL and $\delta^{15}\text{N}$ for both LC and DS green turtles ($R^2 = 0.18$, $p \leq 0.05$), with larger turtles presenting higher $\delta^{15}\text{N}$ values (Figure 2).

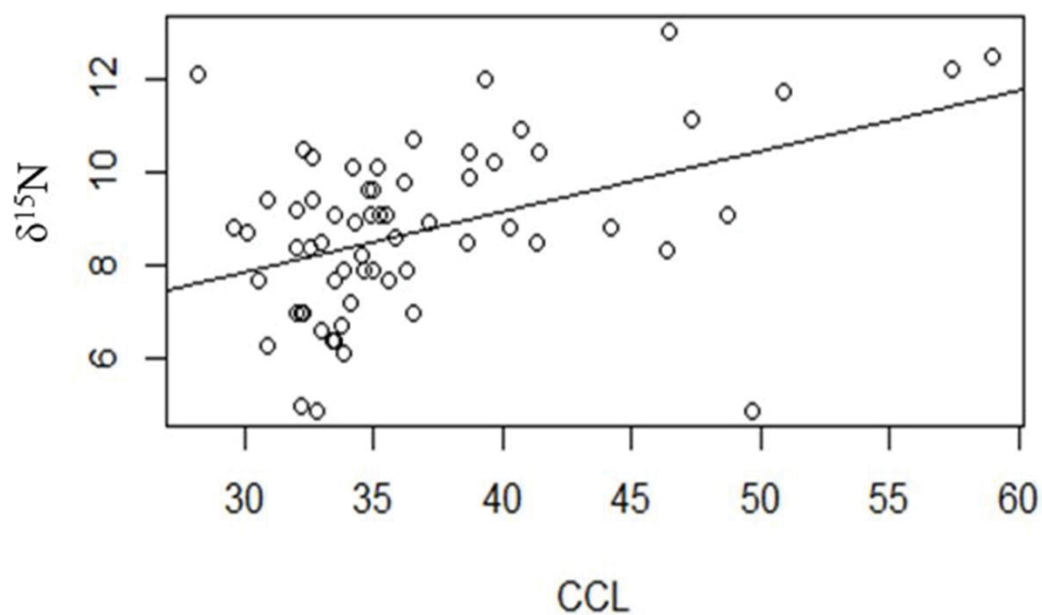


Figure 2. Linear regression showing a significant relationship between curved carapace length and stable-nitrogen isotope values of 66 dead-stranded juvenile green turtles recovered along the Paraná coast of southern Brazil between 2017 and 2018.

Among years, a Tukey *post-hoc* comparison showed significant variability in $\delta^{13}\text{C}$ values for LC turtles from 2016 and LC turtles from 2018, and for LC turtles from 2017 and 2018. There was no difference in the isotope values of DS turtles among all the years. When looking at the differences between LC and DS groups, there was significant inter-annual variability within and between the LC and DS turtle groups for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 3).

Table 3. Results from the Tukey *post-hoc* comparison test for mean annual skin tissue $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ (bottom) of the live-captured (LC) and dead-stranded (DS) juvenile green turtles encountered along the Paraná coast, southern Brazil. The values in bold show pairs of means that are significantly different.

$\delta^{13}\text{C}$					
Abs (Dif)-LSD	Difference means	in	Lower values	Upper values	p-value
LC ₂₀₁₇ - LC ₂₀₁₆	-1.00	-2.63	0.62	0.430	
LC ₂₀₁₈ - LC ₂₀₁₆	-2.25	-3.63	-0.87	<0.001	
DS ₂₀₁₇ - LC ₂₀₁₆	-2.23	-3.68	-0.78	<0.001	
DS ₂₀₁₈ - LC ₂₀₁₆	-2.48	-3.96	-0.99	<0.001	
LC ₂₀₁₈ - LC ₂₀₁₇	-1.24	-2.26	-0.23	0.007	
DS ₂₀₁₇ - LC ₂₀₁₇	-1.22	-2.32	-0.12	0.020	
DS ₂₀₁₈ - LC ₂₀₁₇	-1.47	-2.62	-0.32	0.004	
DS ₂₀₁₇ - LC ₂₀₁₈	0.01	-0.66	0.70	0.990	
DS ₂₀₁₈ - LC ₂₀₁₈	-0.22	-0.99	0.54	0.920	
DS ₂₀₁₈ - DS ₂₀₁₇	-0.24	-1.12	0.62	0.930	
$\delta^{15}\text{N}$					
Abs (Dif)-LSD	Difference means	in	Lower values	Upper values	p-value
LC ₂₀₁₇ - LC ₂₀₁₆	-0.38	-2.11	1.34	0.970	
LC ₂₀₁₈ - LC ₂₀₁₆	-0.58	-2.05	0.88	0.800	
DS ₂₀₁₇ - LC ₂₀₁₆	-1.84	-3.38	-0.31	0.009	
DS ₂₀₁₈ - LC ₂₀₁₆	-2.65	-4.23	-1.07	<0.001	
LC ₂₀₁₈ - LC ₂₀₁₇	-0.20	-1.27	0.87	0.980	
DS ₂₀₁₇ - LC ₂₀₁₇	-1.46	-2.63	-0.29	0.006	
DS ₂₀₁₈ - LC ₂₀₁₇	-2.26	-3.49	-1.04	<0.001	
DS ₂₀₁₇ - LC ₂₀₁₈	-1.26	-1.99	-0.53	<0.001	
DS ₂₀₁₈ - LC ₂₀₁₈	-2.06	-2.88	-1.25	<0.001	
DS ₂₀₁₈ - DS ₂₀₁₇	-0.80	-1.73	0.12	0.120	

Among forage items the mean isotope values ranged from -28.3 ± 0.2 ‰ to -13.8 ± 0.5 ‰ for $\delta^{13}\text{C}$; and from 3.1 ± 0.4 ‰ to 9.7 ± 1.4 ‰ for $\delta^{15}\text{N}$ (Table 1). The “seagrass” prey group

had the highest mean $\delta^{13}\text{C}$ value (-13.8 ± 0.5 ‰) and the “mangrove” group had the lowest mean $\delta^{13}\text{C}$ (-28.3 ± 0.2 ‰). For $\delta^{15}\text{N}$, the “mangrove” and “invertebrates” prey groups had the lowest mean (3.1 ± 0.4 ‰) and the highest (9.7 ± 1.4 ‰) mean values, respectively (Table 1). Among local macroalgae, *Hypnea spinella* had the lowest $\delta^{13}\text{C}$ value (-20.1 ‰) and *Hypnea* sp. the highest $\delta^{13}\text{C}$ value (-13.8 ‰), whereas *Hypnea pseudomusciformis* had the lowest $\delta^{15}\text{N}$ value (4.9 ‰) and *Ulva lactuca* had the highest $\delta^{15}\text{N}$ value (9.1 ‰; Supplementary Table 1).

3.3. Turtle Isotope Ellipse Space

SIBER analyses yielded a CHA area of 47.8 for DS turtles and of 25.8 for LC turtles. The standard ellipse areas (SEA) were 7.9 (DS) and 4.0 (LC) (Figure 3). Dead-stranded green turtles had a greater range in $\delta^{15}\text{N}$ values and a larger isotopic niche space than live turtles (Figure 3).

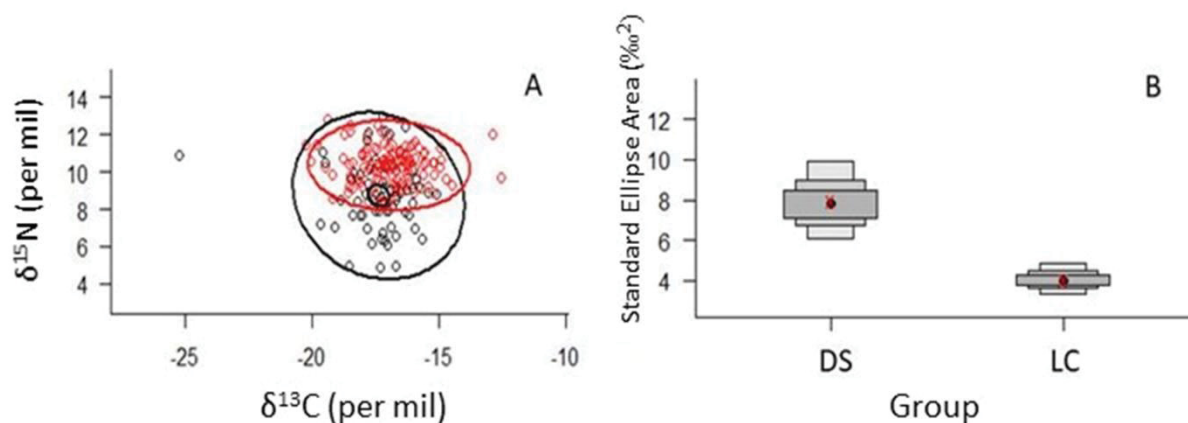


Figure 3. (A) Standard Ellipses, corrected for sample size, which was calculated using a maximum likelihood approach. The red ellipse corresponds to the live-captured green turtles, whereas the black ellipse represents the dead-stranded green turtles. (B) Bayesian SEA estimates for dead-stranded (DS) and live-captured (LC) juvenile green turtles, where black circles represent the mean values, and grey boxes represent the 50, 75, and 95% credible intervals.

3.4. Mixing Model Outputs

Our model that includes five dietary prey groups (Figure 4A and 4B) indicated that “invertebrates” were the most consumed prey group by live-captured turtles, with a mean probable dietary contribution of 41.9% (range = 14.6% to 62.2%; Figure 4A). For dead-stranded juvenile green turtles the most dominant prey groups were “green algae” (24.8% mean probable contribution, range = 2.6% to 57.1%) and “seagrass” (24.2%, range = 8.4% to 37.6%) (Figure 4B).

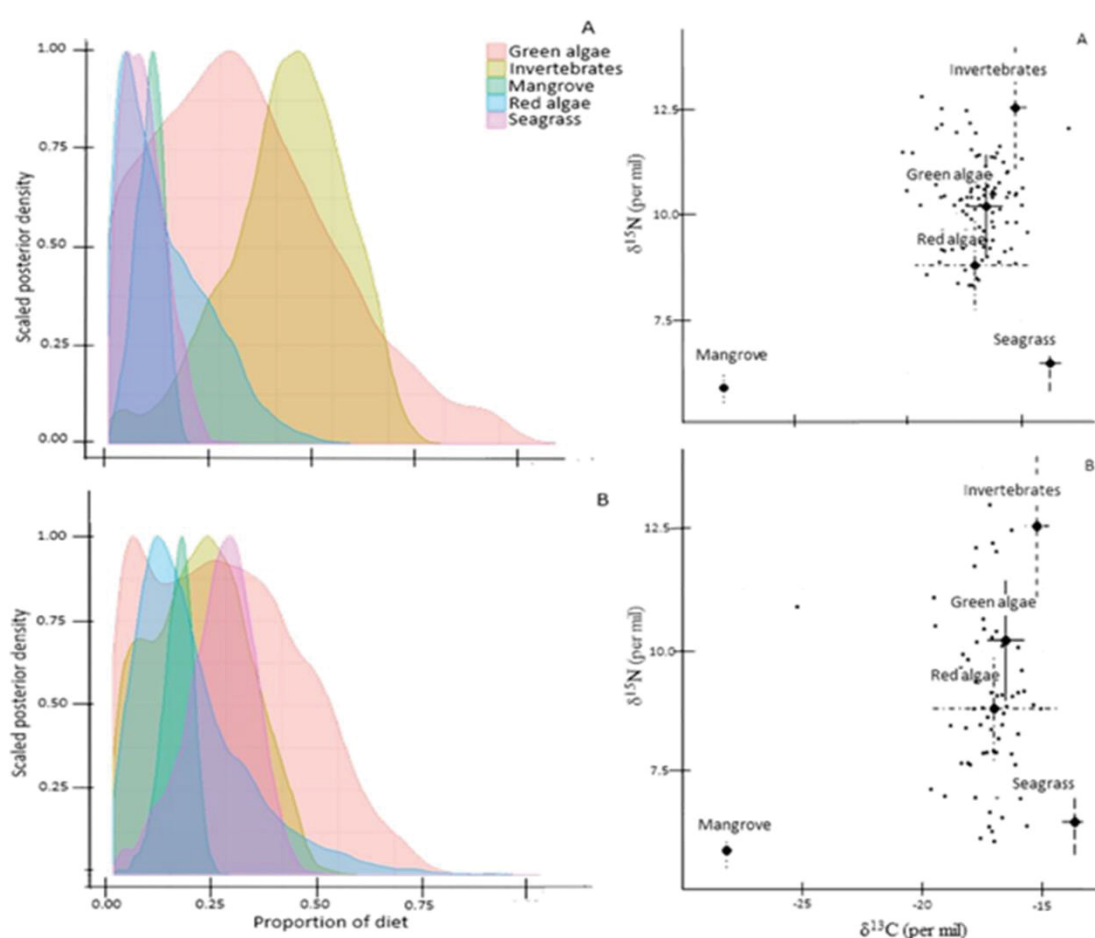


Figure 4: MixSIAR model outputs for (A) live-captured and (B) dead-stranded juvenile green turtles in Paraná coast, southern Brazil and with each respective raw data beside them, resulting from the MixSIAR analysis considering their main five food items isotopic values.

