Diet composition of juvenile green turtles in the Southwestern Atlantic Ocean: long-term insights from a beach stranding program

Running page head: Green turtles long-term diet study.

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Abstract

Long-term diet studies provide information on the temporal variation in diet composition, habitat use and foraging ecology of species. Assessment of dead-stranded sea turtles by stranding programs allows systematic diet sampling over a broad temporal scale, which can help elucidate potential ecological and environmental changes. Off the Southwestern Atlantic Ocean, the Paraná coast, Brazil, is an important foraging ground for juvenile green turtles (*Chelonia mydas*). To determine seasonal and interannual diet variability, 351 dead-stranded individuals had their dietary contents analyzed to the major taxa level from 2008-2020. We identified 13 major prey groups that made up green turtles' diets. A subset of turtles had diet identified to the lowest taxonomic level possible. Interannual differences were found, with the Chlorophyte *Ulva lactuca* highly important in 2008, 2011–2018; Bivalvia and Gastropoda in 2016 and 2017. During La Niña events (2011, 2012, 2013, 2014, 2017, 2018, 2020), Chlorophyta, Mollusca, Crustacea and Hydrozoa were the most frequently encountered diet items; during El Niño events (2015, 2016, 2019) Ochrophyta was the most consumed taxon. Seasonal differences were found, such that Echinodermata and Teleostei were important in autumn and winter; Hydrozoa and Gastropoda in all seasons. Our results underscore individual dietary plasticity, including inter-seasonal and annual differences, which likely reflects their ability to respond to changing prey availabilities and environmental characteristics driven by natural and perhaps anthropogenic influences. Understanding potential links between diet, habitat use, and the effects of a shifting diet and foraging grounds are key information for monitoring impacts and guiding conservation actions.

Keywords: *Chelonia mydas*; feeding ecology; behavioral plasticity; spatial-temporal scale; macroalgae; Mollusca; conservation.

1. INTRODUCTION

Long-term diet studies are key for evaluating temporal changes in food intake and habitat use patterns of consumers, which help identify areas of biological importance and give insight into what foraging areas most need protection (Fuentes et al. 2006, Marcovaldi & Santos 2011, Vélez-Rubio et al. 2018a). Indeed, foraging ecology studies have been identified among the most important themes in sea turtle conservation (Hamann et al. 2010, Wildermann et al. 2018), especially in the context of ongoing climate change and cumulative anthropogenic effects (Hawkes et al. 2009, Fuentes et al. 2020).

When studying green turtle foraging ecology, knowledge about the extrinsic influences such as prey availability, sea surface temperature, cumulative rainfall rates, and habitat quality is fundamental to interpret behaviors, diet intake, and health of local green turtles (Wildermann et al. 2018). Also, understanding the influences of decadal-scale climate shifts on habitats is essential to assess long-term ecological changes (Hawkes et al. 2009, Esteban et al. 2020). For example, in southern South America, El Niño (which increases rainfall and temperature) and La Niña (which decreases rainfall and temperature) events influence climate variability, rainfall patterns and intensity, and sea surface temperatures (Grimm et al. 2000). Therefore, these and other climatic events may drive biological and ecological changes (e.g. habitat dynamics, prey availability, predator-prey interaction), leading to diet variation among turtles in these areas (Saba et al. 2007, Quiñones et al. 2010, Esteban et al. 2020).

The cryptic nature of sea turtles and the logistic difficulties of capturing live turtles in the wild are challenges for studying their diet intake and overall foraging ecology across large spatial and temporal scales (Reich et al. 2007, Vander Zanden et al. 2014, Wildermann et al. 2018). In many areas worldwide, sea turtles are exposed to significant cumulative human threats, resulting in stranding of live and/or dead turtles along shores (Monteiro et al. 2016, Cantor et al. 2020). In such areas, ongoing systematic and long-term sea turtle stranding monitoring programs present an opportunity to encounter and study these individuals for health and ecological assessments, such as analysis of digestive tract contents to gain insights about diet composition for the local population (Hart et al. 2006).

Based on stranding records, southern and southeastern Brazil have a large number of juvenile green turtles (*Chelonia mydas*) that dead-strand each year, particularly in Paraná (25° S) and the central area of Santa Catarina states (26° S) (Cantor et al. 2020). Green turtles in this area are part of the Southwestern Atlantic Ocean (SWAO) Regional Management Unit (Wallace et al. 2010) and include individuals originating from at least 12 rookeries throughout the SWAO (Savada et al. 2021), that can be resident in the area (Guebert et al. 2011, Marcovaldi & Santos 2011, Gama et al. 2016; 2021, Coelho et al. 2018, Fuentes et al. 2020). This region is a biodiversity hotspot (UNESCO 2021) and hosts one of the most impressive mangrove/estuarine systems globally (https://www.ramsar.org/news/brazil-designates-three-ramsar-sites), with nearly 1,000 km of interior coastline that provides a diversity of habitats and prey types for green turtles (Lana et al. 2001, Gama et al. 2016; 2021, Santos & Lana 2017). However, more than 1,000 juveniles are found dead-stranded each year in Paraná (Cantor et al. 2020), with mortality attributed to a variety of local threats, such as habitat degradation, debris ingestion, chemical pollutants, fisheries bycatch, and emergent diseases (Domiciano et al. 2019, Fuentes et al. 2020, Nunes et al. 2021, Sulato et al. 2022).

Since 2004, several studies have been ongoing in this area focusing on green turtles, including beach monitoring and stranding response programs (Guebert-Bartholo et al. 2011, Cantor et al. 2020, Gama et al. 2021, Sulato et al. 2022). Previous studies on green turtle diet in the SWAO show a high diversity of consumed prey items, including seagrasses, macroalgae, mangrove leaves and seeds, and animal matter

(Bugoni et al. 2003, Guebert-Bartholo et al. 2011, Marcovaldi & Santos 2011, Nagaoka et al. 2012, Awabdi et al. 2013, Reisser et al. 2013, Gonzalez-Carman et al. 2014, Santos et al. 2015, Gama et al. 2016, 2021, Vélez-Rubio et al. 2016). However, despite this substantial information on green turtle diet, little information is available regarding the ability of green turtles to shift their diet intake in response to environmental change.

Here, we build upon previous green turtle diet studies in the region to — for the first time — explore long-term variation and trends related to seasonal, annual, and intermittent environmental (El Niño/La Niña) cycles. The present study examined gut contents of dead-stranded green turtles encountered in this area between 2008–2020. In addition to describing temporal patterns in green turtle diet, our efforts underscore the value that beach stranding recovery programs provide for understanding the ecology of and ongoing threats to encountered animals.

2. MATERIALS AND METHODS

2.1. Study site

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 turtle species that are present in the SWAO (Wallace et al. 2010, Marcovaldi & Santos 2011, Cantor et al. 2020). 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 (*Halodule wrightii*) meadows, mangrove-lined (including *Avicennia schaueriana*) estuaries, and rocky subtidal habitats dominated by marine macroalgae (Angulo 1992, Sordo et al. 2011, Pellizzari et al. 2014, Bumbeer et al. 2016, Pellizzari et al. 2020). Macroalgal diversity along the

Paraná coast and islands is considered low (~130 taxa) compared to other tropical areas in Brazil (Pellizzari et al. 2014). Nevertheless, several species of green macroalgae (Chlorophyta), red macroalgae (Rhodophyta), and brown macroalgae (Ochrophyta) occur in high biomass (Pellizzari et al. 2007, 2014, 2021, Pellizzari & Reis 2011).

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

2.2. Dead-stranded turtle collection

Dead-stranded green turtles were collected along the Paraná coast (Fig. 1) during systematic beach surveys from 2008 to 2020; however, only fresh-dead juveniles or animals in early-decomposition stages (Codes 2 and 3, respectively; according to the decomposition stages ranking adapted from Geracy & Lounsbury 2005) with intact digestive tracts were considered for this study. Between 2015–2020 the samples were obtained as part of the PMP-BS (Santos Basin Beach Monitoring Project or *Projeto de Monitoramento de Praia da Bacia de Santos*). All the specimens had their curved carapace length (CCL; to 0.1 cm precision, measured with a flexible tape from the nuchal scute notch to the posterior-most edge of the carapace) recorded and biological samples collected for further analysis. The digestive tracts were removed and stored frozen at –15°C until analysis. The sampling year, locality, date, season, and body size were recorded for each recovered green turtle. Also, some specimens obtained from PMP-BS (n = 238) had their body condition score calculated (e.g. Limpus et al. 2012).

2.3. Diet analysis

To determine diet composition, all recovered items were washed, separated, and identified. The invertebrates, except cephalopod beaks, and debris were washed and dried at 60°C; vegetal matter items were preserved in 70% ethyl alcohol; and cephalopod beaks were preserved in 70% ethyl alcohol and 5% glycerin.

Three different diet analyses were conducted:

i. LT (Low Taxonomic, all prey species): to achieve low taxonomic resolution identification, 351 green turtles had their digestive tract contents identified to the phylum or class level with stereoscopic and optical equipment;

ii. HTM (High Taxonomic, Macroalgae only): a total of 148 turtles recorded from 2008-2014, and 2017-2018 had their macroalgae contents identified to finer taxonomic level (e.g. genus, species) based on the morphology of reproductive and vegetative structures, according to 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 (2019);

iii. HTA (High Taxonomic, Animal prey only): a total of 142 green turtles recorded from 2015 to 2020 had their animal matter (invertebrate and vertebrate) contents identified to the genus or species level according to

Ruppert & Barnes (1996), Wiggers (2003), Pimpão (2004), Xavier & Cherel (2009), Absher (2015), followed by specialists' support.

The global algae database AlgaeBase (Guiry & Guiry, 2023) and the World Register of Marine Species website WoRMS (2023) were also used to validate all the species found. The digestive tracts of all green turtles were also analyzed to quantify the presence of marine debris. All types of debris, including hard and sheet-like plastic, threadlike, nylon, straws, balloons, and fishery debris were visually identified and counted, following the classification of Nunes et al. (2021).

2.4. Statistical analysis

To quantify the digestive tract contents recovered during both efforts, the frequency of occurrence (*%FO*) (Silveira et al. 2020) was calculated for each food category as a percentage between the number of stomachs in which the food category *f* occurred (Sf_f) and the total number of stomachs with food assessed (Sf) [Eq.1]:

$$\%FO = \left(\frac{Sf_f}{Sf}\right) \cdot 100$$

Specific to the macroalgae, which is the prey item whose weight has been measured, the gravimetric frequency (*%W*) was calculated representing a percentage between the weight of the food category *f* consumed by a given specimen i (W_{fi}) and the total weight of all food categories consumed by this specimen ($\sum W_{fi}$). It was weighted by the total number of analyzed stomachs with food (Sf) [Eq. 2] [Eq. 2]:

$$\%W = \frac{1}{Sf_f} \cdot \sum_{i=1}^{Sf} \left(\frac{W_{fi}}{\sum_{i=1}^{f} W_{fi}}\right) \cdot 100$$

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

To test for interannual variation (from 2008 to 2020) in diet composition and the potential influence of climatic events on diet, extreme climatic events were used as a proxy (weak, moderate, or strong El Niño (EN) /La Niña (LN)). The climatic data were obtained from http://enos.cptec.inpe.br/; 08/2021. To test intra-annual differences and seasonal cycles in diet composition ('season of the year'), austral seasons were considered, with January, February, and March corresponding to the summer (late wet); April, May, and June, to the autumn (early dry); July, August, and September, to the winter (late dry); and October, November, and December, to the spring (early wet). This seasonal variation was based on previous studies conducted in the same area (Gama et al. 2016; Possatto et al. 2016).

For $\%FO$ data, a two-way PERMANOVA (year + climatic event, Euclidian distance, 9999 permutations) (Anderson 2001, Anderson & Willis 2003) was performed on logit-transformed data (Warton & Hui 2011). For $\%W$, a two-way PERMANOVA (year + season, Euclidian distance, 9,999 permutations) was used with Hellinger and log-transformed data (log x + 1) (Legendre & Legendre 2012, Borcard et al. 2018). The *p-value* considered was 0.05. Principal Component Analysis (PCA) (Legendre & Legendre 2012, Borcard et al. 2018) highlights differences in a multivariate dataset, hence, it was performed to visually interpret PERMANOVA results. All analyses were performed using R 4.0 software (R Core Team 2019).

3. RESULTS

3.1. General demographic results

The dead-stranded green turtles analyzed for low taxonomic resolution, ranged in size from 23.2 cm to 68.0 cm CCL (38.77±7.16 cm; n = 351). Turtles analyzed for high taxonomic resolution of macroalgae ranged in size from 28.2 cm to 62.0 cm CCL (38.83±6.53 cm; n = 148), with the largest sample sizes in 2017 (n = 32) and 2018 (n = 21). Finally, turtles for which diet was analyzed for high taxonomic resolution of invertebrates ranged in CCL from 23.2 cm to 68.0 cm (38.39±7.85 cm; n = 142). All turtles were in the early decomposition stages, and according to the body condition score established by Limpus et al (2012), which was calculated for 238 turtles, 158 presented a good to great score (score 3); 55 a poor one (score 2); and 25 a very poor score (score 1).

