



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

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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 coast of Paraná, Brazil, is an important foraging ground for juvenile green turtles *Chelonia mydas*. To determine seasonal and interannual diet variability, we analyzed the dietary contents of 351 dead-stranded individuals to the major taxa level from 2008 to 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 and 2011–2018, and 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, and Hydrozoa and Gastropoda in all seasons. Our results underscore individual dietary plasticity, including inter-seasonal and annual differences, which likely reflects the ability of green turtles 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.

**KEY WORDS:** *Chelonia mydas* · Feeding ecology · Behavioral plasticity · Spatial–temporal scale · Macroalgae · Mollusca · Conservation

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## 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, for-

aging 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 *Chelonia mydas* foraging ecology, knowledge about the extrinsic influences such as prey availability, sea surface temperature (SST), cumulative rainfall rates, and habitat quality is fundamental to interpret behaviors, diet intake, and health of local green turtles (Wildermann et al. 2018). Understanding the influences of decadal-scale climate shifts on habitats is also essential to assess long-term ecological changes (Hawkes et al. 2009, Esteban et al. 2020). For example, in southern South America, El Niño (EN), which increases rainfall and temperature, and La Niña (LN), which decreases rainfall and temperature, events influence climate variability, rainfall patterns and intensity, and SSTs (Grimm et al. 2000). Therefore, these and other climatic events may drive biological and ecological changes (e.g. habitat dynamics, prey availability, predator–prey interactions), 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, areas in southern and southeastern Brazil have a large number of juvenile green turtles that dead-strand each year, particularly in Paraná (25° S) and the central area of Santa Catarina (26° S) (Cantor et al. 2020). Green turtles in these areas 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-Bartholo 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 1000 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, Moreira dos Santos & Lana 2017). However, more than 1000 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 showed 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 explore for the first time long-term variation and trends related to seasonal, annual, and intermittent environmental (EN/LN) cycles. We examined gut contents of dead-stranded green turtles encountered in this area between 2008 and 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 coast of Paraná, southern Brazil (25° 20' to 25° 35' S, 48° 17' 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, including the Paranaguá Estuarine Complex (PEC), a 612 km<sup>2</sup> 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, Pellizzari et al. 2014, 2020a, Bumbeer et al. 2016). Macroalgal diversity along the coast of Paraná 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, Pellizzari & Reis 2011).

The coast of Paraná is influenced by the Brazilian Current, which brings warm waters to the south during the austral summer (wet season), and the Falklands Current, which introduces cold waters during

the winter (dry season) (Piola et al. 2000, Matano et al. 2010). The PEC is composed of 3 different haline zones: estuarine, estuarine outlets, and open-ocean coasts (Angulo & Araújo 1996), that result in a salinity gradient and hence, differences in local habitats (Krelling & Turra 2019). The average SST values range from 21.60 to 26.71°C, and the monthly average rainfall values range from 120.66 to 276.63 mm (data obtained from <http://enos.cptec.inpe.br/>; accessed August 2021).

## 2.2. Dead-stranded turtle collection

Dead-stranded green turtles were collected along the coast of Paraná (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-stage ranking adapted from Geraci & Lounsbury 2005) with intact digestive tracts were consid-

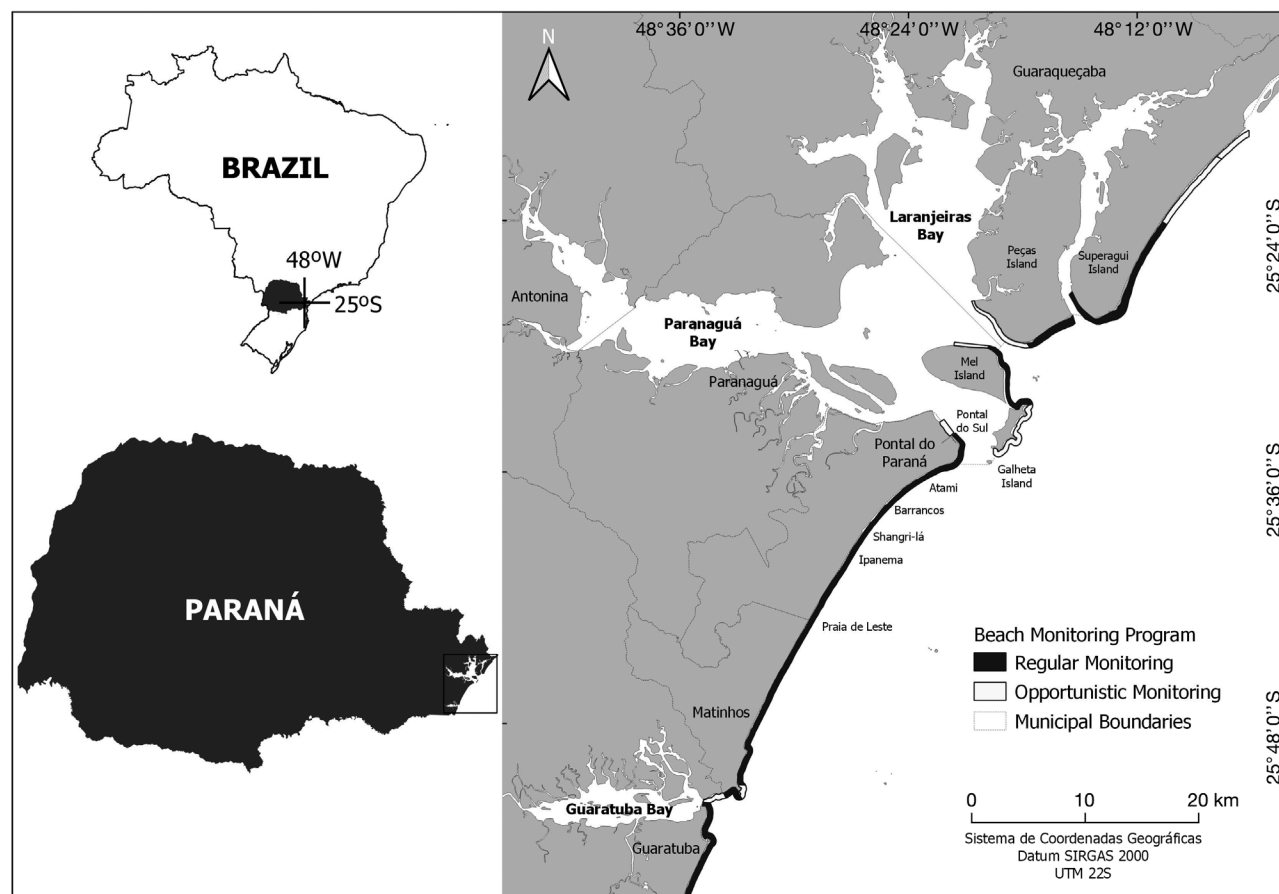


Fig. 1. Coast of Paraná, Brazil, showing the Paranaguá Estuarine Complex and Guaratuba Bay, where the beach surveys were performed and dead-stranded green turtles were recovered. Thick black lines along the coast represent the regularly monitored areas, whereas white lines represent areas where monitoring occurred sporadically