Among all green turtles encountered during this study in Paraná, which included both LC and DS individuals, “invertebrates” and “green algae” were the most important prey groups (Figure 5), with mean probable contributions of 30.5% (ranging from 5.2% to 60.0%) and 23.2% (ranging from 3.5% to 59.8%), respectively (Figure 6A).

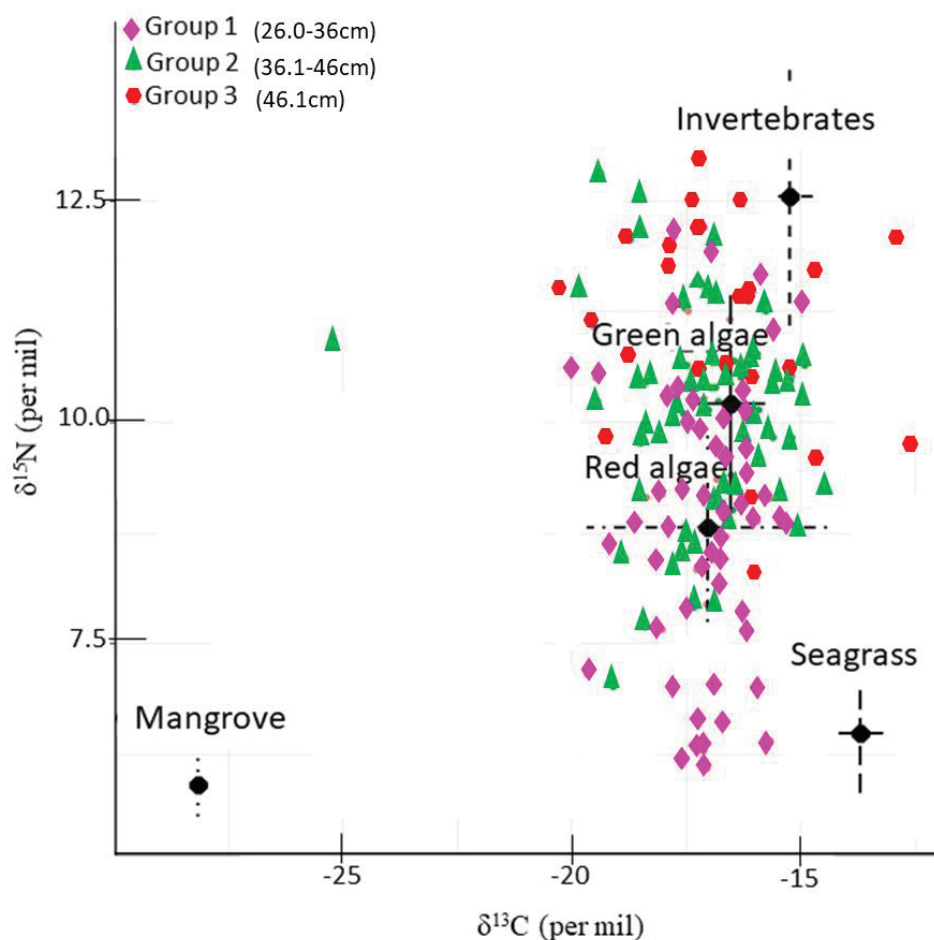


Figure 5. Raw data for live-captured and dead-stranded juvenile green turtles in Paraná coast, southern Brazil, among size classes (Group 1: 26.0–36cm; Group 2: 36.1–46cm; Group 3: ≥ 46.1 cm) resulting from the MixSIAR analysis considering their main five food items isotopic values.

When separating by turtle size category, “green algae” was the most prominent diet group consumed by the smallest turtles (Size Group 1), with a 43.7% mean probable diet contribution, ranging from 8.0% to 86.6% (Figure 6B). For turtles in Size Group 2 (mid-sized turtles), “invertebrates” and “green algae” had the highest mean probable contributions (32.7% and 31.7%, respectively) (Figure 6C). Turtles in Size Group 3 (largest turtles) had the “invertebrates” prey group as that with the highest mean probable contribution (52.6%, range = 5.1% to 74.1%) (Figure 6D).

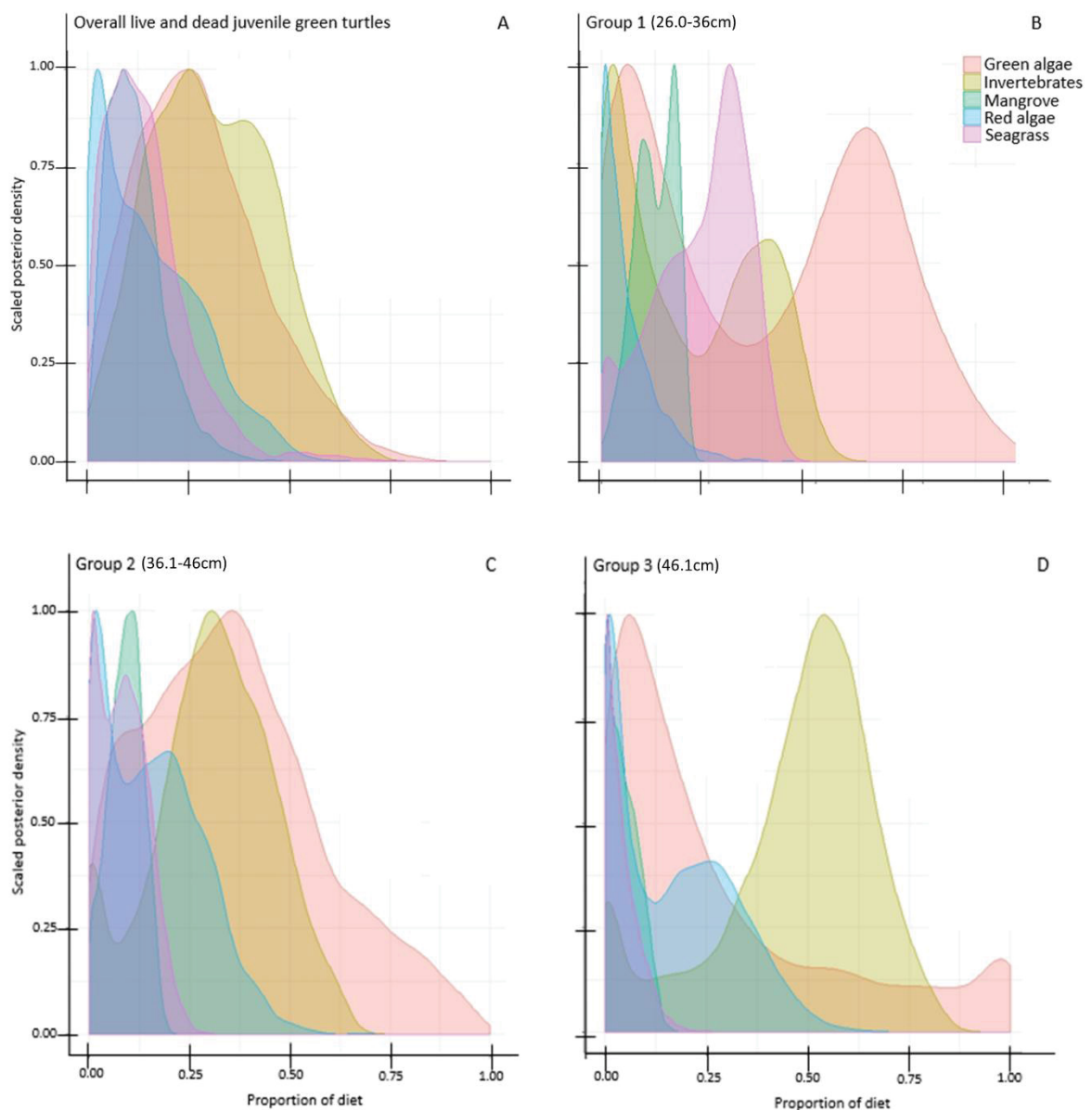


Figure 6. MixSIAR model outputs for overall and different size classes of live-captured and dead-stranded juvenile green turtles in Paraná coast, southern Brazil. (A) Overall turtles; (B) Group 1: 26.0–36cm; (C) Group 2: 36.1–46cm; (D) Group 3: ≥ 46.1 cm.

4. DISCUSSION

Our study highlights the importance of integrating multiple research approaches to better understand trophic status and the ecological diversity of turtle diet. Here we provide additional insights into the diet consumption and dietary diversity of both live-captured and dead-stranded green turtles encountered along the southern Brazilian coast. Concurrent evaluation of turtles from both origins is infrequent, and our study was successful at depicting isotopic differences between the groups that likely reflect diverse ecological strategies between the groups, underscoring the species' omnivorous foraging strategy in the SWAO.

When evaluating the stable isotope values of turtles in different size classes, stable isotope values indicate differing diets among the groups, and suggest recent recruitment from oceanic to neritic habitats for some—usually among the smallest—individuals. As juvenile green turtles grow and develop, their diet shifts from an algae-dominant diet to one that includes more coastal invertebrates. When we analysed live-captured and dead-stranded turtles separately, there was a disparity between groups for the most likely consumed prey items, which is highlighted by the large probable contribution of seagrass only in dead stranded turtles. Whereas the live-captured turtles mostly consumed foods in the “invertebrates” and “green algae” prey groups, dead-stranded turtles most frequently ingested “green algae” and “seagrass”, the latter of which was especially important in the smallest size group. However, it is important to clarify that because the seagrass isotopic values available in the literature are from areas with a significant oceanic water intrusion (Lazzari 2012, Corbisier et al. 2014), the isotope value for “seagrass” used in MixSIAR models may mimic isotopic values of oceanic

prey, as reported elsewhere in the SWAO (Vélez-Rubio et al. 2016). For example, the isotope values attributed in our MixSIAR models to seagrass may reflect the consumption of oceanic items, such as sea jellies as has been reported for green turtles in Uruguay (Vélez-Rubio et al. 2016). Indeed, the lack of isotopic specificity between neritic seagrasses and oceanic prey makes the mixing model results equivocal and brings some bias to our knowledge about feeding ecology of these smallest stranded turtles. These factors highlight the need for further isotopic study of this green turtle lifestage in the SWAO.

SIBER analysis indicated that dead-stranded green turtles had substantially different isotopic niche ellipse space and an overall larger isotopic niche width relative to live-captured green turtles included in this study. Both groups had highly similar $\delta^{13}\text{C}$ ranges, but the DS group had substantially more turtles with low $\delta^{15}\text{N}$ values, which was responsible for the larger niche space of this group. This result suggests these individuals may be recent arrivals to the Paraná study region, originating from areas that have a lower baseline $\delta^{15}\text{N}$ than found locally, or perhaps forage at lower trophic positions than their live-captured counterparts. Considering that most green turtles in the SWAO recruit from offshore areas to coastal waters at ≤ 35 cm CCL (Andrade et al. 2016), turtles of this size and smaller would be expected to be oceanic juveniles and thus consume prey of oceanic nutrient pathways, which typically have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than neritic systems (Hatase et al. 2010, Piovano et al. 2020).