3.2.Diet composition

Considering the entire diet content database (LT), a total of 13 different major taxa was encountered in digestive tracts of green turtles (Fig. 2): Magnoliophyta (including mangrove and seagrass), Rhodophyta (red macroalgae), Mollusca, Chlorophyta (green macroalgae), Ochrophyta (brown macroalgae), Bryozoa, Hydrozoa, Echinodermata, Annelida, Cyanobacteria, Arthropoda (including Crustacea and Insecta), and Chordata (Teleostei). More than half (69.23%; n = 243) of sampled green turtles had some sort of plastic or other anthropogenic-derived debris recovered from their digestive tracts (Fig. 2). Among the diet items encountered, the phylum Magnoliophyta was the most frequent (*%FO* = 60.11), followed by Rhodophyta (*%FO* = 41.31), and Mollusca (*%FO* = 41.02) (Fig. 2).

Regarding HTM analysis, a total of three major taxa was identified, including 49 different taxa of macroalgae. The most frequent macroalgae was *Ulva spp.*

(*%FO* = 45.94), followed by *Sargassum cymosum* (*%FO* = 40.54), and *Gracilaria domingensis* (*%FO* = 20.27) (Table 1).

When considering the HTA analysis, a total of 98 taxa was found. The most frequent major group was Bivalvia (*%FO* = 43.66), followed by Teleostei (*%FO* = 10.56) (Table 2).

3.3.Interannual variation of diet

Consumption of food categories by green turtles was significantly different among years for both the low taxonomic diet analysis ($F\text{-value}_{12} = 2.197$, *p-value* < 0.0001) (Table 3) and high taxonomic diet analyses, macroalgae ($F\text{-value}_{8} = 3.2422$; *p-value* < 0.001) (Table 4) and animal ($F\text{-value}_{5} = 2.7995$; *p-value* = 0.003) (Table 5).

For the LT identified in low taxonomic resolution, the first four axes of PCA explained 82.74% of data variance (*d.v.*). Axis 1 (47.07% *d.v.*) highlighted annual trends in the diet of all the sampled green turtles from 2008 to 2020 concerning the consumption of the categories Magnoliophyta (axis score, *a.s.* = -0.73), Rhodophyta (*a.s.* = -0.61), Chlorophyta (*a.s.* = -0.55), Mollusca (*a.s.* = -0.53), Ochrophyta (*a.s.* = -0.45) and debris (*a.s.* = 1.61) (Fig. 3). In 2008, 2013, 2015, 2016 and 2018, Magnoliophyta was the most recurrent consumed category, with *%FO* varying from 61.54% to 87.50%, followed by debris (*%FO* varying from 25.00% to 58.82%) and Rhodophyta (*%FO* varying from 7.69% to 62.50%) (Fig. 4). In the remaining years, debris was the most recurrent consumed category, with *%FO* varying from 58.82% to 91.67%, followed by Magnoliophyta (*%FO* varying from 37.14% to 69.57%) and Rhodophyta (*%FO* varying from 11.43% to 54.17%) (Fig. 4).

In respect of the HTM sampling, the first four axes of PCA explained 97.10% of *d.v.*. Axes 1 (61.55% *d.v.*) and 2 (16.92% *d.v.*) highlighted the consumption of *U. lactuca*, *G. domingensis* and, *S. cymosum* by green turtles sampled from 2008–2014, 2017, and 2018 (Fig. 5). The multivariate subspaces of the years 2008 and 2011–2014 were elongated in both axes 1 and 2 due to the importance of *U. lactuca* ($a.s._{Axis1}$ = -3.05; $a.s._{Axis2}$ = 0.12), *Gracilaria. domingensis* ($a.s._{Axis1}$ = -0.17; $a.s._{Axis2}$ = -1.48) and *S. cymosum* ($a.s._{Axis1}$ = 0.18; $a.s._{Axis2}$ = 0.59). During these years, *%W* of *U. lactuca* varied from 0.60% to 82.36% (*vs.* 0.01% to 2.43% in the remaining years), of *G. domingensis* from <0.01% to 31.24% (*vs.* absent to 47.46), and of *S. cymosum* from 0.02 to 23.59% (*vs.* <0.01 to 43.05) (Fig. 6). The multivariate subspaces representing the years 2009-2010 were elongated in axis 2 (Fig. 5) due to not only the high importance of *G. domingensis* (*%W* 47.46% and 16.93%, respectively), *S. cymosum* (*%W* 43.05% and 10.35%, respectively) and *U. lactuca* (*%W* 2.43% and 0.41%, respectively), but also to the consumption of *Pyropia* sp. (*a.s.* = 0.12; absent and 12.26%, respectively) and of *Rhizoclonium* sp (*a.s.* = 0.004; 22.66% and 63.00%, respectively) (Fig. 6). Both *Pyropia* sp. and *Rhizoclonium* sp were absent in 2008 and 2011-2014. Axis 3 (13.95% *d.v.*) confirmed the importance of *S. cymosum* (*a.s.* = -1.34) and *G. domingensis* (*a.s.* = -0.55) in the diet of green turtles in all years (Fig. 5). Axis 4 (4.67% *d.v.*) highlighted the importance of *Pyropia* sp. (*a.s.* = -0.82) in the diet of green turtles in 2010, 2017 (*%W* 48.76%) and 2018 (38.98%) (Figs. 5 and 6).

Considering the HTA analysis, the first four axes of PCA explained 79.69% of the *d.v.*. Axis 1 (38.22% *d.v.*) highlights general trends in the diet of green turtles: Bivalvia, Gastropoda and Hydrozoa were the most recurrent consumed food categories, besides the presence of debris in all years (Fig. 7). Despite this generality, Bivalvia (*a.s.* = -0.98) and Gastropoda (*a.s.* = -0.89) were mainly consumed in 2015-2018

(Fig. 7). In this period, *%FO* of Gastropoda varied from 34.48% to 80.00% (*vs.* 28.57% to 32.26% in the remaining years), and of Bivalvia from 47.37% to 69.57% (*vs.* 20.00% to 38.71%) (Fig. 8). Conversely, Hydrozoa (*a.s.* = 0.95) and debris (*a.s.* = 0.63) were mainly exploited between 2017–2020, with *%FO* varying from 21.05% to 38.71% (Fig. 7). Debris was greatly ingested between 2017-2020 (*a.s.* = 0.63), and from 88.57% to 93.55%, respectively (Figs. 7 and Fig. 8). In the remaining years, the recurrence of Hydrozoa varied from 13.04% to 40.00%, and of debris from 40.00% to 56.52% (Fig. 8). Axis two (22.85% *d.v.*) confirmed the importance of Bivalvia in the diet of green turtles during 2016-2018, and revealed that Crustacea was recurrently exploited (*a.s.* = -0.31) in 2016 (*%FO* 13.04% *vs.* absent to 2.86% in the remaining years) and that Echinodermata (*a.s.* = 1.17) was an important food resource in 2015 and 2019-2020 (*%FO* varying from 19.35% to 40.00% *vs.* 3.45% to 15.79% in the remaining years) (Figs. 7 and 8). Axis 3 (10.80% *d.v.*) and 4 (7.81% *d.v.*) confirmed the food trends revealed in Axes 1 and 2, confirming the importance of Gastropoda (*a.s.* = 0.33) in green turtle diet from 2016 to 2020, and revealing the exclusive consumption of Insecta (*a.s.* = 0.33) in 2017 and 2019-2020 (*%FO* varying from 2.86% to 6.45%) (Figs. 7 and 8). Axis 4 revealed the exclusive consumption of Perciformes (*a.s.* = –0.48) in 2016 (*%FO* 8.70%), 2019 (6.45%) and 2020 (5.71%), and of Clupeiformes (*a.s.* = 0.22) in 2015 (20.00%), 2019 (6.45%) and 2020 (5.71%) (Figs. 7 and 8).

3.4. Influence of El Niño /La Niña on diet composition

Considering the influence of El Niño/La Niña on low taxonomic diet analysis (whole sample; n = 351; 2008–2020), 106 turtles were encountered during EN events (years of 2015, 2016, 2019), and 245 turtles during LN events (years of 2011, 2012, 2013, 2014, 2017, 2018, 2020). A significant difference was found in diet composition among climatic events considering all the sampling years (2008–2020) (PERMOVA, *F*-value$_3$ = 1.6350*; p-value* = < 0.0479) (Table 3).

The positive portion of Axis 1 was related to the exclusive consumption of debris (*%FO* = 100%) in 2008 during moderate La Niña event (*a.s.* = 1.61) (Fig. 3). Axis 2 (19.09% *d.v.*) highlighted seasonal trends in food consumption, revealing the exploitation of Hydrozoa (*a.s.* = -0.61), Crustacea (*a.s.* = -0.46), Chlorophyta (*a.s.* = -0.44) and Mollusca (*a.s.* = -0.28) mainly during weak and strong LN episodes (Fig. 3). In these periods, *%FO* of Hydrozoa in green turtle diet varied from 17.50% to 18.18% (*vs.* 6.25% to 13.87% in remaining periods), of Crustacea from 5.00% to 18.18% (*vs.* 4.88% to 12.14%), of Chlorophyta from 22.50% to 36.36% (*vs.* 14.63% to 35.84%), and of Mollusca from 47.50% to 54.55% (*vs.* 21.88 to 47.40%) (Fig. 4). Axis 2 also highlighted the consumption of Ochrophyta (*a.s.* = 0.75), Bryozoa (*a.s.* = 0.44), and Rhodophyta (*a.s.* = 0.39) not only in moderate LN periods but also during moderate and strong EN episodes (Fig. 3). During these periods, *%FO* of Ochrophyta varied from 27.75% to 43.90% (*vs*. 12.12% to 12.50% in the remaining periods), of Bryozoa from 7.32% to 25.00% (*vs*. absent to 12.12%), and of Rhodophyta from 25.00% to 49.13% (*vs.* 30.00% to 48.48%) (Fig. 4). Axes 3 (9.50% *d.v.*) and 4 (0.07% *d.v.*) revealed food categories complementary to those highlighted in Axis 1, however, without clear seasonal trends (Fig. 3). Axis 3 was negatively related to the consumption of Cyanobacteria (*a.s.* = -0.58), Echinodermata (*a.s.* = -0.31), and Crustacea (*a.s.* = -0.29) during periods of moderate EN and weak to moderate LN (Fig. 3). During these periods, *%FO* of Cyanobacteria varied from 2.50 to 12.50% (*vs.* absent to 12.12% in the remaining periods), of Echinodermata from 1.56% to 13.29% (*vs.* absent to 2.44%), and of Crustacea from 5.00% to 12.14% (*vs.* 4.88% to 18.18%) (Fig. 4). The negative portion of Axis 4 confirmed the consumption of Crustacea (*a.s.* = -0.36), Echinodermata (*a.s.* = -0.34), and Bryozoa (*a.s.* = -0.26) during periods of moderate to strong EN (*%FO* 4.88%, 2.44% and 7.32%, respectively) and weak LN (*%FO* 5.00%, 7.50% and absent, respectively) to strong LN (*%FO* 18.18%, absent and 12.12%, respectively) (Fig. 4). And positive portion of Axis 4 confirmed the exploitation of Hydrozoa (*a.s.* = 0.29), Cyanobacteria (*a.s.* = 0.31), and Rhodophyta (*a.s.* = 0.36) during episodes of weak LN (*%FO* 17.50%, 2.50% and 30.00%, respectively) to moderate LN (*%FO* 13.87%, 5.78% and 49.13%, respectively) and moderate EN (*%FO* 6.25%, 12.50% and 25.00%, respectively) to strong EN (*%FO* 2.44%, absent and 39.02%, respectively) (Figs. 3 and 4).

3.5. Seasonal diet variation

Although no significant seasonal difference was found by HTM regarding macroalgae consumption, only six species of macroalgae were encountered during summer (late wet) and spring (early wet), whereas in autumn (early dry) and winter (late dry) 49 taxa were found. The filamentous Cyanobacteria *Lyngbya majuscula* Harvey ex Gomont was found in digestive tracts of 17 turtles, only in winter (*%W* 79.77%) and autumn (20.23%). The green macroalga *U. lactuca* was found in green turtle digestive tracts throughout the year, with highest levels in spring (*%W* 65.72%) and Autumn (16.96%) seasons (Fig. 6).

Concerning seasonal variation in food consumption by HTA, there was significant difference (PERMOVA, F_3-value = 1.9586; *p-value* = 0.0292) (Table 5). According to axis 1, Bivalvia (*a.s.* = -0.98) and Gastropoda (*a.s.* = -0.89) were mainly consumed in autumn and spring (Fig. 7). For these categories, *%FO* varied from 39.02% to 67.57% (*vs.* 30.00% to 34.09% in the remaining seasons), and from 39.02% to 45.95% (*vs.* 20.00% to 36.36%), respectively (Fig. 8). On the other hand, Hydrozoa (*a.s.* = 0.95) were mainly ingested in summer (*%FO* 40.00%) and winter (31.71%), whereas debris (*a.s.* = 0.63) were mainly ingested in winter (88.64%) and summer (85.00%) (Fig. 7 and 8). Axis 2 (22.85% *d.v.*) confirmed the high consumption of Bivalvia (*a.s.* = –0.65) from autumn to spring, also revealing that Echinodermata (*a.s.* = 1.17) was an important food resource in all seasons (*%FO* varying from 15.00% to 22.73%) (Fig. 7 and 8). Axis 3 confirmed the importance of Gastropoda (*a.s.* = 0.33) in the diet of green turtles in autumn and revealed the exclusive consumption of Insecta (*a.s.* = 0.33) during the autumn (*%FO* 5.41%) and winter (4.55%) (Fig. 7 and 8). Axis 4 confirmed the importance of Hydrozoa (*a.s.* = 0.42) and Gastropoda (*a.s.* = 0.36) in the diet of green turtles in spring, and revealed the consumption of Perciformes (*a.s.* = -0.48) mainly in the autumn and winter, with *%FO* varying from 10.81% to 2.27%, respectively (*vs.* 2.44% and 5.00% in the remain seasons) (Fig. 7 and 8).