ered for this study. Between 2015 and 2020, the samples were obtained as part of the Santos Basin Beach Monitoring Project (Projeto de Monitoramento de Praia da Bacia de Santos, PMP-BS). 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) was recorded for all specimens, and biological samples were collected for further analysis. The digestive tracts were removed and stored frozen at  $-15^{\circ}\text{C}$  until analysis. The sampling year, locality, date, season, and body size were recorded for each recovered green turtle. Also, for some specimens obtained from PMP-BS ( $n = 238$ ), we calculated their body condition score (e.g. Limpus et al. 2012).

### 2.3. Diet analysis

To determine diet composition, all recovered items were washed, separated, and identified. Invertebrates, except cephalopod beaks, and debris were washed and dried at  $60^{\circ}\text{C}$ ; vegetal matter was preserved in 70% ethyl alcohol; and cephalopod beaks were preserved in 70% ethyl alcohol and 5% glycerin.

Three different diet analyses were conducted:

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

(2) High taxonomic resolution, macroalgae only (HTM): a total of 148 turtles collected in 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 (1999, 2005), Moura (2000), Barata (2004), Coto (2007), Crispino (2007), Pereira-Filho et al. (2011, 2012), and Pellizzari et al. (2014). Taxonomical updates followed Guiry & Guiry (2019).

(3) High taxonomic resolution, animal prey only (HTA): a total of 142 green turtles collected in 2015–2020 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), and Absher et al. (2015), followed by specialist taxonomists.

The global algae database AlgaeBase (Guiry & Guiry 2019) and the World Register of Marine Species website (WoRMS Editorial Board 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 plastic, 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 in low and high resolutions, the frequency of occurrence (%FO) (Silveira et al. 2020) was calculated for each food category as the number of stomachs in which the food category  $f$  occurred ( $Sf_f$ ) divided by the total number of stomachs with food assessed ( $Sf$ ):

$$\%FO = \left( \frac{Sf_f}{Sf} \right) \times 100 \quad (1)$$

Specific to the macroalgae, the prey item for which weight was measured, the gravimetric frequency (%W) was calculated as the weight of the food category  $f$  consumed by a given specimen  $i$  ( $W_{fi}$ ) divided by 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 ( $Sf$ ):

$$\%W = \frac{1}{Sf_f} \times \sum_{i=1}^{Sf_f} \left( \frac{W_{fi}}{\sum_{i=1}^{Sf_f} W_{fi}} \right) \times 100 \quad (2)$$

This index was used in addition to %FO because all macroalgae species were weighed and %W 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 EN/LN). The climatic data were obtained from <http://enos.cptec.inpe.br/> (accessed August 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 summer (late wet); April, May, and June, to autumn (early dry); July, August, and September, to winter (late dry); and October, November, and December, to spring (early wet). This seasonal variation was based on previous studies conducted in the same area (Gama et al. 2016, Possatto et al. 2017).

For %FO data, a 2-way permutational multivariate analysis of variance (PERMANOVA) (year + climatic event, Euclidian distance, 9999 permutations) (An-

derson 2001, Anderson & Willis 2003) was performed on logit-transformed data (Warton & Hui 2011). For %W, a 2-way PERMANOVA (year + season, Euclidian distance, 9999 permutations) was used with Hellinger and log-transformed data ( $\log x + 1$ ) (Legendre & Legendre 2012, Borcard et al. 2018). Results were considered significant at  $p < 0.05$ . Principal component analysis (PCA) (Legendre & Legendre 2012, Borcard et al. 2018) highlights differences in a multivariate data set; hence, it was performed to visually interpret PERMANOVA results. All analyses were performed using R 4.0 software (R Core Team 2021).

### 3. RESULTS

#### 3.1. General demographic results

The dead-stranded green turtles analyzed for low taxonomic resolution ranged in size from 23.2 to 68.0 cm CCL ( $38.77 \pm 7.16$  cm SD;  $n = 351$ ). Turtles analyzed for high taxonomic resolution of macroalgae ranged in size from 28.2 to 62.0 cm CCL ( $38.83 \pm 6.53$  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 animal prey ranged in CCL from 23.2 to 68.0 cm ( $38.39 \pm 7.85$  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 pre-

sented a good 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 analysis), a total of 13 different major taxa was encountered in digestive tracts of green turtles (Fig. 2): Magnoliophyta (including mangroves and seagrasses), 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 (41.31%) and Mollusca (41.02%) (Fig. 2).

Regarding the HTM analysis, a total of 3 major taxa was identified, including 49 different taxa of macroalgae. The most frequent macroalgae were *Ulva lactuca* (%FO = 45.94%), followed by *Sargassum cymosum* (40.54%) and *Gracilaria domingensis* (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 (10.56%) (Table 2).