Although the origins of dead-stranded turtles are unknown, it is possible that they originate from both offshore and coastal zones. In the South Pacific, Piovano et al. (2020) found a similar result, with two groups of turtles at a Fijian foraging habitat, including one group of turtles that had different $\delta^{15}\text{N}$ values than the local habitat and were considered to be recently settled from offshore waters and not yet in isotopic steady state with the coastal habitat. The possibility that at least some of the dead-stranded turtles in this study were recent arrivals from

offshore waters is also supported by isoscape mapping in the region conducted by Troina et al. (2020) that found higher $\delta^{15}\text{N}$ values among zooplankton collected along the shelf break in the SWAO relative to plankton collected in offshore waters. If so, then green turtles occupying offshore waters would also be expected to have lower $\delta^{15}\text{N}$ values than turtles living in coastal shelf habitats.

In addition to offshore origins, it is possible that at least some turtles in this study transitioned to Paraná from other coastal foraging areas in the region (Gonzalez Carman et al. 2012, Fuentes et al. 2020). Indeed, there is similarity in stable isotope values among green turtles at multiple foraging areas in the SWAO. For dead-stranded turtles from the Paraná, their $\delta^{15}\text{N}$ values are similar to those for green turtles in Argentina (González Carman et al. 2014) and in northeast Brazil (Bezerra et al. 2015); and their $\delta^{13}\text{C}$ values are similar to those found for Rio de Janeiro (Di Benedetto et al. 2017) and northeast Brazil (Bezerra et al. 2015). Green turtle $\delta^{13}\text{C}$ values (range = -20.2‰ to -12.6‰) in Paraná are similar to those for green turtles in northeast and southeast Brazil (Campos & Cardona 2019) (Table 4). For live-captured turtles in this study, the mean $\delta^{15}\text{N}$ value ($10.3 \pm 0.98\text{‰}$) is similar to values reported for green turtles in northeast and southeast Brazil (Bezerra et al. 2015, Di Benedetto et al. 2017) (Table 4). Likewise, González Carman et al. (2014) report $\delta^{13}\text{C}$ values for live green turtles in Argentina (mean = $-16.5 \pm 0.2\text{‰}$) that are similar to live turtles from our study in Paraná. The similarity between the isotope values at all these sites, despite their spatial separation by more than 1000 kilometres, suggests a notable level of connectivity among green turtle foraging populations throughout the SWAO. Consistency in isotope values among green turtles assembled in disparate foraging areas of the SWAO could also reflect the relatively small spatial variability in regional $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isoscapes in the SWAO (McMahon et al. 2013). This makes it

challenging to assign prior origins of recently arrived green turtles in the region but does support our use of prey isotope values from areas outside of Paraná in the mixing models.

Table 4. Literature review of the stable isotope studies with green turtles performed along the Southwestern Atlantic Ocean. Study sites are listed from north to south; isotope data are presented as mean $\pm$ SD or ranges, depending on how data were presented in the source literature. *The size range reflects animals included in the gut analysis. Only a subset of this had stable isotope information.

Study site	Sample size (n)	Size range (CCL; cm)	Tissue	$\delta^{13}\text{C}$ (‰) range/mean	$\delta^{15}\text{N}$ (‰) range/mean	Reference
Ceará and Bahia, Northeast Brazil	31	27.0 – 62.0	Muscle Scute	-17.1 ± 0.9 -18.9 ± 0.8	10.4 ± 0.22 9.6 ± 0.22	Bezerra et al. 2015
Bahia and Ubatuba, Northeast and Southeast Brazil	30	31.1 – 104	Scute	-21.7 to -13.9	5.3 to 14.0	Campos & Cardona 2019
Rio de Janeiro, Southeast Brazil	45	27.3 – 48	Muscle	-17.4 ± 0.8	9.9 ± 1.8	Di Benedetto et al. 2017
Paraná, south Brazil	66 dead 117 alive	28.2 59.0 33.4 54.0	Skin	-17.4 ± 1.4 -16.9 ± 1.3	8.7 ± 1.8 10.3 ± 1.0	This study
Argentina	7 dead; 7 alive	31.3 52.2 *	Skin	-15.5 ± 0.7 -16.5 ± 0.2	9.5 ± 1.0 11.1 ± 1.1	González Carman et al. 2014
Uruguay	126	27.8 – 66.8	Skin	-18.2 to -13.6	6.7 to 15.6	Velez-Rubio et al. 2016
Uruguay	20	27.8 – 66.8	Scute	-19.8 to -14.8	5.8 to 15.8	Velez-Rubio et al. 2018

The presence of algae and invertebrates in the SWAO is reported in all studies that have been conducted in the region; however, for the Paraná coast specifically, the low contribution of seagrass to the diets of live-captured green turtles may signal impacts of anthropogenic

activities that affect the Paraná and wider PEC region. Even the smallest live-captured turtles do not present seagrass as an important dietary item, which was common finding of previous diet studies in this area (e.g., Guebert-Bartholo et al. 2011, Gama et al. 2016).

It is also known from previous studies that marine algae are the most frequently consumed food type among green turtles in the SWAO (Gama et al. 2016, Santos et al. 2015, Vélez-Rubio et al. 2016). For instance, in Uruguay 69% of juvenile green turtles with CCL from 35 cm to 45 cm had consumed macroalgae, with *Ulva* sp. being the most-consumed species (58.6%) (Vélez-Rubio et al. 2016). Along the Paraná coast, *Ulva* sp. comprised 43% of green turtle diet (Gama et al., 2016), which is a macroalgae species that proliferates in polluted areas; thus, its high consumption could be reflective of low habitat quality (Bordean et al. 2016, Bonanno et al. 2020).

The high importance of the “invertebrates” prey group in live-captured juvenile green turtle diet may be reflective of changes in juvenile green turtle foraging strategy, specifically in Paraná coast, where prior gut content analyses have shown that turtles of this lifestage most frequently consumed vegetal prey items such as seagrass and macroalgae (Guebert-Bartholo et al. 2011, Gama et al. 2016). Dependence on invertebrate prey species has been reported throughout subtropical and temperate areas of Brazil (González Carman et al. 2014; Vélez-Rubio et al. 2016). These changes could be a consequence of widespread habitat degradation and a resulting lower availability of vegetal prey items.

The study of both live-captured and dead-stranded turtles provided novel insights on potential differences in their diet, habitat use, and foraging behavior. The isotopic similarities found among this and prior SWAO studies suggest that juvenile green turtle foraging ecology is relatively consistent throughout the region and reinforces the importance of this area as a key foraging ground for the species. As a result, every effort should be made to build effective

management actions that promote population recovery and habitat protection throughout the SWAO region.

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Supplementary Tables

Table 1. Stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of marine algae, seagrass, mangrove, and invertebrates from the Southwestern Atlantic Region. SP = Sao Paulo, SC = Santa Catarina. *The results presented are a combination of both studies.

Site	Habitat item	Genus / species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Reference
Itanhaém/SP, Brazil	Rhodophyta	<i>Hypnea pseudomusciformis</i>	- 18.0	4.9	This study
Itanhaém/SP, Brazil	Rhodophyta	<i>Hypnea spinella</i>	- 20.1	6.3	This study
Ubatuba/SP, Brazil	Rhodophyta	<i>Hypnea spinella</i>	- 17.0	7.3	Corbisier et al. 2006
Southeast Brazil	Rhodophyta	<i>Hypnea</i> sp.	- 13.8	5.4	Vinagre et al. 2008
Itanhaém/SP, Brazil	Chlorophyta	<i>Ulva fasciata</i>	- 17.0	6.6	This study
Penha/SC, Brazil	Chlorophyta	<i>Ulva lactuca</i>	- 15.6	9.1	This study
Ubatuba/SP, Brazil	Chlorophyta	<i>Ulva fasciata</i>	- 17.2	6.4	Corbisier et al. 2006
South Brazil	Chlorophyta	<i>Ulva</i> sp.	- 17.1	7.7	Velez Rubio et al. 2016
Guaratuba/PR, Brazil	Black mangrove	<i>Avicennia schaueriana</i>	- 28.3 $\pm$ 0.2	3.1 $\pm$ 0.4	Larcher et al. 2016
Northeast Brazil	Seagrass	<i>Halodule wrightii</i>	- 14.2 $\pm$ 0.4	3.2 $\pm$ 1.7	Lazzari et al. 2012
Southeast Brazil	Seagrass	<i>Halodule</i> sp.	- 13.5	4.2	Corbisier et al. 2014
Southeast Brazil	Invertebrates	Depositivore	- 15.9 $\pm$ 2.2	9.5 $\pm$ 1.0	Corbisier et al. 2006
Southeast Brazil	Invertebrates	Carnivore	- 14.9 $\pm$ 1.1	11.3 $\pm$ 0.8	Corbisier et al. 2006
Southeast Brazil	Invertebrates	Suspensivorous	- 15.5 $\pm$ 1.6*	8.4 $\pm$ 0.6*	Corbisier et al. 2006; Vinagre et al. 2008

4.CAPÍTULO 2

Long-term dietary shifts of juvenile green turtles in the Southwestern Atlantic Ocean

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Abstract

Long-term diet studies are essential to understand the foraging ecology of a species and its variation in terms of the diet composition. Dead-stranded sea turtles assessed by stranding monitoring programs allows the systematic sampling over a long temporal scale, providing information on foraging and population ecology. Off the Southwestern Atlantic Ocean, the Paraná coast is an important foraging ground for juvenile green turtles (*Chelonia mydas*), which are one of the most frequent species in the region. Globally, the stranding rates of the species in Paraná are ~1000 individuals per year, and from 2008 to 2020, 351 dead-stranded individuals had their digestive tracts removed and contents analyzed to the phylum level. For finer-scale

analysis, a subset of turtles from different periods had macroalgae (n=148) or invertebrates (n=142) contents identified to the lowest taxonomic level possible. We found 11 different Phyla that made up the diets of green turtles, including 49 species of macroalgae, 36 of Mollusca, and 11 of Piscis. The most consumed prey items were Magnoliophyta, followed by Rhodophyta and Mollusca. We found interannual differences represented by Magnoliophyta, Rhodophyta, Chlorophyta, Mollusca and Phaeophyceae, in 2008, 2011, 2015-2020. *Ulva lactuca* was important in 2008, 2011-2018; Bivalvia and Gastropoda in 2016 and 2017; Crustacean in 2016; and Echinoderm in 2018. Considering the climatic events, we can highlight Hydrozoa, Chlorophyta, Crustacean and Mollusca during La Niña. Regarding the seasons, Echinoderm was important in autumn and winter; Hydrozoa and Gastropoda in all seasons. The results underscore the dietary plasticity of green turtles, which could be driven by natural/anthropogenic changes. Understanding the potential effects of these variations in turtles' health and fitness might be key information to guide future conservation plans.

Keywords: sea turtle; feeding ecology; behavioural plasticity; Southwestern Atlantic; spatial-temporal scale; seaweeds; bivalve; conservation.

INTRODUCTION

Diet, nutrition, and the way sea turtles use foraging areas all influence their growth, development, reproductive output, fitness and health condition, but also have implications for habitat preferences and thus, population susceptibility to spatially explicit anthropogenic threats (e.g. marine debris ingestion, bycatch mortality) and recovery potential (Schoener 1987; Vander Zanden et al. 2014; Trites & Spitz 2018). Long-term diet studies are key for deciphering temporal changes in feeding behavior and habitat use patterns, which are crucial to identify areas of biological importance, prioritizing what foraging areas most need protection (Fuentes et al. 2006; Marcovaldi and Santos 2011; Vélez-Rubio et al. 2018). Indeed, studies of the links between sea turtles and their foraging areas have been identified among the most important themes in sea turtle conservation (Hamann et al. 2010; Wildermann et al. 2018), especially in the context of ongoing climate change (Hawkes et al. 2009; Fuentes et al. 2020).

When studying green turtles in foraging areas, knowledge about the extrinsic influences such as prey availability, the temperature and rainfall rates in their key-habitat, and other

parameters to evaluate habitat quality is fundamental to our understanding on diet, nutrition and turtles health condition. Also, understanding the influences of long-term and decadal-scale climate on habitats is essential to assess long-term ecological changes (Hawkes et al. 2009; Esteban et al. 2020). The El Niño and La Niña events, for instance, influence the climate variability in southern South America via changes in rainfall patterns and intensity and shifts in sea surface temperatures (Grimm et al. 2000). Therefore, these and other climatic events may drive biological changes (e.g. habitat dynamics, prey availability), leading to diet variation among turtles in these areas (Saba et al. 2008; Quiñones et al. 2010, Esteban et al., 2020).