4. DISCUSSION

.. Green turtles found stranded along the Paraná coast are part of a mixed stock composed of individuals from more than 12 rookeries, which travel across different areas of the SWAO (Gonzalez-Carman et al. 2012; Naro Maciel et al. 2014; Savada et al. 2021). The present study provides one of the largest datasets on green turtle diet in the SWAO and underscores the substantial temporal in SWAO green turtle diet variability. Although prey densities were not measured in Paraná, it is likely that the observed temporal shifts in green turtle diet are likely responses to changing prey availabilities driven by large-scale environmental variability observed during the 13 years of this study (2008–2020). We observed that green turtles presented a more diverse diet than in the previous studies (Guebert-Bartholo et al. 2011; Gama et al. 2016) with higher consumption of invertebrates and fish, which is similar to findings from Vélez-Rubio et al. (2016), Piovano et al. (2020), Quiñones et al. (2022), whose results showed high occurrences of invertebrate foods, including Cnidaria. Indeed, in our previous study (Gama et al. 2021), we verified that live green turtles intentionally captured in Paraná presented invertebrates as one of the most important prey items in their diet. These findings advance our knowledge of the population ecology of juveniles and opens the opportunity to in the future evaluate ecological theories, such as understanding how density-dependence and competition can affect green turtle foraging decisions.

The juveniles herein analyzed presented a mixed diet consisting almost exclusively of benthic prey, which is common among green turtles that forage in estuarine and bay areas, as found by Santos et al. (2015), and reviewed by Esteban et al. (2020). The omnivorous feeding habit of green turtles has been verified in several diet studies (Seminoff et al. 2006, Arthur et al. 2008, Cardona et al. 2009, Lemons et al. 2011, Santos et al. 2015, Holloway-Adkins & Hanisak 2017, Gillis et al. 2020, Howell & Shaver 2021), but the wide range of forage items identified at the species level is unique in our study, and includes more than 90% taxa that have not been reported for the area before. Although Gama et al. (2016) identified a few prey items in our study region, our study benefited from further identification of macroalgae and invertebrate groups, as a result of including taxonomists for each group to identify prey.

The invertebrates represented basically by Mollusca and the vertebrates represented by Teleostei were largely consumed by juveniles throughout our sampling analysis, and it may be related to their availability along the Paraná coast, as shown by Bumbeer et al. (2016) and Cattani et al. (2022), and to the individualized foraging preferences among green turtles that aggregate in the area. Further, Mollusca consumption may be related to the fact that in estuarine areas they may coexist with macroalgae in the benthic habitat, as verified by Santos et al. (2015); this finding contrasts other studies in the SWAO that found only sporadic occurrence of mollusks in green turtle diets (Morais et al. 2012, Vélez-Rubio et al. 2015). Live green turtles along the Paraná coast foraged mostly on invertebrates, highlighting the unique dietary tendencies for the species in this estuarine complex (Gama et al. 2021). Nevertheless, we did not identify any gelatinous zooplankton in green turtle digestive tracts, as has been reported in other green turtle diet studies (Burkholder et al. 2011, Santos et al. 2015, Vélez-Rubio et al. 2016, Gama et al. 2021, Stubbs et al. 2022). This is likely due to this prey type's rapid digestion (González-Carman et al. 2014, Hays et al. 2018), which suggests gelatinous prey may be underrepresented in our study.

With respect to anthropogenic influences on green turtle diet, our study indicates marine debris consumption across all years, with the greatestoccurrence from 2017 to 2020, especially in 2018; these are mostly La Niña years (CPTEC 2016) that presented low temperature and low rainfall rates (*appendices* Fig. 1). However, the occurrence of debris was high and similar when comparing the winter (*FO%* = 88.64), which is the low rain season, and the summer (*FO%* = 85.00), which is the high rain season. Because of that it is important to mention that other oceanographic, physical, and geographic factors may be responsible for higher debris concentrations in the estuarine area of PEC (Krelling & Turra 2019) and they should be measured in future studies to better address debris availability and ingestion by fauna in this area. For instance, extensive dredging was conducted along the PEC in 2018, which moved sediments and sheltered materials from the sea bottom (Soares et al. 2022). This process might re-mobilize debris, making them more available to be ingested by the marine fauna.

Moreover, debris consumption by green turtles may occur during their recruitment to the coast (Vélez-Rubio et al. 2018b) and reflect its high availability in the foraging area (Schuyler et al. 2014). Debris ingestion is considered a major threat to green turtle conservation status and health condition, as it can cause digestive tract obstruction and tissue injury, leading to starvation and death (Di Beneditto & Awabdi 2014, Domiciano et al. 2019). We thus recommend further evaluation of the relationship between diet and the presence of debris to clarify the severity of this problem and inform management plans that promote habitat quality and the conservation of green turtles in the SWAO.

4.1.Seasonal variability

Macroalgae consumption varied among seasons, which is perhaps related to temporal fluctuations in relative availability for different taxa in the area (Pellizzari et al. 2014). In autumn and winter, macroalgae dietary diversity among green turtles was higher than in spring and summer, with diet samples from the latter season only revealing six species of macroalgae being consumed. This is consistent with findings by Pellizzari et al. (2014) that reported higher species richness and higher biomass along the Paraná coast in winter versus summer. Lower macroalgae species richness in diet samples may be related to higher water turbidity from sedimentation introduced via coastal runoff in summer, which decreases the photic zone in coastal waters, thus reducing rates of photosynthesis and inhibiting macroalgae growth (Júnior et al. 1991, Bezerra & Marinho-Soriano 2010).

With respect to animal matter consumption, the highest consumption of invertebrate prey and fishes occurred during the autumn and winter, which is probably related to the fact that the energy intake obtained from this food source may be advantageous compared to vegetal prey, which improves the turtle’s metabolism during these seasons (Bjorndal 1980, Brand-Gardner et al. 1999). It is important to consider that both the dietary transit times and the turtle metabolism are slower in lower temperatures, as shown by González-Paredes et al. (2021), which may have influenced the higher occurrence of undigested invertebrates found in this study. Despite that, invertebrates such as Mollusca and Hydrozoa were consumed in every season, and this pattern may be related to the prey species' presence throughout the year in some islands along the Paraná coast (Bumbeer et al. 2016), making them available for consumption in all seasons. Furthermore, it is important to consider that the absorption of nutrients from these prey items is higher when compared to the plant matter prey, as both the intake passage time and the digestion are faster (Amorocho & Reina 2008). However, as shown by Quiñones et al. (2022), it is possible that some of the juveniles herein analyzed do not present the gut specialization to digest vegetal matter items, consuming more animal origin prey items afterwards. Also, as verified by Meylan et al. (2020), turtles may adapt to changes in prey availability, which impacts foraging effort and areas, and perhaps survival. It is worth mentioning that some of the turtles foraging in this area may be both recent recruits that were previously foraging in higher latitudes, as shown by Gama et al. (2021).

Even though fishes and cephalopods were found ingested by green turtles and are a good energy source, we did not evaluate foraging strategies, and some items might be caught dead or moribund. Some fishes predated by turtles are cited as a bycatch of trawlers fisheries (Cattani et al., 2011), which occurs in the Paraná state and adjacent coastal areas throughout the year. Moreover, floating dead squids may be consumed by green turtles because of their scavenging foraging behavior as shown by Morais et al. (2012) and Vélez-Rubio et al. (2015). However, this information is speculative, and future studies focusing on prey-predator strategies can be conducted to clarify this ecological point.

4.2. Annual diet variability

Clear annual trends were observed, considering the dietary shift from Bivalvia and Gastropoda in the first years to Hydrozoa in the last couple years of our analysis, despite the constant consumption of Mollusca over the years. In terms of macroalgae consumption, the continuous consumption of Rhodophyta and Chlorophyta reinforces them as key dietary items for green turtles in the SWAO (Reisser et al. 2013, Santos et al. 2015, Vélez-Rubio et al. 2016).

Green turtle dietary shifts observed during this study (2008 to 2020) are likely related to the climatic variation resulting from the onset of El Niño events, probably to the high rainfall rates that are expected for this event. Rainfall dynamics have been known to flush some floating algae species, such as the *S. cymosum* from estuary sites to nearby open coasts (Witherington et al. 2012). In particular, higher consumption of Ochrophyta (especially *S. cymosum*) in our study may be resulting from these changes during EN events in 2015, 2016, and 2019. As found elsewhere (Hawkes et al. 2009, Esteban et al. 2020), climate events may lead to changes in sea surface temperature, in both diet and food resource availability, driving changes in habitat use, behavior, and exposure to threats. Indeed, climate change affects marine herbivores mostly because of their vulnerability to temperature changes, but may also disrupt trophic chains in the marine ecosystem, as observed by Hu et al. (2022).

5. CONCLUSIONS

Our results highlight the importance of the estuarine and bay areas of Paraná state as habitats for juvenile green turtle foraging and development. This is reinforced not only by the diversity of food items consumed across years, seasons, and climate events, but also by green turtles' capacity to be resilient to these changes with individualized and adaptive foraging selection. Nevertheless, it is important to use caution when evaluating those changes, as they may represent a higher exposure to impacted foraging grounds and conservation risks. Although most of our study group is composed of individuals in a good body condition, we cannot say their diet reflects the items consumed only by healthy individuals that use Paraná coast due to the fact that no necropsy analyses were included to look at overall health prior to death. Additionally, the only diet data of live green turtles in Paraná are based on stable isotopic analysis (Gama et al. 2021) and this is similar to our findings, which showed invertebrates and green algae as the most consumed and important prey items. Despite the punctual information available (Gonzalez Carman et al. 2014; Fuentes et al. 2020), species resilience may be enhanced by the fact that many turtles remain in this foraging area and use different habitats within the Paraná, including islands, rocky shores, meadows, and mangroves. Thus, delimitating diet changes across the years and how the species responds to climate variability helps decipher the species foraging intake throughout time and individual variability in terms of habitat use and exposition to threats. This helps delimitate food resources changes and track the impacts over both the foraging habitat and the species itself. Hence, this study contains data that may help to delimitate areas to be protected and managed in the SWAO, besides to inform and prioritize further conservation actions based on the distribution of foraging resources used by the species.

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LITERATURE CITED

Absher TM, Ferreira Junior AL, Christo SW (2015) Conchas de Moluscos Marinhos do Paraná. In: Publiki, Rio de Janeiro.

Amorocho DF, Reina RD (2008) Intake passage time, digesta composition and digestibility in East Pacific green turtles (*Chelonia mydas agassizii*) at Gorgona National Park, Colombian Pacific. Journal of Experimental Marine Biology and Ecology 360:117−124

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Australian Ecology 26:32−46

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511−525

Angulo JR (1992) Geologia da planície costeira do Estado do Paraná. PhD dissertation, Universidade de São Paulo, São Paulo, Brazil

Angulo RJ, Araújo ADD (1996). Classificação da costa paranaense com base na sua dinâmica, como subsídio à ocupação da orla litorânea. Boletim Paranaense de Geociências 44:7−17

Ansari AA, Khan FA, Gill SS, Varshney J (2010) Aquatic Plant Diversity in Eutrophic

Ecosystems. In: Ansari A, Gill S, Lanza G, Rast W (eds) Eutrophication: causes, consequences and control. Springer, Dordrecht, 247–263

Arizza V, Vecchioni L, Caracappa S, Sciurba G, Berlinghieri F, Gentile A (2019) New insights into the gut microbiome in loggerhead sea turtles *Caretta caretta* stranded on the Mediterranean coast. PLoS ONE 14:e0220329.

Arthur KE, Boyle MC, Limpus CJ (2008) Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. Mar Ecol Prog Ser 362:303–311

Awabdi DR, Siciliano S, Di Beneditto APM (2013) First information about the stomach contents of juvenile green turtles, *Chelonia mydas*, in Rio de Janeiro, south-eastern Brazil. Mar Biodivers Res 6:e5

Barata D (2004) Clorofíceas Marinhas Bentônicas do Estado do Espírito Santo. Masters dissertation, Instituto de Botânica da Secretaria do Meio Ambiente, São Paulo, Brazil.

