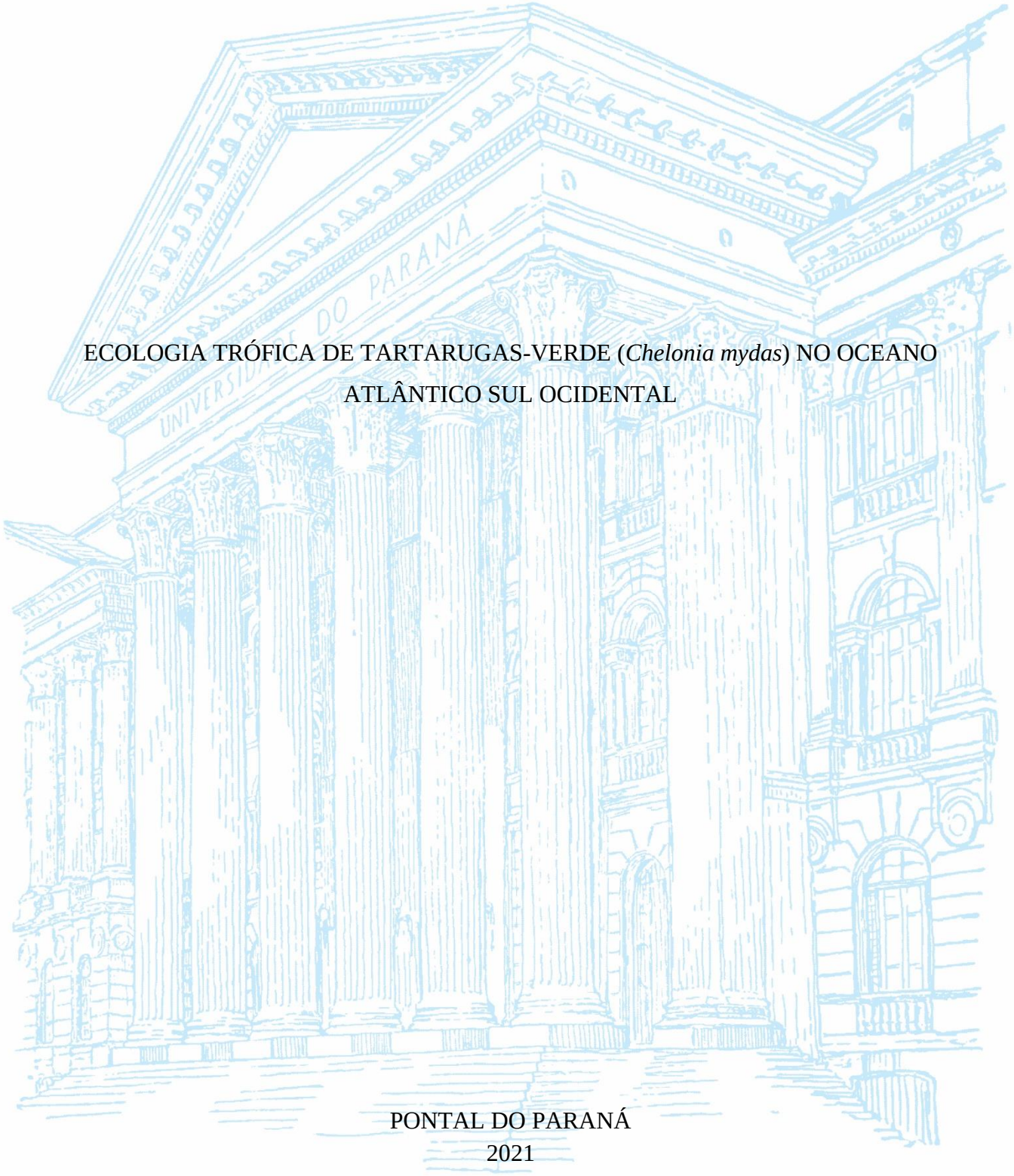
UNIVERSIDADE FEDERAL DO PARANÁ

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

PONTAL DO PARANÁ
2021

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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 tartarugas marinhas na região costeira do Oceano Atlântico Sul-Ocidental (ASO), região composta pelas costas do Brasil, Argentina e Uruguai. No sul do Brasil, o litoral do Paraná é parte do corredor migratório da espécie, além de ser área de alimentação e desenvolvimento para os juvenis. Anualmente mais de 1000 indivíduos são encontrados mortos na região devido a diferentes fatores, incluindo mortalidade natural, e interações diretas e indiretas com atividades antrópicas. Esse elevado número de carcaças permite a realização de diversos estudos ecológicos, incluindo os de ecologia trófica, desenvolvidos no Paraná desde 2004. Avaliações de ecologia trófica podem ser desenvolvidas por meio de diferentes metodologias, incluindo análises de tratos digestórios e análises isotópicas. Seus resultados podem evidenciar variações na dieta da espécie, bem como comportamentos adaptativos frente a alterações de habitat de origem natural e antrópica. Tais informações são essenciais para a identificação de recursos e áreas prioritárias de conservação, assim como para o planejamento territorial e para a conservação. Utilizando dados de dieta obtidos por meio das análises de trato digestório ao longo dos anos e análise de isótopos estáveis de tartarugas capturadas vivas intencionalmente e de indivíduos encalhados mortos, esta tese objetivou em três capítulos: 1) contribuir com o entendimento sobre a forma de uso do habitat pelas tartarugas-verde juvenis; 2) avaliar a variação sazonal da dieta e como ela se relaciona com a disponibilidade dos recursos alimentares; 3) caracterizar a dieta da agregação local de *Chelonia mydas* e investigar variações interanuais. As análises isotópicas mostraram que tartarugas-verde mortas e vivas apresentam nicho trófico diferente, bem como há diferença na contribuição dos itens alimentares na dieta dos respectivos grupos. As tartarugas mortas tiveram seus tratos digestórios analisados, consumiram 15 diferentes grupos taxonômicos de itens alimentares, sendo 49 espécies diferentes de macroalgas marinhas e espécies tóxicas de cianobactérias. Os juvenis apresentam variação na dieta resultante de parâmetros abióticos, mas também de comportamento alimentar individual. Coletivamente, os resultados permitem compreender a diversidade da dieta e comportamento alimentar da espécie, identificar alterações que indicam mudanças na disponibilidade de recursos e evidenciar ações prioritárias para conservação dos juvenis de tartarugas-verde no ASO.

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 three 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, consuming fifteen different taxonomic-prey groups, including 49 different species of macroalgae as well as toxic cyanobacteria species. There is interannual variation on green turtles diet resulting of abiotic parameters, and individual foraging behavior. 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

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PREFÁCIO

A primeira parte do trabalho, em português, é composta por uma introdução geral; objetivo geral do trabalho e específicos de cada capítulo; e por uma metodologia geral, escrita em subtópicos, referentes aos capítulos presentes nesta tese. A segunda parte do trabalho é comporta por três capítulos, cada um deles formado por artigos científicos elaborados seguindo as normas das respectivas revistas científicas. A última parte desta tese traz as considerações finais, nas quais a compilação dos principais resultados encontrados é realizada de forma a destacar a contribuição científica deste estudo.

No primeiro capítulo, 'Trophic ecology of juvenile green turtles in the Southwestern Atlantic Ocean: insights from stable isotope analysis and niche modelling', o objetivo foi analisar isotopicamente as tartarugas-verde que utilizam o litoral paranaense para se alimentar. Como resultados, verificou-se que a população é composta tanto por indivíduos residentes quanto por recém recrutados, sendo possível melhor compreender a diversidade ecológica existente dos juvenis que transitam e se alimentam na região do Oceano Atlântico Sul Ocidental, 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 foi submetido e aceito pelo periódico *Marine Ecology Progress Series*, (ISSN: 0171-8630; IF = 2.32, Qualis A1 biodiversidade), a qual aborda pesquisas relacionadas à ecologia no ambiente marinho.

No segundo capítulo, 'What macroalgae's diversity and richness may represent about green turtle (*Chelonia mydas*) foraging behavior in the Southwestern Atlantic Ocean', a avaliação da variação sazonal da diversidade de itens consumidos pela espécie foi realizada, com enfoque em uma análise minuciosa das macroalgas registradas no trato digestório das tartaruga-verde juvenis encalhadas no Paraná. Os resultados incluem um maior consumo de itens nas estações de inverno e de outono, bem como a presença de cianobactérias tóxicas e de macroalgas resistentes a regiões eutrofizadas. O capítulo será submetido ao periódico *European Journal of Phycology*, (ISSN: 0967-0262; IF = 2.75, Qualis A2 biodiversidade), o qual aborda pesquisas relacionadas a algas e cianobactérias.

No terceiro capítulo, 'Long-term dietary shifts of immature green turtles in the Southwestern Atlantic Ocean', o objetivo foi de compreender a dinâmica ecológica das tartarugas-verde juvenis que se agregam e alimentam no litoral do Paraná em uma longa escala temporal (12 anos de estudos), por meio da análise da dieta acessada pela avaliação dos tratos

digestórios de espécimes encontrados encalhados mortos. Foram verificadas variações quali e quantitativas na dieta da espécie, as quais puderam ser relacionadas a diferentes fatores ambientais e dinâmica ecossistêmica regional. Este capítulo será submetido ao periódico *Estuarine, Coastal and Shelf Science*, (ISSN: 0272-7714, IF = 2.33, Qualis A1 biodiversidade), especializado em pesquisas realizadas no ambiente estuarino e costeiro.

1. INTRODUÇÃO GERAL

Chelonia mydas Linnaeus 1758 (tartaruga-verde) é a espécie de tartaruga marinha mais frequente na região costeira do Oceano Atlântico Sul ocidental (ASO), utilizando a região para alimentação e desenvolvimento (Bugoni et al. 2003; Guebert-Bartholo et al. 2011; Marcovaldi & Santos 2011; Reisser et al. 2013; Andrade et al. 2016; Gama et al. 2016; Coelho et al. 2018; Vélez-Rubio et al. 2018). Esta espécie desenvolve a maior parte do ciclo de vida no habitat costeiro (Lutz et al. 1996).

Durante o desenvolvimento ontogenético, os juvenis de *C. mydas* são recrutados da zona oceânica para a costeira, e em algumas regiões alteram a dieta do padrão onívoro para o herbívoro (Bjorndal & Bolten 1988). No entanto, este processo não é uniforme entre indivíduos de mesma classe de tamanho e idade, nem 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). Em zonas temperadas e subtropicais do ASO, após o recrutamento costeiro, juvenis de *C. mydas* migram de maneira errática entre áreas oceânicas e costeiras para se alimentar, o que possivelmente acarreta em uma dieta mais diversificada (González Carman et al. 2012; Reisser et al. 2013; Vélez-Rubio et al. 2018).

Além disso, a temperatura da superfície da água também é um fator na variação da dieta, como observado por Esteban et al. (2020), onde em regiões de maior latitude, e, consequentemente mais frias, o consumo de itens de origem animal é maior quando comparado com regiões mais quentes, onde a predominância é da herbivoria. Em uma mesma área de alimentação no ASO, fatores intrínsecos (ex. idade e haplótipo) e extrínsecos (disponibilidade de alimento, sazonalidade, variação temporal e região) interagem e atuam na variação comportamental e alimentar dos juvenis da espécie (Santos et al. 2015; Andrade et al. 2016; Gama et al. 2016; Vélez-Rubio et al. 2016; Coelho et al 2018).

Estudos relacionados ao comportamento de alimentação de *C. mydas* foram realizados no ASO utilizando metodologias distintas: telemetria (González Carman et al. 2012; Vélez-Rubio et al. 2018); 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 análise de isótopos estáveis (González Carman et al. 2014; Bezerra et al. 2015; Vélez-Rubio et al. 2016; Di Beneditto et al. 2017; Vélez-Rubio et al. 2018; Campos & Cardona 2019; Gama et al. 2021). A análise dos tratos digestórios possibilita a identificação e mensuração dos itens recém consumidos, bem

como inferência da possível área de alimentação dos espécimes, quando é conhecido o bioma de dada localidade.

Uma técnica que, associada às análises de dieta, permite avaliar os itens consumidos a longo prazo (~ 6 meses) é a de isótopos estáveis (IE) de carbono (C) e nitrogênio (N), pois provê informações quanto à posição ocupada pelos animais na teia trófica e gradiente de latitude (isótopos de nitrogênio, $\delta^{15}N$) e quanto ao habitat costeiro e/ou oceânico de forrageio (isótopos de carbono, $\delta^{13}C$) (Seminoff et al. 2006; Reich et al. 2007; Bisi et al. 2013; Vélez Rubio et al. 2018). A mudança de dieta ou de área de alimentação acarreta mudanças no sinal isotópico do tecido analisado, sendo que os valores isotópicos de carbono serão maiores em indivíduos que forrageiam perto da costa, assim como valores isotópicos de nitrogênio serão maiores em indivíduos topo de cadeia (Peterson & Fry 1987).

A velocidade desta mudança corresponde à taxa de reposição (*turnover*) das matrizes biológicas e varia entre tecidos analisados, fase de desenvolvimento do indivíduo, intervalo de tempo no qual a espécie assimila os nutrientes da dieta nos tecidos, e parâmetros abióticos do ecossistema de ocorrência do espécime (Manetta & Benedito-Cecilio 2003). Por exemplo, tecidos metabolicamente mais ativos (fígado e sangue total) refletem a dieta em um intervalo de tempo curto, enquanto os menos ativos (músculo, tegumento e osso) refletem uma dieta referente a intervalos de tempo mais longos (Hobson & Clark 1992; Tieszen et al. 2017). Desta forma, a análise conjunta de $\delta^{13}C$ e $\delta^{15}N$ e o uso de diferentes tecidos possibilitam determinar padrões de deslocamento e residência (isto é, se os indivíduos são residentes ou migratórios) e suas áreas de forrageamento (Seminoff et al. 2006; Bradshaw et al. 2017).

As composições isotópicas dos tecidos dos consumidores integram as informações isotópicas do habitat ("*isoscapes*") das áreas de alimentação (Deniro & Epstein 1981). Além disso, elas permitem avaliar o uso do habitat com menor custo mesmo sem a precisão de métodos de rastreio simultâneo (e.g. telemetria), permitindo a determinação das áreas pelas quais as tartarugas migram e a composição de sua dieta. Portanto, quando um animal marinho migra entre teias alimentares distintas isotopicamente, os valores de isótopos estáveis nos tecidos podem informar quanto ao uso de área (Hobson 1999; Hobson & Wassenaar 2008; Newsome et al. 2010; Turner-Tomaszewicz et al. 2018).

Adicionalmente, a análise isotópica de animais encontrados encalhados mortos e de animais capturados vivos em uma mesma área 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 e nos padrões de migração podem ser observadas (Newsome

et al. 2010; Vélez-Rubio et al. 2013; 2018; Turner Tomaszewicz et al. 2018). Os estudos de dieta de *C. mydas* utilizando isótopos estáveis já realizados no ASO indicaram tanto uma predominância de itens de origem animal (González Carman et al. 2014), quanto destacaram a predominância de macroalgas (Di Beneditto et al. 2017), além do aumento do consumo de macroalgas por tartarugas-verde com comprimento curvilíneo de carapaça maior (Vélez-Rubio et al. 2016). A diversidade atual de resultados evidencia uma variação individual, regional, ou mesmo sazonal.

Ao longo do ASO e, especificamente no litoral sul e sudeste brasileiro, estoques genéticos mistos de juvenis de *C. mydas* se agregam para alimentação e utilizam a plataforma costeira como corredor migratório, movimentando-se entre diferentes áreas de alimentação (González Carman et al. 2012; Jordão et al. 2015). Dados de monitoramento por satélite acusam variação no comportamento migratório e no tempo de residência das tartarugas-verde em diferentes áreas, relacionada principalmente à adaptação ao habitat das regiões temperadas (González Carman et al. 2012; Godley et al. 2003; Vélez-Rubio et al. 2018). Entretanto, as áreas costeiras se sobrepõem com áreas onde diversos tipos e intensidades de atividades antrópicas impactantes podem ameaçar a espécie, atualmente classificada como ameaçada pela IUCN (International Union for Conservation of Nature and Natural Resources 2004).

Na região sul do Brasil, o litoral do Paraná, apesar de seus reduzidos e aproximados 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, costões rochosos, baías permeadas por substratos consolidados naturais e artificiais para contenção de erosão e avanço portuário, assim como ilhas costeiras (Guebert-Bartholo et al. 2011; Pellizzari et al. 2014; Andrade et al. 2016; Gama et al. 2016). Nesta região são registrados mais de 1000 indivíduos mortos ao ano (Cantor et al. 2020), com predominância de indivíduos entre dois e oito anos de idade, ou seja, recém-recrutados de zona oceânica e em deslocamento entre áreas de alimentação costeiras (Andrade et al. 2016). Os indivíduos são geralmente originários de sítios reprodutivos do Atlântico e Caribe, tais como Ascenção, Guiné-Bissau e Ilha das Aves (Jordão et al. 2015; Coelho et al 2018). Delimitar as variações existentes na dieta da espécie é importante para a compreensão do comportamento alimentar das tartarugas-verde juvenis no ASO e a capacidade adaptativa deles às alterações. 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 e se este consumo é sazonal, traz

contribuição essencial para melhor compreender o uso do habitat pela espécie e os possíveis impactos incidentes.

Portanto, na primeira parte deste estudo, a análise de isótopos estáveis de indivíduos mortos e vivos que utilizam o litoral do Paraná para alimentação foi feita, visando inferir sobre a ecologia trófica das *C. mydas* no Atlântico Sul, bem como avaliar a diversidade ecológica existente entre os espécimes vivos e mortos, além de identificar potenciais impactos sobre as áreas de alimentação e a espécie. Na segunda parte, a identificação e mensuração dos itens alimentares, incluindo a análise minuciosa das espécies de macroalgas consumidas por 190 indivíduos foi realizada, visando avaliar a variação sazonal da diversidade de itens e impactos incidentes. Já na terceira parte, a análise em longo prazo (doze anos) dos tratos digestórios de indivíduos encontrados mortos foi realizada, visando evidenciar as flutuações ao longo dos anos e mudanças na forma como estes animais migratórios utilizam as áreas de alimentação.