The cryptic nature of sea turtles and the logistic difficulties of capturing live turtles in the wild are challenges for studying their diet intake and overall foraging ecology (Reich et al. 2007; Vander Zanden et al. 2014; Wildermann et al. 2018). However, in many areas worldwide, sea turtles are exposed to significant human threats, resulting in often live- or dead- strand along shores in areas adjacent to where the source of threats exist. In such areas, ongoing systematic and long-term sea turtle stranding monitoring programs present an opportunity to encounter and recover these individuals for health and ecological assessments. There are several biological samples obtained from dead-stranded sea turtles via stranding response programs, including soft tissues and bones, which allow studies related to demography, age, pathologies, sex ratios, and the frequency of occurrence of the species in the area (Vélez-Rubio et al. 2003; Maldini et al. 2005). For turtles recovered in a relatively well-preserved state (McMichael et al. 2008; Peckham et al. 2008; Orós et al. 2016; Arizza et al. 2019), intact gut contents can yield information about the entire array of consumed prey items (Seminoff et al. 2002; Vélez-Rubio et al. 2018).

In addition to biological specimen collection, such monitoring efforts can identify stranding hotspots (Hart et al. 2006; Cantor et al. 2020) and sometimes even cause of death (Monteiro et al. 2016; Santos et al. 2018; Tagliatto et al. 2019). For example, a local stranding program in Baja California, Mexico, revealed the dramatic impact of bycatch mortality of loggerhead turtles (*Caretta caretta*) in locally-based artisanal gillnet and long-line Pisciseries (Peckham et al. 2008; Senko et al. 2017). In the Mediterranean, Dimitriadis et al. (2022) used stranding data to map risk areas for sea turtles, making management actions possible.

Based on stranding records, southern and southeastern Brazil have relatively high mortality rates for juvenile green turtles, particularly in Paraná and the central area of Santa Catarina state (Cantor et al. 2020). The Paraná coast is also a hotspot of threats to juvenile green

turtles (Fuentes et al., 2020). Conversely, it hosts one of the most impressive mangrove / estuarine systems in the region with nearly 1,500 km of interior coastline (Lana et al. 2001; Santos and Lana 2017) and is a biodiversity hotspot (UNESCO 2021). Several long-term studies have been ongoing in this area since 2004, including beach monitoring and stranded marine animal recovery. After 2015, the stranding monitoring project in this region was encapsulated by the ongoing project Santos Basin Beach Monitoring Project (PMP-BS), which is a requirement set by the Brazilian Institute of the Environment (IBAMA) for the environmental licensing of the oil and natural gas production and transport by Petrobras. Daily, this project systematically covered beaches from the states of Santa Catarina to Rio de Janeiro.

One of the most commonly encountered species is the green turtle (*Chelonia mydas*), of which more than 1,000 individuals are found dead-stranded each year (Cantor et al. 2020). Green turtle mortality has been attributed to a variety of local negative threats such as ongoing habitat degradation, bycatch, marine debris ingestion, chemical pollutants, and emergence diseases (Domiciano et al. 2019). Green turtles use the Paraná coast throughout the year and are originated from at least 12 rookeries (Savada et al. 2021). The area is an important foraging ground for juveniles in the Southwestern Atlantic Ocean (SWAO) (Marcovaldi and Santos 2011; Gama et al. 2016; Vélez-Rubio et al. 2018).

Previous studies on green turtle diet in the SWAO showed a high diversity of the consumed prey items, including seagrasses (Guebert-Bartholo et al. 2011); macroalgae (Nagaoka et al. 2012; Awabdi et al. 2013; Santos et al. 2015; Gama et al. 2016); mangrove leaves and seeds (Nagaoka et al. 2012; Gama et al. 2016), and animal matter, in higher latitudes (Bugoni et al. 2003; Gonzalez-Carman et al. 2014; Santos et al. 2015; Gama et al. 2021). However, no study in the SWAO has explored together seasonal and annual variability in diet, particularly based on long-term monitoring. Therefore, considering the importance of the Paraná coast as a stopover for juvenile green turtles from the SWAO RMU, the present study examined gut contents of dead-stranded green turtles encountered along this area between 2008-2020, in an effort to determine seasonal and interannual diet variability, disclosing potential ecological changes and drivers. To achieve this goal, three different analyses were conducted, including (i) low taxonomic resolution (*i.e.*, to phylum level) diet analysis to check the main changes in items ingestions throughout the years, (ii) high taxonomic resolution (*i.e.*, to species level) diet analysis focusing on macroalgae identification and their seasonal variation, and (iii) high taxonomic resolution diet analysis focusing on invertebrates identification and seasonal

variation, considering their importance and high occurrence in green turtles diet in Paraná coast. Collectively, the results were evaluated regarding the potential changes caused by extreme climate events.

MATERIALS & METHODS

Study site

The Paraná coast, southern Brazil ($25^{\circ}20'S$ to $25^{\circ}35'S$ / $48^{\circ}17'W$ to $48^{\circ}42'W$), is a migratory corridor for multiple sea turtle species that are present in the SWAO (Marcovaldi & Santos 2011; Wallace et al., 2010). Paraná has ~90 km of sandy beaches, and several bays and estuaries, such as the Paranaguá Estuarine Complex (PEC), a 612-km² semi-enclosed inlet, that comprises ~1000 km of estuarine interior coastline (Lana et al. 2001) (Fig. 1).

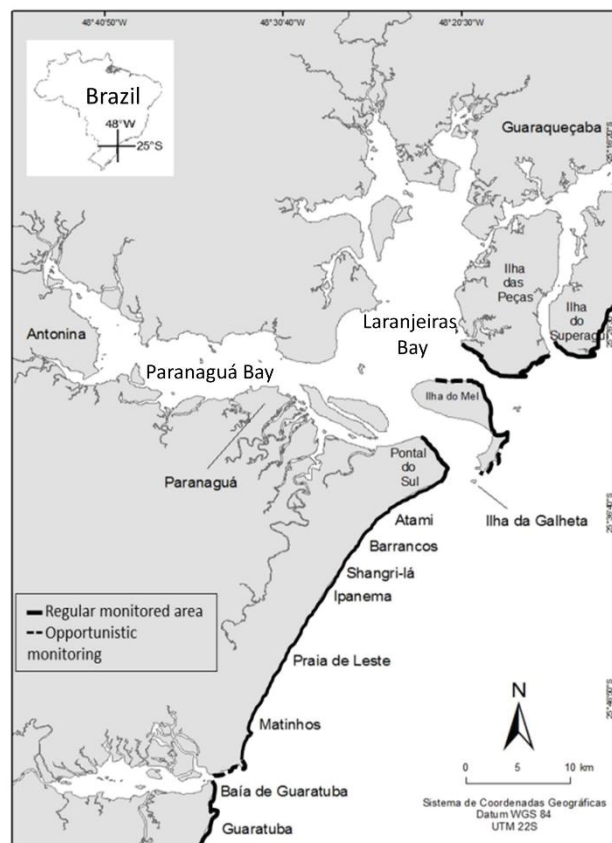


Figure 1. Map of the Paraná coast of Brazil, including the Paranaguá Estuarine Complex (PEC), in south Brazil, where the beach surveys were performed, and dead-stranded green turtles were

recovered. The thick lines represent the regular monitored area, whereas the dashed one represents the areas where the monitoring has been made occasionally.

The area is in the subtropical climatic zone and hosts a diversity of marine habitats such as seagrass meadows (*Halodule wrightii*), mangrove-lined (mainly *Avicennia schaueriana*) estuaries, and rocky subtidal habitats dominated by marine macroalgae (Angulo 1992; Sordo et al. 2011; Pellizzari et al. 2014; Bumbeer et al. 2016; Pellizzari et al. 2020). Macroalgal diversity along the Paraná coast and islands is considered low (~130 taxa) compared to other tropical areas in Brazil (Pellizzari *et al.* 2014). Nevertheless, several species of green macroalgae (Chlorophyta), red macroalgae (Rhodophyta), and brown macroalgae (Phaeophyceae) occur in high biomass (Pellizzari et al. 2007, 2014, 2021; Pellizzari & Reis 2011).

Paraná is influenced by the Brazilian Current, which brings warm waters to the south during the austral summer (wet season), and the Falklands Current which introduces cold waters during the winter (dry season) (Piola et al. 2000; Matano et al. 2010). The PEC is composed by three different haline zones (estuarine, estuarine outlets and open-ocean coasts) (Angulo and Araujo 1996), that result in a salinity gradient and hence, differences in local habitats (Krelling & Turra 2019). The average sea surface temperature (SST) values ranged from 21.60°C in 2008 to 26.71°C in 2014; whereas the monthly average rainfall values ranged from 120.66 in 2014 to 276.63 in 2010 (Fig. 1; *supplementary material*).

Dead-stranded turtle collection

Dead stranded green turtles were collected along the Paraná coast (Fig. 1) during daily beach surveys from 2008 to 2020; however, only fresh-dead juveniles with intact tissues were considered. All the specimens had their body size, represented by their curved carapace length (CCL; cm measured with a flexible metric tape from the nuchal scute notch to the posterior-most edge of the carapace) recorded and biological samples collected for further necropsy analysis. During necropsy, the digestive tracts were removed and stored frozen at -10°C until analysis. The sampling year, locality, date, season, and body size were recorded for each recovered green turtle

Diet analysis

To determine diet composition, all recovered items were washed, separated, and identified, then re-stored frozen at -10°C . Two separate datasets are evaluated here because different groups of researchers analyzed the guts contents: one including turtles recorded between 2008 and 2014, plus 2017 and 2018 (Group I); and another one between 2015 and 2020 (Group II - part of the PMP-BS program). Both groups evaluated macroalgae and invertebrate contents with stereoscopic and optical equipment; however, the identified items in a low taxonomic level by the groups of researchers were different. In addition, all digestive tracts were analyzed to quantify the presence of marine debris.

Green turtles analyzed by Group I had all their digestive tract contents identified to the phylum level; however, the absence of an invertebrate specialist resulted in only macroalgae contents being identified to the species level. The morphology of reproductive and vegetative structures was used as distinguishing features for algae identification, which was based on Cordeiro-Marino (1978), Nunes *et al.* (1999), Moura (2000), Barata (2004), Nunes (2005), Coto (2007), Crispino (2007), Pereira-Filho *et al.* (2011; 2012), and Pellizzari *et al.* (2014). Taxonomical updates followed Guiry & Guiry (2021).

Green turtles evaluated by the Group II also identified all diet contents to the phylum level, but the lack of a phycologist resulted in only invertebrates being keyed to the genus or species level. All the invertebrates were identified using appropriate books and identification keys (Ruppert & Barnes, 1996; Wiggers, 2003; Pimpão, 2004; Xavier & Cherel, 2009; Absher, 2015), followed by specialists' support.

Statistical analysis

To analyze the digestive tract contents recovered during both the Group I and II efforts, the frequency of occurrence ($\%FO$) (Hyslop 1980) was calculated for each diet item [Eq.1]:

$$\%FO = \frac{\text{Number of samples containing diet item}}{\text{Total number of samples}} * 100$$

Specific to the macroalgae, the relative wet biomass ($\%Biomass$; g.) was calculated [Eq. 2]:

$$\%Biomass = \frac{\text{Total weight (in g) of a certain prey}}{\text{Total weight of all the prey items}} * 100$$

This index was used in addition to *%FO* because all the macroalgae species were weighed and *%Biomass* is considered a more accurate index when compared to the *%FO* only (Silveira et al. 2020).

In addition, to test for interannual variation (from 2008 to 2020) in diet composition and influence of climatic events on diet (weak, moderate, or strong El Niño - which increases the rainfall and the temperature; or La Niña – which decreases the rainfall and the temperature). The climatic data was obtained from <http://enos.cptec.inpe.br/>. A two-factor PERMANOVA was performed on logit-transformed (Warton & Hui, 2011) *%FO* data (year + climatic event, Euclidian distance, 9999 permutations) (Anderson, 2001; 2003). A PCA (Legendre & Legendre, 2012; Borcard et al. 2018) was performed to visually interpret the PERMANOVA results. In a PCA, the first axis highlights annual trends in the diet of green turtles; the second one highlights seasonal trends in food consumption; whereas the third reveals food categories complementary to those highlighted in axis 1; and the fourth axis reveals complementary information related to the second axis. All analyses were performed using R 4.0 software (R Core Team 2019).