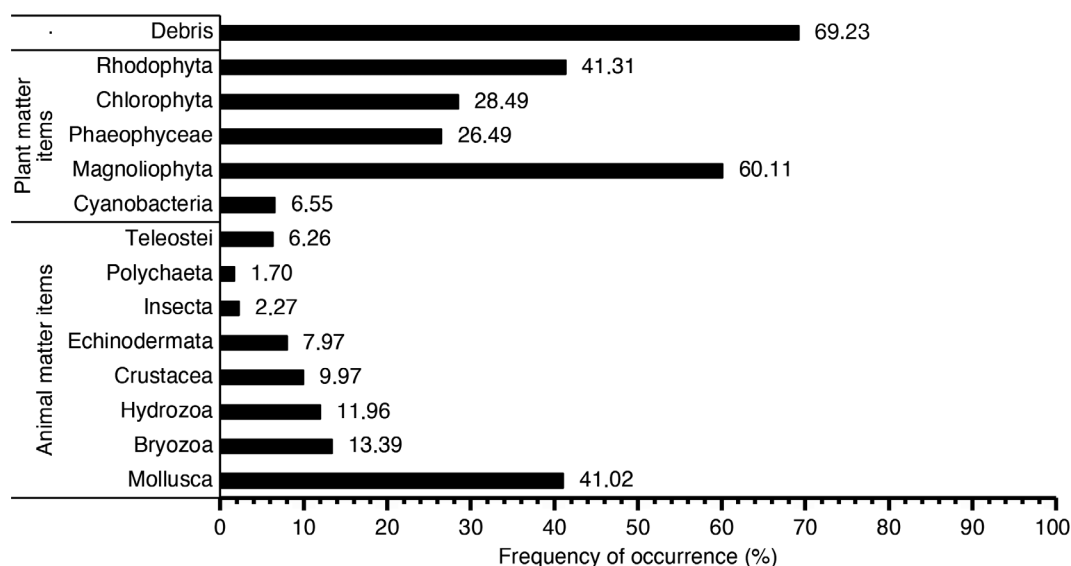


Fig. 2. Frequency of occurrence (%FO) of all prey items and debris found in the digestive tracts of stranded juvenile green turtles *Chelonia mydas* ( $n = 351$ ) along the coast of Paraná, Brazil, for the entire study period (2008–2020)



Table 1. Frequency of occurrence (%FO) and weight (%W) of macroalgae at high taxonomic resolution (see Section 2.3 for details) registered in digestive tract (DT) contents of juvenile green turtles *Chelonia mydas* (n = 148) collected dead-stranded along the coast of Paraná, Brazil, 2008–2014 and 2017–2018. nd: value did not reach the minimum accuracy scale

Taxa	No. of DTs	%FO	%W
<b>CHLOROPHYTA</b>			
<i>Caulerpa</i> sp.	2	1.351	nd
<i>Chaetomorpha aerea</i>	5	3.378	0.008
<i>Chaetomorpha antennina</i>	2	1.351	nd
<i>Chaetomorpha</i> sp.	1	0.675	nd
<i>Cladophora catenata</i>	1	0.675	nd
<i>Cladophora vagabunda</i>	7	4.729	0.036
<i>Cladophora</i> sp.	6	4.054	0.016
<i>Cladophoropsis membranacea</i>	1	0.675	nd
<i>Rhizoclonium</i> sp.	6	4.054	0.010
<i>Ulva chaetomorphaeoides</i>	1	0.675	nd
<i>Ulva fasciata</i>	1	0.675	nd
<i>Ulva flexuosa</i>	1	0.675	nd
<i>Ulva lactuca</i>	68	45.940	58.920
<i>Willeella brachyclados</i>	1	0.675	nd
Total	68	45.940	
<b>OCHROPHYTA</b>			
<i>Chnoospora minima</i>	4	2.702	nd
<i>Dictyota</i> sp.	7	4.729	0.011
<i>Padina</i> sp.	8	5.405	0.050
<i>Sargassum cymosum</i>	60	40.540	2.400
Total	60	40.540	
<b>RHODOPHYTA</b>			
<i>Aglaothamnion uruguayense</i>	1	0.675	nd
<i>Aglaothamnion</i> sp.	1	0.675	nd
<i>Amphiroa beauvoisii</i>	1	0.675	nd
<i>Asparagopsis taxiformis</i>	2	1.351	nd
<i>Bostrychia binderi</i>	2	1.351	nd
<i>Bostrychia radicans</i>	1	0.675	nd
<i>Bostrychia</i> sp.	4	2.702	0.001
<i>Bostrychia tenella</i>	2	1.351	nd
<i>Caloglossa</i> sp.	1	0.675	nd
<i>Ceramium</i> sp.	3	2.027	0.015
<i>Chondracanthus</i> sp.	1	0.675	nd
<i>Chondracanthus teedei</i>	3	2.027	0.005
<i>Chondria</i> sp.	1	0.675	nd
<i>Dipterosiphonia</i> sp.	1	0.675	nd
<i>Gelidium pusillum</i>	5	3.378	0.023
<i>Gelidium</i> sp.	5	3.378	0.014
<i>Gracilaria domingensis</i>	30	20.270	5.090
<i>Heterosiphonia crispella</i>	1	0.675	nd
<i>Heterosiphonia</i> sp.	3	2.027	0.041
<i>Hypnea pseudomusciformis</i>	8	5.405	0.020
<i>Hypnea</i> sp.	8	5.405	0.015
<i>Hypnea spinella</i>	4	2.094	0.007
<i>Neosiphonia</i> sp.	1	0.675	nd
<i>Plocamium</i> sp.	1	0.675	nd
<i>Polysiphonia howei</i>	1	0.675	nd
<i>Polysiphonia</i> sp.	1	0.675	nd
<i>Pterocladia</i> sp.	2	1.351	nd
<i>Pterosiphonia parasitica</i>	3	2.027	0.001
<i>Pterosiphonia pennata</i>	6	4.054	0.015
<i>Pterosiphonia</i> sp.	1	0.675	nd
<i>Pyropia</i> sp.	17	11.486	0.490
Total	49	33.100	

### 3.3. Interannual variation in diet

Consumption of food categories by green turtles was significantly different among years for the LT diet analysis ( $F_{12} = 2.1973$ ,  $p < 0.0001$ ) (Table 3) as well as the HTM ( $F_8 = 3.2422$ ;  $p < 0.001$ ) (Table 4) and HTA ( $F_5 = 2.799$ ;  $p = 0.003$ ) diet analyses (Table 5).

For the LT analysis (low taxonomic resolution), the first 4 axes of the PCA explained 82.74% of data variance (d.v.). Axis 1 (47.07% d.v.) highlighted annual trends in the diet of all green turtles sampled from 2008 to 2020 concerning the consumption of the categories Magnoliophyta (axis score, a.s. =  $-0.73$ ), Rhodophyta ( $-0.61$ ), Chlorophyta ( $-0.55$ ), Mollusca ( $-0.53$ ), Ochrophyta ( $-0.45$ ), and debris (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 (25.00–58.82%) and Rhodophyta (7.69–62.50%) (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 (37.14–69.57%) and Rhodophyta (11.43–54.17%) (Fig. 4).