1.2. OBJETIVOS E HIPÓTESES

Este estudo objetiva compreender a ecologia trófica e o comportamento alimentar de juvenis de tartaruga-verde no litoral do Paraná, por meio da (i) análise isotópica da dieta de espécimes encontrados mortos e capturados vivos, visando avaliar a diversidade ecológica de indivíduos encontrada na área; (ii) avaliação da variação sazonal da dieta das tartarugas-verde na região, incluindo mensuração de itens consumidos e identificação à nível de espécie das macroalgas, um dos principais itens alimentares durante certas fases do desenvolvimento de *C mydas*, além de relacionar estes resultados com habitat de forrageio e possíveis impactos; (iii) análise da dieta de espécimes encalhados encontrados mortos ao longo de 12 anos de monitoramentos, bem como da avaliação da variação desta ao longo deste período. O estudo foi realizado no litoral do Paraná, importante área de alimentação e desenvolvimento para as tartarugas-verde, e corredor migratório do Oceano Atlântico Sul-Ocidental (ASO) (Marcovaldi & Santos, 2011).

A principal hipótese do estudo é a de que se existe variação na dieta e na composição isotópica das tartarugas-verde, então os indivíduos que utilizam o litoral do Paraná para se alimentarem, adaptam-se e forrageiam sobre os itens alimentares disponíveis no habitat, além de constituírem uma população formada por residentes e por indivíduos advindos de outras regiões. 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, os subitens testados da hipótese, em cada capítulo, foram:

- Se os dados de isótopos estáveis variam entre os espécimes de *C. mydas* encontradas mortas e os espécimes capturados vivos na mesma área de coleta, então o conjunto de espécimes que forrageiam no litoral do Paraná podem ser formados por residentes, em equilíbrio com os valores isotópicos locais; e transientes, advindos de outras áreas do ASO; Se os dados de isótopos estáveis evidenciam um nicho trófico amplo para os juvenis de tartarugas-verde, é possível inferir que os indivíduos encontrados no Paraná se alimentam de outros recursos alimentares disponíveis em outras regiões do ASO, e que existe conectividade entre as áreas de alimentação desta espécie (Capítulo 1);

- Se há variação sazonal da diversidade e biomassa de itens alimentares consumidos, especificamente de espécies ou de gêneros de macroalgas, item predominante e analisado detalhadamente em tratos digestórios de *C. mydas* em caráter inédito no ASO, e esta variação se relaciona com a disponibilidade do recurso no habitat, então é possível inferir sobre seletividade do recurso alimentar e possíveis impactos de poluição e contaminação aos quais a espécie está submetida (Capítulo 2);

- Se variações nas frequências de ocorrência dos itens mais frequentemente consumidos pelas tartarugas-verde juvenis são evidenciadas ao longo dos anos, então é possível inferir que alterações na disponibilidade de recursos ocorrem e são responsáveis pelas alterações na dieta da espécie, a qual apresenta capacidade adaptativa a estas alterações, uma vez que permanece na área (Capítulo 3).

Sendo assim, os objetivos deste estudo foram:

1. Definir as razões de isótopos estáveis de Carbono ($\delta^{13}C$) e de Nitrogênio ($\delta^{15}N$) para os juvenis de *C. mydas* encontradas encalhadas mortas e intencionalmente capturadas vivas 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. Avaliar a dieta qualitativa e quantitativamente (biomassa dos itens consumidos) dos juvenis de tartarugas-verde encontrados mortos no litoral do Paraná, com enfoque na variação sazonal da diversidade de itens, com foco no detalhamento de espécies de macroalgas consumidas pelos espécimes, e estabelecer provável relação com impactos nas áreas de alimentação (Capítulo 2);

3. 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 agregam no litoral do Paraná (Capítulo 3).

2. MATERIAL E MÉTODOS GERAIS

2.1. ÁREA DE ESTUDO

O estudo foi realizado nos litorais do Paraná, Santa Catarina e São Paulo, totalizando uma extensão de 1511.4 km. Estas áreas foram escolhidas para a coleta de macroalgas consumidas por tartarugas-verde com base em um estudo de telemetria realizado no ASO, no qual 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) (González Carman et al. 2012; Vélez-Rubio et al. 2018).

Especificamente, o litoral paranaense tem apenas 90 km de linha de costa, no entanto, 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, planícies de maré, ilhas e manguezais (Lana et al. 2001), os quais provêm recurso alimentar de origem vegetal para *C. mydas*, tornando esta área importante para alimentação e desenvolvimento dos espécimes (Guebert-Bartholo et al. 2011; Gama et al. 2016).

O litoral de Santa Catarina apresenta 561,4 km de extensão, situado na zona climática temperada (Rodrigues et al. 2004). Nele está o Cabo de Santa Marta Grande, situado no município de Laguna, limitando os litorais sudeste (à norte) e sul (ao sul), contando com 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 (Nimer 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.

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 indivíduos com carcaças nos estágios iniciais de decomposição (com perda parcial de tecidos; carapaça, plastrão e nadadeiras íntegras; inchaço ausente a moderado; órgãos intactos) foram amostrados. 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 ao sul (ex. Uruguai, Vélez-Rubio et al. 2018) e ao norte (Fuentes et al. 2020).

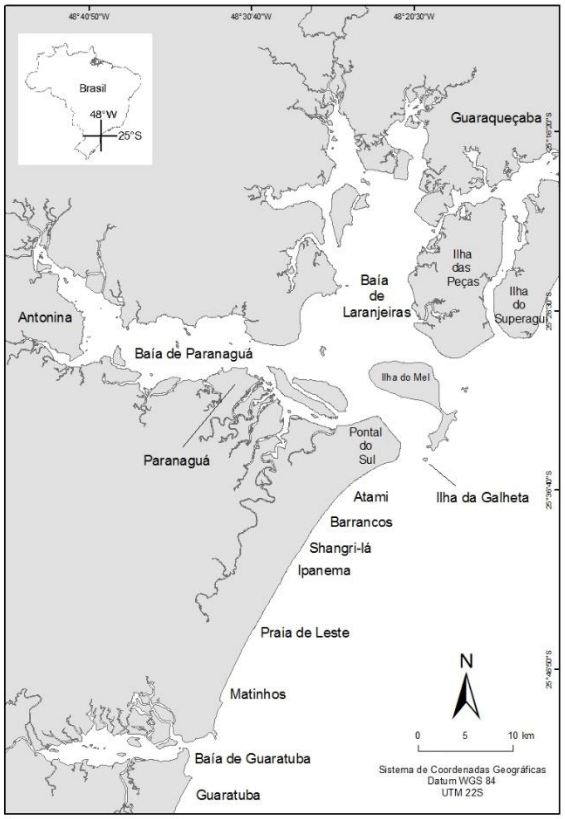


Figura 1: Mapa do litoral paranaense, incluindo o Complexo Estuarino de Paranaguá (CEP), onde foram realizados os monitoramentos de praia e coleta dos espécimes de tartarugas-verde juvenis.

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). Na zona continental (entre Pontal do Paraná e Guaratuba) foram percorridos diariamente cerca de 60 km de extensão praial, além do monitoramento nas ilhas do Mel, Peças e Superagui (± 40 km). 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 longo 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 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 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 pesagem. Todas as tartarugas vivas foram anilhadas e soltas na área dentro de duas horas após a captura.

2.4. COLETAS EM ÁREAS DE ALIMENTAÇÃO

2.4.1. Coleta de macroalgas

As coletas das macroalgas foram realizadas em seis áreas ao longo do sul e sudeste do Brasil, incluindo áreas de agregação alimentar e permanência de tartarugas-verde no Oceano Atlântico Sul ocidental (González Carman et al. 2012; Vélez-Rubio et al. 2018; Fuentes et al. 2020): Ilha das Cabras (23°49'42’’; 45°23'32’’) e Portinho (23°51'51’’; 45°25'48’’), em Ilha de São Sebastião 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; Arquipélago de Currais (25°44'09''; 48°21'55''), no Paraná; na Praia da Armação do Itapocaroi (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; Bumbeer et al. 2016; Gama et al. 2016).

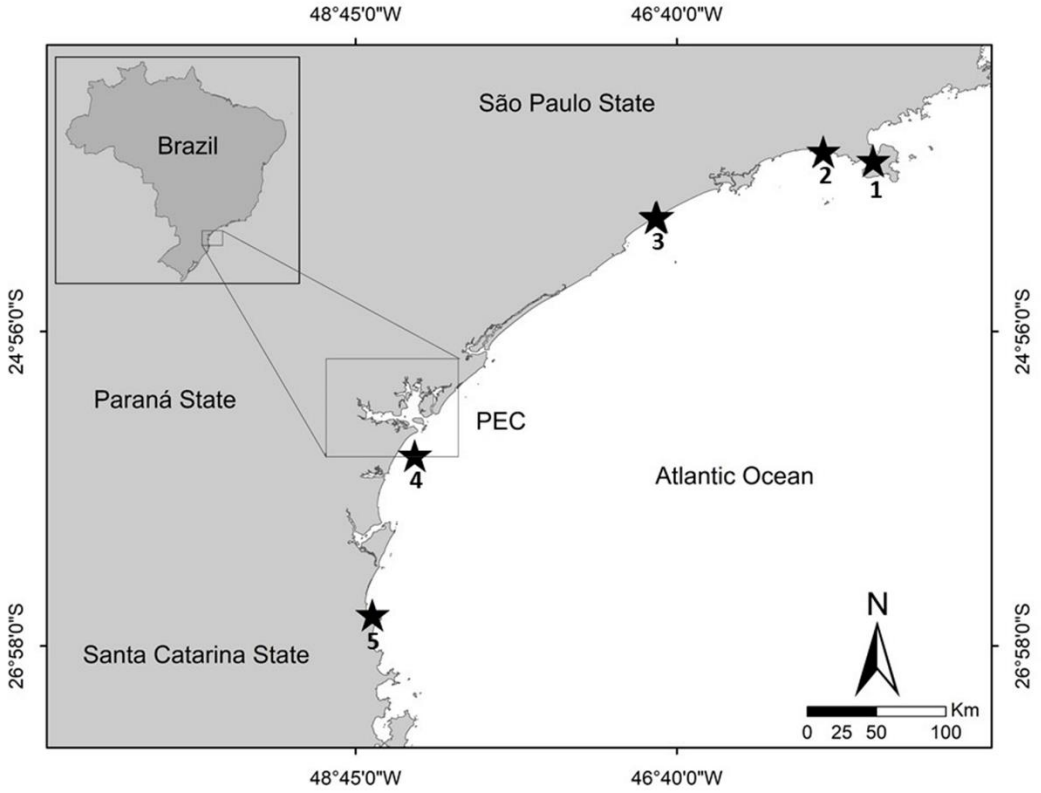


Figura 2: Mapa das áreas de coletas de macroalgas, incluindo (no sentido sul-norte): 5. Armação do Itapocaroi, em Santa Catarina; 4. o Arquipélago de Currais, no Paraná; 3. Praia dos Sonhos e Cama de Anchieta, em Itanhaém, São Paulo; 2. Portinho e 1. Ilha das Cabras, em Ilha de São Sebastião.

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 em duas estações climáticas, agrupando primavera e verão (de outubro a março); e outono e inverno (de abril a setembro; *c.f.* Possatto et al. 2017), visando avaliar possíveis variações sazonais na disponibilidade de recursos alimentares entre as áreas de alimentação.

As macroalgas que compõem a dieta das tartarugas-verde seguindo dados da literatura (Nagaoka et al. 2012; Gama et al. 2016; Corbisier et al. 2014; Vinagre et al. 2018), e

visualmente mais abundantes em cada local, 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 agregadas, 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 foi retirada e armazenada em formaldeído 4% diluído em água do mar filtrada, para posterior identificação, via cortes histológicos e análises microscópicas de estruturas vegetativas e reprodutivas das macroalgas (quando possível devido ao grau de degradação do material), mantendo o restante da amostra congelada.

2.5.ANÁLISE DE ISÓTOPOS ESTÁVEIS

Para esta análise apenas amostras de tecido epidérmico foram utilizadas. 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). 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 $\delta^{15}N$ e 100% para $\delta^{13}C$, e o IAEA-600, com recuperação de 97% para $\delta^{15}N$ e 100% para $\delta^{13}C$.

As amostras de macroalgas (potenciais itens da dieta) já descritas na dieta da espécie e presentes nas seis áreas de coleta também 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 o 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 a análise de isótopos estáveis. Os itens alimentares foram identificados sob microscópios e estereomicroscópios e com auxílio de guias, livros e de pranchas de identificação, de acordo com sua classificação taxonômica.

Informações secundárias e parte de 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, a idade das tartarugas-verde, o sexo dos indivíduos 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 analisados e comparados com

estudos prévios (Gama et al. 2016), visando análise temporal da dieta e 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 $\delta^{13}C$ e $\delta^{15}N$. 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 sazonal dos recursos alimentares consumidos e sua relação com disponibilidade no habitat de forrageamento e possíveis impactos, a análise de variância multivariada permutacional (PERMANOVA) e a análise de componentes principais (PCA) foram aplicadas. No terceiro capítulo, para verificar a variação interanual da dieta de *C. mydas*, a PERMANOVA e PCA também foram aplicadas.

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3. CAPÍTULO 1

Aceito na Marine Ecology Progress Series (https://doi.org/10.3354/meps13868)

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 ($\delta^{13}C$) and -nitrogen ($\delta^{15}N$) 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 $\delta^{15}N$ 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 $\delta^{15}N$ 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

3.1. 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 ($\delta^{13}C$) 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 $\delta^{13}C$ 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 $\delta^{13}C$ values relative to seagrass and marine macroalgae located only a few meters away (Lepoint et al. 2004). Conversely, stable nitrogen isotope ($\delta^{15}N$) 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 $\delta^{15}N$ 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 Paraná 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 Paraná 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 ($\delta^{13}C$, $\delta^{15}N$) 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.

3.2. MATERIALS AND METHODS

3.2.1. 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-km^2 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).

3.2.2. 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.

3.2.3. 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.

3.2.4. 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*.

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

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

where R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) 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 $\delta^{15}N$ and $\delta^{13}C$ measurements, respectively.

3.2.6. 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 ($\delta^{13}C$ and $\delta^{15}N$). 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 $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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.

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 depositovorous (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 Group 3: ≥ 46.1 cm) that reflect the entire size range (CCL) of turtles examined. For all models, we applied turtle-prey trophic discrimination factors (TDFs) from Seminoff et al. (2006; 0.17 ± 0.03 ‰ for $\delta^{13}C$; 2.8 ± 0.11‰ for $\delta^{15}N$), as these were derived for green turtles of similar size (i.e., life-history phase) to individuals included in this study.

3.3. RESULTS

3.3.1. Live-capture and dead-stranded turtle samples

A total of 117 individuals was captured alive (LC) during 2016 (n = 8), 2017 (n = 14), and 2018 (n = 89), with six turtles recaptured in multiple years. Curved carapace length ranged from 30.6 to 63.2 cm (mean = 39.6 ± 6.9 cm). For dead-stranded turtles (DS), a total of 66 individuals was sampled, with CCL ranging from 28.2 to 59.0 cm (mean = 36.6 ± 6.3 cm).

3.3.2. Isotopic values of turtle samples and forage items

The mean $\delta^{13}C$ value of LC turtles was −16.9 ± 1.3 ‰ (range = −20.2 ‰ to −12.6 ‰), whereas that for DS turtles was −17.4 ± 1.4 ‰ (range = −25.2 ‰ to −15.1 ‰). Mean $\delta^{15}N$ value of LC turtles was 10.3 ± 1.0 ‰ (range = 8.3 ‰ to 12.8 ‰), and for DS turtles was 8.7 ± 1.8 ‰ (range = 4.9 ‰ to 12.9 ‰). Further details on the $\delta^{13}C$ and $\delta^{15}N$ values, and the elemental concentrations (%C and %N), of LC and DS green turtles are presented in Table 2. Differences between the size groups were observed (ANOVA, $p \leq 0.05$), but there was no relationship between turtle size (CCL) and $\delta^{13}C$ for either group; however, there was a significant positive relationship between CCL and $\delta^{15}N$ for both LC and DS green turtles ($R^2 = 0.18$, $p \leq 0.05$), with larger turtles presenting higher $\delta^{15}N$ values (Figure 2). Among years, a Tukey *post-hoc* comparison showed significant variability in $\delta^{13}C$ 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 $\delta^{13}C$ and $\delta^{15}N$ (Table 3).

Among forage items the mean isotope values ranged from –28.3 ± 0.2 ‰ to –13.8 ± 0.5 ‰ for $\delta^{13}C$; and from 3.1 ± 0.4 ‰ to 9.7 ± 1.4 ‰ for $\delta^{15}N$ (Table 1). The “seagrass” prey group had the highest mean $\delta^{13}C$ value (−13.8 ± 0.5 ‰) and the “mangrove” group had the lowest mean $\delta^{13}C$ (−28.3 ± 0.2 ‰). For $\delta^{15}N$, 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 $\delta^{13}C$ value (−20.1 ‰) and *Hypnea* sp. the highest $\delta^{13}C$ value (−13.8 ‰), whereas *Hypnea pseudomusciformis* had the lowest $\delta^{15}N$ value (4.9 ‰) and *Ulva lactuca* had the highest $\delta^{15}N$ value (9.1 ‰; Supplementary Table 1).