Bezerra AF, Marinho-Soriano E (2010) Cultivation of the red seaweed *Gracilaria birdiae* (Gracilariales, Rhodophyta) in tropical waters of northeast Brazil. Biomass and Bioenergy 34:1813–1817

Bjorndal KA (1980) Nutrition and grazing behavior of the green turtle, *Chelonia mydas*. Marine Biology 56:147–154

Borcard D, Gillet F, Legendre P (2018) Numerical Ecology with R. 2nd ed. Springer

Brand-Gardner SJ, Limpus CJ, Lanyon JM (1999) Diet selection by immature green turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. Australian Journal of Zoology 47:181–191

Bugoni L, Krause L, Petry LV (2003) Diet of sea turtles in Southern Brazil.Chelonian conservation and biology 4:685–688

Bumbeer J, Cattani AP, Chierigatti NB, Rocha RM (2016) Biodiversity of benthic macroinvertebrates on hard substrates in the Currais Marine Protected Area, in southern Brazil. Biota Neotrop 16:e20160246

Burkholder DA, Heithaus MR, Thomson JA, Fourqurean JW (2011) Diversity in trophic interactions of green sea turtles *Chelonia mydas* on a relatively pristine coastal foraging ground. Mar Ecol Prog Ser 439:277-293

Campos P, Cardona L (2020) Trade-offs between nutritional quality and abundance determine diet selection in juvenile benthic green turtles. Journal of Experimental Marine Biology and Ecology 527:151373

Cantor M, Barreto AS, Taufer RM, Giffoni B, Castilho PV, Maranho A, Beatriz C, Kolesnikovas C, Godoy D, Rogério DW, Dick JL, Groch KR, Rosa L, Cremer MJ, Cattani PE, Valle RR, Domit C (2020) High incidence of sea turtle stranding in the southwestern Atlantic Ocean. ICES J Mar Sci 77:1864–1878

Cardona L, Aguilar A, Pazos L (2009) Delayed ontogenic dietary shift and high levels of omnivory in green turtles (*Chelonia mydas*) from the NW coast of Africa. Mar Biol 156:1487–1495

Cattani AP, Santos LDO, Spach HL, Budel BR, Gondim JHD (2011). Avaliação da ictiofauna da fauna acompanhante da pesca do camarão sete-barbas do município de Pontal do Paraná, litoral do Paraná, Brasil. *Boletim do Instituto de Pesca*, *37*(2), 247-260.

Cattani AP, Gerke Y, Pichler HA, Adelir-Alves J, Spach HL, Schwingel PR (2022) Fish assemblage patterns in a subtropical estuary in southern Brazil. *Biota Neotropica*, *22*, e20211194.

Clutton-Brock T, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology and Evolution 25:562–573

Coelho VF, Domit C, Broadhurst MK, Prosdocimi L, Nishizawa H, Almeida FS (2018) Intra-specific variation in skull morphology of juvenile *Chelonia mydas* in the southwestern Atlantic Ocean. Mar Biol 165:174.

Cordeiro-Marino M (1978) Rodofíceas bentônicas marinhas do estado de Santa Catarina, Rickia. Série criptogâmica dos Arquivos de Botânica do Estado de São Paulo. Secretaria da Agricultura, Coordenadoria da Pesquisa de Recursos Naturais, Instituto de Botânica, São Paulo, Brazil

Coto ACSP (2007) Biodiversidade de Clorófitas Marinhas bentônicas do litoral do estado de São Paulo. Masters dissertation, Instituto de Botânica da Secretaria do Meio Ambiente, São Paulo, Brazil

Crispino LMB (2007) Cianobactérias Marinhas Bentônicas do litoral do Estado de São Paulo. PhD dissertation, Instituto de Botânica da Secretaria de Meio ambiente, São Paulo, Brazil

Di Beneditto APM, Awabdi DR (2014) How marine debris ingestion differs among megafauna species in a tropical coastal area. Marine Pollution Bulletin, 88:86–90

Domiciano IG, Broadhurst MK, Domit C, Flaiban KKMC, Goldberg DW, Fritzen JTT, Bracarense APFRL (2019) Chelonid alphaherpesvirus 5 DNA in fibropapillomatosis-affected *Chelonia mydas*. EcoHealth 16:248–259

Donaton J, Durham K, Cerrato R, Schwerzmann J, Thorne LH (2019) Long-term changes in loggerhead sea turtle diet indicate shifts in the benthic community associated with warming temperatures. Estuarine, Coastal and Shelf Science, 218:139–147

Esteban N, Mortimer JA, Stokes HJ, Laloe J, Unsworth RKF, Hays GC (2020) A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. Mar Biol 167,183

Fuentes MMPB, Lawler IR, Gyuris E (2006) Dietary preferences of juvenile green turtles (*Chelonia mydas*) on a tropical reef flat. Wildl Res 33:671–678

Fuentes MMPB, Wildermann N, Gandra TBR, Domit C (2020) Cumulative threats to juvenile green turtles in the coastal waters of southern and southeastern Brazil. Biodiversity and Conservation 29:1783–1803

Gama LR, Domit C, Broadhurst MK Fuentes MMPB, Millar RB (2016) Green turtle *Chelonia mydas* foraging ecology at 25°S in the western Atlantic: evidence to support a feeding model driven by intrinsic and extrinsic variability. Mar Ecol Prog Ser 542:209–219

Gama LR, Fuentes MMPB, Trevizani TH, Pellizzari F, Lemons GE, Seminoff JA, Domit C (2021) Trophic ecology of juvenile green turtles in the Southwestern Atlantic Ocean: insights from stable isotope analysis and niche modelling. Marine Ecology Progress Series, 678:139–152

Geraci JR, Lounsbury VL (2005) Marine mammals ashore:a field guide for strandings. Texas A&M University Sea Grant College Program, National Aquarium in Baltimore

Gillis AJ, Wildermann NE, Ceriani SA, Seminoff JA, Fuentes MM (2020) Evaluating different spatial scales of forage item availability to determine diet selection of juvenile green turtles (*Chelonia mydas*). Marine Biology, 167,170

Gonzalez Carman V, Falabella V, Maxwell S, Albareda D (2012) Revisiting the ontogenetic shift paradigm: The case of juvenile green turtles in the SW Atlantic. J Exp Mar Bio Ecol 429:64–72

Gonzalez Carman V, Botto F, Gaitán E, Albareda D, Campagna C, Mianzan H (2014) A jelly Piscis diet for the herbivorous green turtle *Chelonia mydas* in the temperate

SW Atlantic. Mar Biol 161:339–349

González-Paredes D, Ariel E, David MF, Ferrando V, Marsh H, Hamann M (2021) Gastrointestinal transit times in juvenile green turtles: An approach for assessing digestive motility disorders. J Exp Mar Bio Ecol 544,151616

Grimm AM, Barros VR, Doyle ME (2000) Climate variability in southern South America associated with El Niño and La Niña events. Journal of climate 13:35–58

Guebert-Bartholo FM, Barletta M, Costa MF, Monteiro-Filho ELA (2011) Using gut contents to assess foraging patterns of juvenile green turtles *Chelonia mydas* in the Paranaguá Estuary, Brazil. Endanger Species Res 13:131–143

Guiry MD, Guiry GM (2019) AlgaeBase. Worldwide electronic publication, National University of Ireland, Galway. Available: http://www.algaebase.org (accessed Sep. 15 2021)

Hamann M, Godfrey M, Seminoff JA, Arthur K, Barata P, Bjorndal KA, Bolten AB, Broderick AC, Campbell L, Carreras C, Casale P, Chaloupka M, Chan SKF, Coyne M, Crowder LB, Diez C, Dutton PH, Epperly SP, FitzSimmons NN, Formia A, Girondot M, Hays GC, Cheng IJ, Kaska Y, Lewison RL, Mortimer J, Nichols WJ, Reina RD, Shanker K, Spotila JR, Tomás J, Wallace BP, Work TM, Zbinden JA, Godley BJ (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. Endangered Species Research 11:245–269

Hart KM, Mooreside P, Crowder LB (2006) Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. Biol Conserv 129:283–290

Hawkes L, Broderick A, Godfrey M, Godley B (2009) Climate change and marine turtles. Endangered Species Research 7:137–154

Hays GC, Doyle TK, Houghton JD (2018) A paradigm shift in the trophic importance of jellyfish? Trends in ecology & evolution 33:874-884

Holloway-Adkins KG, Dennis Hanisak M (2017) Macroalgal foraging preferences of juvenile green turtles (*Chelonia mydas*) in a warm temperate/subtropical transition zone. Marine Biology 164:161

Howell LN, Shaver DJ (2021) Foraging habits of green sea turtles (*Chelonia mydas*) in the northwestern Gulf of Mexico. Frontiers in Marine Science 8:418-430

Hu N, Bourdeau PE, Harlos C, Liu Y, Hollander J. (2022). Meta-analysis reveals variance in tolerance to climate change across marine trophic levels. *The Science of the total environment*, 827:154244.

Hyslop EJ (1980) Stomach contents analysis – a review of methods and their application. Journal of Piscis Biology 17:411–429

International Union for Conservation of Nature and Natural Resources (2004) The IUCN red list of threatened species. IUCN Global Species Programme Red List Unit

Jatmiko TH, Prasetyo DJ, Poeloengasih CD, Khasanah Y (2019). Nutritional Evaluation of Ulva sp. from Sepanjang Coast, Gunungkidul, Indonesia. In IOP Conference Series: Earth and Environmental Science 251,012011

Júnior ON, Dip MR, Góes RM (1991) Macroalgae of a stream in southeastern Brazil: composition, seasonal variation and relation to physical and chemical variables. Hydrobiologia 213:241–250

Krelling AP, Turra A (2019) Influence of oceanographic and meteorological events on the quantity and quality of marine debris along an estuarine gradient. Marine Pollution Bulletin, 139:282–298

Lana PC, Marone E, Lopes RM, Machado EC (2001) The Subtropical Estuarine Complex of Paranaguá Bay, Brazil. In: Seeliger U, Kjerfve B (eds) Coastal Marine

Ecosystems of Latin America. Ecological Studies, Springer, Berlin, Heidelberg

Legendre P, Legendre L (2012). Numerical Ecology. 3rd ed. Elsevier, Amsterdam.

Lemons G, Lewison R, Komoroske L, Gaos A, Lai C-T, Dutton P, Eguchi T, LeRoux R, Seminoff JA (2011) Trophic ecology of green sea turtles in a highly urbanized bay: insights from stable isotopes and mixing models. Journal of Experimental Marine Biology and Ecology, 405:25–32

Limpus CJ, Limpus DJ, Savige M, Shearer Damon (2012) Health Assessment of Green Turtles in South and Central Queensland Following Extreme Weather Impacts on Coastal Habitat During 2011. Department of Environment and Heritage Protection, issuing body. Brisbane: Department of Environment and Heritage Protection, Queensland.

Littler MM, LittlerDS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. The American Naturalist, 116:25–44

Maldini D, Mazzuca L, Atkinson S (2005) Odontocete stranding patterns in the main Hawaiian Islands (1937–2002): How do they compare with live animal surveys? Pacific Science, 59:55–67

Marcovaldi A, Santos A (2011) Plano de ação nacional para conservação das tartarugas marinhas. Brasília Inst Chico Mendes Conserv da Biodiversidade, Icmbio 120

Matano RP, Palma ED, Piola AR (2010) The influence of the Brazil and Malvinas Currents on the Southwestern Atlantic Shelf circulation. Ocean Sci 6:983–995

McMichael E, Seminoff JA, Carthy R (2008) Growth rates of wild greenturtles, *Chelonia mydas*, at a temperate foraging habitat in the northern Gulf of Mexico: assessing short-term effects of cold-stunning on growth, *Journal of Natural History*, 42:43–44

Meylan PA, Hardy RF, Gray JA, Meylan AB (2022) A half-century of demographic changes in a green turtle (Chelonia mydas) foraging aggregation during an era of seagrass decline. *Marine Biology*, 169:74.

Monteiro DS, Estima SC, Gandra TBR, Silva AP, Bugoni L, Swimmer Y, Seminoff JÁ (2016). Long-term spatial and temporal patterns of sea turtle strandings in southern Brazil. *Marine Biology*, 163:247

Morais RA, Longo GO, Santos RA, Yoshida ETE, Stahelin GD, Horta PA (2012) Cephalopod ingestion by juvenile green sea turtles (*Chelonia mydas*): predatory or scavenging behavior? *Herpetological Review* 43,47

Moura CWN (2000) Coralináceas com genículo (Rhodophyta, Corallinales) do litoral do Brasil. PhD dissertation, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

Nagaoka SM, Martins AS, dos Santos RG (2012) Diet of juvenile green turtles (*Chelonia mydas*) associating with artisanal Piscising traps in a subtropical estuary in Brazil. Mar Biol 159:573–581

Naro-Maciel E, Reid BN, Alter SE, Amato G, Bjorndal KA, Bolten AB, Martin M, Nairn CJ, Shamblin B, Pineda-Catalan O (2014). From refugia to rookeries: Phylogeography of Atlantic green turtles. *Journal of Experimental Marine Biology and Ecology*, *461*:306-316.