For the HTM sampling, the first 4 axes of the PCA explained 97.10% of d.v. Axes 1 (61.55% d.v.) and 2 (16.92% d.v.) highlighted the consumption of *Ulva lactuca*, *Gracilaria domingensis*, and *Sargassum cymosum* by green turtles sampled from 2008–2014 and 2017–2018 (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.<sub>Axis1</sub> =  $-3.05$ ; a.s.<sub>Axis2</sub> = 0.12), *G. domingensis* (a.s.<sub>Axis1</sub> =  $-0.17$ ; a.s.<sub>Axis2</sub> =  $-1.48$ ) and *S. cymosum* (a.s.<sub>Axis1</sub> = 0.18; a.s.<sub>Axis2</sub> = 0.59) (Fig. 6). During these years, %W of *U. lactuca* varied from 0.60 to 82.36% (0.01–2.43% in the remaining years), of *G. domingensis* from  $<0.01$  to 31.24% (vs. absent to 47.46%), and %W of *S. cymosum* varied from 0.02 to 23.59% (vs.  $<0.01$  to 43.05%). The multivariate sub-

Table 2. Frequency of occurrence (%FO) of animal prey at high taxonomic resolution (see Section 2.3 for details) registered in digestive tract (DT) contents of juvenile green turtles (n = 142) collected dead-stranded along the coast of Paraná, Brazil, from 2015 to 2020. The most frequent taxa are in **bold**

Taxon	No. of DTs	%FO	Taxon	No. of DTs	%FO
Phylum Mollusca	96	67.60	Family Mactridae	1	0.70
Gastropoda	50	<b>35.21</b>	Family Mytilidae	5	<b>2.92</b>
<i>Acteocina lepta</i>	1	0.70	<i>Noetia bisulcate</i>	2	1.40
<i>Acteocina</i> sp.	1	0.70	<i>Nucula</i> sp.	4	<b>2.81</b>
Family Architectonicidae	1	0.70	Family Ostreidae	5	<b>2.92</b>
Family Atlantidae	3	2.11	Family Pectinidae	3	2.11
<i>Bittiolium varium</i>	1	0.70	<i>Perna perna</i>	1	0.70
Family Calyptraeidae	2	1.40	<i>Semele nuculoides</i>	3	2.11
<i>Cavolinia</i> sp.	7	<b>4.92</b>	<i>Strigilla</i> sp.	3	2.11
<i>Cavolinia tridentata</i>	1	0.70	Cephalopoda	11	<b>7.74</b>
Family Cavolinidae	1	0.70	<i>Doryteuthis pleii</i>	1	0.70
Family Cerithiidae	1	0.70	Decapodiformes	2	1.40
<i>Cerithium</i> cf. <i>algicola</i>	1	0.70	Octopodiformes	2	1.40
Family Collumbelidae	9	<b>6.33</b>	Family Spirulidae	1	0.70
<i>Costoanachis sertularium</i>	2	1.40	Scaphopoda	2	1.40
<i>Costoanachis</i> sp.	4	<b>2.81</b>	Phylum Bryozoa	5	<b>2.92</b>
<i>Diacria</i> sp.	2	1.40	Phylum Hydrozoa	5	<b>2.92</b>
<i>Diacria trispinosa</i>	2	1.40	Plumularioidea	1	0.70
<i>Diodora</i> sp.	1	0.70	Crustacea	5	<b>2.92</b>
Family Epitoniidae	1	0.70	Family Balanidae	1	0.70
<i>Epitonium angulatum</i>	1	0.70	Balanomorpha	1	0.70
<i>Epitonium</i> sp.	1	0.70	Family Barleeiidae	1	0.70
<i>Eulithidium affine</i>	1	0.70	Cirripedia	4	<b>2.81</b>
<i>Heleobia australis</i>	1	0.70	Decapoda	1	0.70
Family Hipponicidae	1	0.70	Paguroidea	1	0.70
<i>Melanella hypsela</i>	1	0.70	Pleocyemata	1	0.70
<i>Mitrella</i> cf. <i>Moleculina</i>	1	0.70	Phylum Echinodermata	<b>4</b>	<b>2.81</b>
Family Nassaridae	2	1.40	Echinoidea	1	0.70
Family Neritidae	1	0.70	Insecta	4	<b>2.81</b>
<i>Neritina virginea/Vitta virginea</i>	3	2.11	Pycnogonida	1	0.70
<i>Olivella</i> sp.	2	1.40	Pterygota	1	0.70
Family Olividae	2	1.40	Coleoptera	2	1.40
<i>Parvanachis</i> sp.	1	0.70	Coccinellidae	1	0.70
Family Tateidae	1	0.70	Polychaeta	4	<b>2.81</b>
<i>Turbonilla</i> sp.	2	1.40	Phylum Chordata	20	<b>14.08</b>
Family Turritelidae	1	0.70	Teleostei	15	<b>10.56</b>
Bivalvia	62	<b>43.66</b>	Family Engraulidae	1	0.70
<i>Anadara ovalis</i>	2	1.40	<i>Harengula clupeiola</i>	1	0.70
<i>Anadara</i> sp.	3	2.11	<i>Lycengraulis grossidens</i>	1	0.70
Family Arcidae	1	0.70	<i>Pellona harroweri</i>	1	0.70
<i>Brachidontes</i> sp.	1	0.70	<i>Ctenosciaena gracilicirrus</i>	2	1.40
<i>Carditamera</i> sp.	1	0.70	<i>Isopisthus parvipinnis</i>	2	1.40
<i>Corbula</i> sp.	5	<b>2.92</b>	<i>Micropogonias furnieri</i>	2	1.40
Family Corbulidae	1	0.70	<i>Paralanchurus brasiliensis</i>	2	1.40
<i>Crassatella riograndensis</i>	1	0.70	Family Sciaenidae	2	1.40
<i>Crassostrea</i> sp.	1	0.70	<i>Stellifer brasiliensis</i>	1	0.70
<i>Ctena</i> cf. <i>pectinella</i>	1	0.70	<i>Stellifer rastrifer</i>	2	1.40
<i>Ctena</i> sp.	1	0.70	<i>Stellifer</i> sp.	1	0.70
Family Donacidae	1	0.70	<i>Raneya brasiliensis</i>	1	0.70

spaces representing the years 2009–2010 were elongated in Axis 2 (Fig. 5) due not only to 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