3.3.3. 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 $\delta^{15}N$ values and a larger isotopic niche space than live turtles (Figure 3).

3.3.4. 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).

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). 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).

3.4.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 $\delta^{13}C$ ranges, but the DS group had substantially more turtles with low $\delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ 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 (González 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 $\delta^{15}N$ 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 $\delta^{13}C$ values are similar to those found for Rio de Janeiro (Di Beneditto et al. 2017) and northeast Brazil (Bezerra et al. 2015). Green turtle $\delta^{13}C$ 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 $\delta^{15}N$ value (10.3 ± 0.98 ‰) is similar to values reported for green turtles in northeast and southeast Brazil (Bezerra et al. 2015, Di Beneditto et al. 2017) (Table 4). Likewise, González Carman et al. (2014) report $\delta^{13}C$ values for live green turtles in Argentina (mean = –16.5 ± 0.2 ‰) 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 $\delta^{15}N$ and $\delta^{13}C$ 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.

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

Prey group	N	$\delta^{13}C$	$\delta^{15}N$	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

Table 2. Mean stable isotope ($\delta^{13}C$, $\delta^{15}N$) values and elemental concentrations (%C, %N) for live-captured and dead-stranded juvenile green turtles found along the Paraná coast, southern Brazil, from 2016 to 2018. There are six specimens whose capture year is not known, because they were recaptured in multiple years.

Year	N	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		%C		%N	
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Live-captured									
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

Table 3. Results from the Tukey *post-hoc* comparison test for mean annual skin tissue $\delta^{13}C$ (top) and $\delta^{15}N$ (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.

$\delta^{13}C$

Abs (Dif)-LSD	Difference in means	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

$\delta^{13}N$

Abs (Dif)-LSD	Difference in means	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

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 ± 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	$\delta^{13}C$ (‰) range/ mean	$\delta^{15}N$ (‰) range/ mean	Reference
Ceará and Bahia, Northeast Brazil	31	27.0 – 62.0	Muscle	–17.1 ± 0.9	10.4 ± 0.22	Bezerra et al. 2015
			Scute	–18.9 ± 0.8	9.6 ± 0.22	
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 Beneditto et al. 2017
Paraná, south Brazil	66 dead	28.2 – 59.0	Skin	–17.4 ± 1.4	8.7 ± 1.8	This study
	117 alive	33.4 – 54.0		–16.9 ± 1.3	10.3 ± 1.0	
Argentina	7 dead;	31.3 – 52.2	Skin	–15.5 ± 0.7	9.5 ± 1.0	González Carman et al. 2014
	7 alive	*		–16.5 ± 0.2	11.1 ± 1.1	
Uruguay	126	27.8 – 66.8	Skin	–18.2 to –13.6	6.7 to 15.6	Vélez-Rubio et al. 2016
Uruguay	20	27.8 – 66.8	Scute	–19.8 to –14.8	5.8 to 15.8	Vélez-Rubio et al. 2018

Supplementary Tables

Table 1. Stable isotope values ($\delta^{13}C$, $\delta^{15}N$) 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	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Reference
Itanhaém/SP, Brazil	Rhodophyta	*Hypnea pseudomusciformis*	– 18.0	4.9	This study
Itanhaém/SP, Brazil	Rhodophyta	*Hypnea spinella*	– 20.1	6.3	This study
Ubatuba/SP, Brazil	Rhodophyta	*Hypnea spinella*	– 17.0	7.3	Corbisier et al. 2006
Southeast Brazil	Rhodophyta	*Hypnea* sp.	– 13.8	5.4	Vinagre et al. 2008
Itanhaém/SP, Brazil	Chlorophyta	*Ulva fasciata*	– 17.0	6.6	This study
Penha/SC, Brazil	Chlorophyta	*Ulva lactuca*	– 15.6	9.1	This study
Ubatuba/SP, Brazil	Chlorophyta	*Ulva fasciata*	– 17.2	6.4	Corbisier et al. 2006
South Brazil	Chlorophyta	*Ulva* sp.	– 17.1	7.7	Vélez Rubio et al. 2016
Guaratuba/PR, Brazil	Black mangrove	*Avicennia schaueriana*	– 28.3 ± 0.2	3.1 ± 0.4	Larcher et al. 2016
Northeast Brazil	Seagrass	*Halodule wrightii*	– 14.2 ± 0.4	3.2 ± 1.7	Lazzari et al. 2012
Southeast Brazil	Seagrass	*Halodule* sp.	– 13.5	4.2	Corbisier et al. 2014
Southeast Brazil	Invertebrates	Depositivere	– 15.9 ± 2.2	9.5 ± 1.0	Corbisier et al. 2006
Southeast Brazil	Invertebrates	Carnivore	– 14.9 ± 1.1	11.3± 0.8	Corbisier et al. 2006

Southeast Brazil	Invertebrates	Suspensivorous	– 15.5 ± 1.6*	8.4 ± 0.6*	Corbisier et al. 2006; Vinagre et al 2008

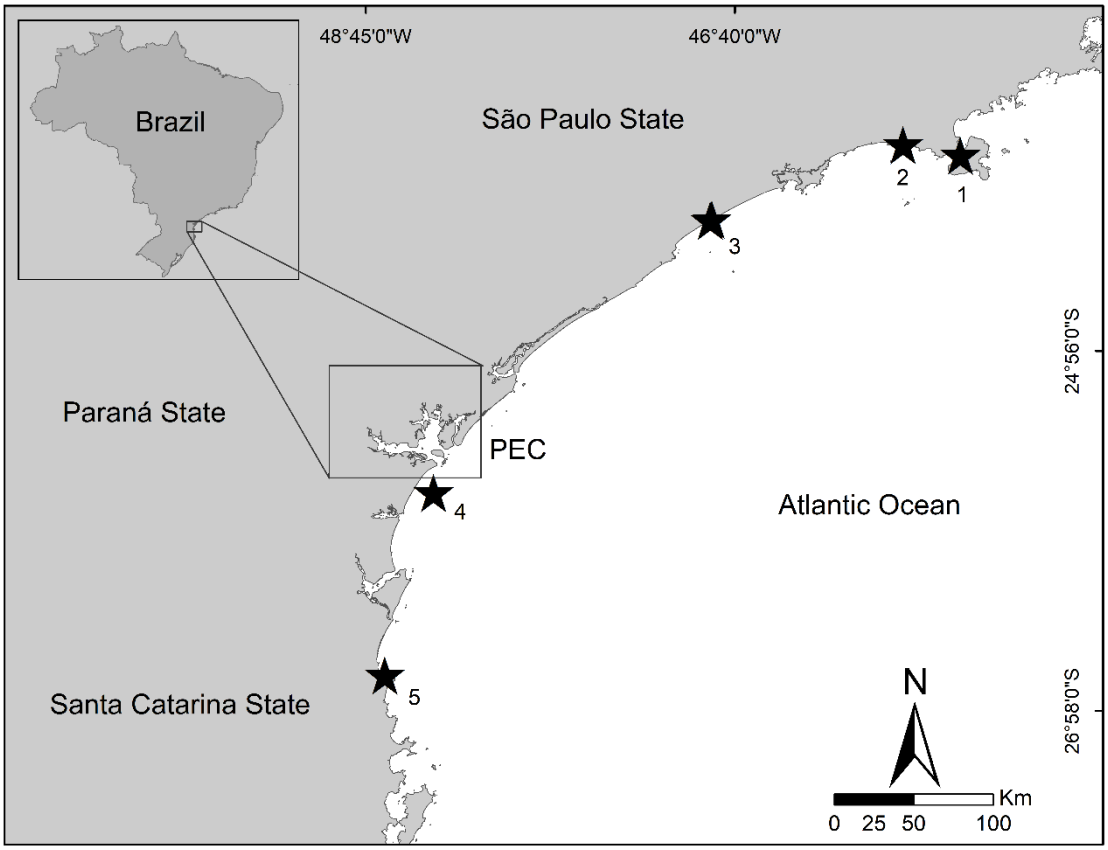


Figure 1. Map of the marine algae sampling areas along the coast of the Southwestern Atlantic Ocean, where site 1 is "Ilha das Cabras" and site 2 is "Portinho", in Ilha Bela (São Paulo state); 3 is "Cama de Anchieta" and "Praia dos Sonhos", in Itanhaém (São Paulo state); 4 is "Currais" in Paraná; and 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.

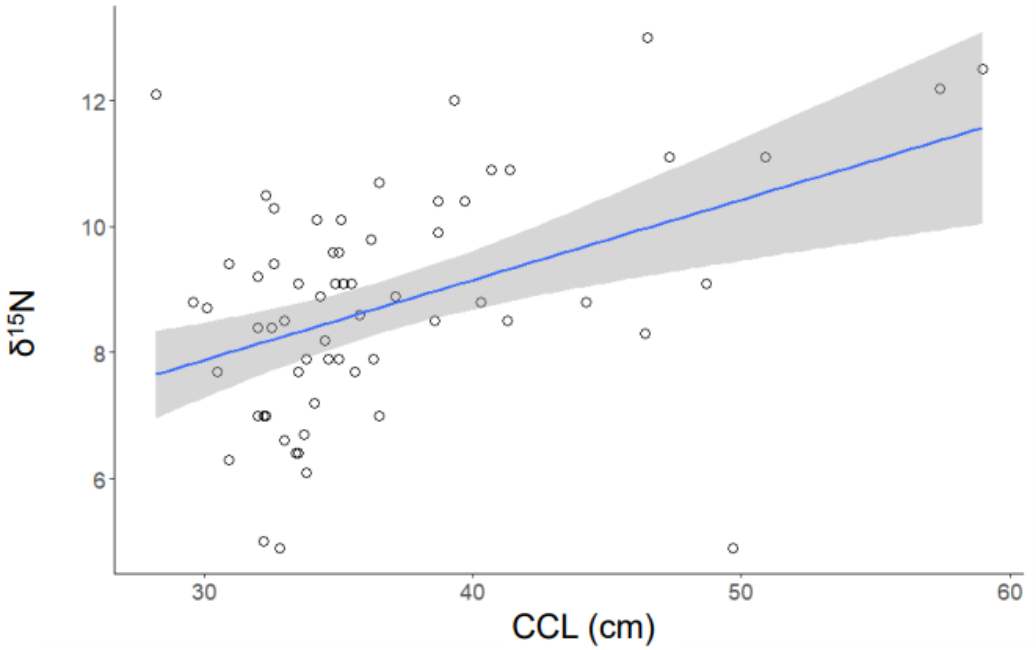


Figure 2. Linear regression showing a significant relationship between curved carapace length and stable-nitrogen isotope values of 66 dead-stranded juvenile green turtles recovered along the Paraná coast of southern Brazil between 2017 and 2018.

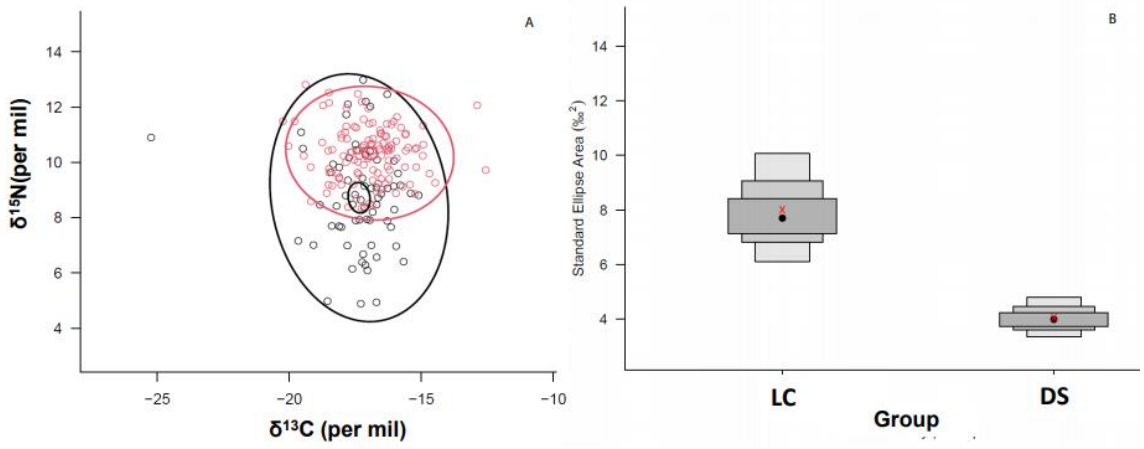


Figure 3. (A) Standard Ellipses, corrected for sample size, which was calculated using a maximum likelihood approach. The red ellipse corresponds to the live-captured green turtles, whereas the black ellipse represents the dead-stranded green turtles. (B) Bayesian SEA estimates for dead-stranded (DS) 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.

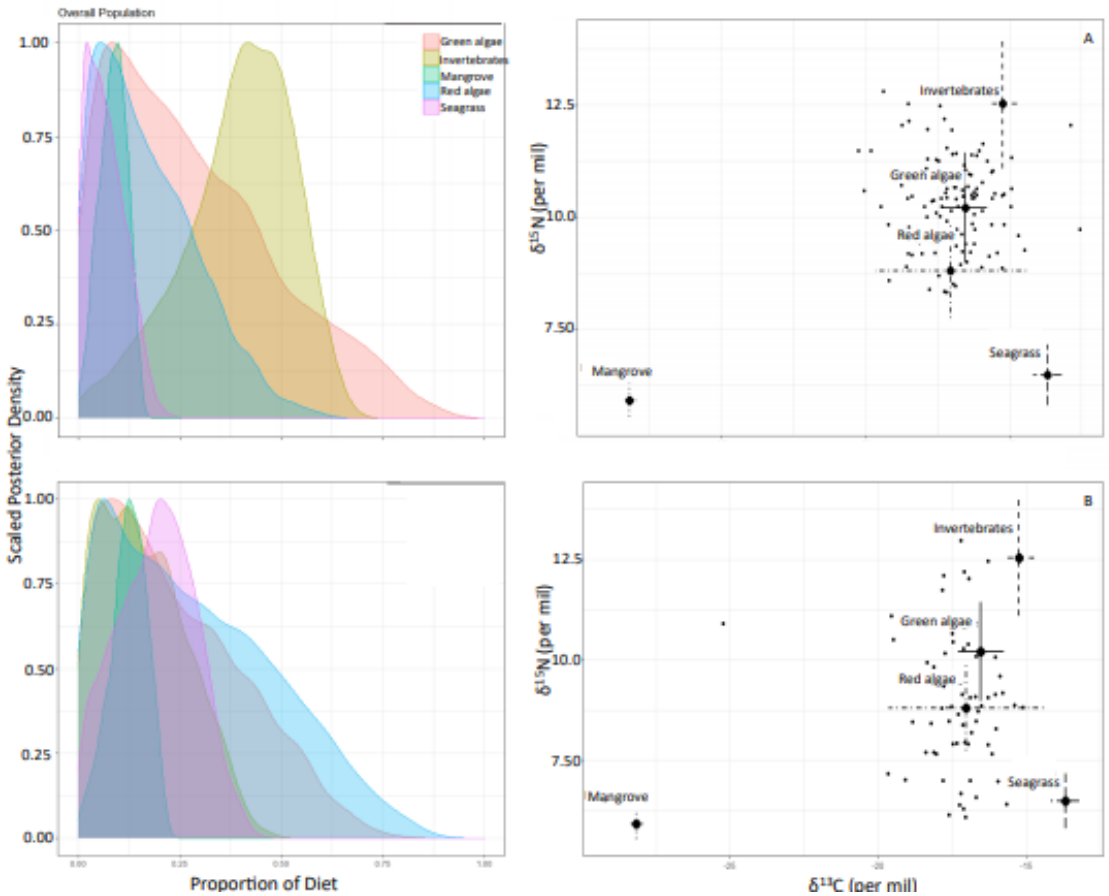


Figure 4: MixSIAR model outputs for (A) live-captured and (B) dead-stranded juvenile green turtles in Paraná coast, southern Brazil and with each respective raw data beside them, resulting from the MixSIAR analysis considering their main five food items isotopic values.

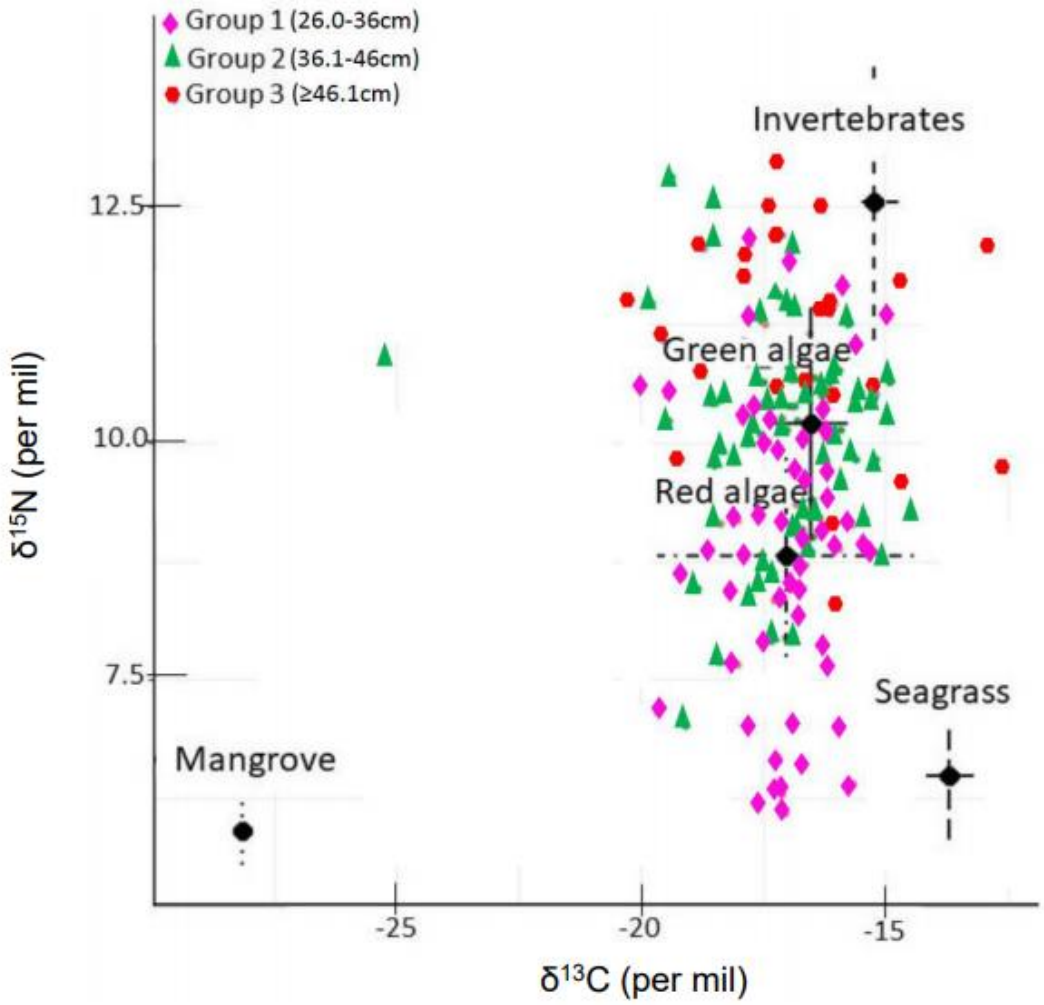


Figure 5. Raw data for live-captured and dead-stranded juvenile green turtles in Paraná coast, southern Brazil, among size classes (Group 1: 26.0–36cm; Group 2: 36.1–46cm; Group 3: ≥46.1cm) resulting from the MixSIAR analysis considering their main five food items isotopic values.