Also, to determine the intra-annual differences in diet composition based on ‘season of the year’, a PERMANOVA with transformed data ($\log x + 1$; Euclidian distance) was used. The austral seasons were the considered, with January, February, and March corresponding to the summer (late wet); April, May, and June, to the autumn (early dry); July, August, and September, to the winter (late dry); and October, November, and December, to the spring (early wet). A PCA (Legendre & Legendre, 2012; Borcard et al. 2018) was performed to evaluate variation in diet composition among the collected individuals and to determine which food items were the most influential in explaining variation in green turtle diet.

RESULTS

General demographic results

In the present study 351 dead-stranded green turtles were collected, ranging in size from 23.2 cm to 68 cm CCL (mean $\pm$ SD, 38.77 ± 7.16 cm). A total of 148 green turtles were evaluated by Group I (mean CCL = 38.83 ± 6.53 cm; range = 28.2– 62.0 cm), whereas 142 turtles were studied by the Group II (mean CCL = 38.39 ± 7.85 cm, range = 23.2 – 68.0 cm). In all cases these body sizes correspond to immature individuals, based on adult carapace size thresholds (Mendonça et al. 2007). While Group I had the largest sample sizes in 2017 (n = 32) and 2018 (n = 21), the highest annual sample size for Group II was in 2020 (n = 35) (Fig. 2).

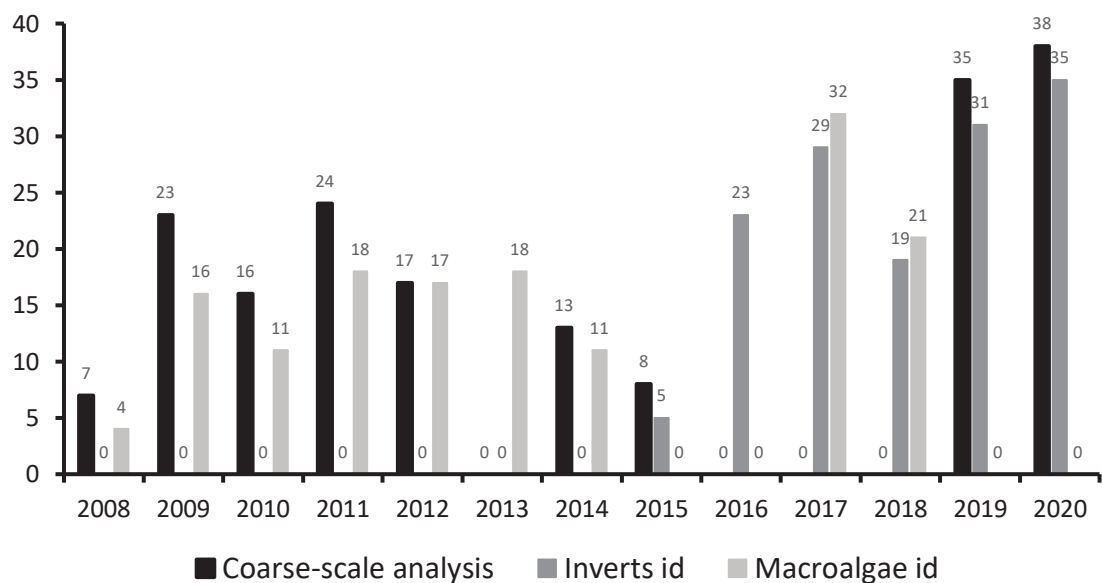


Figure 2: Number of strandings of juvenile green turtles, sampled in the Paraná coast, which had their digestive tracts analyzed with the coarse-scale analysis; by the invertebrate specialists (2015-2020); and by the macroalgal specialists (2008-2014, 2017, 2018), in each year of the study. The years of 2015, 2016, 2019 and 2020 did not have any macroalgae identification at the species level.

Diet composition

Considering the entire database, a total of 11 different Phyla: Magnoliophyte (including mangrove and seagrass), Rhodophyta, Mollusca, Chlorophyta, Phaeophyceae, Bryozoa, Hydrozoa, Echinoderm, Annelida, Cyanobacteria, Piscis; and two classes: Crustacea and Insecta, were encountered in digestive tracts of green turtles (Fig. 3). Among the diet items encountered, the phylum Magnoliophyta was the most frequent ($FO\% = 60.11$), followed by

Rhodophyta (%FO = 41.31), and Mollusca (FO% = 41.02) (Fig. 3). Regarding marine debris occurrence, 69.23% (n = 243) of sampled green turtles has some sort of plastic or other anthropogenic-derived debris recovered from their digestive tracts (Fig. 3).

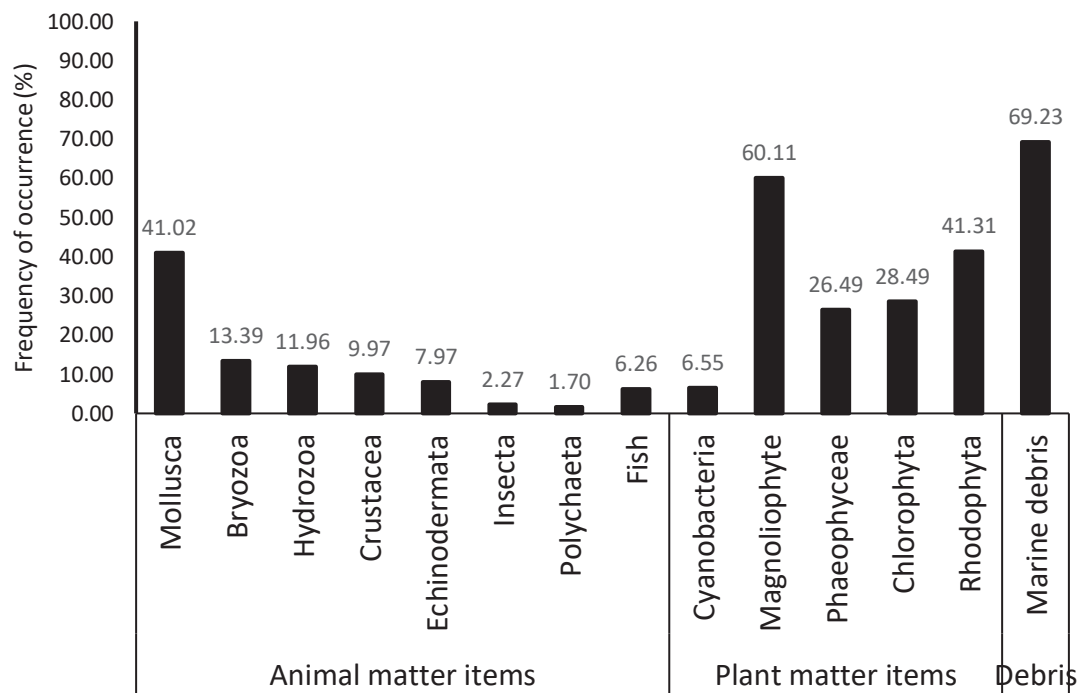


Figure 3: Frequency of occurrence (FO%) of all the prey items found in the digestive tracts stranded immature green turtles (n = 351) in Paraná coast from 2008 to 2020.

A total of 49 species of macroalgae were identified in the Group I dataset, comprised of 31 species of Rhodophyta (red macroalgae), 14 species of Chlorophyta (green macroalgae), and four species of Phaeophyceae (brown macroalgae) (Table 1). The most frequent macroalgae found in the digestive tracts was *Ulva lactuca* Linnaeus 1753 (n = 68 digestive tracts; %FO = 45.94), followed by *Sargassum cymosum* C. Agardh (n = 60; %FO = 40.54), and *Gracilaria domingensis* (Kützinger) Sonder ex Dickie 1874 (n = 30; %FO = 20.27) (Table 1). Parts of the mangrove tree *Avicennia schaueriana* (Stapf & Leechm) and the seagrass *Halodule wrightii* (Ascherson) were the only identified angiosperm species (n = 23; %FO = 15.26). Only 14 specimens presented animal matter items in their digestive tracts (%FO = 9.48).

Table 1: Frequency of occurrence (%*FO*) and biomass (%*Biomass*) of macroalgal species registered in digestive tract (DT) contents of juvenile green turtles (n = 148) collected dead-stranded along the Paraná coast from 2008-2014 and 2017-2018.

Taxa	Author	N of DT	%FO	%Biomass
CHLOROPHYTA				
<i>Caulerpa</i> sp.		2	1.047	n.d.
<i>Chaetomorpha aerea</i>	(Dillwyn) Kützing	5	2.617	0.008
<i>Chaetomorpha antennina</i>	(Bory) Kützing	2	1.047	n.d.
<i>Chaetomorpha</i> sp.		1	0.523	n.d.
<i>Cladophora catenata</i>	Kützing	1	0.523	n.d.
<i>Cladophora vagabunda</i>	(Linnaeus) Hoek	7	3.644	0.036
<i>Cladophora</i> sp.		6	3.141	0.016
<i>Cladophoropsis membranacea</i>	(Hofman Bang ex C. Agardh)	1	0.523	n.d.
<i>Rhizoclonium</i> sp.		6	3.141	0.010
<i>Ulva</i> cf. <i>chaetomorphoides</i>	(Børgesen) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	1	0.523	n.d.
<i>Ulva fasciata</i>	Delile	1	0.523	n.d.
<i>Ulva flexuosa</i>	Wulfen	1	0.523	n.d.
<i>Ulva lactuca</i>	Linnaeus	77	40.31	58.92
<i>Willeella brachyclados</i>	(Montagne) M.J.Wynne	1	0.523	n.d.
Total		77	40.52	
OCHROPHYTA/PHAEOPHYCEAE				
<i>Chnoospora minima</i>	(Hering) Papenfuss	4	2.094	n.d.
<i>Dictyota</i> sp.		7	3.644	0.011
<i>Padina</i> sp.		8	4.188	0.05
<i>Sargassum cymosum</i>	C. Agardh	40	20.942	2.40
Total		40	21.05	
RHODOPHYTA				
<i>Aglaothamnion uruguayense</i>	(W.R.Taylor) N.E.Aponte, D.L.Ballantine & J.N.Norris	1	0.523	n.d.
<i>Aglaothamnion</i> sp.		1	0.523	n.d.
<i>Amphiroa beauvoisii</i>	J.V.Lamouroux	1	0.523	n.d.
<i>Asparagopsis taxiformis</i>	(Delile) Trevisan	2	1.047	n.d.
<i>Bostrychia binderi</i>	Harvey	2	1.047	n.d.
<i>Bostrychia radicans</i>	(Montagne) Montagne	1	0.523	n.d.
<i>Bostrychia</i> sp.		4	2.094	0.001
<i>Bostrychia tenella</i>	(J.V.Lamouroux) J.Agardh	2	1.047	n.d.
<i>Caloglossa</i> sp.		1	0.523	n.d.
<i>Ceramium</i> sp.		3	1.570	0.015
<i>Chondracanthus</i> sp.		1	0.523	n.d.
<i>Chondracanthus teedei</i>	(Mertens ex Roth) Kützing	3	1.570	0.005
<i>Chondria</i> sp.		1	0.523	n.d.
<i>Dipterosiphonia</i> sp.		1	0.523	n.d.