Table 3. Results from 2-factor PERMANOVA (year + climatic event) for the diet (at low taxonomic resolution) of all Paraná green turtles analyzed herein ( $n = 351$ ). Values in **bold** indicate significant differences ( $\alpha = 0.05$ )

Sources	df	SS	Pseudo-R <sup>2</sup>	F	p
Years	12	473.4	0.0719	2.1973	<b>0.0001</b>
Climatic events	3	88.1	0.0133	1.6350	<b>0.0479</b>
Residual	335	6014.4	0.9146		
Total	350	6575.8	1.0000		

Table 4. Results from 2-factor PERMANOVA (year + season) regarding species identification (at high taxonomic resolution) of macroalgae consumed by Paraná green turtles ( $n = 148$ ) from 2008 to 2014, and 2017 to 2018. Values in **bold** indicate significant differences ( $\alpha = 0.05$ )

Sources	df	SS	Pseudo-R <sup>2</sup>	F	p
Year	8	36.4	0.1583	3.2422	<b>0.0003</b>
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 2-factor PERMANOVA (year + season) regarding identification (at high taxonomic resolution) of animal prey consumed by Paraná green turtles ( $n = 142$ ) from 2015 to 2020. Values in **bold** indicate significant differences ( $\alpha = 0.05$ )

Sources	df	SS	Pseudo-R <sup>2</sup>	F	p
Year	5	241.7	0.092	2.799	<b>0.0003</b>
Season	3	101.4	0.038	1.959	<b>0.0292</b>
Year:Season	10	170.8	0.065	0.989	0.4803
Residual	123	2124.1	0.805		
Total	141	2638.1			

(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 & 6).

Considering the HTA analysis, the first 4 axes of the 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. 28.57–32.26% in the remaining years), and of Bivalvia from 47.37 to 69.57% (vs. 20.00–38.71%) (Fig. 8). Conversely, Hydrozoa (a.s. = 0.95) and debris (a.s. = 0.63) were mainly exploited between 2017 and 2020, with %FO varying from 21.05 to 38.71% (Fig. 7). Debris ingestion was very high between 2017 and 2020 (a.s. = 0.63), from 88.57 to 93.55%, respectively (Figs. 7 & 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 2 (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. 3.45–15.79% in the remaining years) (Figs. 7 & 8). Axes 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 & 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 & 8).

### 3.4. Influence of EN/LN on diet composition

Considering the influence of EN/LN on low taxonomic diet analysis (whole sample;  $n = 351$ ; 2008–2020), 106 turtles were encountered during EN events (2015, 2016, 2019), and 245 turtles during LN events (2011, 2012, 2013, 2014, 2017, 2018, 2020). A significant difference was found in diet composition among climatic events considering all sampling years (2008–2020) (PERMANOVA,  $F_3 = 1.6350$ ;  $p = 0.0479$ ) (Table 3).

The positive portion of Axis 1 was related to the exclusive consumption of debris (%FO = 100%) in 2008 during a moderate LN 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 ( $-0.46$ ), Chlorophyta ( $-0.44$ ), and Mollusca ( $-0.28$ ) mainly during weak and strong LN episodes (Fig. 3). During the weak and the strong LN episodes, %FO of Hydrozoa in green turtle diet varied from 17.50 to 18.18% (vs. 6.25–13.87% in remaining periods); for Crustacea,