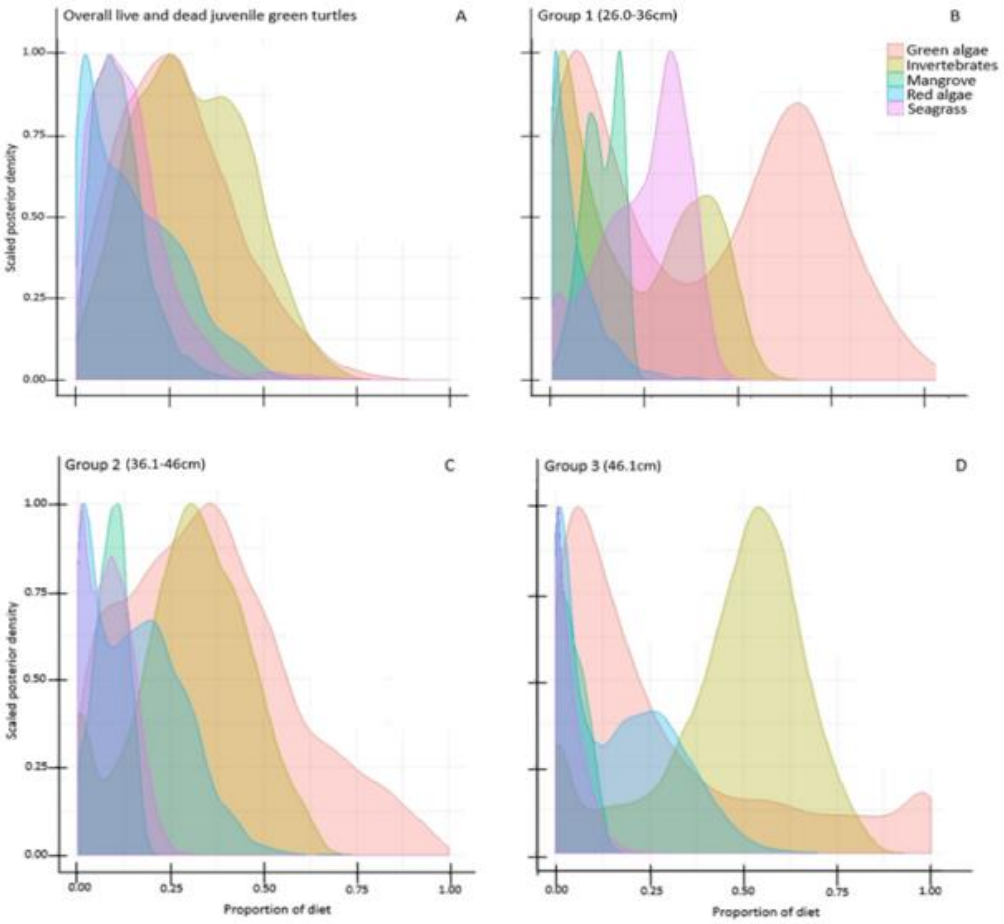


Figure 6. MixSIAR model outputs for overall and different size classes of live-captured and dead-stranded juvenile green turtles in Paraná coast, southern Brazil. (A) Overall turtles; (B) Group 1: 26.0–36cm; (C) Group 2: 36.1–46cm; (D) Group 3: ≥46.1cm.

4. CAPÍTULO 2

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What macroalgae's diversity and richness may represent about green turtle (*Chelonia mydas*) foraging behavior in the Southwestern Atlantic Ocean

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Abstract

Macroalgae are important bioresources in marine coastal ecosystems and oceanic islands. They are frequently ingested by several species, including the green turtle *Chelonia mydas*, which is one of the most common sea turtle species in coastal areas of the Southwestern Atlantic Ocean, including the Paraná coast in South Brazil. Across 10 years, 190 juvenile green turtles were collected dead-stranded during beach monitoring in this area. They had their digestive tracts collected to further analyze dietary content. The most frequent macroalgae group was Rhodophyta, followed by Chlorophyta, and Phaeophyceae. When looking at frequency of occurrence, biomass, and the relative importance, the Chlorophyte *Ulva lactuca* was the most consumed, followed by the Rhodophyte, and by the Phaeophyceae *Sargassum cymosum*. High frequencies of red and green macroalgae suggest that their consumption by green turtles is influenced by their high nutritional content and selectivity by the species, as verified in other diet studies. There was significant diet variation among seasons, with the austral winter and

autumn presenting higher macroalgae richness than spring and summer. Also, during the winter and autumn, the cyanobacteria *Lyngbya majuscula* was found, which is toxic and usually encountered in polluted habitats. Despite the resources availability in the habitat, it's known that green turtles select them, seeking high lipids, oligoelements and carbohydrates (polyssacharides)-content ones, which can be verified by the highly consumed macroalgae herein presented. This study provides a baseline of macroalgae species consumed by green turtles in the South Atlantic Ocean, and sheds light on seasonal changes in dietary importance of macroalgae in green turtles' diet. Finally, these data highlight which macroalgae, and habitats, should be prioritized for conservation.

Key words: seaweeds; diet; foraging plasticity; pollution; habitat use; seasonal variation.

Highlights

The richness of macroalgae in turtle digestive tracts is higher during winter and autumn.

Green turtles forage on pollution-resistant macroalgae, mainly chlorophytes.

Macroalgae consumption by *C. mydas* is related to the plant-based availability.

Introduction

Macroalgae are important sources of lipids, vitamins, minerals, aminoacids, and other trace elements (Chennubhotla 1996; Norziah & Ching 2000) for marine consumers and they are responsible for ca. of 80% of the primary productivity in coastal regions (Israel *et al.* 2010). Macroalgae assemblages can be used to describe the coastal habitat features and are a sensitive way to evaluate anthropic impact (Soltan *et al.* 2001; Arévalo *et al.* 2007). Macroalgae often show high species richness in coastal and insular areas (Pellizzari *et al*. 2014, 2017, 2020), and can be classified into morpho-functional groups which are related to their shapes, thickness, photosynthetic and carbon assimilation efficiency resulting from abiotic and biotic interactions (Litler & Litler 1980). Some functional groups, such as foliose, filamentous, and leathery algae may be more abundant, or present higher biomass than other groups (e.g. terete or fleshy, calcareous, or balloon) in stressed or contaminated regions (Balata *et al.* 2011). Moreover, the

same photosynthetic and bio-chemical pathways that determine classification also lead to morphological differences that affect their consumption by herbivorous species, which tend to forage on filamentous, foliose, or fleshy species, rather than on branched calcareous ones, which have rigid walls and are more resistant to predation (Mendes *et al.* 2015; Yin 2020).

Several marine invertebrates and vertebrates consume macroalgae (Steneck *et al.* 2017), including the circum-global green turtle *Chelonia mydas* - the only sea turtle species able to digest cellulose (Bjorndal 1979). *C. mydas* presents a mixed diet in temperate and subtropical areas, ingesting macroalgae, seagrasses, mangrove seeds and propagules, but also invertebrates and even small fish (Limpus & Limpus 2000; Lemons *et al.* 2011; Gama *et al.* 2016; Vélez-Rubio *et al.* 2016; Esteban *et al.* 2020*).*

The green turtle is one of the most frequent species of sea turtles in the coastal area of Southwestern Atlantic Ocean (SWAO), encompassing Uruguay, Argentina, and Brazil (Marcovaldi & Santos 2011). Specifically in southern Brazil, Paraná coast is an important year-round foraging and development ground for juvenile *C. mydas* (Andrade *et al.* 2016; Gama *et al.* 2016). In this area, turtles mostly feed close to rocky shores and mangroves, both high productivity habitats (Moreno & Rocha 2012; Santos & Lana 2017).

Macroalgae richness along the Paraná coast and islands is considered low (ca of. 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) show high biomass (Pellizzari *et al.* 2007, 2014, 2021; Pellizzari & Reis 2011). However, in estuaries, mangroves, and coastal areas nearby, some green algae species such as *Ulva* spp., have their growth stimulated by high levels of dissolved inorganic nutrients, which is related to the eutrophication process and pollution (Teichberg *et al.* 2010). Indeed, this chlorophyte genus is opportunistic and highly tolerant to eutrophic areas (Scherner *et al.* 2013; Pellizzari *et al*. 2020b). This environmental eutrophication impact is also applied to the mangrove habitats, along Paraná coast, which are critical nursery habitats to many species of fauna and flora, while also containing high levels of contaminants (Songjun *et al.* 2015).

Previous studies developed in Paraná coast showed the seagrass *Halodule wrightii* and the macroalgae *Ulva* spp. were the most important items consumed by green turtles, with a progressive increase in the importance of *Ulva* spp. (Guebert-Bartholo *et al.* 2011; Gama *et al.* 2016). This general increase in macroalgae consumption may have been caused by a decline

and even a loss of seagrasses abundance and distribution in eutrophic waters (Greening & Janicki 2006; Holmer *et al*. 2016; Ruesink 2016).

The composition and variations across seasons on green turtles' diet could help understand changes in macroalgae habitat and the effects of marine disturbances. Additionally, several studies showed that green turtles select macroalgae as a food resource and present foraging plasticity, which exposes them to several impacts (Seminoff *et al.* 2002; Fuentes *et al.* 2006; López-Mendilaharsu *et al.* 2008; Santos *et al.* 2015). Therefore, identifying the macroalgae species recently consumed by green turtles in Paraná, southern Brazil, is one of the steps that help assess ecological changes in the turtle habitat and prioritize conservation areas that they constantly use. This study details the macroalgae species consumed by green turtles and discusses their seasonal variation in an important subtropical foraging area, supporting a better understanding of regional impacts and risks.

Materials and methods

Study area

The Paraná coast of Brazil in the Southwestern Atlantic Ocean, (25°20'S to 25°35'S // 48°17'W to 48°42'W) is an important foraging, development, and migratory region for all the five sea turtle species that occur in Brazil, including *C. mydas* (Marcovaldi & Santos 2011). This area presents several bays, sandy beaches, and estuaries, including the Paranaguá Estuarine Complex (PEC), with an area of 612km^2 (Lana *et al.* 2001) (Figure 1). PEC is surrounded by mangroves in the inner sector, and by sandy beaches and rocky shores in the outer sector of the estuary (Lana *et al*. 2001).

The Paraná coast, despite its short coastline (ca. of 90 km), is considered a hotspot for biodiversity (UNESCO 2021), presenting seagrass meadows composed by *Halodule wrightii* Ascherson 1868, mangroves (Angulo 1992; Sordo *et al.* 2011), and rocky shores with more than a hundred species of macroalgae (Pellizzari *et al.* 2014).

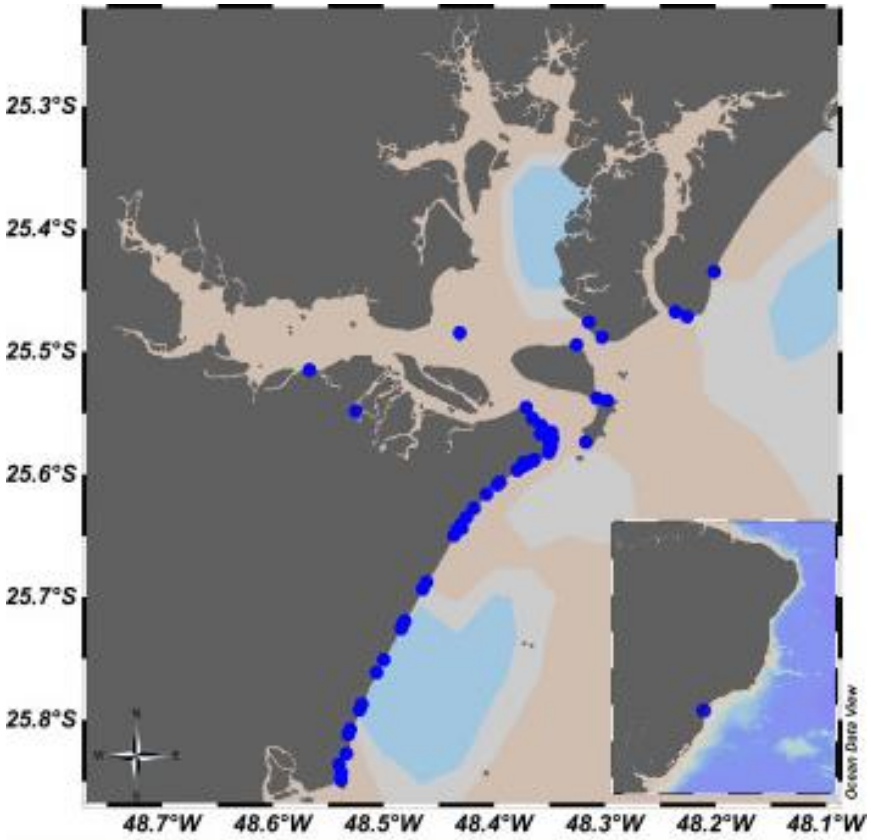


Figure 1. Map of the Paraná coast in Southeastern Brazilian coast, including the Paranaguá Estuarine Complex (PEC), where the beach surveys were performed, and dead-stranded green turtles (blue dots) were collected. Map generated in ODV, with the shaded colors indicating bathymetry.

This estuarine complex is negatively impacted by urbanization, agriculture in the continental area, and the port areas of Paranaguá and Antonina; fishery activities; constant vessel traffic; and the presence of many marinas in Pontal do Paraná, Paranaguá and Antonina (Sordo *et al*. 2011; López-Barrera *et al*. 2012; Passos *et al*. 2013; Gama *et al*. 2016).

Dead-stranded juvenile green turtles' collection

Daily beach monitoring was performed to collect dead-stranded juvenile green turtles along the Paraná coast from 2008 to 2018 (Figure 1). Each encountered turtle was measured (CCL = curved carapace length, in cm) for further necropsy and digestive tract analysis. Each turtle was categorized into 10-cm size classes, for graphical purposes, following classifications published in previous studies for the area (Guebert-Bartholo *et al*. 2011; Gama *et al*. 2016;

Coelho *et al*. 2018). Only fresh and early-decomposition stage specimens were evaluated (ranks 2 and 3; adapted from Geraci & Lounsbury, 2005).

Besides size (CCL), the season of collection (austral seasons) was recorded. Average rainfall data (in mm) was obtained from the Paranaguá meteorologic station at 25°31'S, 48°30'W by SIMEPAR (Meteorological System of Paraná) (data retrieved from http:www.simepar.br).

Macroalgae and other plant-based material screening, and identification

After necropsy, the digestive tracts were removed and stored frozen at –10°C. For diet analysis, all the items were separated, washed and re-stored frozen at –10°C. Macroalgae were identified using histological and microscopy techniques to observe the morphology of the specimens, considering the reproductive and vegetative structures of each diet item. Diet samples were prepared on glass slides and analyzed via stereoscopic and optical microscopy with image capture (Olympus CX31). For the comparative identification of macroalgae diet items we used several articles, thesis, and identification keys including 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). The morpho-functional macroalgae group classification followed Steneck & Detier (1984).

Numerical and Statistical analysis

Three distinct indices were used to determine the dietary importance of each prey species: frequency of occurrence (*%FO*; Hyslop 1980), relative wet biomass (*%Biomass*; g.) and the index of relative importance (*%IRI*; Bjorndal et al. 1997).

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

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

$$\%IRI = \frac{\%FO \text{ of a certain prey} * \ \%W \text{ of a certain prey} * 100}{\sum \quad \%FO * \%W}$$

Multivariate analysis was performed to test differences in macroalgae species consumption by green turtles. Permutational MANOVA (PERMANOVA; Anderson 2001) with transformed data (log x + 1; Euclidian distance) was used to determine the relationship between the prey items ingested by turtles and the explanatory term 'season of the year'. The austral seasons were the considered, with the months of January, February, and March corresponding to the summer; April, May, and June, to the autumn; July, August, and September, to the winter; and October, November, and December, to the spring. A Principal Component Analysis (PCA; Legendre & Legendre, 2012; Borcard *et al*. 2018) (PCA function, FactoMineR package, Lê *et al*. 2008) was performed to evaluate variation in diet composition among the collected individuals and to determine which food items were most influential in explaining variation in green turtle diet.