<i>Gelidium pusillum</i>	(Stackhouse) Le Jolis	5	2.617	0.023
<i>Gelidium</i> sp.		5	2.617	0.014
<i>Gracilaria domingensis</i>	(Kütz) Sond. Ex Dickie	27	14.136	5.09
<i>Heterosiphonia crispella</i>	(C.Agardh) M.J.Wynne	1	0.523	n.d.
<i>Heterosiphonia</i> sp.		3	1.570	0.041
<i>Hypnea pseudomusciformis</i>	Nauer, Cassano & M.C.Oliveira	8	4.188	0.020
<i>Hypnea</i> sp.		8	4.188	0.015
<i>Hypnea spinella</i>	(C.Agardh) Kützinger	4	2.094	0.007
<i>Neosiphonia</i> sp.		1	0.523	n.d.
<i>Plocamium</i> sp.		1	0.523	n.d.
<i>Polysiphonia howei</i>	Hollenberg in W.R. Taylor	1	0.523	n.d.
<i>Polysiphonia</i> sp.		1	0.523	n.d.
<i>Pterocladia</i> sp.		2	1.047	n.d.
<i>Pterosiphonia parasitica</i>	(Hudson) Falkenberg	3	1.570	0.001
<i>Pterosiphonia pennata</i>	(C.Agardh) Sauvageau	6	3.141	0.015
<i>Pterosiphonia</i> sp.		1	0.523	n.d.
<i>Pyropia</i> sp.		17	8.900	0.49
Total		49	25.78	

Regarding the Group II identification, a total of five phyla (Mollusca, Bryozoa, Hydrozoa, Echinodermata, Piscis, two sub-phyla (Crustacean and Insecta), seven classes (Gastropoda, Bivalvia, Cephalopod, Scaphopod, Polychaeta, Pycnogonida, Echinoidea), two infraclasses (Cirripedia, Teleostei), one superorder (Octopodiformes, Decapodiformes), two orders (Balanomorpha, Decapoda), one suborder (Pleocyemata), one superfamily (Paguroidea), and 28 families were registered. A total of 36 species of Mollusca and 11 species of Piscis were identified (Table 2). The most frequent invertebrate taxon found in the digestive tracts was Bivalvia ($FO\% = 43.66$) (Table 2). Moreover, 87 specimens presented Magnoliophyta in their digestive tracts ($FO\% = 61.26$ (87); and 47 ($FO\% = 33.09$), Phaeophyceae; 55 ($FO\% = 38.73$), Chlorophyta; and 71 ($FO\% = 50$), Rhodophyta.

Table 2: Frequency of occurrence ($FO\%$) of the taxonomic groups of invertebrates registered in digestive tract (DT) contents of juvenile green turtles ($n = 142$) collected dead-stranded along the Paraná coast from 2015 to 2020. The most frequent species are in bold.

Taxon	Number of digestive tracts	Frequency of occurrence ($FO\%$)
Phylum Mollusca	96	56.14
Gastropoda	50	29.23
<i>Acteocina leptota</i>	1	0.58
<i>Acteocina</i> sp.	1	0.58

Family Architectonicidae	1	0.58
Family Atlantidae	3	1.75
<i>Bitiolium varium</i>	1	0.58
Family Calyptraeidae	2	1.16
<i>Cavolinia</i> sp.	7	4.09
<i>Cavolinia tridentata</i>	1	0.58
Family Cavolinidae	1	0.58
Family Cerithiidae	1	0.58
<i>Cerithium</i> cf. <i>algicola</i>	1	0.58
Family Collumbelidae	9	5.26
<i>Costoanachis sertularium</i>	2	1.16
<i>Costoanachis</i> sp.	4	2.33
<i>Diacria</i> sp.	2	1.16
<i>Diacria trispinosa</i>	2	1.16
<i>Diodora</i> sp.	1	0.58
Family Epitoniidae	1	0.58
<i>Epitonium angulatum</i>	1	0.58
<i>Epitonium</i> sp.	1	0.58
<i>Eulithidium affine</i>	1	0.58
<i>Heleobia australis</i>	1	0.58
Family Hipponicidae	1	0.58
<i>Melanella hypsela</i>	1	0.58
<i>Mitrella</i> cf. <i>moleculina</i>	1	0.58
Family Nassaridae	2	1.16
Family Neritidae	1	0.58
<i>Neritina virginea/Vitta virginea</i>	3	1.75
<i>Olivella</i> sp.	2	1.16
Family Olividae	2	1.16
<i>Parvanachis</i> sp.	1	0.58
Family Tateidae	1	0.58
<i>Turbonilla</i> sp.	2	1.16
Family Turritelidae	1	0.58
Bivalvia	62	43.66
<i>Anadara ovalis</i>	2	1.16
<i>Anadara</i> sp.	3	1.75
Family Arcidae	1	0.58
<i>Brachidontes</i> sp.	1	0.58
<i>Carditamera</i> sp.	1	0.58
<i>Corbula</i> sp.	5	2.92
Family Corbulidae	1	0.58
<i>Crassatella riograndensis</i>	1	0.58
<i>Crassostrea</i> sp.	1	0.58
<i>Ctena</i> cf. <i>pectinella</i>	1	0.58
<i>Ctena</i> sp.	1	0.58
Family Donacidae	1	0.58
Family Mactridae	1	0.58
Family Mytilidae	5	2.92
<i>Noetia bisulcate</i>	2	1.16
<i>Nucula</i> sp.	4	2.33
Family Ostreidae	5	2.92
Family Pectinidae	3	1.75
<i>Perna perna</i>	1	0.58
<i>Semele nuculoides</i>	3	1.75
<i>Strigilla</i> sp.	3	1.75
Cephalopod	11	6.43
<i>Doryteuthis pleii</i>	1	0.58
Octopodiformes	2	1.16

Family Spirulidae	1	0.58
Scaphopod	2	1.16
Phylum Bryozoa	5	2.92
Phylum Hydrozoa	5	2.92
Plumularioidea	1	0.58
Crustacean	5	2.92
Family Balanidae	1	0.58
Balanomorpha	1	0.58
Family Barleeiidae	1	0.58
Cirripedia	4	2.33
Decapoda	1	0.58
Decapodiformes	2	1.16
Paguroidea	1	0.58
Pleocyemata	1	0.58
Phylum Echinoderm	4	2.33
Echinoidea	1	0.58
Insecta	4	2.33
Pycnogonida	1	0.58
Pterygota	1	0.58
Coleoptera	2	1.16
Coccinellidae	1	0.58
Polychaeta	4	2.33
Phylum Piscis	20	11.69
Teleostei	15	8.77
Family Engraulidae	1	0.58
<i>Harengula chupeola</i>	1	0.58
<i>Lycengraulis grossidens</i>	1	0.58
<i>Pellona harroweri</i>	1	0.58
<i>Ctenosciaena gracilicirrus</i>	2	1.16
<i>Isopisthus parvipinnis</i>	2	1.16
<i>Micropogonias furnieri</i>	2	1.16
<i>Paralichthys brasiliensis</i>	2	1.16
Family Sciaenidae	2	1.16
<i>Stellifer brasiliensis</i>	1	0.58
<i>Stellifer rastriifer</i>	2	1.16
<i>Stellifer</i> sp.	1	0.58
<i>Raneya brasiliensis</i>	1	0.58

Interannual variation of diet

According to PERMANOVA results, consumption of food categories by green turtles was significantly different between years (from 2008 to 2020) ($F\text{-value} = 2.1973$; $p\text{-value} = < 0.0001$; $DF = 12$) ($n = 351$) (Table 3); for the macroalgae identification ($n = 148$) (from 2008 to 2014, 2017 and 2018) ($F\text{-value} = 3.2422$; $p\text{-value} = 0.0003$; $DF = 8$) (Table 4); and for the invertebrate identification ($n = 142$) (from 2015 to 2020) ($F\text{-value} = 2.7995$; $p\text{-value} = 0.003$; $DF = 5$) (Table 5).

Table 3. Results from two-factor PERMANOVA (year + climatic event) for the low-taxonomic resolution diet of all Paraná green turtles herein analyzed ($n = 351$). Df = degrees of freedom;

SS = sum of squares; R^2 = pseudo- R^2 . Values in bold indicate significant differences ($\alpha = 0.05$).

* marginally significant

Sources	Df	SS	R^2	F-value	P-value
Years	12	473.4	0.07199	2.1973	0.0001
Climatic events	3	88.1	0.01339	1.6350	0.0479*
Residual	335	6014.4	0.91462		
Total	350	6575.8	1.00000		

Table 4. Results from two-factor PERMANOVA (year + season) regarding macroalgae species identified and consumed by Paraná green turtles ($n = 148$) from 2008 to 2014, 2017 – 2018. Df = degrees of freedom; SS = sum of squares; R^2 = pseudo- R^2 . Values in bold indicate significant differences ($\alpha = 0.05$).

Sources	Df	SS	R^2	F-value	p-value
Year	8	36.497	0.15836	3.2422	0.0003
Season	3	2.613	0.01134	0.619	0.7486
Residual	136	191.366	0.83031		
Total	147	230.477	1		
Sources	Df	SS	R^2	F-value	p-value

Table 5. Results from two-factor PERMANOVA (year + season) regarding the invertebrates identified and consumed by Paraná green turtles ($n = 142$) from 2015 to 2020. Df = degrees of freedom; SS = sum of squares; R^2 = pseudo- R^2 . Values in bold indicate significant differences ($\alpha = 0.05$). * marginally significant

Sources	Df	SS	R^2	F-value	P-value
Year	5	241.73	0.09163	2.7995	0.0003
Season	3	101.47	0.03846	1.9586	0.0292*
Year:Season	10	170.83	0.06475	0.9892	0.4803
Residual	123	2124.14	0.80516		
Total	141	2638.17	1		

The first four axes of PCA explained 82.74% of data variance (*d.v.*). Axis 1 (47.07% *d.v.*). Axis 1 (47.07% *d.v.*) highlighted annual trends in the diet of all the sampled green turtles from 2008 to 2020. This axis was negatively related to Magnoliophyte (axis score, *a.s.* = -0.73), Rhodophyta (*a.s.* = -0.61), Chlorophyta (*a.s.* = -0.55), Mollusca (*a.s.* = -0.53) and

Phaeophyceae ($a.s. = -0.45$), foods categories high important in the diet of green turtles in all year analysed, highlighting 2008, 2011 and 2015-2020 (Fig. 4).

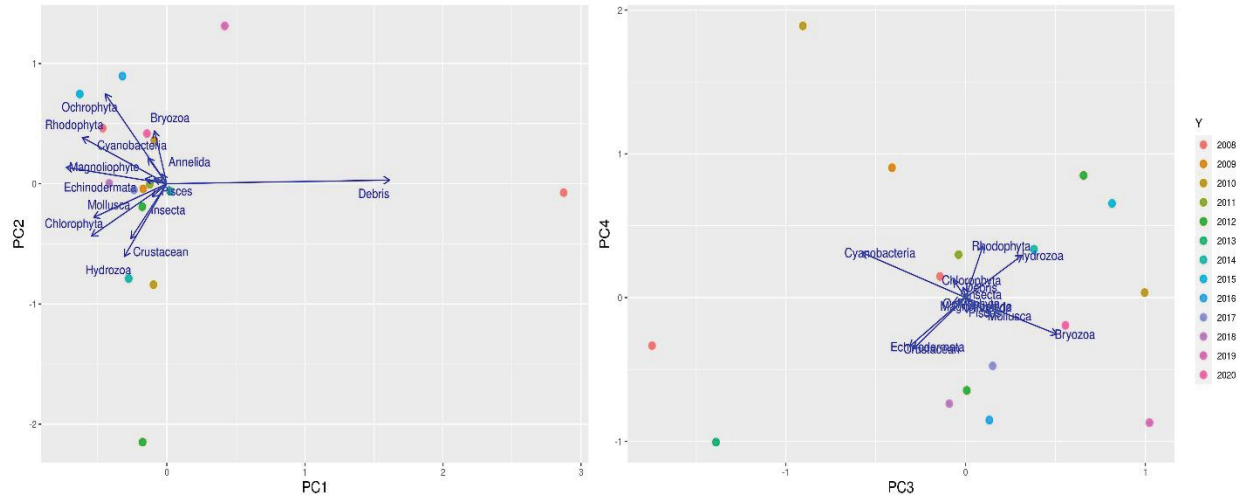


Figure 4: PCA showing the interannual tendencies of green turtles diet ($n = 351$) across 12 years of analysis in Paraná coast, south Brazil.

Regarding macroalgae species, the first four axes of PCA explained 97.10% of data variance ($d.v.$). Axes 1 (61.55% $d.v.$) and 2 (16.92% $d.v.$) highlighted the consumption of *U. lactuca*, *G. domingensis* e *S. cymosum* by green turtles sampled from 2008-2014, 2017 and 2018 (Fig. 5).