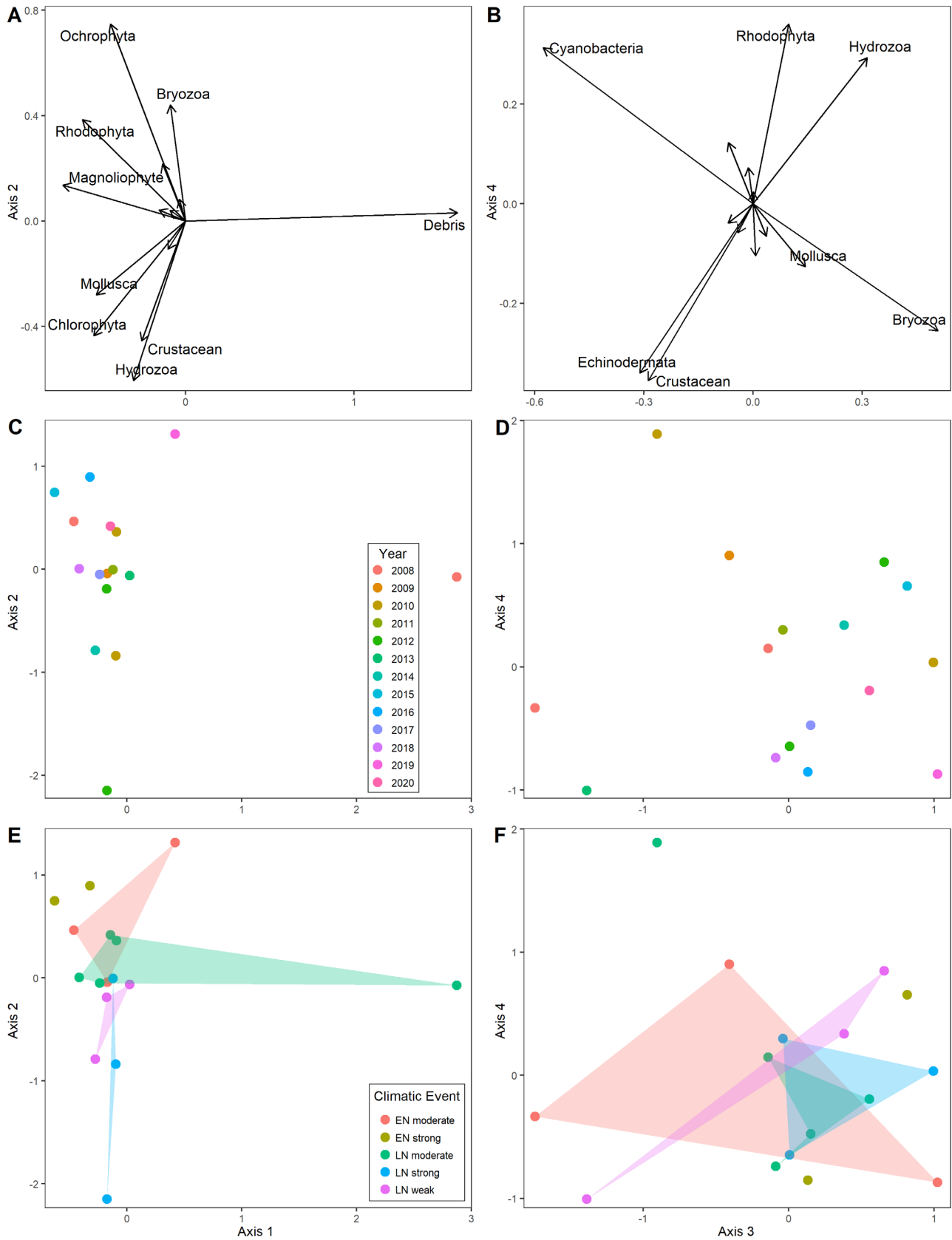


Fig. 3. PCA showing diet tendencies of green turtles *Chelonia mydas* ( $n = 351$ ) in Paraná, southern Brazil, based on (A,C,E) Axes 1 and 2 and (B,D,F) Axes 3 and 4. Interannual diet tendencies (2008–2020) (C,D) and diet tendencies by climatic events (EN: El Niño; LN: La Niña) (E,F) are also shown. Shaded regions: multivariate subspaces

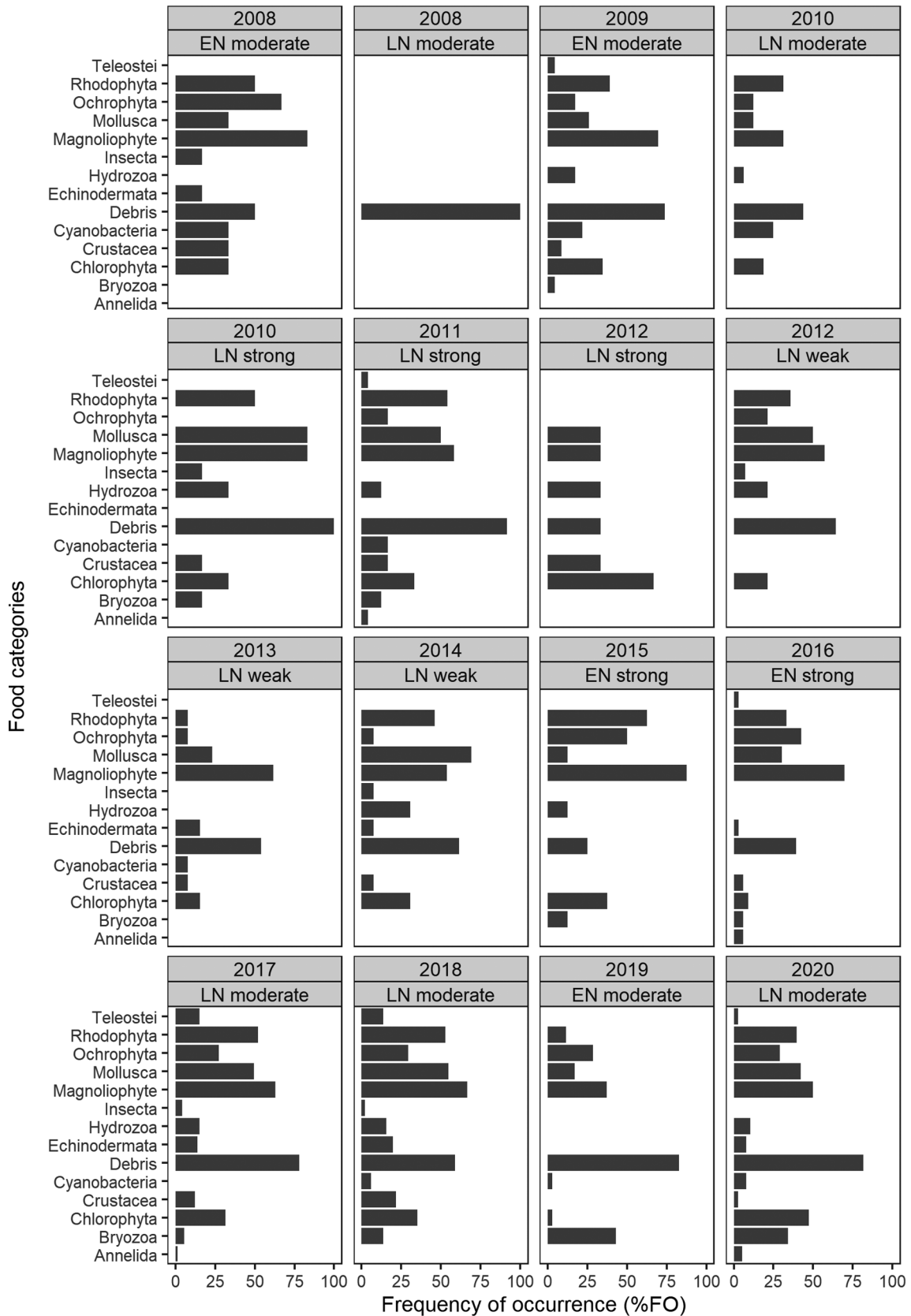


Fig. 4. Frequency of occurrence (%FO) of all prey species in the entire database (resulting in low taxonomic resolution; see Section 2.3 for details) found in the digestive tracts of juvenile green turtles (n = 351) found dead-stranded along the coast of Paran, southern Brazil, from 2008 to 2020. EN: El Nio; LN: La Nia