Results

C. mydas general data

A total of 190 juvenile green turtles were collected, with CCL ranging from 28.2 cm to 62.0 cm (38.83 ± 6.53 cm). The most frequent size class was of specimens ranging from 35.0cm to 49.9cm CCL (n = 96; *%FO* = 50.52) (Figure 2). The average sizes within each size class were: 40.01 cm in spring; 39.99 cm in summer; 38.48 cm in autumn; and 38.83 cm in winter.

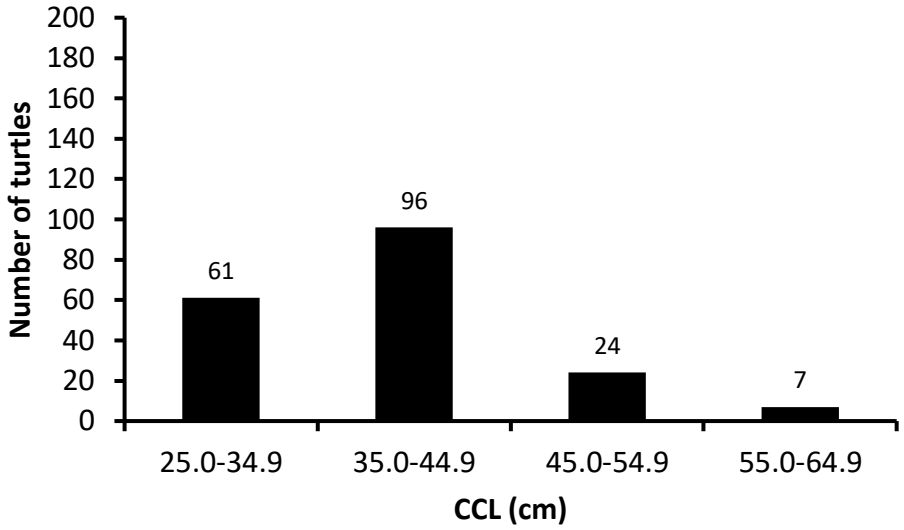


Figure 2: Distribution of the sampled juvenile green turtles among 10-cm curved carapace length size classes from 2008 to 2018 in Paraná coast.

The autumn and the winter were the seasons with the highest numbers of turtles stranding (62 turtles, *%FO* = 32.63%; and 61 turtles, *%FO* = 32.10%; respectively). The average rainfall was highest in the summer months (251.80 mm) (Figure 3).

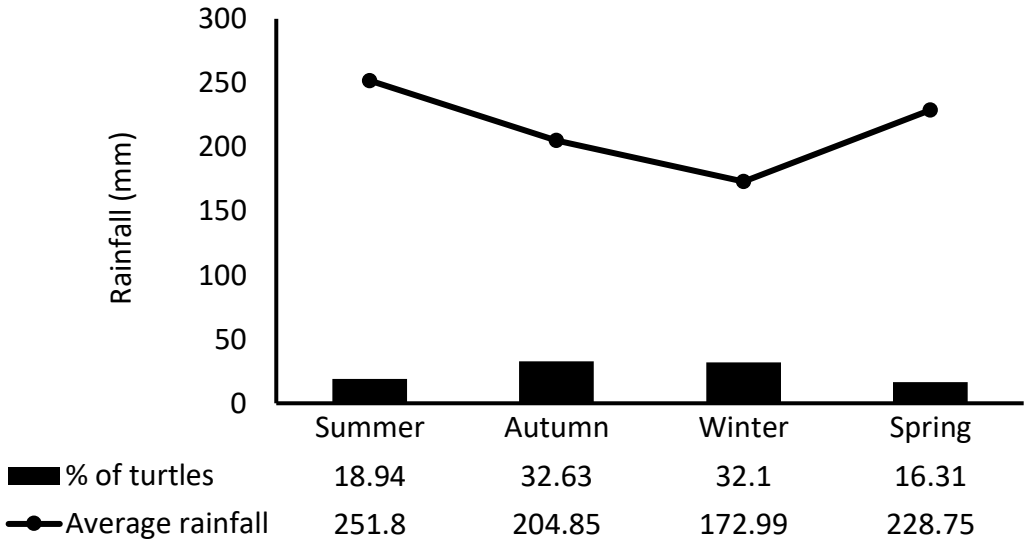


Figure 3: Average rainfall (in mm) and percentage of dead-stranded juvenile green turtles throughout the seasons in Paraná coast, SE Brazilian coast.

Macroalgae richness in digestive tract contents

A total of 49 species of macroalgae were identified, comprising 31 species of Rhodophyta (red macroalgae); 14 species of Chlorophyta (green macroalgae); and four species of Phaeophyceae (brown macroalgae) (Table 1). All the macroalgae herein presented were found in *C. mydas* specimens dead-stranded during the winter and the autumn seasons, whereas during summer and spring, only six species of macroalgae were found (two species of Chlorophyta – *Rhizoclonium* sp. and *Ulva lactuca*; two species of Rhodophyta - *Gracilaria domingensis* and *Pyropia* sp.; and one species of Phaeophyceae, *Sargassum cymosum*. The mangrove *Avicennia schaueriana* and the seagrass *Halodule wrightii* were the only identified species of angiosperms, as well as Cyanobacteria *Lyngbya majuscula*, the latter of which was found only in the winter and autumn samples.

Table 1: Frequency of occurrence (*%FO*) and biomass (*%Biomass*) of macroalgae species registered in digestive tracts contents of juvenile green turtles along the Paraná coast from 2008 to 2018. Functional groups: FI = filamentous, FO = foliose, CT = corticated terete (fleshy), CF = corticated foliose, TL = thin leathery, AC = articulated calcareous.

Taxa	**Author**	**Functional Group**	**N of digestive tracts**	***%FO***	***%Biomass***
CHLOROPHYTA					
Caulerpa sp.		**FI**	**2**	**1.047**	**0**
Chaetomorpha aerea	(Dillwyn) Kützing	**FI**	**5**	**2.617**	**0.008**
Chaetomorpha antennina	(Bory) Kützing	**FI**	**2**	**1.047**	**0**
Chaetomorpha sp.		**FI**	**1**	**0.523**	**0**
Cladophora catenata	Kutzing	**FI**	**1**	**0.523**	**0**
Cladophora vagabunda	(Linnaeus) Hoek	**FI**	**7**	**3.644**	**0.036**
Cladophora sp.		**FI**	**6**	**3.141**	**0.016**
Cladophoropsis membranacea	(Hofman Bang ex C. Agardh)	**FI**	**1**	**0.523**	**0**
Rhizoclonium sp.		**FI**	**6**	**3.141**	**0.010**
Ulva cf. *chaetomorphoides*	(Børgesen) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	**FI**	**1**	**0.523**	**0**
Ulva fasciata	Delile	**FO**	**1**	**0.523**	**0**
Ulva flexuosa	Wulfen	**FI**	**1**	**0.523**	**0**
Ulva lactuca	Linnaeus	**FO**	**77**	**40.31**	**58.92**
Willeella brachyclados	(Montagne) M.J.Wynne	**FI**	**1**	**0.523**	**0**
Total			***77***	***40.52***	
OCHROPHYTA/PHAEOPHYCEAE					
Chnoospora minima	(Hering) Papenfuss	**CT**	**4**	**2.094**	**0**
Dictyota sp.		**CT**	**7**	**3.644**	**0.011**
Padina sp.		**CF**	**8**	**4.188**	**0.05**
Sargassum cymosum	C. Agardh	**TL**	**40**	**20.942**	**2.40**
Total			***40***	***21.05***	

Continue

Continuation of Table 1					
RHODOPHYTA					
Aglaothamnion uruguayense	(W.R.Taylor) N.E.Aponte, D.L.Ballantine & J.N.Norris	**FI**	**1**	**0.523**	**0**
Aglaothamnion sp.		**FI**	**1**	**0.523**	**0**
Amphiroa beauvoisii	J.V.Lamouroux	**AC**	**1**	**0.523**	**0**
Asparagopsis taxiformis	(Delile) Trevisan	**FI**	**2**	**1.047**	**0**
Bostrychia binderi	Harvey	**FI**	**2**	**1.047**	**0**
Bostrychia radicans	(Montagne) Montagne	**FI**	**1**	**0.523**	**0**
Bostrychia sp.		**FI**	**4**	**2.094**	**0.001**
Bostrychia tenella	(J.V.Lamouroux) J.Agardh	**FI**	**2**	**1.047**	**0**
Caloglossa sp.		**FO**	**1**	**0.523**	**0**
Ceramium sp.		**FI**	**3**	**1.570**	**0.015**
Chondracanthus sp.		**CT**	**1**	**0.523**	**0**
Chondracantus teedei	(Mertens ex Roth) Kützing	**CT**	**3**	**1.570**	**0.005**
Chondria sp.		**CT**	**1**	**0.523**	**0**
Dipterosiphonia sp.		**FI**	**1**	**0.523**	**0**
Gelidium pusillum	(Stackhouse) Le Jolis	**CT**	**5**	**2.617**	**0.023**
Gelidium sp.		**CT**	**5**	**2.617**	**0.014**
Gracilaria domingensis	(Kütz) Sond. Ex Dickie	**CT**	**27**	**14.136**	**5.09**
Heterosiphonia crispella	(C.Agardh) M.J.Wynne	**FI**	**1**	**0.523**	**0**
Heterosiphonia sp.		**FI**	**3**	**1.570**	**0.041**
Hypnea pseudomusciformis	Nauer, Cassano & M.C.Oliveira	**CT**	**8**	**4.188**	**0.020**
Hypnea sp.		**CT**	**8**	**4.188**	**0.015**
Hypnea spinella	(C.Agardh) Kützing	**CT**	**4**	**2.094**	**0.007**
Neosiphonia sp.		**FI**	**1**	**0.523**	**0**
Plocamium sp.		**CT**	**1**	**0.523**	**0**
Polysiphonia howei	Hollenberg in W.R. Taylor	**FI**	**1**	**0.523**	**0**
Polysiphonia sp.		**FI**	**1**	**0.523**	**0**
Pterocladiella sp.		**CT**	**2**	**1.047**	**0**
Pterosiphonia parasitica	(Hudson) Falkenberg	**FI**	**3**	**1.570**	**0.001**
Pterosiphonia pennata	(C.Agardh) Sauvageau	**FI**	**6**	**3.141**	**0.015**
Pterosiphonia sp.		**FI**	**1**	**0.523**	**0**
Pyropia sp.		**FO**	**17**	**8.900**	**0.49**
Total			***49***	***25.78***	

Regarding the morpho-functional macroalgae groups, the filamentous was the most frequent within the identified species (FI; n = 29 spp; *%FO* = 59.18), followed by the terete (CT; n = 13 spp; *%FO* = 26.53) (Figure 4).

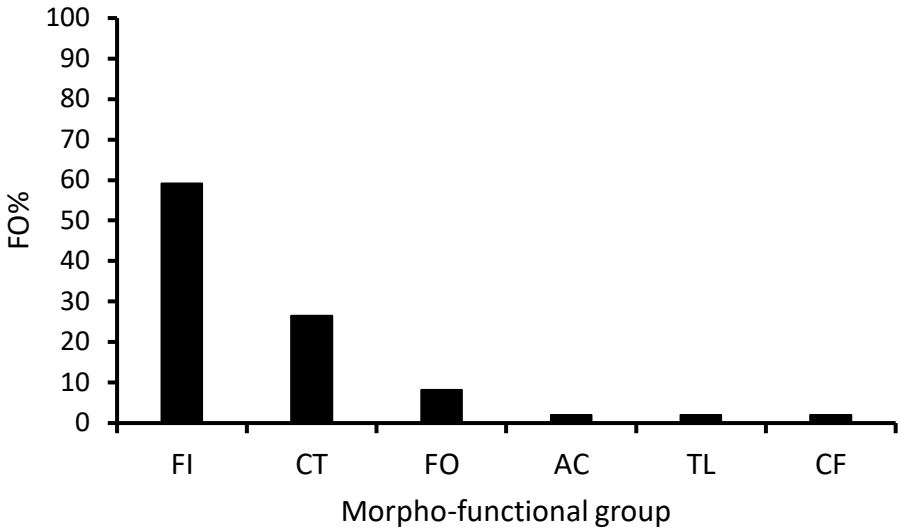


Figure 4: Frequency of occurrence of the morpho-functional groups of identified macroalgae species found in digestive tracts of juvenile green turtles along the Paraná coast from 2008 to 2018. Where FI = filamentous, FO = foliose, CT = corticated terete (fleshy), CF = corticated foliose, TL = thin leathery, AC = articulated calcareous.

Diet composition of green turtles in the Southwestern Atlantic Ocean

The most frequent macroalgae found in the digestive tracts was *Ulva lactuca* Linnaeus 1753 (n = 77; *%FO* = 40.31), followed by *Sargassum cymosum* C. Agardh (n = 40; *%FO* = 20.94), and *Gracilaria domingensis* (Kützing) Sonder ex Dickie 1874 (n = 27; *%FO* = 14.13) (Table 1). Considering the index of relative importance (*%IRI*), only the items that presented biomass were included, and *Ulva lactuca* was the prey item with the highest dietary relevance, followed by the seagrass *Halodule wrightii* Ascherson 1868 (Table 2). The filamentous Cyanobacteria *Lyngbya majuscula* Harvey ex Gomont was found in digestive tracts of 23 turtles (*%FO* = 12.04), in winter and autumn seasons only. Besides the predominance of main three groups of macroalgae, another plant prey items also showed high *%IRI*, including seagrass, mangrove, and cyanobacteria (Table 2).

Table 2: Plant matter prey items ingested by juvenile green turtles, including their specific frequency of occurrence (*%FO*), biomass (*% Biomass*) and index of relative importance (*%IRI*).

Feeding item	***%FO***	***%Biomass***	***%IRI***
CHLOROPHYTA			
Ulva lactuca	40.31	58.92	11.8400
Cladophora sp.	3.64	0.036	0.0006
Cladophora vagabunda	3.14	0.016	0.0002
Rhizoclonium	3.14	0.01	0.0001
Chaetomorpha aerea	2.61	0.008	0.0001
PHAEOPHYCEAE			
Sargassum cymosum	20.94	2.40	0.2500
Dictyota sp.	3.64	0.011	0.0002
RHODOPHYTA			
Gracilaria domingensis	14.13	5.09	0.3600
Pyropia sp.	8.9	0.49	0.0200
Hypnea pseudomusciformis	4.18	0.02	0.0004
Gelidium sp.	2.61	0.023	0.0003
Heterosiphonia sp.	1.57	0.041	0.0003
Hypnea sp.	4.18	0.015	0.0003
Ceramium sp.	1.57	0.015	0.0001
Gelidium pusillum	2.61	0.014	0.0001
Pterosiphonia pennata	3.14	0.015	0.00024
Chondracanthus teedei	0.52	0.005	1.29E-05
Bostrychia sp.	2.09	0.001	1.04E-05
Hypnea spinella	2.09	0.007	7.29E-05
Pterosiphonia parasitica	1.57	0.001	7.83E-06
SEAGRASS			
Halodule wrightii	17.36	25.38	2.1900
MANGROVE			
Avicennia schaueriana	34.73	6.61	1.1400
CYANOBACTERIA			
Lyngbya majuscula	12.04	0.033	0.0020
INVERTEBRATES			
Cephalopod's beaks	6.84	0.15	0.0050

Along the seasons, it's important to highlight the higher frequency of occurrence (*%FO*) of the filamentous cyanobacteria *Lyngbya majuscula* (*%FO* = 36.06) during winter. The mangrove species *Avicennia schaueriana* and the green macroalgae *Ulva lactuca* also showed high frequencies (*%FO* = 57.37 and *%FO* = 47.54, respectively) (Figure 5). The summer and the spring were the seasons when *L. majuscula* was not found, and the latter was the season with the highest occurrence of the seagrass *H. wrightii* (*%FO* = 38.70). The green macroalgae *Ulva lactuca* was found in green turtle digestive tracts during all seasons studied (Figure 5).

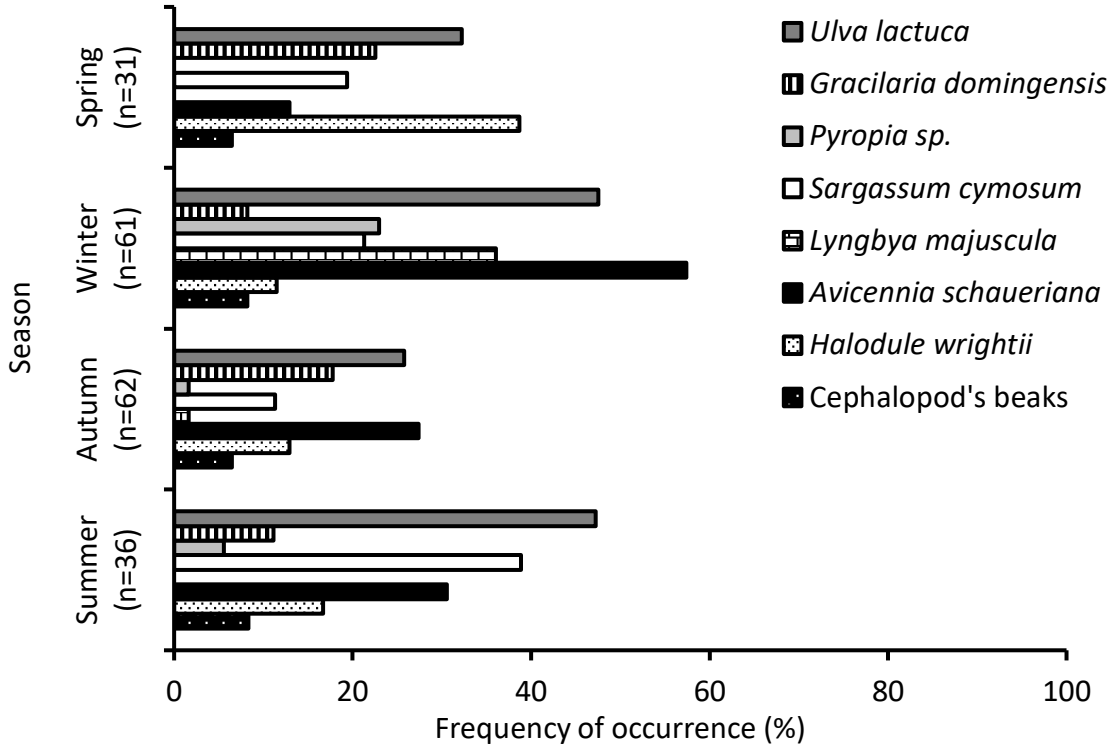


Figure 5: Frequency of occurrence of the main feeding items found in the digestive tracts of juvenile green turtles along the Paraná coast per season between 2008 and 2018.