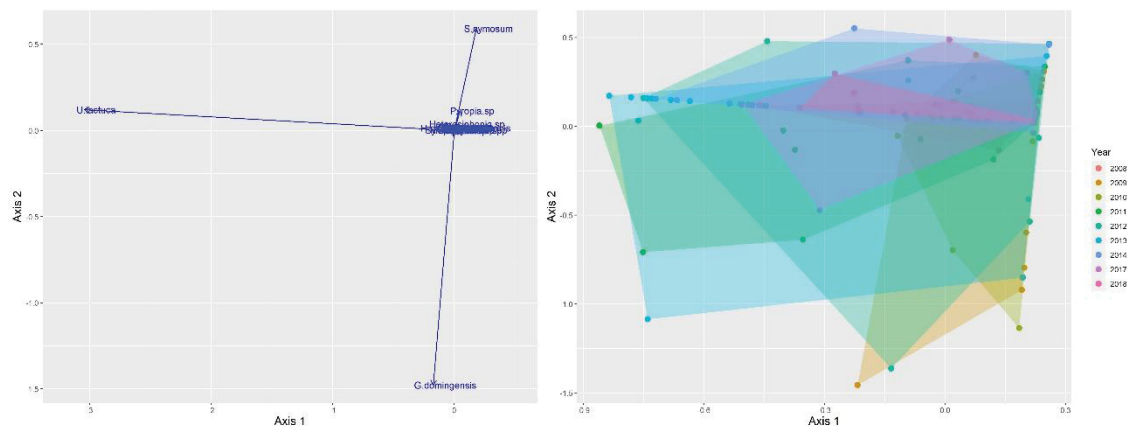


Figure 5: PCA showing the annual tendencies of green turtles diet based on macroalgae occurrence ($n = 148$) from 2008 to 2014, 2017 and 2018 in Paraná coast, south Brazil.

In axis 1, the multivariate subspaces of the years 2008 and 2011-2018 were elongated due to the importance of *U. lactuca* (axis score, $a.s. = -3.05$) in the diet of green turtles,

representing from 59.48% to 96.72% of the biomass ingested. *Gracilaria domingensis* ($a.s. = -0.17$) and *S. cymosum* ($a.s. = 0.18$) complemented the diet of green turtles in 2008 and 2011-2014. In axis 2, *G. domingensis* ($a.s. = -1.48$) was highlighted due its importance in the diet of green turtles in 2009-2010, representing 83.05% and 70.19% of the ingested biomass, respectively. Axis 3 (13.95% $d.v.$) confirmed the importance of *S. cymosum* ($a.s. = -1.34$) as complementary food for all years, and the importance of *G. domingensis* ($a.s. = -0.55$) both as main consumed food in 2009-2010 and as complementary food for the remain years analysed (2008, 2001-2014, 2017 and 2018). And axis 4 (4.67% $d.v.$) revealed the importance of *Pyropia* sp. ($a.s. = -0.82$) for the diet of green turtles in 2010 and 2017-2018, when this food represented from 8.45% to 26.99% of ingested biomass (Fig. 5).

Regarding invertebrate consumption, the first four axes of PCA explained 79.69% of the data variance ($d.v.$). Axis 1 (38.22% $d.v.$) highlighted global trends in the diet of green turtles: Bivalvia, Gastropoda, Debris and Hydrozoa were the most recurrent consumed food categories, being exploited in all years (Fig. 6).

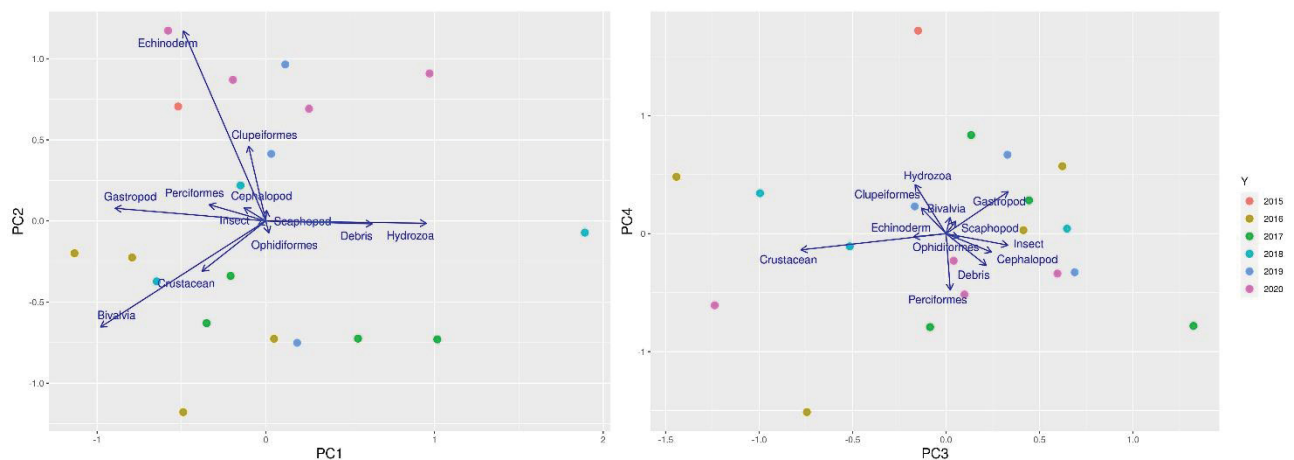


Figure 6: PCA showing the tendencies of green turtles ($n = 142$) diet based on invertebrate occurrence from 2015 to 2020 in Paraná coast, south Brazil.

Despite of this generality, Bivalvia ($a.s. = -0.98$) and Gastropoda ($a.s. = -0.89$) were mainly consumed in 2016 and 2017, whilst Hydrozoa ($a.s. = 0.95$) and debris ($a.s. = 0.63$) were mainly exploited between 2017-2020. Axis two (22.85% $d.v.$) confirmed the high consumption of Bivalvia ($a.s. = -0.65$) in 2016-2017 and revealed that Crustacean was recurrently exploited ($a.s. = -0.31$) in 2016. Axis 2 also revealed that Echinoderm ($a.s. = 1.17$) was an important food resource in 2020 and 2019. Axis 3 (10.80% $d.v.$) and 4 (7.81% $d.v.$) confirmed the food trends

revealed in axes 1 and 2. Axis 3 confirmed the consumption of Crustacean ($a.s. = -0.78$) in 2016 and revealed its exploitation in 2018 and 2020. In addition, this axis confirmed the importance of Gastropoda ($a.s. = 0.33$) in the diet of green turtles from 2016 to 2020, and revealed the consumption of Insect ($a.s. = 0.33$) in 2017, 2019 and 2020. Axis 4 revealed a recurrent consumption of Perciformes ($a.s. = -0.48$) in 2016, 2019 and 2020, and confirmed the importance of Hydrozoa ($a.s. = 0.42$) and Gastropod ($a.s. = 0.36$) in the diet of green turtles in the different years.

Influence of climatic events on diet composition

We analyzed 106 turtles encountered during El Niño events (years of 2015, 2016, 2019), and 245 during La Niña events (years of 2011, 2012, 2013, 2014, 2017, 2018, 2020) (Fig 1., *supplementary material*). Based on PERMANOVA results, we found significant differences in diet composition among climatic events considering all the sampling years (2008 – 2020) ($F\text{-value} = 1.6350$; $p\text{-value} = < 0.0479$; $DF = 3$) (Table 3).

Concerning the positive portion of axis 1, it was related to the exclusive consumption of debris ($a.s. = 1.61$) in 2008. Axis 2 (19.09% $d.v.$) highlighted seasonal trends in food consumption, revealing the exploitation of Hydrozoa ($a.s. = -0.61$), Chlorophyta ($a.s. = -0.46$), Crustacean ($a.s. = -0.44$) and Mollusca ($a.s. = -0.28$) mainly during LN strong and weak episodes, and the consumption of Phaeophyceae ($a.s. = 0.75$), Bryozoa ($a.s. = 0.44$) and Rhodophyta ($a.s. = 0.39$) not only during EN moderate and strong episodes, but also in LN moderate periods. Axes 3 (9.50% $d.v.$) and 4 (0.07% $d.v.$) revealed food categories complementary to those highlighted in axis 1 without, however, highlight clear seasonal trends. Axis 3 was negatively related to the consumption of Cyanobacteria ($a.s. = -0.58$), Echinoderm ($a.s. = -0.31$) and Crustacean ($a.s. = -0.29$) during periods of EN moderate and LN weak to moderate. The negative portion of axis 4 confirmed the consumption of Crustacean ($a.s. = -0.36$), Echinoderm ($a.s. = -0.34$) and Bryozoa ($a.s. = -0.26$) during periods of EN moderate to strong and LN weak to strong. And positive portion of axis 4 confirmed the exploitation of Hydrozoa ($a.s. = 0.29$), Cyanobacteria ($a.s. = 0.31$) and Rhodophyta ($a.s. = 0.36$) during episodes of EN moderate to strong and LN weak to moderate (Fig. 7).

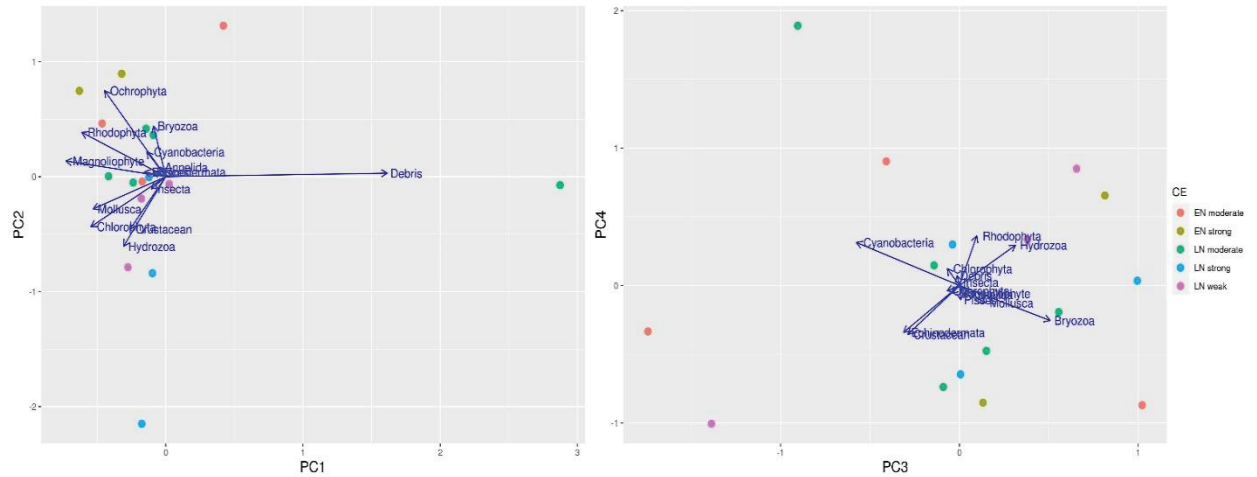


Figure 7: PCA showing the interannual tendencies of green turtles diet ($n = 351$) across 12 years of analysis in Paraná coast, south Brazil, considering the climatic events. ENMod = El Niño moderate; ENstg = El Niño strong; LNmod = La Niña moderate; LNstg = La Niña strong; LNweak = La Niña weak.

Seasonal diet variation

Although no significant seasonal difference was found regarding macroalgae consumption, only six species of macroalgae were encountered during summer and spring, whereas in the autumn and winter, all 49 species were found. The filamentous Cyanobacteria *Lyngbya majuscula* Harvey ex Gomont was found in digestive tracts of 17 turtles (%FO = 11.48), only in winter and autumn. The green macroalgae *Ulva lactuca* was found in green turtle digestive tracts throughout the year, with highest levels in winter and autumn seasons.

From PERMANOVA results, we found significant difference in invertebrate consumption among seasons (sampled turtles from 2015 to 2020) ($F\text{-value} = 1.9586$; $p\text{-value} = 0.0292$; $DF = 3$) (Table 5). Bivalvia ($a.s. = -0.98$) and Gastropoda ($a.s. = -0.89$) were consumed in autumn and spring, whilst Hydrozoa ($a.s. = 0.95$) and debris ($a.s. = 0.63$) were consumed in winter and spring. Axis two (22.85% d.v.) confirmed the high consumption of Bivalvia ($a.s. = -0.65$) from autumn to spring. Axis 2 also revealed that Echinodem ($a.s. = 1.17$) was an important food resource mainly in autumn and winter. Axis 3 confirmed the importance of Gastropoda ($a.s. = 0.33$) in the diet of green turtles in all the seasons and revealed the consumption of Insect ($a.s. = 0.33$) during the autumn and winter. Axis 4 revealed a recurrent consumption of Perciformes ($a.s. = -0.48$) in the autumn and winter and confirmed the importance of Hydrozoa ($a.s. = 0.42$) and Gastropoda ($a.s. = 0.36$) in the diet of green turtles in the different seasons (Fig. 8).