Nunes JM, Paula EJ (1999) Phaeophyta da região metropolitana de Salvador, Bahia, Brasil. Masters dissertation, Instituto de Biociências Universidade de São Paulo, São Paulo, Brazil

Nunes JMC (2005) Rodofíceas marinhas bentônicas do estado da Bahia, Brasil. PhD dissertation, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

Nunes TY, Broadhurst MK, Domit C (2021) Selectivity of marine-debris ingestion by juvenile green turtles (*Chelonia mydas*) at a South American World Heritage Listed area. Marine Pollution Bulletin, 169:112574

Orós J, Montesdeoca N, Camacho M, Arencibia A, Calabuig P (2016) Causes of stranding and mortality, and final eisposition of loggerhead sea turtles (*Caretta caretta*) admitted to a wildlife rehabilitation center in Gran Canaria Island, Spain (1998-2014): A long-term retrospective study. PLoS ONE 11(2): e0149398

Peckham SH, Maldonado Diaz D, Koch V, Mancini A, Gaos A, Tinker MT, Nichols WJ (2008) High mortality of loggerhead turtles due to bycatch, human consumption and strandings at Baja California Sur, Mexico, 2003 to 2007. Endangered Species Research 5:171–183

Pellizzari FM, Yokoya NS, Oliveira EC (2007) Cultivation of the edible green seaweed *Gayralia* (Chlorophyta) in southern Brazil. Journal of Applied Phycology, 19:63–69

Pellizzari FM, Reis RP (2011) Seaweed cultivation on the Southern and Southeastern Brazilian Coast. Braz. J. Pharmacog. 21:305–312

Pellizzari FM, Bernardi J, Silva EM, Silva MC, Yokoya NS (2014) Benthic marine algae from the insular areas of Paraná, Brazil: new database to support the conservation of marine ecosystems. Biota Neotropica 14:e20130011

Pellizzari F, Silva MC, Silva EM, Medeiros A, Oliveira MC, Yokoya NS, Pupo D, Rosa LH, Colepicolo P (2017) Diversity and spatial distribution of seaweeds in the South Shetland Islands, Antarctica: an updated database for environmental monitoring under climate change scenarios. Polar Biology, 40:1671–1685

Pellizzari F, Osaki VS, Santos-Silva MC (2020) New records of seaweeds and filamentous cyanobacteria from Trindade island: an updated checklist to support conservation guidelines and monitoring of environmental changes in the southern Atlantic archipelagos. Scientia Marina 84:227–242

Pellizzari F, Rosa LH, Yokoya NS (2020b) Biogeography of Antarctic Seaweeds Facing Climate Changes. In: Gómez I., Huovinen P. (eds) Antarctic Seaweeds. Springer, Cham.

Pereira-Filho GH, Amado-Filho GM, Guimarães SMPB, Moura RL, Sumida PYG, Abrantes DP, Bahia RG, Güth AZ, Jorge RR, Filho RBF (2011) Reef Piscis and benthic assemblages of the trindade and Martin Vaz island group, SouthWestern Atlantic. Brazilian Journal of Oceanography 59:201–212

Pereira-Filho GH, Amado-Filho GM, de Moura RL, Bastos AC, Guimarães SMPB, Salgado LT, Francini-Filho RB, Bahia RG, Abrantes DP, Guth AZ, Brasileiro PS (2012) Extensive rhodolith beds cover the summits of Southwestern Atlantic Ocean seamounts. J. Coast. Res. 279:261–269

Pimpão DM (2004) Moluscos bivalves da Plataforma Externa e Talude Superior ao largo de Rio Grande, Rio Grande do Sul, Brasil. Dissertation, Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Rio Grande do Sul, Brazil

Piola AR, Campos EJ, Möller Jr, Charo M, Martinez C (2000) Subtropical shelf front off eastern South America. Journal of Geophysical Research: Oceans 105:6565–6578.

Piovano S, Lemons GE, Ciriyawa A, Batibasaga A, Seminoff JA (2020) Diet and recruitment of green turtles in Fiji, South Pacific, inferred from in-water capture and stable isotope analysis. *Marine Ecology Progress Series*, 640:201-213

Possatto FE, Broadhurst MK, Gray CA, Spach HL, Lamour MR (2016) Spatiotemporal variation among demersal ichthyofauna in a subtropical estuary bordering World Heritage-listed and marine protected areas: implications for resource management. *Marine and Freshwater Research*, *68*:703-717.

Quiñones J, González Carman V, Zeballos J, Purca S, Mianzan H (2010) Effects of El Niño-driven environmental variability on black turtle migration to Peruvian foraging grounds. Hydrobiologia 645:69–79

Quiñones J, Paredes-Coral E, Seminoff JA (2022) Foraging ecology of green turtles (*Chelonia mydas*) in Peru: relationships with ontogeny and environmental variability. Mar Biol 169,139

Rasyid A (2017) Evaluation of nutritional composition of the dried seaweed *Ulva lactuca* from Pameungpeuk Waters, Indonesia. Tropical Life Sciences Research, 28:119–125

Reich KJ, Bjorndal KA, Bolten AB (2007) The "lost years" of green turtles: using stable isotopes to study cryptic lifestages. Biol Lett 3:712–4

Reisser J, Proietti M, Sazima I, Kinas P, Horta P, Secchi E (2013) Feeding ecology of the green turtle (*Chelonia mydas*) at rocky reefs in western South Atlantic. Marine biology, 160:3169–3179

Ruppert E, Barnes RD (1996) Zoologia dos Invertebrados. 6ª ed., Roca Ed., São Paulo. 1029p.

Saba VS, Santidrián-Tomillo PILAR, Reina RD, Spotila JR, Musick JA, Evans DA, Paladino FV (2007) The effect of the El Niño Southern Oscillation on the reproductive frequency of eastern Pacific leatherback turtles. Journal of Applied Ecology, 44:395–404

Santos RG, Martins AS, Farias JN, Horta PA, Pinheiro HT, Torezani E, Baptistotte C, Seminoff JA, Balazs GH, Work TM (2011) Coastal habitat degradation and green sea turtle diets in Southeastern Brazil. Mar Pollut Bull 62:1297–1302

Santos RG, Martins AS, Batista MB, Horta PA (2015) Regional and local factors determining green turtle *Chelonia mydas* foraging relationships with the environment. Mar Ecol Prog Ser 529:265–277

Santos NM, Lana P (2017) Present and past uses of mangrove wood in the subtropical Bay of Paranaguá (Paraná, Brazil). Ocean & Coastal Management 148:97–103

Santos BS, Friedrichs MAM, Rose SA, Barco SG, Kaplan DM (2008) Likely locations of sea turtle stranding mortality using experimentally-calibrated, time and space-specific drift models. Biological Conservation 226:127–143

Savada CS, Prosdocimi L, Domit C, Almeida FSD (2021) Multiple haplotypes of *Chelonia mydas* juveniles in a threatened hotspot area in Southern Brazil. Genetics and Molecular Biology 44:e20200410

Schoener TW (1987) A Brief History of Optimal Foraging Ecology. In: Kamil AC, Krebs JR, Pulliam HR (eds) Foraging Behavior. Springer, Boston, MA.

Schuyler Q, Hardesty BD, Wilcox C, Townsend K (2014) Global analysis of anthropogenic debris ingestion by sea turtles. Conservation biology 28:129–139

Seminoff JA, Resendiz A, Nichols WJ (2002) Diet of East Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, Mexico. Journal of Herpetology, 36:447–453

Seminoff JA, Jones TT, Eguchi T, Jones DR, Dutton PH (2006) Stable isotope discrimination ($\delta^{13}C$ and $\delta^{15}N$) between soft tissues of the green sea turtle *Chelonia mydas* and its diet. Mar Ecol Prog Ser 308:271–278

Silveira EL, Semmar N, Cartes JE, Tuset VM, Lombarte A, Ballester ELC, Vaz-dos-Santos AM (2020) Methods for trophic ecology assessment in Piscises: A critical review of stomach analysis. Reviews in Pisciseries Science & Aquaculture, 28:71–106

Soares ED, Cantor M, Bracarense APFRL, Groch KR, Domit C (2022) Health conditions of Guiana dolphins facing cumulative anthropogenic impacts. Mammalian Biology 1–16

Stubbs JL, Revill AT, Pillans RD, Vanderklift MA (2022) Stable isotope composition of multiple tissues and individual amino acids reveals dietary variation among life stages in green turtles (*Chelonia mydas*) at Ningaloo Reef. Marine Biology 169 (6) 72.

Sulato ET, Luko-Sulato K, Pedrobom JH, de Oliveira LMDS, dos Santos Lima G, Govone JS, Barreto AS, de Araújo Júnior MAG, Menegário AA (2022) Metals and metalloids in green turtle hepatic tissue (Chelonia mydas) from Santos Basin, Brazil. Environmental Research, 203:111835

Trites AW, Spitz J (2018) Diet. Encyclopedia of Marine Mammals (Third Edition), Academic Press. Eds: Bernd Würsig, Thewissen JGM, Kovacs KM 255-259, ISBN 9780128043271,1.00105-9.

UNESCO (United Nations Educational, Scientific and Cultural Organization) (2021) UNESCO World Heritage Centre. Available at https://whc.unesco.org

Vander Zanden HB, Pfaller JB, Reich KJ (2014) Foraging areas differentially affect reproductive output and interpretation of trends in abundance of loggerhead turtles. Marine Biology 161:585–598.

Vélez-RubioGM, Estrades A, Fallabrino A. (2013) Marine turtle threats in Uruguayan waters: insights from 12 years of stranding data. Marine Biology 160, 2797–2811 Vélez-Rubio GM, Tomás J, Míguez-Lozano R, Xavier JC, Martinez-Souza G, Carranza A (2015) New insights in Southwestern Atlantic Ocean Oegopsid squid distribution based on juvenile green turtle (*Chelonia mydas*) diet analysis. Marine Biodiversity 45:701–709

Vélez-Rubio GM, Cardona L, López-Mendilaharsu M, Martínez Souza G, Carranza A, González-Paredes D, Tomás J (2016) Ontogenetic dietary changes of green turtles (Chelonia mydas) in the temperate southwestern Atlantic. Mar Biol 163:1–16

Vélez-Rubio GM, Cardona L, López-Mendilaharsu M, Martínez Souza G, Carranza A, Campos P, González-Paredes D, Tomás J (2018a) Pre and post-settlement movements of juvenile green turtles in the Southwestern Atlantic Ocean. J Exp Mar Bio Ecol 501:36–45

Vélez-Rubio GM, Teryda N, Asaroff PE, Estrades A, Rodriguez D, Tomás J (2018b). Differential impact of marine debris ingestion during ontogenetic dietary shift of green turtles in Uruguayan waters. Marine pollution bulletin, 127:603–611

Xavier JC, CherelY (2009) Cephalopod Beak Guide For The Southern Ocean. British Antarctic Survey, Cambridge, UK. 129 p

Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM, Bolten AB, Chaloupka MY, Hutchinson BJ, Abreu-Grobois FA, Amorocho D, Bjorndal KA, Bourjea J, Bowen BW, Briseño Dueñas R, Casale P, Choudhury BC, Costa A, Dutton PH, Fallabrino A, Girard A, Girondot M, Godfrey MH, Hamann M, López-Mendilaharsu M, Marcovaldi MA, Mortimer JA, Musick JA, Nel R, Pilcher NJ, Seminoff JA, Troëng S, Witherington B, Mast RB (2010) Regional Management Units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 5:e15465

Warton DI, Hui FK (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10

Wiggers F (2003) Moluscos gastrópodes da plataforma continental externa e talude continental ao largo da Laguna dos Patos – Rio Grande do Sul, Brasil. Dissertation. Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Rio Grande do Sul, Brazil

Wildermann NE, Gredzens C, Avens L, Barrios-Garrido HA, Bell I, Blumenthal J, Bolten AB, McNeill JB, Casale P, Di Domenico M, Domit C, Epperly SP, Godfrey MH, Godley BJ, González-Carman V, Hamann M, Hart KM, Ishihara T, Mansfield KL, Metz TL, Miller JD, Pilcher NJ, Read MA, Sasso C, Seminoff JA, Seney EE, Willard AS, Tomás J, Vélez-Rubio GM, Ware M, Williams JL, Wyneken J, Fuentes MMPB (2018) Informing research priorities for immature sea turtles through expert elicitation. Endangered Species Research 37:55–76

Witherington B, Hirama S, Hardy R (2012) Young sea turtles of the pelagic Sargassum-dominated drift community: Habitat use, population density, and threats. Marine Ecology Progress Series 463:1–22

WoRMS Editorial Board (2023). World Register of Marine Species. Available https://www.marinespecies.org at VLIZ. Accessed Nov. 19 2021.

Tables

Table 1: Frequency of occurrence (*%FO*) and weight (*%W*) of High taxonomic macroalgae (HTM) species registered in digestive tract (DT) contents of juvenile green turtles *Chelonia mydas* (n = 148) collected dead-stranded along the Paraná coast from 2008–2014 and 2017–2018. n.d.= the value did not reach the minimum accuracy scale.