Considering the morpho-functional groups, the most frequent (*%FO*) thalli consumed by green turtles was foliose (FO), mainly represented here by *U. lactuca*; followed by the brown thin leathery (TL) *Sargassum cymosum*; and the red corticated terete (CT) *Gracilaria domingensis* (Figure 6).

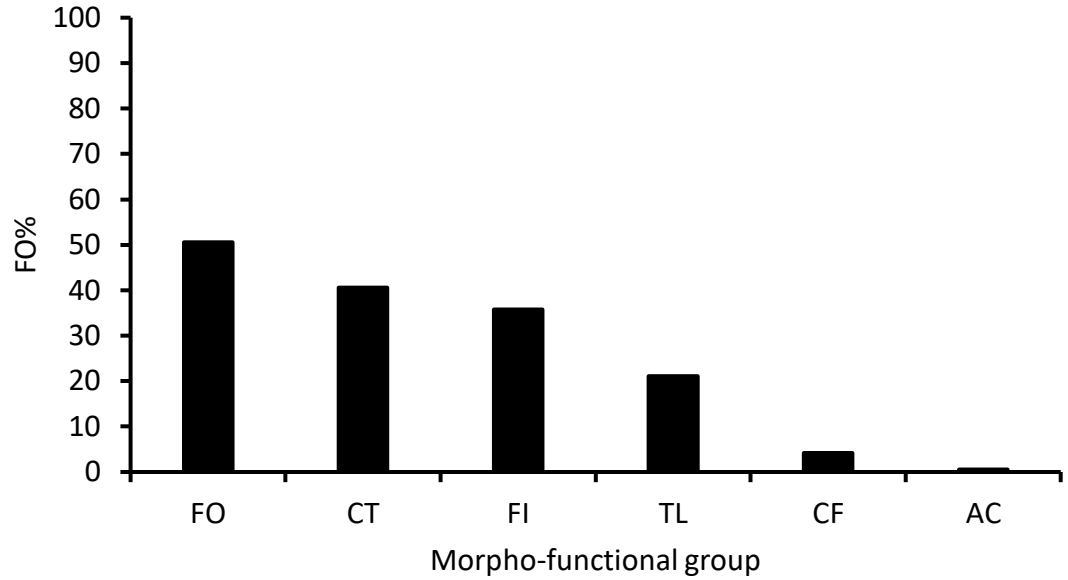


Figure 6: Distribution of the frequency of occurrence of the morpho-functional groups of macroalgae consumed by juvenile green turtles along Paraná coast. Where: FI = filamentous, FO = foliose, CT = corticated terete (fleshy), CF = corticated foliose, TL = thin leathery, AC = articulated calcareous.

PERMANOVA showed significant difference among seasons (F-value = 2.7388; Df = 3; p-value = 0.0024) (Table 3).

Table 3: Results from the permutational MANOVA, including the degrees of freedom (Df), sum of squares (SS), R^2, F-value and p-value. The difference is statistically significative.

Sources	**Df**	**SS**	**R^2**	**F-value**	**p-value**
Season	3	18.430	0.042	2.7388	0.0024
Residual	186	417.140	0.957		
Total	189	435.560	1.000		

Resulting from PCA, *U. lactuca*, the seagrass *H. wrightii* and the mangrove *A. schaueriana* were the main dietary items consumed by green turtles (Figure 7). The first four PCA axes (Fig. 7 A-D) explained 87.11% of data variance. The first (38.36%) and the second (25.58%) revealed general tendencies of *C. mydas* diet. These axes highlighted the most consumed prey items in terms of biomass, including *U. lactuca*, which represented 59.31% of the total biomass consumed by the specimens, followed by *H. wrightii* (25.54%); *G. domingensis* (5.13%) and *A.schaueriana* (6.66%).

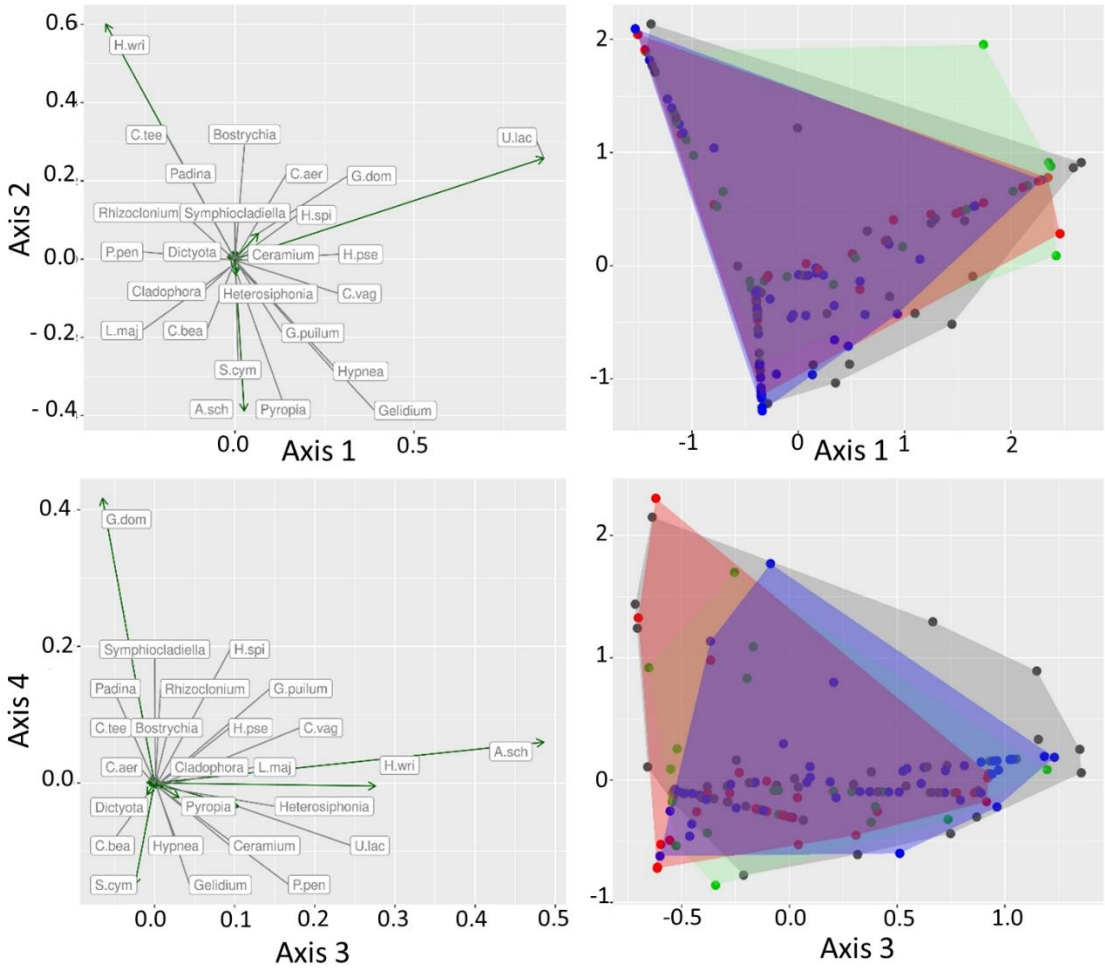


Figure 7: Principal component analysis (PCA) considering the main dietary items of *Chelonia mydas* diet, where "pink" represents austral summer; "grey" austral autumn; "blue" austral winter; and "green" austral spring.

Discussion

This study encountered 49 species of macroalgae, as well as filamentous cyanobacteria in green turtle' digestive tracts collected during ten seasonal cycles. The most frequent macroalgae group in digestive tracts contents was Rhodophyta, followed by Chlorophyta, and Phaeophyceae. Macroalgae richness of the three groups followed the expected pattern for this region, as the findings reported by Pellizzari *et al.* (2014), with Rhodophyta being the most representative group. However, considering biomass and index of relative importance (*%IRI*) of the dietary items, the Chlorophyta *Ulva lactuca* Linnaeus 1753 was the most consumed item, followed by the Rhodophyta *Gracilaria domingensis* (Kützing) Sonder ex Dickie 1874 and by

the Phaeophyceae *Sargassum cymosum* C. Agardh. In part this may be explained by higher biomass of Chlorophyta in Paraná coast throughout the year (Pellizzari *et al.* 2014), which are available food resource to green turtles.

Macroalgae's list and richness vs green turtles diet

Although Rhodophyta was the most representative macroalgae group in the analyzed digestive tracts, the most frequent macroalgae consumed by green turtles was *Ulva lactuca*, showing higher biomass and *%IRI* (Table 2). The same pattern was found by Santos *et al.* (2011) in highly urbanized areas along the Brazilian coast, and by Holloway-Adkins & Hanisak (2017) in Florida. Green turtles exhibit two foraging behaviors: browsing and grazing, as stated by Goatley *et al.* (2012) and Hoey & Bellwood (2011). The browsers forage on leathery macroalgae, whereas the grazers forage on algae turfs (Hoey & Bellwood 2011). Our results suggest that green turtles are displaying both foraging behaviors in the area.

More than the morpho-functional groups of the macroalgae, it's important to highlight the carbohydrates content, which tends to be higher in Chlorophyta, especially in *Ulva lactuca* (Rasyid 2017; Jatmiko *et al*. 2019), and this may be the reason for its higher consumption besides its availability in the area. Also, the low fiber content of this macroalgae (28.4%; Rasyid 2017) makes the turtles' digestion easier and faster, thus, the energy intake is higher (Bjorndal 1980; Brand-Gardner *et al.* 1999).

Another commonly encountered macroalgae was *Sargassum cymosum*, suggesting that juvenile green turtles are foraging in the outer sector of Paranaguá Bay, in areas such as Mel, Calheta and even Currais islands (Pellizzari *et al.* 2014), or even foraging on the floating *Sargassum* spp. (Witherington *et al.* 2012; Devault *et al.* 2021). Thus, some of the specimens whose digestive tracts contained *S. cymosum* may be recent recruiters from the pelagic-oceanic area, once floating Sargassum is a nursery habitat as suggested by Howell & Shaver (2021) and Sissini *et al.* (2017).

Regarding the morpho-functional groups, the highest consumption was of foliose macroalgae (*Ulva lactuca*), followed by thin-leathery (*Sargassum cymosum*) and by corticated-terete (*Gracilaria domingensis*), all robust species considering our subtropical phycoflora. The consumption of *Ulva lactuca* and *Gracilaria domingensis* may be related to their high nutritional value (high nitrogen content and low fiber), which in part define the feeding habit

of green turtles, as verified by Santos *et al.* (2011) and Brand-Gardner *et al.* (1999), respectively. *Sargassum cymosum* high occurrence could be related to its abundance and high biomass, and hence, higher availability in the foraging area.

Seasonal difference in macroalgae's consumption and dietary importance

There was significant diet variation among seasons (Table 3), with the austral winter and autumn seasons presenting higher macroalgae richness when compared to the spring and summer, probably due to the lower rainfall, and hence, increased macroalgae availability to green turtles and their grazing foraging behavior. Also, during the winter and autumn, the cyanobacteria *Lyngbya majuscula* was found, which is toxic and usually encountered in polluted habitats (Pearson *et al.* 2010). Thus, biotoxic effects in green turtles should be assessed in the future to understand better the sea turtles' health, as it could cause immunological disruption, increasing the prevalence of emerging diseases, such as fibropapillomatosis (Santos *et al.* 2010; Van Routan *et al.* 2014; Rossi *et al*. 2019).

The interseason differences were found for macroalgae's species richness, as well as frequencies of occurrence and biomass, all of which may be related to their availability in the foraging area, as observed in other studies (Seminoff *et al.* 2006; López-Mendilaharsu *et al.* 2008; Holloway-Adkins & Hanisak 2017; Gillis *et al.* 2020). In the autumn and winter, macroalgae richness consumed by green turtles was higher when compared to the summer and spring. This is in line with the higher richness and biomass of macroalgae at the Paraná islands reported during the winter (Pellizzari *et al*. 2014). The main foraging items consumed by green turtles in these seasons were *Ulva lactuca* followed by seedlings of *Avicennia schaueriana.*

Regarding the high occurrence of *Avicennia schaueriana* during the autumn and winter, it may be related to the macroalgae ingested in both seasons, all of which are associated to the mangrove habitat (Saengkaew *et al.* 2016), such as: *Caloglossa* sp., *Bostrychia binderi*, *Bostrychia radicans*, *Bostrychia tenella*, *Dipterosiphonia* sp., *Heterosiphonia* spp., *Heterosiphonia crispella*, *Neosiphonia* sp., and *Polysiphonia* spp. (Pellizzari *et al*. 2020b). Also, the frequency of *Pyropia* sp. was higher in green turtles sampled during winter, which may be related to its higher availability in this season in the Mel Islands, in the outer sector of PEC, and Farol Island, surrounding Guaratuba Bay (Pellizzari *et al.* 2014).

During summer, only 6 species of macroalgae were consumed, which is probably related to the documented lower richness of macroalgae in this season (Pellizzari *et al.* 2014). Nevertheless, it is important to stress that the consumed macroalgae in this season are energetically valuable for green turtles. For instance, *Rhizoclonium* sp. is an epiphytic macroalgae of *Ulva* spp. and it was consumed only in this season, probably due to the increased biomass of Ulvales, as observed by Pellizzari *et al.* (2014) and Tavares *et al.* (2020).

Alternatively, during the spring the higher consumption of the seagrass *Halodule wrightii* may be explained by its blooming and growing in this season, which presumably makes it more available to green turtles (Hall *et al*. 1999; Sordo *et al*. 2011). Moreover, this seagrass presented the second highest *%IRI*, especially because of its high biomass in some of the analyzed digestive tracts.

C. mydas macroalgae consumption vs anthropogenic impacts

All the identified macroalgae (n = 49) and the cyanobacteria occurrence were found in the green turtles' digestive tracts collected during the winter and autumn, seasons with a high incidence of stranding animals in Paraná coast (Cantor *et al*. 2020). As we know, green turtles found dead-stranded in Paraná coast present a large isotopic niche width (Gama *et al*. 2021), composed by specimens with different feeding habits. Also, this difference can be an outcome of the low rainfall in the winter, which increases the seawater salinity, transparency, and, hence, the light capture efficiency by the macroalgae, promoting their distribution and abundance increase (Carpenter 1990; Scherner *et al.* 2012), thus, their availability to green turtles is higher. Also, it has been shown that the grazing activity by green turtles is less frequent when turbidity is higher (Goatley *et al*. 2012), which can explain the overall higher macroalgae richness in winter and autumn seasons. Macroalgae richness of the three groups followed the expected for this region, as the findings reported by Pellizzari *et al.* 2014, with Rhodophyta being the most representative group.

The most frequently consumed macroalgae *U. lactuca* is a foliose seaweed, which is tolerant in eutrophic habitats (Ansari *et al*. 2010; Scherner *et al.* 2013). Moreover, they are opportunistic species that may have extremely high growth rates under human impacted and/or altered habitats (Duarte *et al.* 2019), and this may explain its conspicuous occurrence in PEC.

Moreover, Sherner *et al.* (2012) reported the expansion of *Ulva* spp. in contaminated areas, known as a pollution-tolerant species.

The mangrove *A. schaueriana* Stapf. & Leech also was an important dietary item for green turtles in Paraná coast. However, this prey item and associated Rhodophyta macroalgae consumption may be a warning considering how contaminated the mangrove habitat is, once they are excellent bio accumulators of trace elements, including metals, that magnify in polluted areas and stressed environments (Silva *et al.* 2010, Sippo *et al*. 2016, Naidoo *et al*. 2018; Duarte *et al*. 2019). Besides, *Lyngbya majuscula* was highly consumed and found in the green turtles' digestive tracts from Paraná coast in a previous study (Moreira González *et al.* 2020); these cyanobacteria may synthesize toxic compounds and are well bioindicators of aquatic pollution (Alvarenga *et al.* 2015; Pearson *et al.* 2010).

Thus, green turtles along the Paraná coast consume a mixed diet dominated by macroalgae, and showing seasonal variation directly related to their reported availability for the area (e.g. Pellizzari *et al.* 2014). They also forage on highly impacted foraging grounds, which exposes them to contaminated prey items in the area, leading to high incidence of diseases (Domiciano *et al*. 2017). This study provides an accurate dataset and baseline of macroalgae species consumed by green turtles in the South Atlantic Ocean, with focus on their seasonal dietary importance to the species. Finally, this base line data could support further studies aiming to delimitate foraging grounds, which should be prioritized in terms of conservation as turtle’s habitats.