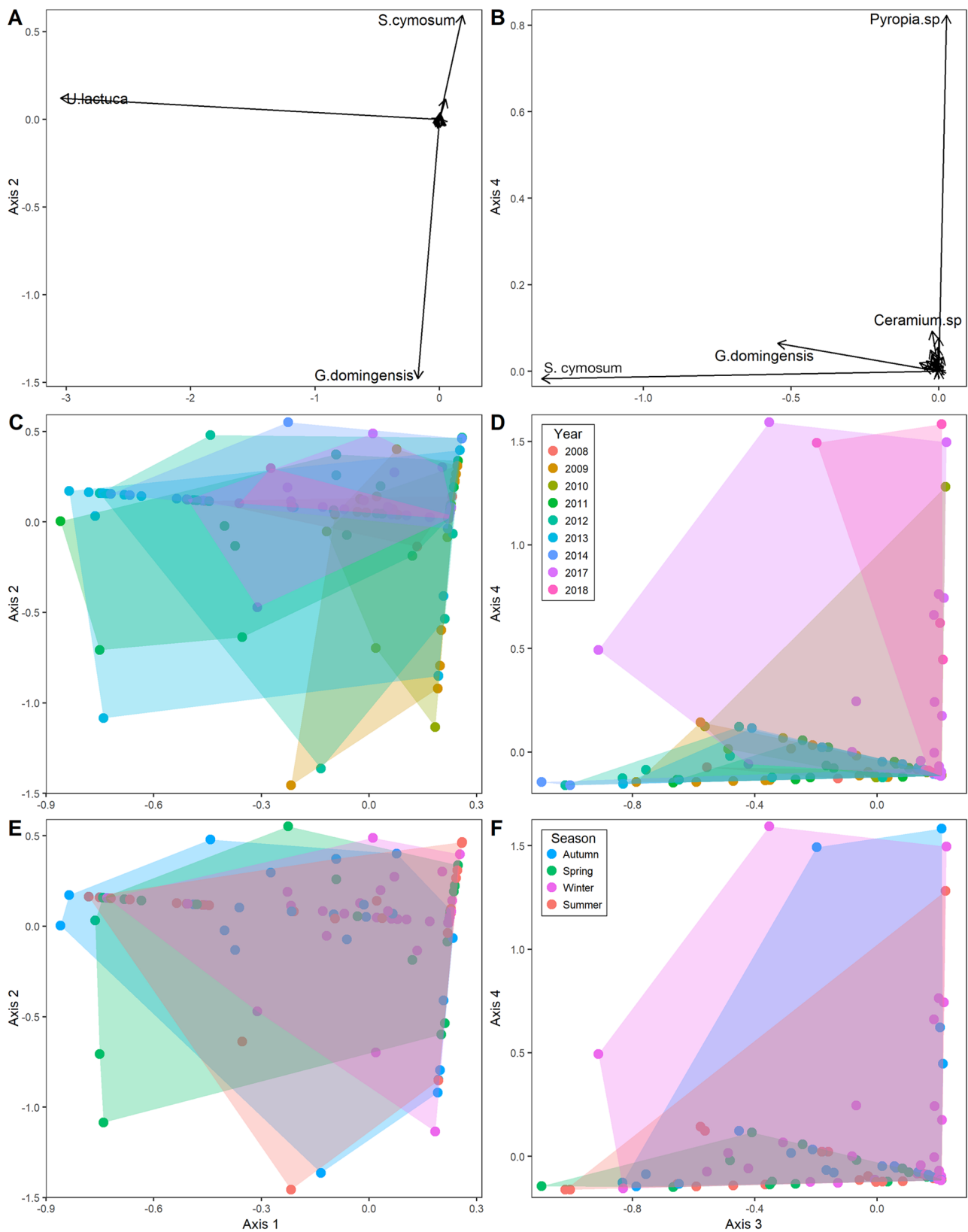


Fig. 5. PCA showing macroalgae consumption tendencies of green turtles *Chelonia mydas* (n = 148) in Paraná, southern Brazil, at high taxonomic resolution, based on (A,C,E) Axes 1 and 2 and (B,D,F) Axes 3 and 4. Interannual diet tendencies (2008–2014, 2017–2018) (C,D) and diet tendencies by seasons (E,F) are also shown. Shaded regions: multivariate subspaces

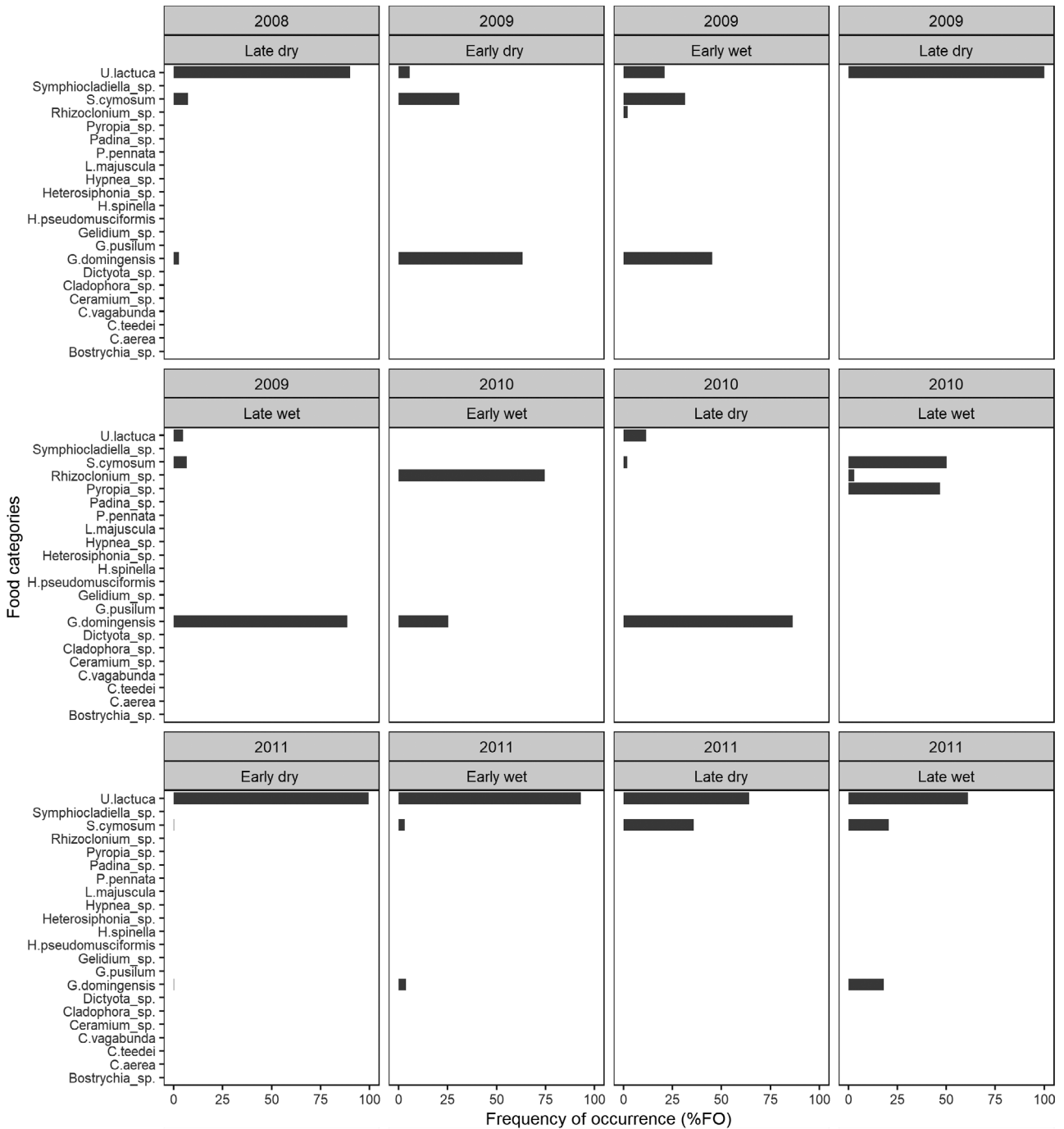


Fig. 6. (continued on next page)