Taxa	**Author**	**N of DT**	***%FO***	***%W***
CHLOROPHYTA				
Caulerpa sp.		**2**	**1.351**	**n.d.**
Chaetomorpha aerea	(Dillwyn) Kützing	**5**	**3.378**	**0.008**

Chaetomorpha antennina	(Bory) Kützing	**2**	**1.351**	**n.d.**
Chaetomorpha sp.		**1**	**0.675**	**n.d.**
Cladophora catenata	Kutzing	**1**	**0.675**	**n.d.**
Cladophora vagabunda	(Linnaeus) Hoek	**7**	**4.729**	**0.036**
Cladophora sp.		**6**	**4.054**	**0.016**
Cladophoropsis membranacea	(Hofman Bang ex C. Agardh)	**1**	**0.675**	**n.d.**
Rhizoclonium sp.		**6**	**4.054**	**0.010**
Ulva cf. *chaetomorphoides*	(Børgesen) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope andWaaland	**1**	**0.675**	**n.d.**
Ulva fasciata	Delile	**1**	**0.675**	**n.d.**
Ulva flexuosa	Wulfen	**1**	**0.675**	**n.d.**
Ulva lactuca	Linnaeus	**68**	**45.94**	**58.920**
Willeella brachyclados	(Montagne) M.J.Wynne	**1**	**0.675**	**n.d.**
Total		***68***	***45.940***	
OCHROPHYTA				
Chnoospora minima	(Hering) Papenfuss	**4**	**2.702**	**n.d.**
Dictyota sp.		**7**	**4.729**	**0.011**
Padina sp.		**8**	**5.405**	**0.050**
Sargassum cymosum	C. Agardh	**60**	**40.540**	**2.400**
Total		***60***	***40.540***	
RHODOPHYTA				
Aglaothamnion uruguayense	(W.R.Taylor) N.E.Aponte, D.L.Ballantin e andJ.N.Norris	**1**	**0.675**	**n.d.**
Aglaothamnion sp.		**1**	**0.675**	**n.d.**
Amphiroa beauvoisii	J.V.Lamourou x	**1**	**0.675**	**n.d.**
Asparagopsis taxiformis	(Delile) Trevisan	**2**	**1.351**	**n.d.**
Bostrychia binderi	Harvey	**2**	**1.351**	**n.d.**
Bostrychia radicans	(Montagne) Montagne	**1**	**0.675**	**n.d.**
Bostrychia sp.		**4**	**2.702**	**0.001**
Bostrychia tenella	(J.V.Lamouro ux) J.Agardh	**2**	**1.351**	**n.d.**
Caloglossa sp.		**1**	**0.675**	**n.d.**
Ceramium sp.		**3**	**2.027**	**0.015**
Chondracanthus sp.		**1**	**0.675**	**n.d.**
Chondracantus teedei	(Mertensex Roth) Kützing	**3**	**2.027**	**0.005**
Chondria sp.		**1**	**0.675**	**n.d.**
Dipterosiphonia sp.		**1**	**0.675**	**n.d.**
Gelidium pusillum	(Stackhouse) Le Jolis	**5**	**3.378**	**0.023**
Gelidium sp.		**5**	**3.378**	**0.014**
Gracilaria domingensis	(Kütz) Sond. Ex Dickie	**30**	**20.270**	**5.090**
Heterosiphonia crispella	(C.Agardh) M.J.Wynne	**1**	**0.675**	**n.d.**
Heterosiphonia sp.		**3**	**2.027**	**0.041**
Hypnea pseudomusciformis	Nauer, Cassano andM.C.Olive ira	**8**	**5.405**	**0.020**
Hypnea sp.		**8**	**5.405**	**0.015**

Hypnea spinella	(C.Agardh) Kützing	**4**	**2.094**	**0.007**
Neosiphonia sp.		**1**	**0.675**	**n.d.**
Plocamiums p.		**1**	**0.675**	**n.d.**
Polysiphonia howei	Hollenberg in W.R. Taylor	**1**	**0.675**	**n.d.**
Polysiphonia sp.		**1**	**0.675**	**n.d.**
Pterocladiella sp.		**2**	**1.351**	**n.d.**
Pterosiphonia parasítica	(Hudson) Falkenberg	**3**	**2.027**	**0.001**
Pterosiphonia pennata	(C.Agardh) Sauvageau	**6**	**4.054**	**0.015**
Pterosiphonia sp.		**1**	**0.675**	**n.d.**
Pyropia sp.		**17**	**11.486**	**0.490**
Total		***49***	***33.100***	

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

Taxon	**Number of digestive tracts**	**Frequency of occurrence (*%FO*)**
Phylum Mollusca	96	67.60
Gastropoda	50	**35.21**
Acteocina lepta	1	0.70
Acteocina sp.	1	0.70
Family Architectonicidae	1	0.70
Family Atlantidae	3	2.11
Bittiolum varium	1	0.70
Family Calyptraeidae	2	1.40
Cavolinia sp.	7	**4.92**
Cavolinia tridentata	1	0.70
Family Cavolinidae	1	0.70
Family Cerithiidae	1	0.70
Cerithium cf. *algicola*	1	0.70
Family Collumbelidae	9	**6.33**
Costoanachis sertularium	2	1.40
Costoanachis sp.	4	**2.81**
Diacria sp.	2	1.40
Diacria trispinosa	2	1.40
Diodora sp.	1	0.70
Family Epitoniidae	1	0.70
Epitonium angulatum	1	0.70
Epitonium sp.	1	0.70
Eulithidium affine	1	0.70
Heleobia australis	1	0.70
Family Hipponicidae	1	0.70
Melanella hypsela	1	0.70
Mitrella cf. *Moleculina*	1	0.70
Family Nassaridae	2	1.40
Family Neritidae	1	0.70
Neritina virginea/Vitta virginea	3	2.11
Olivella sp.	2	1.40
Family Olividae	2	1.40
Parvanachis sp.	1	0.70
Family Tateidae	1	0.70
Turbonilla sp.	2	1.40

Family Turritelidae	1	0.70
Bivalvia	62	**43.66**
Anadara ovalis	2	1.40
Anadara sp.	3	2.11
Family Arcidae	1	0.70
Brachidontes sp.	1	0.70
Carditamera sp.	1	0.70
Corbula sp.	5	**2.92**
Family Corbulidae	1	0.70
Crassatella riograndensis	1	0.70
Crassostrea sp.	1	0.70
Ctena cf.*pectinella*	1	0.70
Ctena sp.	1	0.70
Family Donacidae	1	0.70
Family Mactridae	1	0.70
Family Mytilidae	5	**2.92**
Noetia bisulcate	2	1.40
Nucula sp.	4	**2.81**
Family Ostreidae	5	**2.92**
Family Pectinidae	3	2.11
Perna perna	1	0.70
Semele nuculoides	3	2.11
Strigilla sp.	3	2.11
Cephalopoda	11	**7.74**
Doryteuthis pleii	1	0.70
Decapodiformes	2	1.40
Octopodiformes	2	1.40
Family Spirulidae	1	0.70
Scaphopoda	2	1.40
Phylum Bryozoa	5	**2.92**
Phylum Hydrozoa	5	**2.92**
Plumularioidea	1	0.70
Crustacea	5	**2.92**
Family Balanidae	1	0.70
Balanomorpha	1	0.70
Family Barleeiidae	1	0.70
Cirripedia	4	**2.81**
Decapoda	1	0.70
Paguroidea	1	0.70
Pleocyemata	1	0.70
PhylumEchinodermata	**4**	**2.81**
Echinoidea	1	0.70
Insecta	4	**2.81**
Pycnogonida	1	0.70
Pterygota	1	0.70
Coleoptera	2	1.40
Coccinellidae	1	0.70
Polychaeta	4	**2.81**
PhylumChordata	20	**14.08**
Teleostei	15	**10.56**
Family Engraulidae	1	0.70
Harengula clupeola	1	0.70
Lycengraulis grossidens	1	0.70
Pellona harroweri	1	0.70
Ctenosciaena gracilicirrhus	2	1.40
Isopisthus parvipinnis	2	1.40
Micropogonias furnieri	2	1.40
Paralonchurus brasiliensis	2	1.40
Family Sciaenidae	2	1.40
Stellifer brasiliensis	1	0.70

Stellifer rastrifer	2	1.40
Stellifer sp.	1	0.70
Raneya brasiliensis	1	0.70

Table 3. Results from two-factor PERMANOVA (year + climatic event) for the low-taxonomic resolution diet of all Paraná green turtles herein analyzed (n = 351). Df = degrees of freedom; SS = sum of squares; R^2 = pseudo-R^2. Values in bold indicate significant differences (α = 0.05).

Sources	Df	SS	R^2	F-value	p-value
Years	12	473.4	0.0719	2.1973	**0.0001**
Climatic events	3	88.1	0.0133	1.6350	**0.0479**
Residual	335	6014.4	0.9146		
Total	350	6575.8	1.0000		

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

Sources	Df	SS	R^2	F-value	p-value
Year	8	36.4	0.1583	3.2422	0.0003
Season	3	2.6	0.0113	0.6190	0.7486
Residual	136	191.3	0.8303		
Total	147	230.4	1		

Table 5. Results from two-factor PERMANOVA (year + season) regarding HTA (high taxonomic animal) identification and consumption by Paraná green turtles (n = 142) from 2015 to 2020. Df = degrees of freedom; SS = sum of squares; R^2 = pseudo-R^2. Values in bold indicate significant differences (α = 0.05).

Sources	Df	SS	R^2	F-value	p-value
Year	5	241.7	0.092	2.799	**0.0003**
Season	3	101.4	0.038	1.959	**0.0292**
Year:Season	10	170.8	0.065	0.989	0.4803
Residual	123	2124.1	0.805		
Total	141	2638.1	1		

Figures

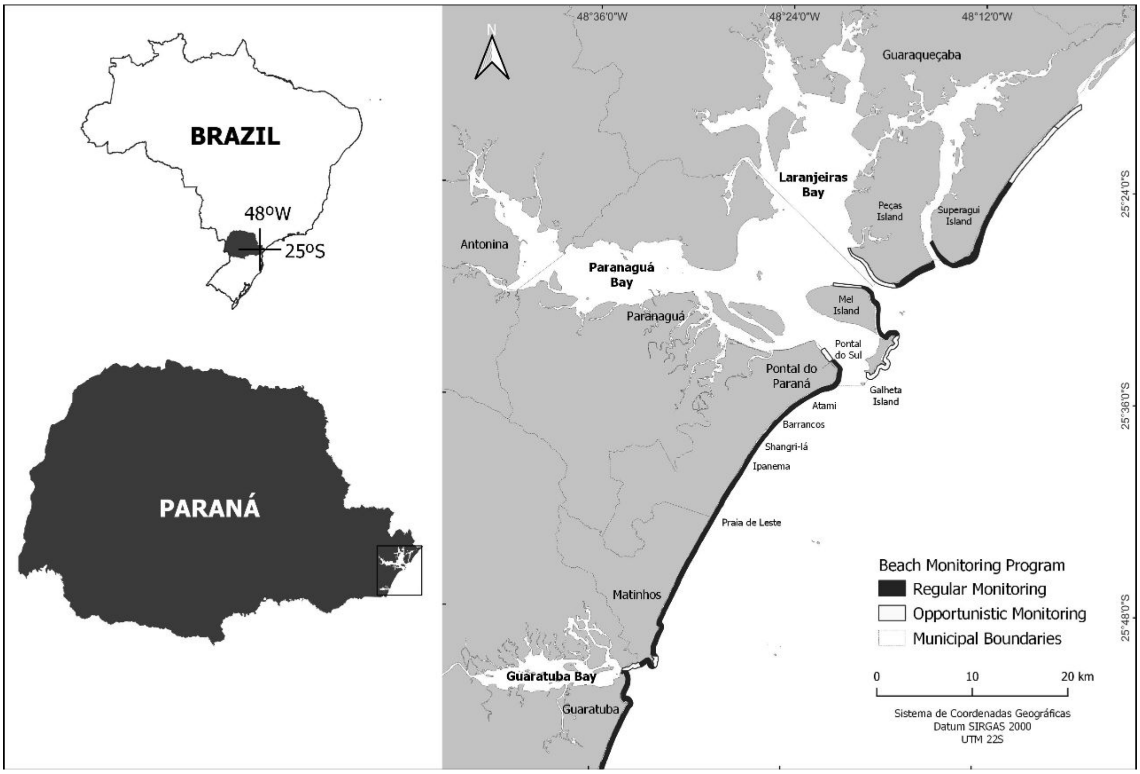


Figure 1. Map of the Paraná coast of Brazil, including the Paranaguá Estuarine Complex (PEC) and Guaratuba Bay, in south Brazil, where the beach surveys were performed, and dead-stranded green turtles were recovered. The lines colored in black represent the regular monitored area, whereas the ones in white represent the areas where monitoring occurred sporadically.

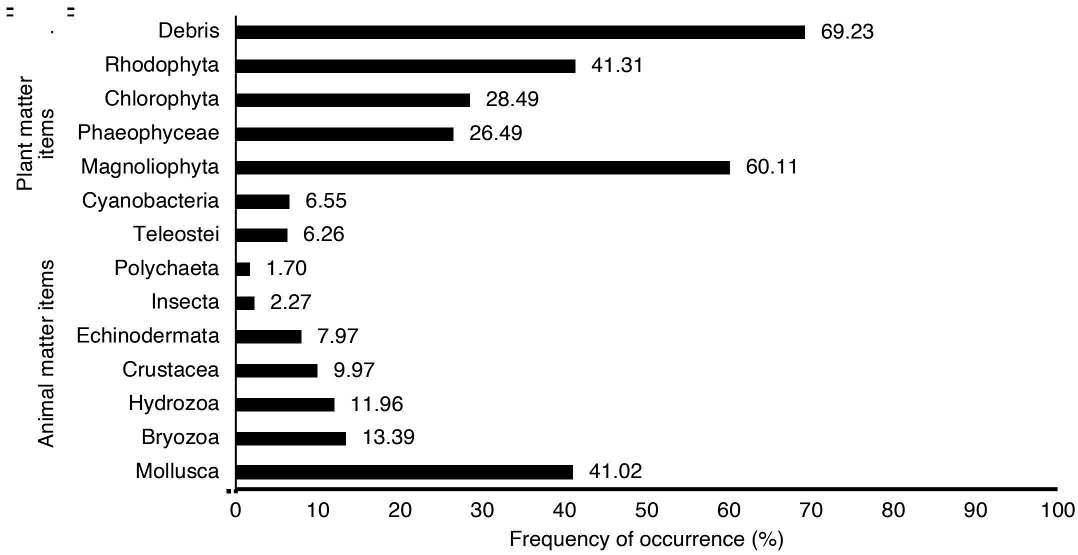


Figure 2: Frequency of occurrence (*%FO)* of all the prey items and debris found in the

digestive tracts of stranded juvenile green turtles *Chelonia mydas* (n = 351) in Paraná coast for all the study period (2008 to 2020).