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5. CAPÍTULO 3

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

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Abstract

Diet analysis is a key to better understanding foraging ecology and the habitat use of wildlife species. When applied to a large sample along a temporal scale, the outcomes can reveal the main diet variation drivers and the patterns, if existing. The green turtle, *Chelonia mydas*, is one of the most frequent sea turtle species in coastal areas of the Southwestern Atlantic Ocean, an important ground for foraging and development of this species. Gut analysis was performed for 315 immature turtles sampled from 2008 to 2020 along the Paraná coast, southern Brazil. A total of 15 different taxa was identified as part of the green turtles diet: Mollusca was the most frequent taxon, followed by Rhodophyta (red macroalgae) and the mangrove propagules *Avicennia schaueriana*. Inter-annual diet variation was observed, highlighting higher interannual frequencies of certain items, which can be related to natural and anthropogenic

changes in this coastal foraging habitat. Furthermore, even mostly consuming macroalgae, other different feeding strategies could be verified: seagrass foraging, invertebrates foraging and mangrove foraging. This study contributes to assessing variations in immature green turtle diet, pinpointing critical changes to their foraging habitat, and potential consequences in the species conservation.

Key words: sea turtle; feeding ecology; Southwestern Atlantic; spatial-temporal scale; seaweeds; bivalve; conservation.

5.1. Introduction

Diet, nutrition, and the way sea turtles use foraging areas influence their development and reproductive output, but also have implications for risks and recovery potential (Vander Zanden et al. 2014). Understanding these aspects may help identify areas of biological importance, temporal changes in feeding behavior and habitat use patterns, but also assess impacts and potential population effects (Fuentes et al. 2006; Marcovaldi and Santos 2011; Vélez-Rubio et al. 2018). Diet studies, especially those with long-term quantitative approaches, are key for prioritizing what foraging areas most need protection and designing more effective conservation initiatives (Hawkes et al. 2009; Hamann et al. 2010; Wildermann et al. 2018).

The cryptic nature of sea turtles and the logistic difficulties of capturing live turtles have resulted in significant challenges for collecting foraging ecology information for many species and populations worldwide (Reich et al. 2007; Vander Zanden et al. 2014; Wildermann et al. 2018). Therefore, methods to study diet, which do not require capture of live turtles in the wild, are crucial to disclose foraging aspects. For example, in many areas, sea turtle stranding programs provide an opportunity to encounter dead-stranded turtles in a relatively well-preserved state, covering a long space and time (McMichael et al. 2007; Peckham et al. 2008; Orós et al. 2016; Arizza et al. 2019). In these cases, it is often possible to recover intact gut contents to yield information about individuals' diet (Vélez-Rubio et al. 2016). Besides the possibility to determine the negative impacts that are detrimental to the species (Fuentes et al. 2020), this approach also has advantages of being inexpensive and relatively easy to conduct with proper training and a systematic stranding monitoring program. When we consider the diet methodologies, analyzing the gut content of dead stranded turtles is useful to better provide information about the entire array of consumed prey items; allowing for taxonomic

identification and, when assessed in a genetic setting, allows for comparison among different stocks mixed at foraging areas (Seminoff et al. 2002; Vélez-Rubio et al. 2018).

When a long-term monitoring is performed, analyses of gut contents from dead-stranded animals can also provide information about temporal shifts in foraging ecology. This information, when evaluated in an environmental context, may yield insights about the intrinsic (size, age, sex) and extrinsic (seasons, years) influences on diet intake, as well as suggest the ecological niche(s) of species and populations, i.e., if it is specialist or generalist (Hawkes et al. 2006; Tomás et al. 2008; Vélez Rubio et al. 2013).

In Brazil, the Santos Basin Beach Monitoring Project (PMP-BS[1]), is a stranding monitoring program systematically covering beaches from the states of Santa Catarina to Rio de Janeiro daily since 2015. The PMP-BS encompasses 1,500 km of coastline, and records were collected for dead stranded mammals, sea turtles and sea birds. However, the Paraná coast, with the second smallest state coastline in Brazil (ca. 90 km), hosts one of the most impressive mangrove / estuarine systems in the region (Lana et al. 2001; Santos and Lana 2017) and is a biodiversity hotspot (UNESCO 2021). The area is particularly important as a foraging ground for juvenile green turtles (*Chelonia mydas*), which occur year-round (Guebert-Bartholo et al. 2011; Gama et al 2016). However, more than 1,000 green sea turtles are found dead-stranded each year (Cantor et al. 2020). The impact is a critical conservation issue, but offering large sample sizes for analysis of stranded animals and a more holistic view of ecological approaches (i.e. dietary intake) and potential anthropogenic impacts.

Green turtles (*Chelonia mydas*) occur in the Southwestern Atlantic Ocean (SWAO) throughout the year, including the Paraná coast, which is an important foraging ground for juveniles (Marcovaldi and Santos 2011; Gama et al. 2016; Vélez-Rubio et al. 2018). This region hosts green turtles from multiple stocks, including the SWAO regional management unit (RMU) and the South Central Atlantic RMU (Wallace et al. 2010). Studying feeding habits of these turtles through time helps better understand the population's behavior and its exposure to anthropogenic impacts. Previous studies on green turtle diet in this area 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

[1] PMP-BS: The Santos Basin Beach Monitoring Project (PMP-BS), an IBAMA constraint related to oil and natural gas exploration in the Brazilian coast by PETROBRAS, is proposed to help elucidate knowledge gaps and improve impact mitigation actions for the species conservation.

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; Gama, *chapter* 1). Prior research has also indicated changes in green turtle presence and ecological parameters related to climatic zone and temperature (Esteban et al. 2020). Given temperature influences on diet, it is essential to include climatic variability as a potential driver for diet variability in the same area. Along the Peruvian coast, large green turtles, known locally as black turtles (*C. m. agassizi*), are primarily herbivorous; however, during El Niño events, they migrate to neritic waters and ingest large amounts of scyphozoan jellies, especially when this prey type is undergoing periodic blooms (Quiñones et al. 2010). It is also known that changes in temperature affect the food resource availability in the habitat, which leads to variation in green turtles diet (Hawkes et al. 2009).

Diet variation among green turtles in the SWAO RMU was also influenced by turtle size, age and seasonality (Gama et al. 2016; Vélez-Rubio et al. 2016); however, so far, no study in the SWAO has tested diet as a way to assess habitat use on long temporal scales. Considering the importance of Paraná coast as a stopover for juvenile green turtles from the SWAO RMU, the present study focused on the interannual diet variability, disclosing potential ecological changes throughout the years.

5.2.Methods

5.2.1. Study area

The Paraná coast, southern Brazil (25°20'S to 25°35'S / 48°17'W to 48°42'W), is a migratory corridor for multiple sea turtles species that are present in the SWAO (Marcovaldi and Santos 2011). Paraná has ~90 km of sandy beaches, and several bays and estuaries, such as the Paranaguá Estuarine Complex (PEC), a 612-km^2 semi-enclosed inlet, that comprises ~1000 km of estuarine interior coastline (Lana et al. 2001) (Fig. 1). 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, mangrove roots 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). Paraná is influenced by the Brazilian Current, which brings warm waters to the south during the austral summer (wet season), and the Falklands Current that introduces cold waters northward during the winter (dry season)

(Piola et al. 2000; Matano et al. 2010). The PEC is composed by three different halines zones (estuarine, estuarine outlets and open-ocean coasts) (Angulo and Araujo 1996), with different dynamics that result in an estuarine gradient and hence, spatial differences in wave and tidal influences (Krelling and Turra 2019).

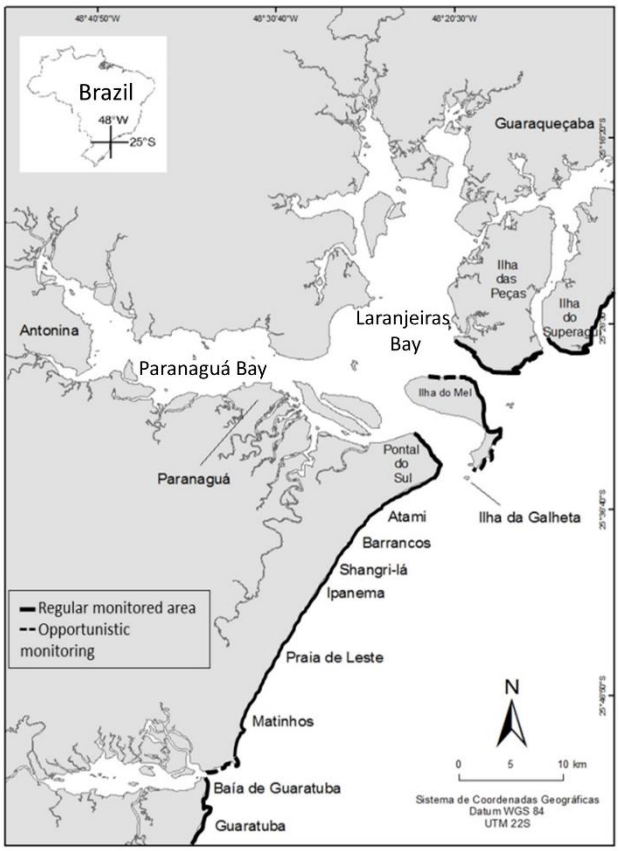


Figure 1. Map of the Paraná coast of Brazil, including the Paranaguá Estuarine Complex (PEC), in south Brazil, where the beach surveys were performed, and dead-stranded green turtles were recovered. The thick lines represent the regular monitored area, whereas the dashed one represents the areas where the monitoring has been made occasionally.

5.2.2. Collecting stranded specimens

Dead stranded green turtles were collected along the Paraná coast (Fig. 1) during daily beach surveys from 2008 to 2020; however, only freshly dead juveniles with intact tissues were considered. All the specimens had their life stage and body size (curved carapace length = CCL; measured in cm with a plastic metric tape from the cranial carapace junction to the caudal margin of the post-central scutes of the carapace) recorded and biological samples collected for further necropsy analysis. Curved carapace length was measured in cm with a plastic metric

tape from the cranial carapace junction to the caudal margin of the post-central scutes of the carapace. The digestive tracts were stored frozen until diet evaluation.

The sampling year, locality, date, season, and body size were recorded for each recovered green turtle. In addition, sex was determined by gonadal histology following Duarte et al. (2011), and age was estimated via the skeletochronology method (Snover et al. 2004), both by the PMP-BS technician team.

5.2.3. Gut content analysis

The dietary items encountered in the digestive tracts were washed, separated using a tablet stereoscopical microscope and re-stored frozen for further analysis. Macroalgae constituents, seagrasses and mangrove seeds were separated, washed, identified to the lowest possible taxonomic level, and the frequency of occurrence was calculated. Macroalgae taxa were determined using morphological and reproductive features in proper microscopy, supported by appropriate identification keys, and illustrated references (Cordeiro-Marino, 1978; Nunes et al. 1999; Moura, 2000; Barata, 2004; Nunes, 2005; Coto, 2007; Crispino, 2007; Nunes and Guimarães, 2008; Pereira-Filho et al. 2011/2012; and Pellizzari et al. 2014). All the invertebrates were identified using appropriate books and identification keys (Ruppert and Barnes, 1996; Wiggers, 2003; Pimpão, 2004; Xavier and Cherel, 2009; Absher, 2015), followed by specialists' support. Non-food ingesta (mainly marine debris) was registered, and frequency of occurrence was also calculated, contributing to understanding the effects of this threat on juvenile green turtles.

5.2.4. Statistical analysis

The frequency of occurrence (*%FO*) (Hyslop 1980) of the prey items found in the digestive tracts was calculated:

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

In order to identify temporal tendencies in green turtles diet the frequency of occurrence (*%FO*) of the prey items was calculated by year (2008–2020) and season (austral summer, autumn, winter and spring). The *%FO* values were logit-transformed (Warton and Hui, 2011) and a two-factor PERMANOVA was performed (year + season, Euclidian distance, 9999 permutations) (Anderson, 2001; 2003); a PCA was performed aiming to better interpret the PERMANOVA results. All analyses were performed using R 4.0 software (give citation for R group). In addition, rainfall data from 2008 to 2020 (in mm from the Paranaguá meteorologic station at 25°31'S, 48°30'W; by SIMEPAR, www.simepar.br) and sea surface temperature (SST) data were obtained from https://coastwatch.pfeg.noaa.gov/, using the average values for each year of analysis.

5.3. Results

5.3.1. General information

In the present study, a total of 315 fresh juvenile green turtles were sampled, with CCL ranging from 23.2 cm to 68.0 cm (38.5 ± 7.3 cm). We analyzed 128 turtles encountered during the spring and summer (between October and March) and 187 turtles from autumn and winter (between April and September). Sex was determined for 231 turtles, including 183 females and 48 males; all were immature individuals, age-estimated from 2 to 17 years old. The years 2017 and 2018 were the ones with more individuals analyzed (Fig. 2), mostly because the sampling effort was greater to collect diet content and skin samples for isotope analysis (e.g. Gama et al. 2021 – *chapter 1*).

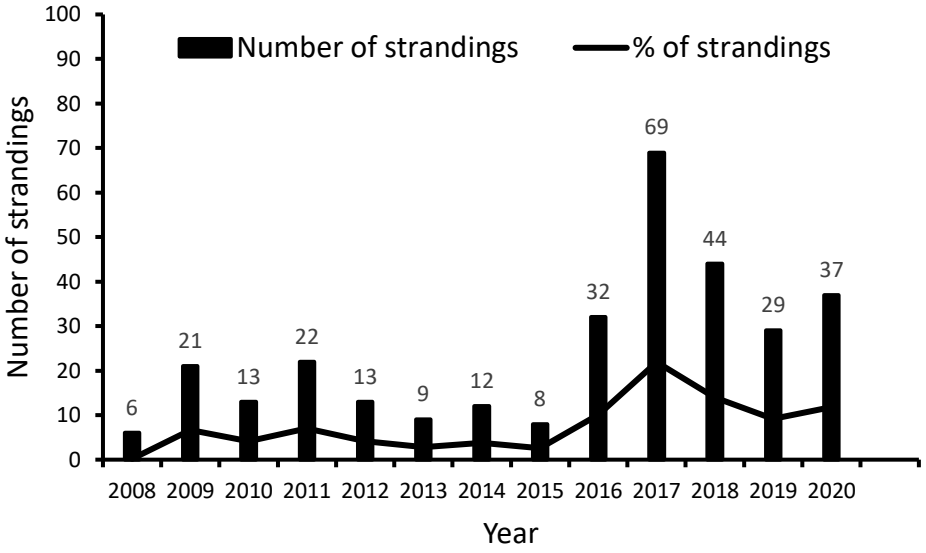


Figure 2: The number (column) and % (line) of immature green turtles, sampled in the Paraná coast, which had their digestive tracts analyzed in each year of study.

The average sea surface temperature (SST) values ranged from 21.60°C in 2008 to 26.71°C in 2014; whereas the average rainfall values ranged from 120.66 in 2014 to 276.63 in 2010 (Fig 3).

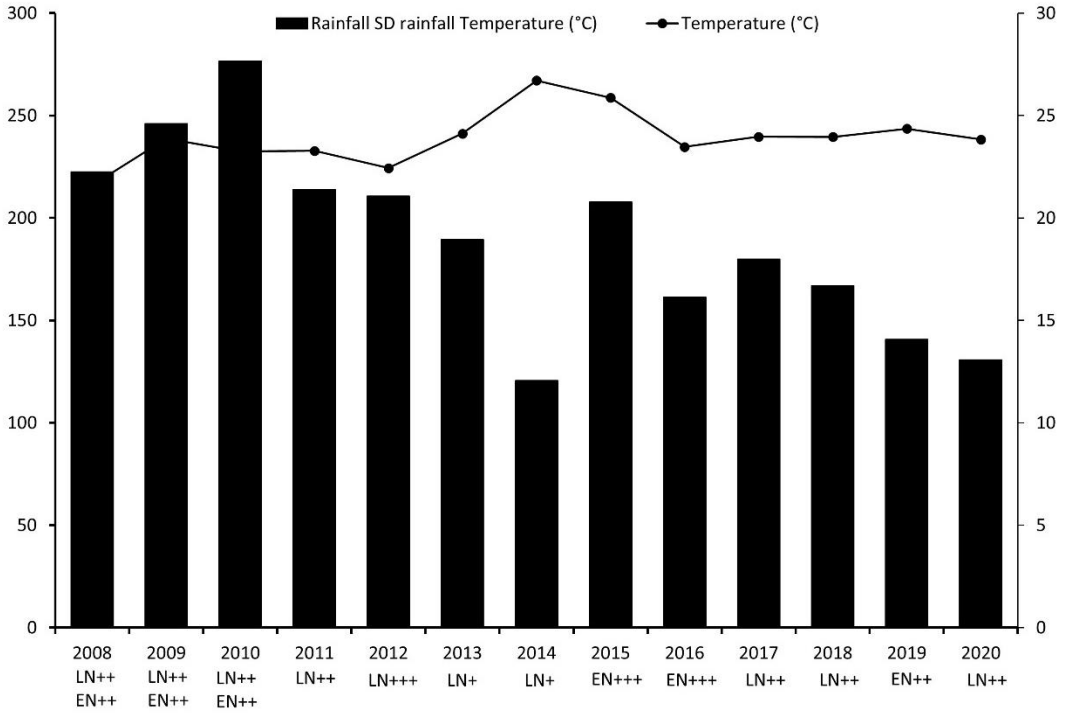


Figure 3: Average rainfall (in mm) values and average temperature (°C) values from 2008 to 2020 in Paraná coast, south Brazil. La Niña (LN) and El Niño (EN) events are included, where "+" means a weak event; "++", moderate; and "+++" strong.

A total of 15 different taxonomic groups were encountered in digestive tracts of green turtles: Mollusca (including Gastropoda, Bivalvia and Cephalopoda), Rhodophyta, Angiosperms (including mangrove, other angiosperms, and seagrass), Chlorophyta, Phaeophyceae, Bryozoa, Hydrozoa, Crustacea, Echinodermata, Cyanobacteria, Fish, and Insecta (Fig. 3). It is important to highlight that the phylum Mollusca was subdivided and analyzed into three classes (Gastropoda, Bivalvia and Cephalopoda) and angiosperms were identified as a distinct group.