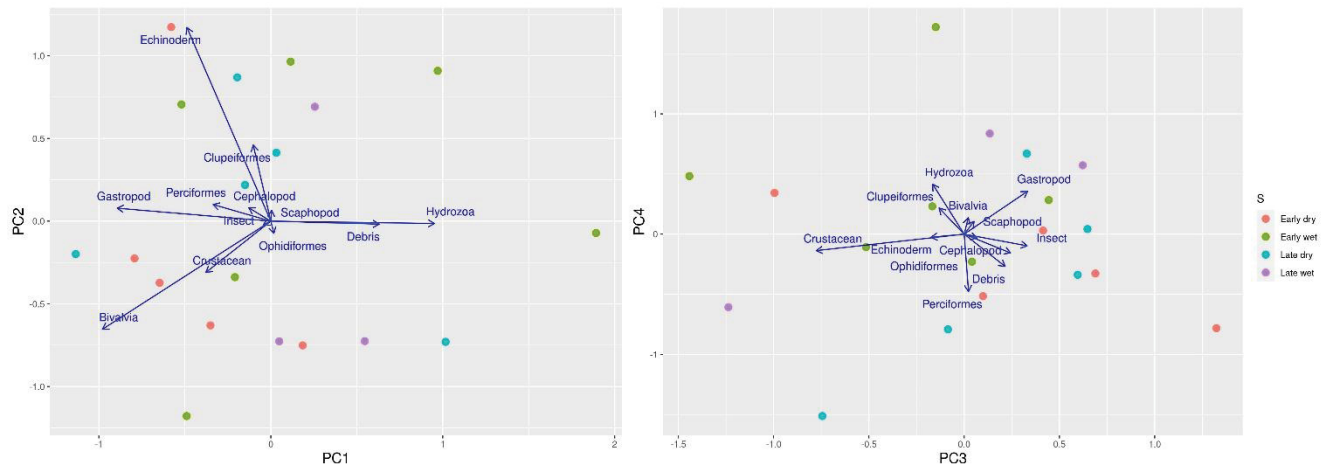


Figure 8: PCA showing the tendencies of green turtles ($n = 142$) diet based on invertebrates occurrence across the seasons of the year in Paraná coast, south Brazil.

DISCUSSION

Long-term diet studies are essential to detect intrinsic and extrinsic variations on ecological interactions, assessing the effects of punctual, local, and temporal changes, but also the ones that happen spread out across the population expressing a new pattern (Clutton-Brock and Sheldon, 2010; Donaton et al. 2019). Data obtained from diet studies help understanding these changes, which can reflect either changes on food resources availability in the habitat or individual foraging behavior (Brand-Gardner et al. 1999; Santos et al. 2015; Campos and Cardona 2020). Moreover, when this dataset is evaluated in a long temporal scale, the diet variation and possible impacts are stressed, which can be accomplished through the stranding monitoring programs (Vélez-Rubio et al. 2003; Monteiro et al. 2016; Cantor et al. 2020).

The juveniles herein analyzed presented a mixed diet and benthic foraging strategy, which are common to specimens that use estuarine and bay areas for foraging, as registered by Santos et al. (2015), and in a review made by Esteban et al. (2020). This omnivorous feeding habit of green turtles has been verified in several diet studies (Arthur et al. 2008, Cardona et al. 2009, Lemons et al. 2011, Santos et al. 2015, Vélez-Rubio et al. 2016, Howell and Shaver 2021) and the consumption of gelatinous prey was observed for small juveniles in Argentina and Uruguay (González Carman et al. 2014, Fukuoka et al. 2016). Although diet changes may be related to environmental parameters, such as the temperature (Esteban et al. 2020) and/or the

foraging behavior itself, green turtles in a same area can present different feeding habits (Santos et al. 2015), making this long-term temporal analysis valuable to detect possible diet shifts and their respective drivers.

We identified an evident annual diet variation comparing samples from 2008-2020, as well as a variation resulted from the climatic events, with progressive higher occurrences of both macroalgae species and invertebrate species in all the sampling periods. Despite of that, we can highlight higher consumptions of macroalgae during El Niño events, resulting from both higher temperature and rainfall. Specifically, about invertebrate consumption, the mollusks and Hydrozoa consumed by the specimens may be related to their availability in the area (Bumbeer et al. 2016) revealing another foraging habitat for juvenile green turtles, as well as feeding habit. Furthermore, it is important to consider that the nutrients absorption of these prey items is higher when compared to the plant matter prey items, because of the faster intake passage time and digestion (Amorocho and Reina 2008). Indeed, most of the invertebrate was consumed during the autumn and winter, when the vegetal matter items are less available, and the energy intake obtained is higher (Bjorndal 1980; Brand-Gardner et al. 1999). Although omnivorous, we found high occurrence of vegetal matter items in green turtles diet, mostly comprised by the three macroalgal groups, which followed the expected pattern for this region, with Rhodophyta being the most representative one in diet and habitat availability (Pellizzari et al. 2014). In accordance with the invertebrate higher consumption during the dry seasons (autumn and winter), the macroalgae diversity was also higher in those seasons, when the temperature is lower, and the vegetal resources availability is lower. Also, we can highlight the high biomass of Chlorophyta (especially of *Ulva lactuca*) herein found, which has also been shown by Santos et al. (2011) in highly urbanized areas along the Brazilian coast, and by Holloway-Adkins & Hanisak (2017) in Florida. The reasons for its higher consumption, besides the availability in the area, may be its high carbohydrates content (Rasyid 2017; Jatmiko et al. 2019); and its low fiber content (28.4%; Rasyid 2017) which makes the turtles' digestion easier and faster. However, this species is tolerant to eutrophic habitats (Ansari et al. 2010; Scherner et al. 2013), and opportunistic that may have extremely high growth rates under human impacted and/or altered habitats (Duarte et al. 2019). Indeed, Sherner et al. (2012) reported the expansion of *Ulva* spp. in contaminated areas, known as a pollution-tolerant species.

Considering marine debris consumption, in a study conducted in southeastern Brazil, the green turtle was the marine species that mostly consumed debris (Di Benedetto and Awabdi,

2014). The hypothesis for debris consumption by green turtles is that they ingest them due to confusion with their prey items and/or by accident (Schuyler et al. 2014). In Paraná coast, specifically, debris consumption is high (Gama et al. 2016; Nunes et al. 2021) and low rainfall is a factor that induces debris presence in the estuarine area (Nunes et al. 2021), making them available to green turtles. Our study reveals marine debris consumption across all the sampled years, with high occurrence from 2017 to 2020, mostly years of La Niña (CPTEC 2016), presenting both low temperature and low rainfall rates (Fig 1; *Supplementary material*).

Our diet findings align with the expected foraging strategies for green turtles that forage in estuarine and bay areas, highlighting an increase on the diversity of dietary items consumed by the species along the years, and this result might be indicating variation in the habitat plant composition. Even though foraging plasticity may be considered for this species, they are exposed to different impacts once it is using different habitats to forage. Delimitating diet changes across the years and how the species respond to climate variability helps to mitigate further conservation actions, not only to the species itself but also to its environment.

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Supplementary material

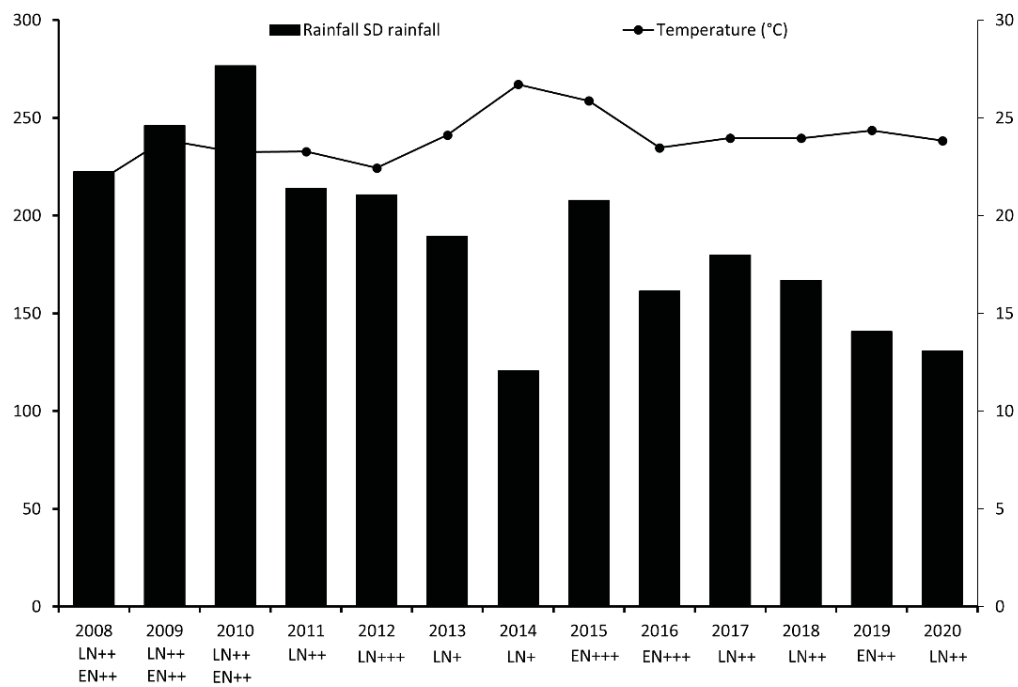


Figure 1: Average rainfall (in mm) values and average temperature (°C) values from 2008 to 2020 in Paraná coast, south Brazil. La Niña (LN) and El Niño (EN) events are included, where “+” means a weak event; “++”, moderate; and “+++” strong.

CONSIDERAÇÕES FINAIS

Os principais objetivos deste estudo foram: i. definir o tamanho do nicho trófico dos juvenis de *C. mydas* encontrados encalhados mortos e intencionalmente capturados vivos na costa do Paraná e a contribuição dos itens alimentares na dieta da espécie, a partir de análises isotópicas; ii. avaliar a variação interanual da dieta da espécie ao longo de 12 anos de estudos no litoral do Paraná, incluindo a variação sazonal da diversidade de itens consumidos pela espécie, com enfoque na análise minuciosa das macroalgas e de invertebrados e relações com eventos climáticos.

Coletivamente, os dados nesta tese apresentados ajudam na compreensão da ecologia alimentar dos juvenis da espécie, esclarecendo questões relacionadas ao uso do habitat, comportamento alimentar e fatores responsáveis por variações na dieta. Estes dados são relevantes para definir quais áreas devem ser priorizadas, bem como auxiliam a traçar planos de manejo em prol da conservação de *Chelonia mydas*.

Concluiu-se que há diversidade ecológica entre os grupos de tartarugas-verde juvenis encontradas mortas e as capturadas vivas intencionalmente no litoral do Paraná, sendo que os espécimes mortos apresentam um nicho isotópico maior, provavelmente formado por indivíduos residentes na área e por recém recrutados, advindos de outras regiões do Oceano Atlântico Sul Ocidental. Além disso, a contribuição dos itens alimentares na dieta também varia entre os grupos, sendo macroalgas e a fanerógama marinha *Halodule wrightii* os itens que mais contribuem na dieta de tartarugas-verde mortas; e os invertebrados e macroalgas, para as tartarugas-verde vivas. Importante ressaltar também o maior consumo de invertebrados em espécimes maiores, resultado inédito encontrado para os juvenis que utilizam o ASO.

No que se refere à variação interanual da dieta, a maior parte dos itens aqui listados é consumida ao longo de todos os anos. No entanto, foram observadas mudanças na dieta de *C. mydas*, sendo possível apresentar diferentes comportamentos alimentares dos indivíduos na área, bem como o alto consumo de invertebrados. Os juvenis de tartarugas-verde apresentam uma dieta heterogênea na região, onívora, com consumo de 49 diferentes espécies de macroalgas marinhas, fanerógamas marinhas, propágulos de mangue e invertebrados. Existe variação interanual e sazonal no consumo dos recursos alimentares, sendo que nas estações de inverno e de outono, a riqueza de espécies consumidas é maior, provavelmente relacionado à disponibilidade nas áreas de alimentação. Foi encontrada variação influenciada pelos eventos

climáticos também, com maior consumo de lixo marinho durante os eventos de La Niña. Esta análise temporal em longa escala permite a compreensão da variação da dieta da espécie em função dos fatores ambientais e a verificação da plasticidade ecológica dos juvenis de tartaruga-verde no ASO, auxiliando a traçar planos de manejo para conservação da espécie.

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