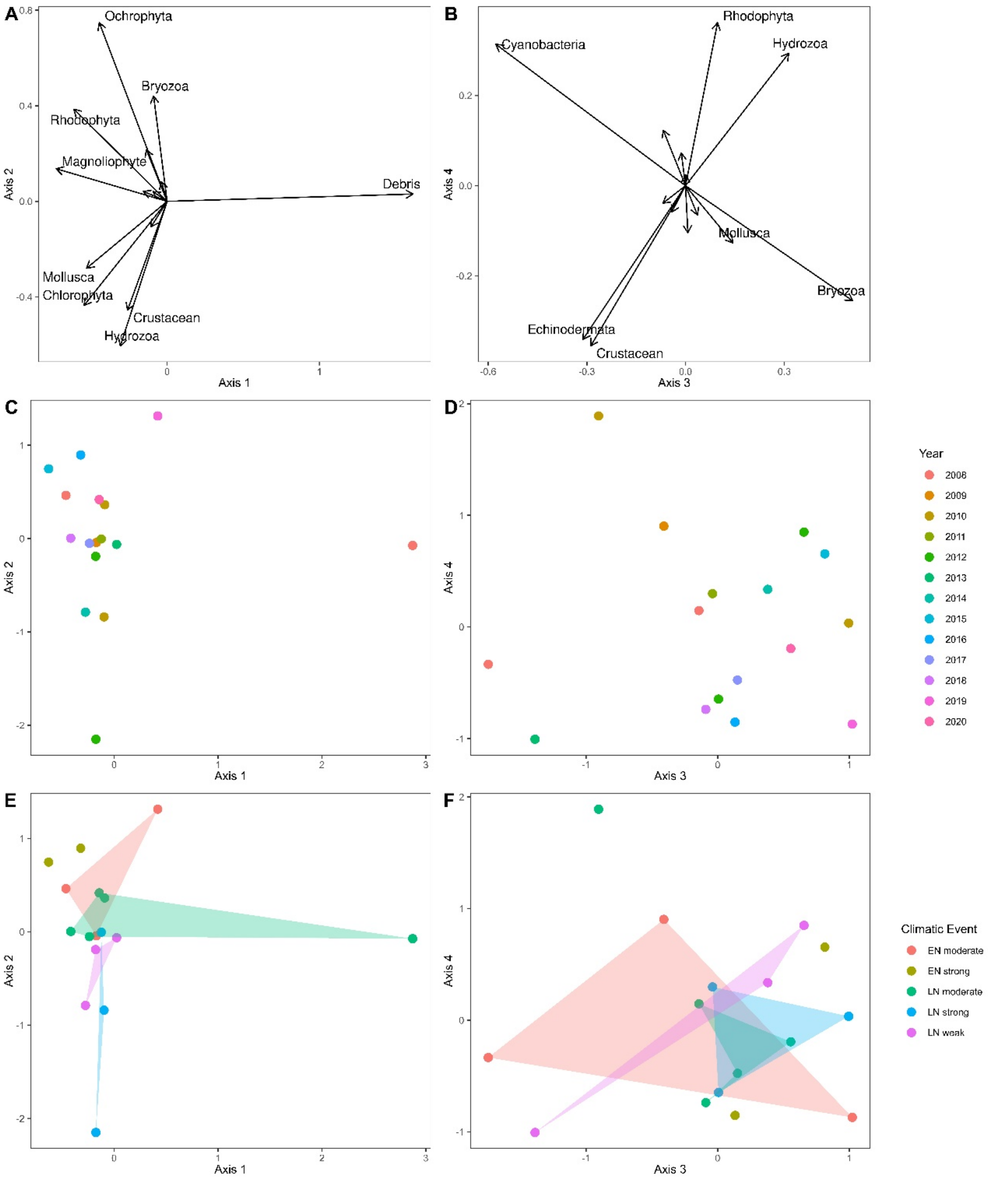
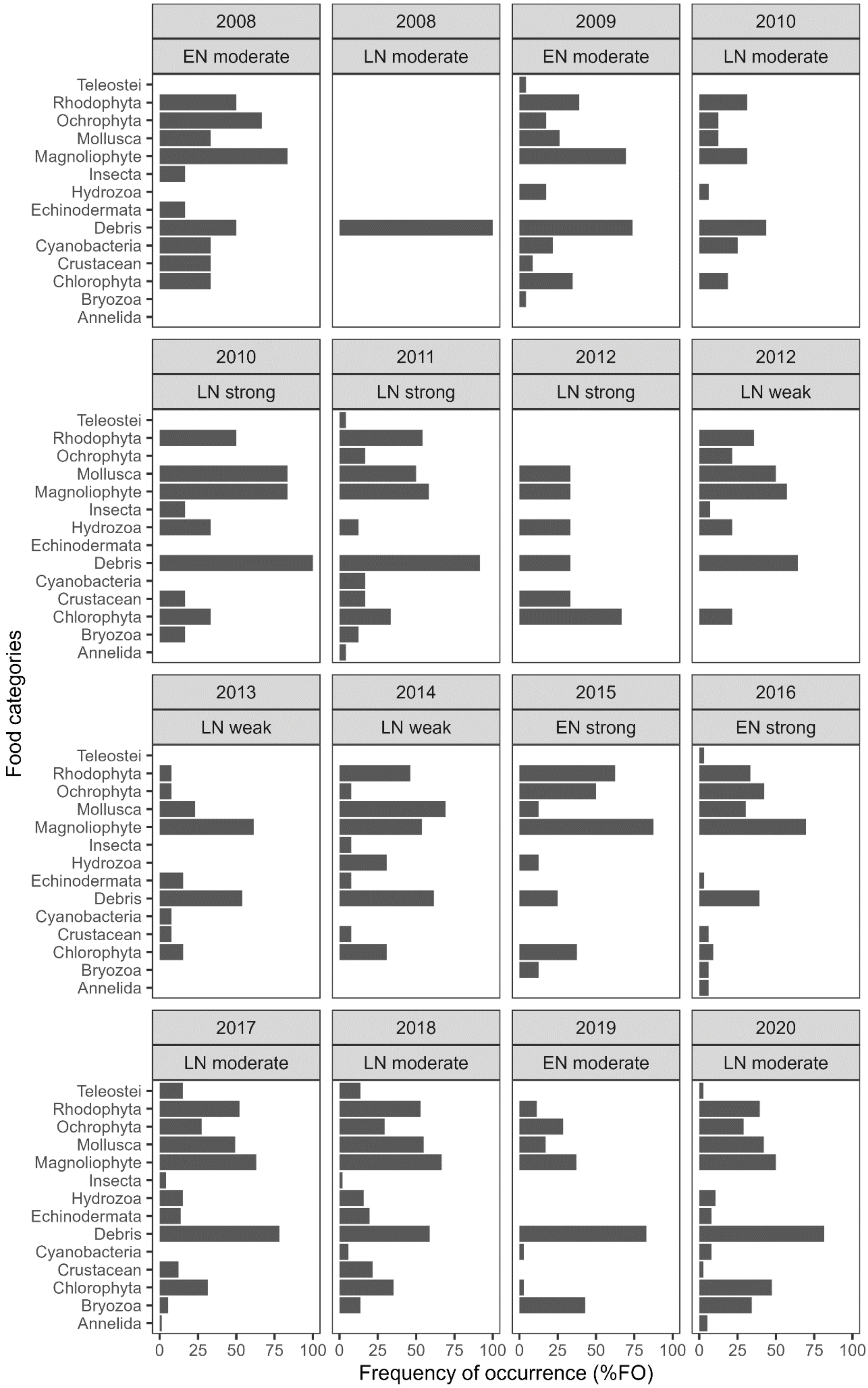


Figure 3: Principal Component Analysis (PCA) showing diet tendencies of green turtles *Chelonia mydas* (n = 351) in Paraná coast, south Brazil. Interannual diet tendencies (2008 to 2020) along axes 1 and 2 (A and C), and 3 and 4 (B and D). Diet tendencies by climatic events (EN = El Niño, LN = La Niña) along axes 1 and 2 (A and E) and 3 and 4 (B and F).



985
986 **Fig. 4:** Bar-plots representing the frequency of occurrence (*%FO*) of the entire database

(LT) found in the digestive tracts of juvenile green turtles (n = 351) found dead-stranded in Paraná coast, south Brazil, from 2008 to 2020.

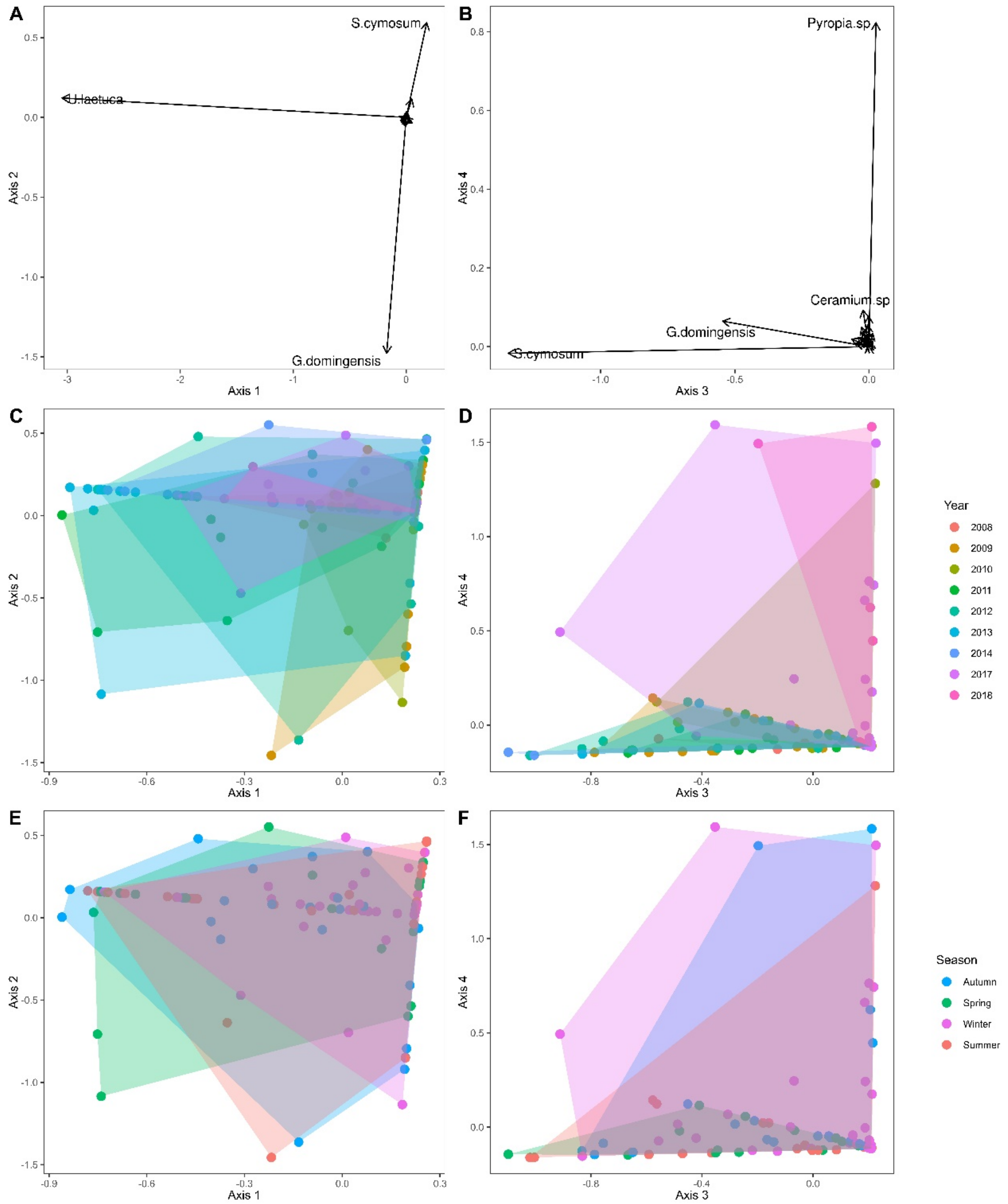
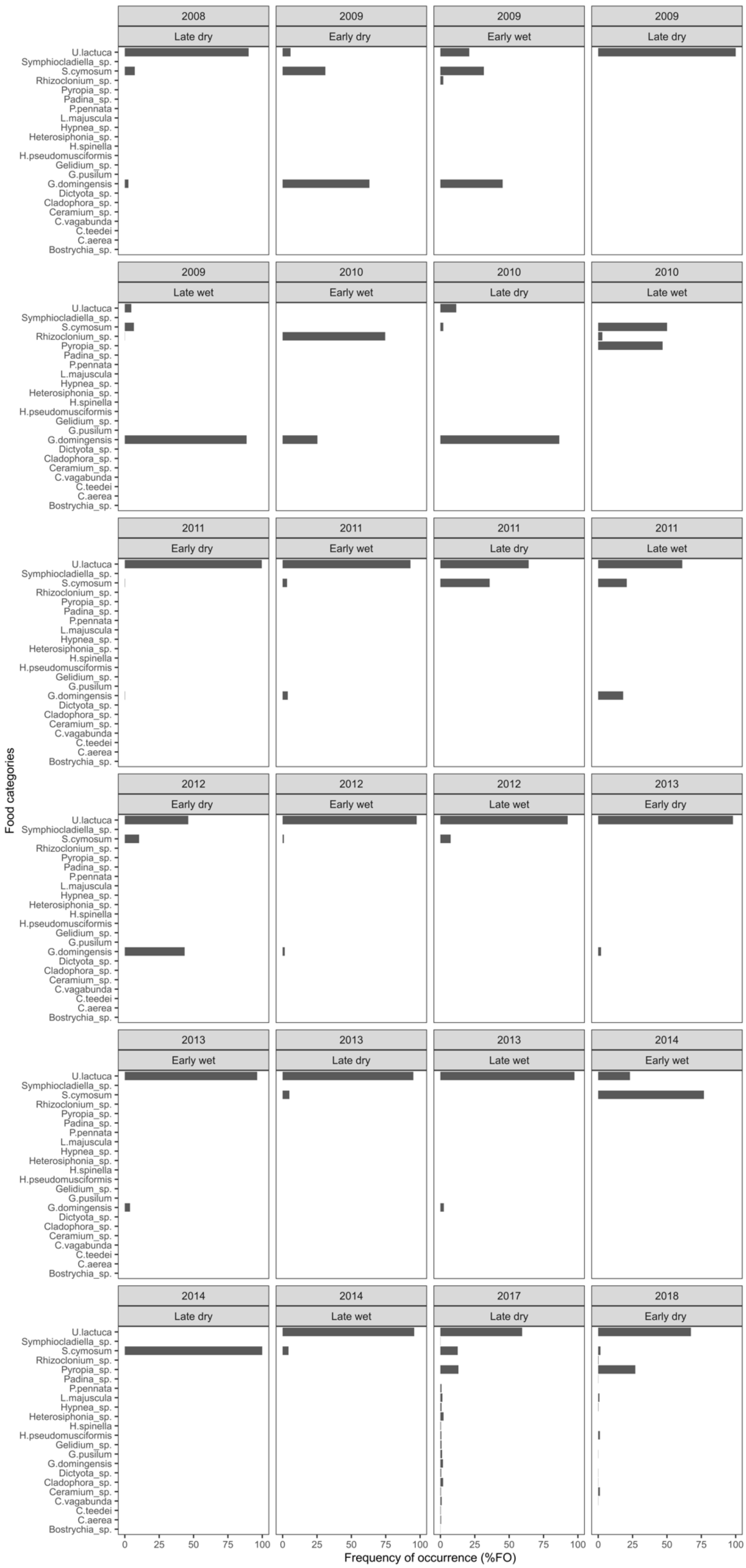