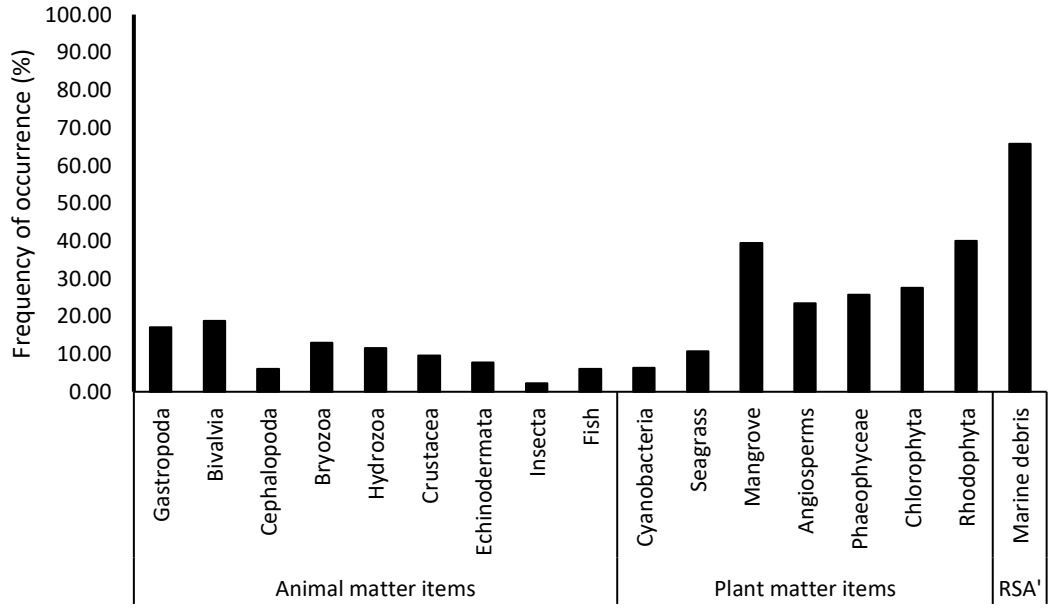


Figure 3: Frequency of occurrence (expressed in %) of all the prey items found in the digestive tracts stranded immature green turtles (n= 315) in Paraná coast from 2008 to 2020.

Among the items revealed, the phylum Rhodophyta was the most frequent (*FO%* = 40.05), followed by the mangrove *Avicennia schaueriana* (*FO%* = 39.5), and Bivalvia (*FO%* = 18.78) (Fig. 3). Regarding marine debris occurrence ('RSA'), 65.71% (n = 207) of sampled green turtles presented marine debris in their digestive tracts (Fig. 3), with 57.48% (n = 119) of those being females and 14.00% (n = 29) males.

5.3.2. Temporal variability in diet contents

The same prey-item distribution was observed across the years, with Rhodophyta, *A. schaueriana* and Bivalvia being the most frequent ones in the samples (Fig. 4). When looking at the distribution of the frequency of occurrence (*FO%*) of the prey items among the years, it

is observed that their distribution is constant throughout time (Fig. 4). Nevertheless, it is important to highlight few occurrences in 2015 (only Mangrove, Chlorophyta and Rhodophyta) and the high richness in 2020 (Fig. 4).

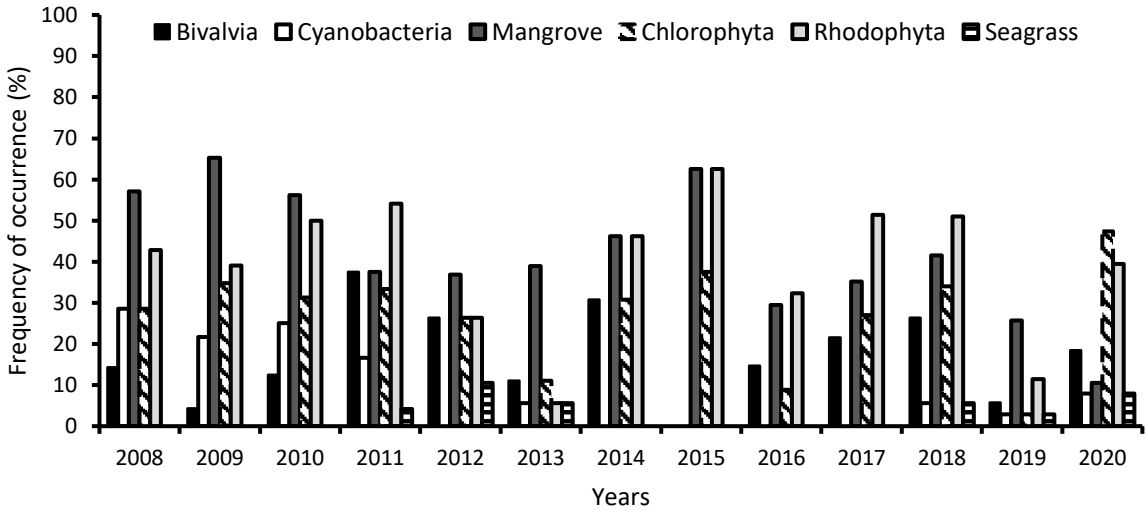


Figure 4: Frequency of occurrence (expressed in %) of the main prey items ingested by immature green turtles throughout the sampling analysis of 12 years in Paraná coast.

PERMANOVA revealed significant differences in green turtle diet across years (F-value = 1.3909; *p*-value = 0.0292) (Table 1). However, no statistical difference between seasons was observed (PERMANOVA: F-value = 0.8081, *p*-value = 0.7638).

Table 1. Results from two-factor PERMANOVA (year + season) for the diet of Paraná green turtles. 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	12	174.74	0.3542	1.3909	**0.0292**
Season	3	25.38	0.0514	0.8081	0.7638
Residual	28	293.14	0.5943		
Total	43	493.26	1.0000		

The four first axes of PCA explained 63.54% of the dataset variance. The first axis (variance % = 24.38%) highlighted the consumption of *Halodule wrightii* (axe score, sc1 –1.25), Chlorophyta (sc1 0.50) and Mollusca (sc1 0.50); and the year of 2018, comprising a diet quite constant in *Halodule wrightii* and Phaeophyceae (sc1 –0.33) (Fig. 4A-4B). The second axis (variance % = 15.98%) highlighted the consumption of *Avicennia schaueriana* (sc2 –0.81),

Cyanobacteria (sc –0.42), Gastropoda (sc2 0.56), Bivalvia (sc2 0.48) and Mollusca (sc2 0.43) (Fig. 4A). *Avicennia schaueriana* was consumed during all sampled years, although its consumption was higher in 2009, 2010, 2013 and 2014, which might be influenced by La Niña events. Cyanobacteria was the most consumed prey type in 2009 and 2010, whereas Mollusca was most consumed from 2011 to 2014 (Fig. 4B).

The axes 3 (variance % = 14.90%) and 4 (variance % = 8.27%) confirmed the annual tendencies of green turtles diet highlighted on the axes 1 and 2; besides showing complementary information. *Avicennia schaueriana* (sc3 –0.47 and sc4 0.35) and Mollusca (sc3 –0.30) were confirmed as constant items during 2013 and 2014, while *Halodule wrightii* (sc3 –0.14) was encountered throughout the year of 2012 in high frequencies (Fig. 4C). Marine debris ('RSA' in the PCA graph) (sc3 0.69), Rhodophyta (sc3 0.63) and other angiosperms (sc4 0.37) were consumed over the years, with marine debris presenting higher consumption frequencies from 2017 to 2020; Rhodophyta in 2010, 2016 and 2017; and other angiosperms from 2015 to 2017. Despite these differences, the three items reached their minimum of consumption in 2012 and 2013. Finally, Chlorophyta (sc4 –0.47) and Cyanobacteria (sc4 –0.23) presented more consumption from 2009 to 2011, besides we should highlight Hydrozoa (sc4 –0.20) in 2012, and Bryozoa (sc4 0.48) in 2019 and 2020 (Fig. 4D).

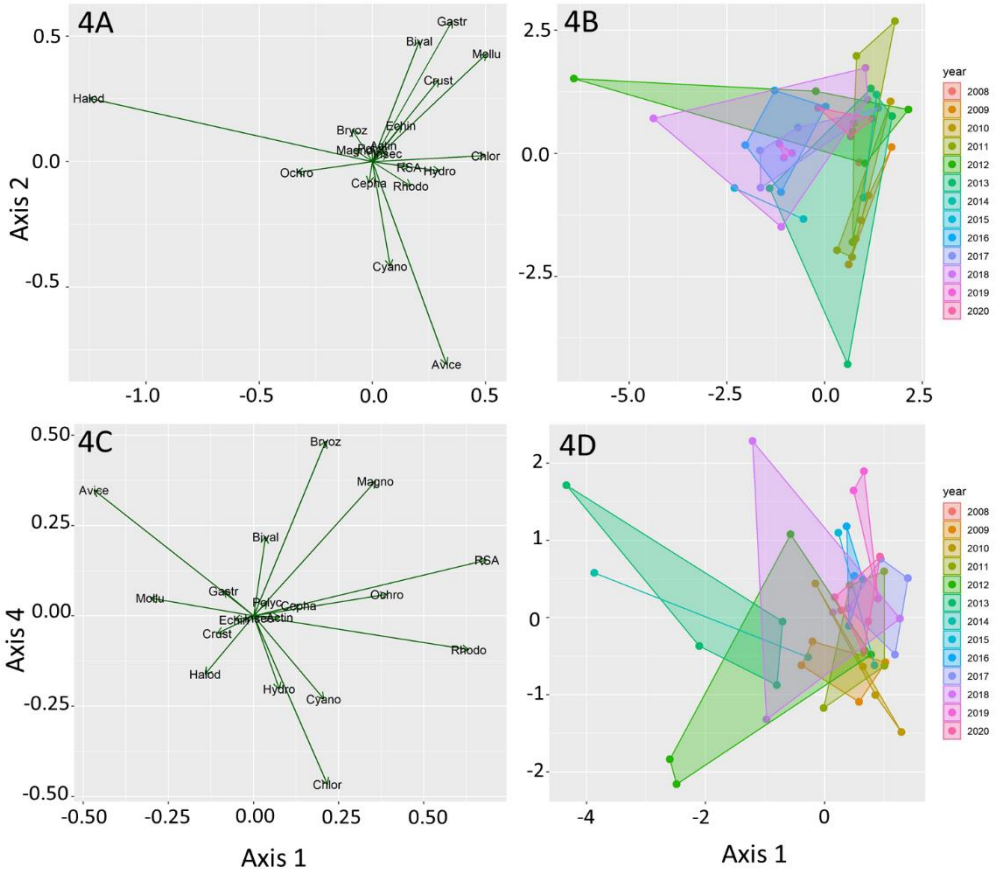


Figure 4: PCA showing the interannual tendencies of green turtles diet across 12 years of analysis in Paraná coast, south Brazil.

5.4.Discussion

5.4.1. Green turtles diet in Paraná coast

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). Indeed, in Paraná coast there are multiple stocks of juvenile green turtles which use the area for foraging (Coelho et al. 2018; Savada et al. 2021), and this can influence on the diet variation herein presented.

For juvenile green turtles from SWAO, analyzing gut contents of 315 individuals found stranded in Paraná coast, we identified individual variation across the years and an evident annual diet variation comparing samples from 2008-2020. All the dead-stranded green turtles herein included are immature juveniles, with 62 cm maximum of curved carapace length, age-estimated from 2 to 17 years old, and they are found in every season (Andrade et al. 2016, Gama et al. 2016; Coelho et al. 2018). We recorded fifteen taxonomic prey items in the present study, including animal and plant matter ones. This mixed diet and benthic foraging strategy 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). Moreover, 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.

5.4.2. Diet shifts in green turtles foraging habit across twelve years

The temporal analysis across twelve years highlights the effect of the interannual changes as the most relevant driver on diet variation of juvenile green turtles that aggregate to the foraging area in Paraná coast, part of the SWAO RMU. It was observed that Rhodophyta (red macroalgae) and Chlorophyta (green macroalgae) consumption is continuous and frequent throughout the sampling years of analysis (seasons of austral winter and autumn), which reinforce macroalgae diet data for the species along the SWAO RMU (Reisser et al. 2013; Santos et al. 2015). Their constant consumption may be related to their easy digestibility by green turtles (Campos and Cardona 2020) and high nitrogen and low fiber content (Brand-Gardner et al. 1999).

However, some prey items showed higher consumption in certain years, which was the case of the seagrass *Halodule wrightii*, for instance. This seagrass presented high occurrence in the spring of 2012, when Chlorophyta, marine debris, and other angiosperms presented

minimum occurrence (Fig 4A-D). This food resource used to be one of the most frequent in green turtles diet in Paraná coast (Guebert-Bartholo et al. 2011; Gama et al. 2016), and presented high frequencies in the spring of 2012 and in the summer of 2018. Despite the little availability of this food resource in the area since 2011 (Gama et al. 2016), this result aligns with the isotope analysis of the dead-stranded turtles found in Paraná coast, which might be selecting seagrass in their diet (Gama, *chapter 1*), stressing one type of foraging strategy.

From diet data across the sampling years, we could observe that juvenile green turtles have been using critical foraging habitats, such as the mangroves. The consumption of *Avicennia schaueriana* may be a warning to green turtles health because this nursery habitat presents high levels of contaminants and pollution in Paraná (Silva et al. 2010; Garcia and Martins 2021). This health negative issue can be verified by the high incidence of individuals with fibropapillomatosis in Paraná coast (Domiciano et al. 2019) and high ingestion of marine debris by juveniles (Gama et al. 2016; Nunes et al. 2021). The mangrove *Avicennia schaueriana* and Cyanobacteria, which are toxic and usually found in polluted habitats (Alvarenga et al. 2015), presented higher occurrences from 2009 to 2014. We can observe that when seagrass was the dominant consumed prey item, the mangrove and Cyanobacteria were absent (Fig 4A-D).

Regarding the invertebrates consumption, Bivalvia and Gastropoda are the most available Mollusca in Paraná coast islands (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, in accordance, stable isotope data of live-captured green turtles from 2016 to 2018 showed a high contribution of invertebrates to their diet (Gama, *chapter 1*).

5.4.3. Feeding habit and impacts

Juvenile green turtles are threatened in Paraná coast because of several impacts, such as fishery, pollution from the urban and port areas, contamination, marine debris, and marine traffic (Domiciano et al. 2017; Fuentes et al. 2020; Nunes et al. 2021). Thus, the estuarine

habitat and the feeding habits herein presented expose the specimens to different risks, once the more polluted an area is, the higher the occurrence of diseases will be (Domiciano et al. 2019).

Considering marine debris consumption, in a study conducted in southeastern Brazil, the green turtle was the marine species that mostly consumed debris (Di Beneditto 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 in 2017 and 2018, years of La Niña (CPTEC 2016), presenting both low temperature and low rainfall rates (Figure 5; as confirmed with our rainfall data).

5.5. Conclusion

Our diet findings align with the expected foraging strategies for green turtles that forage in estuarine and bay areas, highlighting green turtles diet as mixed in these areas (Santos et al. 2015; Esteban et al. 2020). Moreover, years with atypical average rainfall were the ones that green turtles diet was different. This result might be indicating variation in the habitat plant composition; and, hence, variation in green turtles diet. Besides, dredging activities take place in PEC in different years, probably contributing to the habitat changes and degradation. Finally, foraging plasticity must be considered as well as different foraging behaviors presented by green turtles in the same area, as reported by Santos et al. (2015). Conservation actions are urgently needed, once not only sea turtles but also marine fauna and phyco-flora are exposed to this threatened and sensitive environment.

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The Santos Basin Beach Monitoring Project (Projeto de Monitoramento de Praias da Bacia de Santos - PMP-BS) is required by Brazil's federal environmental agency, IBAMA, for the environmental licensing process of oil production and transport by Petrobras (ABIO 640/2015)

5.6. References

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5. CONSIDERAÇÕES FINAIS

Os principais objetivos deste estudo foram: i. definir o tamanho do nicho trófico dos juvenis de *C. mydas* encontradas encalhadas mortas e intencionalmente capturadas vivas na costa do Paraná e a contribuição dos itens alimentares na dieta da espécie, a partir de análises isotópicas; ii. avaliar a variação sazonal da diversidade de itens consumidos pela espécie, com enfoque na análise minuciosa das macroalgas e relações com impactos sobre área de alimentação; iii. avaliar a variação interanual da dieta da espécie ao longo de 12 anos de estudos no litoral do Paraná.

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.

Os juvenis de tartarugas-verde apresentam uma dieta heterogênea, com consumo de 49 diferentes espécies de macroalgas marinhas, fanerógamas marinhas, propágulos de mangue e invertebrados. Especificamente para as macroalgas marinhas, existe variação sazonal no consumo destas, sendo que nas estações de inverno e de outono, a riqueza de espécies consumida é maior, provavelmente relacionado à disponibilidade nas áreas de alimentação. Além disso, é importante salientar o consumo de cianobactérias tóxicas, bem como a utilização de áreas de alimentação impactadas negativamente.

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, além do consumo contínuo de macroalgas: alto consumo de fanerógama marinha *Halodule wrightii*; consumo de invertebrados; e consumo de propágulo de mangue *Avicennia schaueriana*. As tartarugas-verde apresentam variação da dieta relacionada a alterações na temperatura e pluviosidade, mas também ao seu hábito alimentar individual, sendo que apesar

dos impactos a que estão submetidas, há plasticidade alimentar e capacidade adaptativa dos espécimes na região.

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*.

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