Figure 5: Principal Component Analysis (PCA) showing high taxonomic macroalgae (HTM) consumption tendencies of green turtles *Chelonia mydas* (n = 148) in Paraná coast, south Brazil. Interannual diet tendencies (2008 to 2014, 2017 and 2018) along axes 1 and 2 (A and C), and 3 and 4 (B and D). Diet tendencies by seasons along axes 1 and 2 (A and E) and 3 and 4 (B and F).


2008
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Late dry
2014
Late wet
2017
Late dry
2018
Early dry
U.lactuca
Symphiocladiella_sp.
S.cymosum
Rhizoclonium_sp.
Pyropia_sp.
Padina_sp.
P.pennata
L.majuscula
Hypnea_sp.
Heterosiphonia_sp.
H.spinella
H.pseudomusciformis
Gelidium_sp.
G.pusilum
G.domingensis
Dictyota_sp.
Cladophora_sp.
Ceramium_sp.
C.vagabunda
C.teedei
C.aerea
Bostrychia_sp.
Food categories
0 25 50 75 100
Frequency of occurrence (%FO)

Fig. 6: Bar-plots representing the frequency of occurrence (*%FO*) of high taxonomic macroalgae (HTM) found in the digestive tracts of juvenile green turtles (n = 148) found dead-stranded in Paraná coast, south Brazil, from 2008 to 2014; 2017 and 2018.

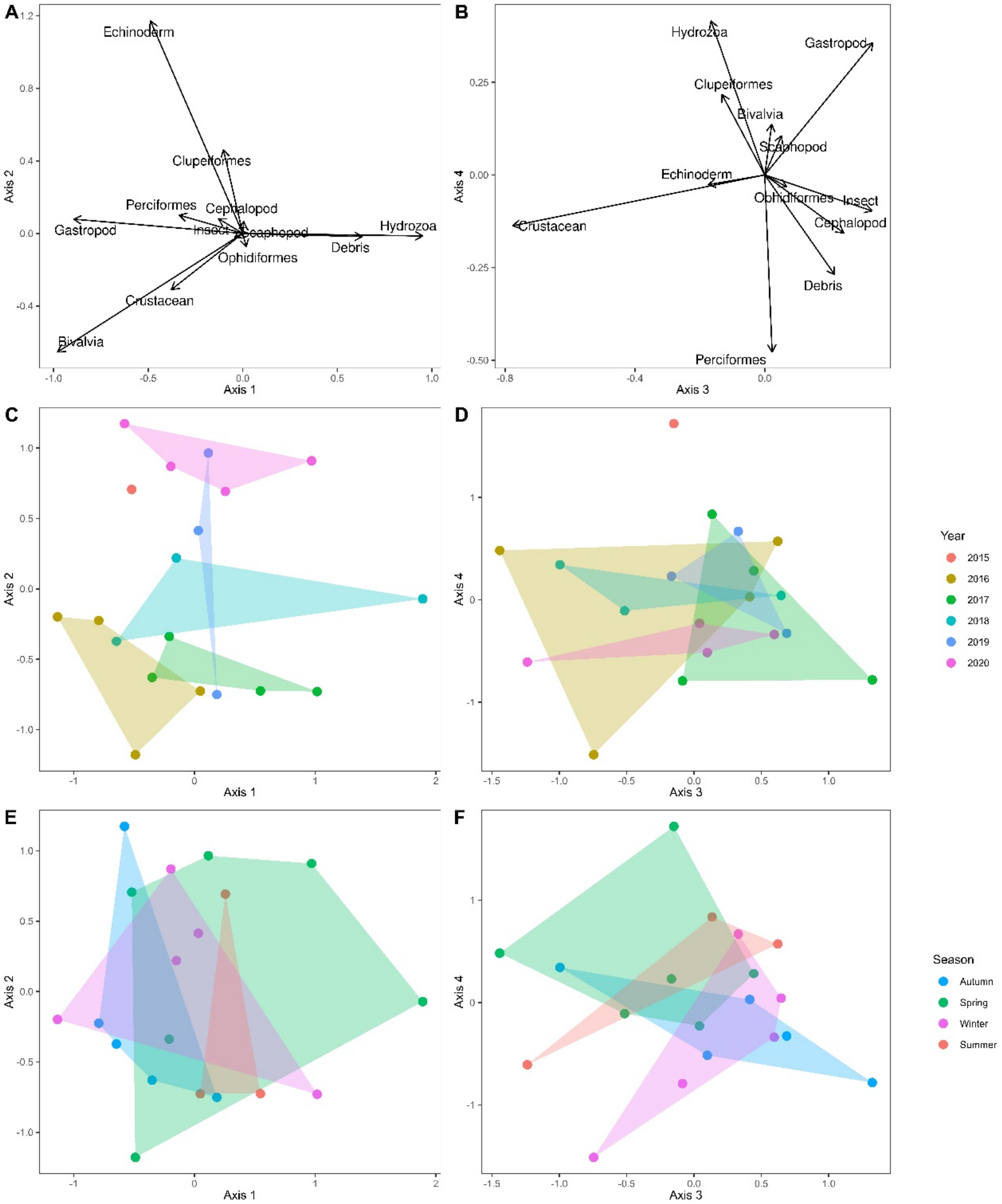
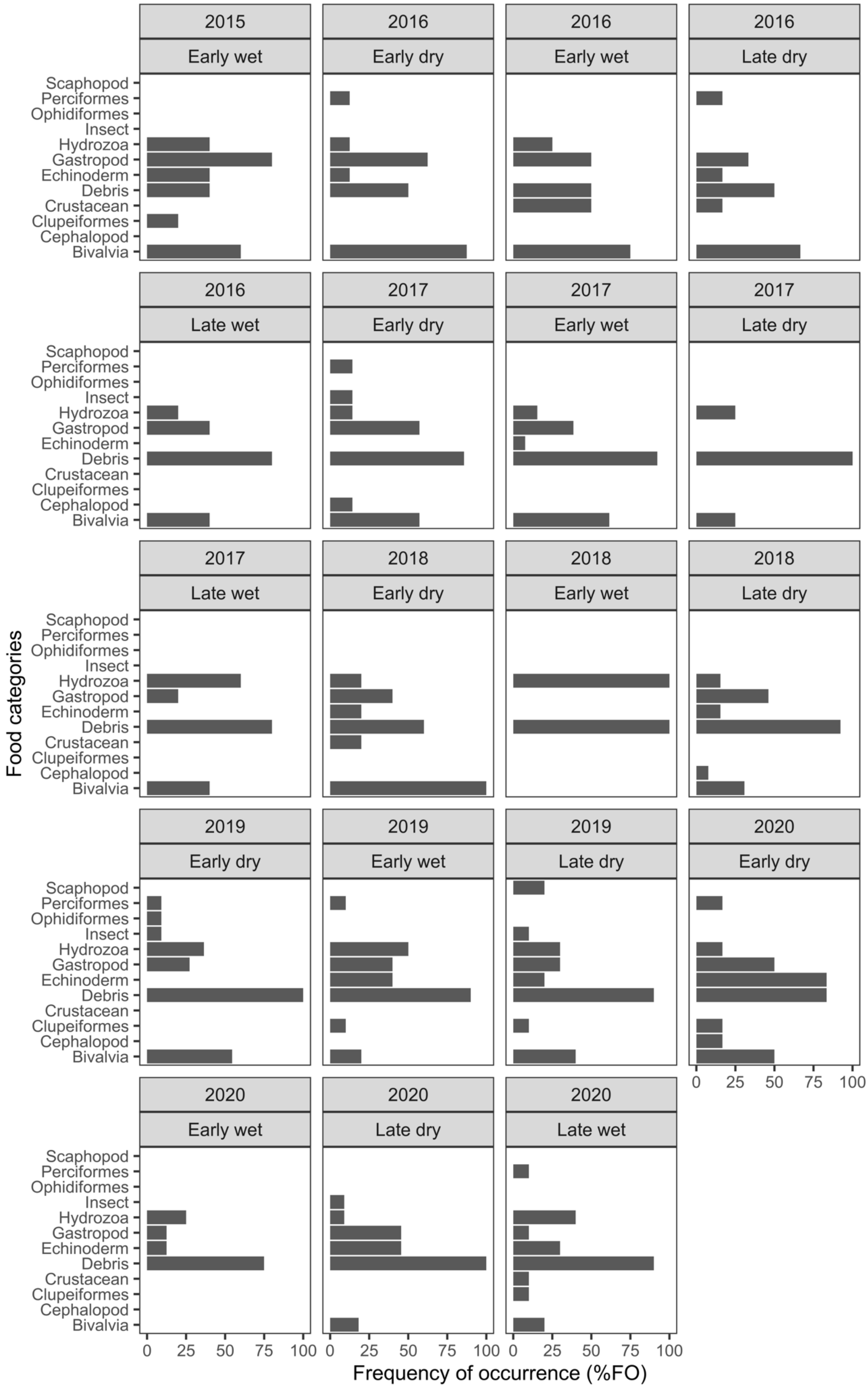


Figure 7: Principal Component Analysis (PCA) showing high taxonomic animal (HTA) consumption tendencies of green turtles *Chelonia mydas* (n = 142) in Paraná coast, south Brazil. Interannual diet tendencies (2015 to 2020) along axes 1 and 2 (A and C), and 3 and 4 (B and D). Diet tendencies by seasons along axes 1 and 2 (A and E) and 3 and 4 (B and F).


2015
Early wet
2016
Early dry
2016
Early wet
2016
Late dry
2016
Late wet
2017
Early dry
2017
Early wet
2017
Late dry
2017
Late wet
2018
Early dry
2018
Early wet
2018
Late dry
2019
Early dry
2019
Early wet
2019
Late dry
2020
Early dry
2020
Early wet
2020
Late dry
2020
Late wet
Scaphopod
Perciformes
Ophidiformes
Insect
Hydrozoa
Gastropod
Echinoderm
Debris
Crustacean
Clupeiformes
Cephalopod
Bivalvia
Food categories
0 25 50 75 100
Frequency of occurrence (%FO)

1010

Fig. 8: Bar-plots representing the frequency of occurrence (*%FO*) of high taxonomic animal (HTA) found in the digestive tracts of juvenile green turtles (n = 142) found dead-stranded in Paraná coast, south Brazil, from 2015 to 2020.