Fig. 6. Frequency of occurrence (%FO) of macroalgae at high taxonomic resolution (see Section 2.3 for details) found in the digestive tracts of juvenile green turtles (n = 148) dead-stranded in Paraná, southern Brazil, from 2008 to 2014 and from 2017 to 2018

%FO varied from 5.00 to 18.18% (vs. 4.88–12.14%); for Chlorophyta, from 22.50 to 36.36% (vs. 14.63–35.84%); and for Mollusca, from 47.50 to 54.55% (vs. 21.88–47.40%) (Fig. 4). Axis 2 also highlighted the consumption of Ochrophyta (a.s. = 0.75), Bryozoa (0.44), and Rhodophyta (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. 12.12–12.50% in the remaining periods); for Bryozoa, %FO varied from 7.32 to 25.00% (vs. absent to 12.12%); and for Rhodophyta, from 25.00 to 49.13% (vs. 30.00–

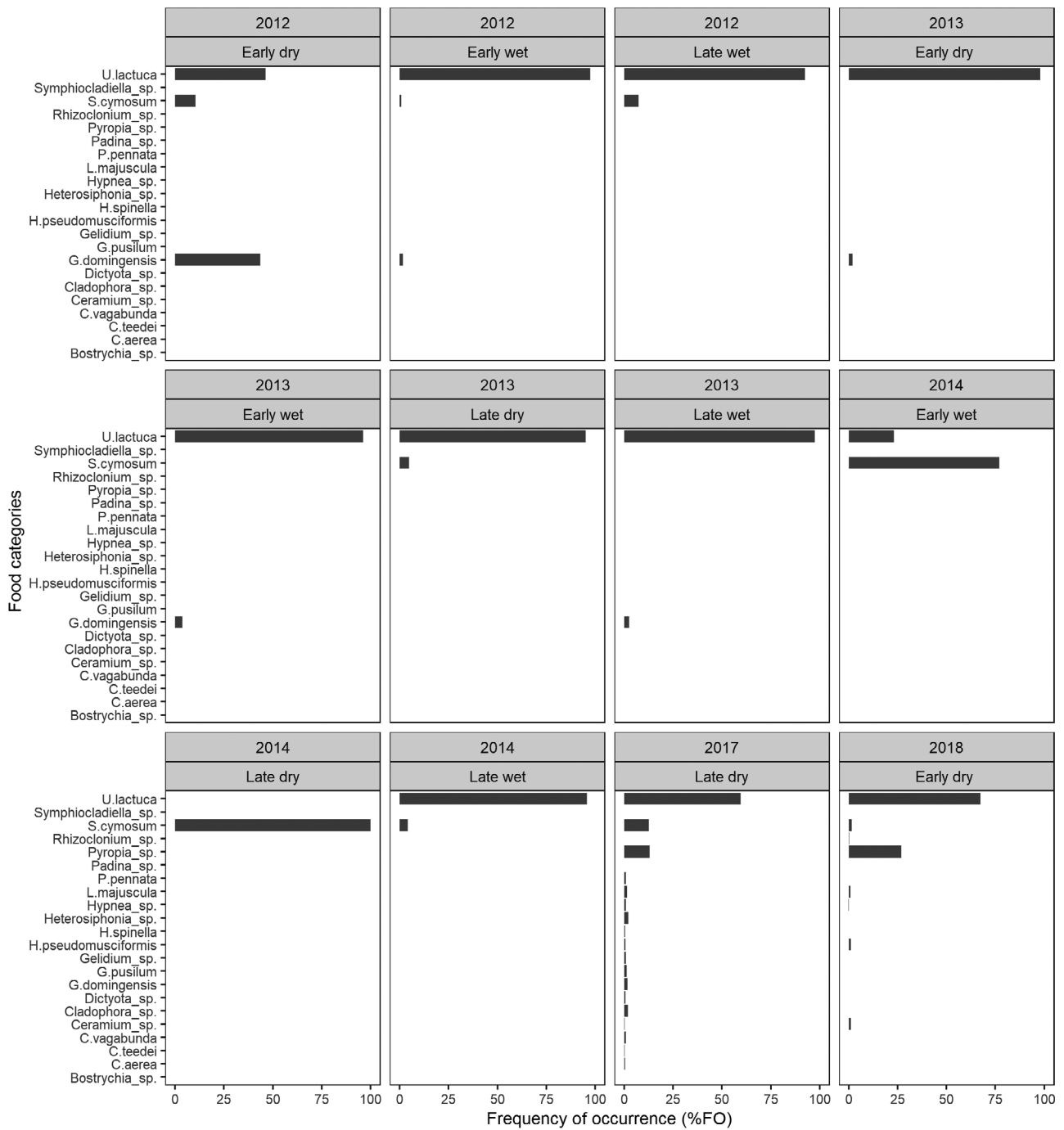


Fig. 6. (continued)

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, but without clear seasonal trends (Fig. 3). Axis 3 was negatively related to the consumption of Cyanobacteria (a.s. = -0.58), Echinodermata (-0.31), and Crustacea (-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), that of Echinodermata varied from 1.56 to 13.29% (vs. absent to 2.44%), and that of Crustacea from 5.00 to 12.14% (vs. 4.88–18.18%) (Fig. 4). The negative portion of Axis 4 confirmed the consumption of Crustacea (a.s. = -0.36), Echinodermata (-0.34), and Bryozoa (-0.26) during periods of moderate to strong EN (%FO: 4.88, 2.44, and 7.32%,



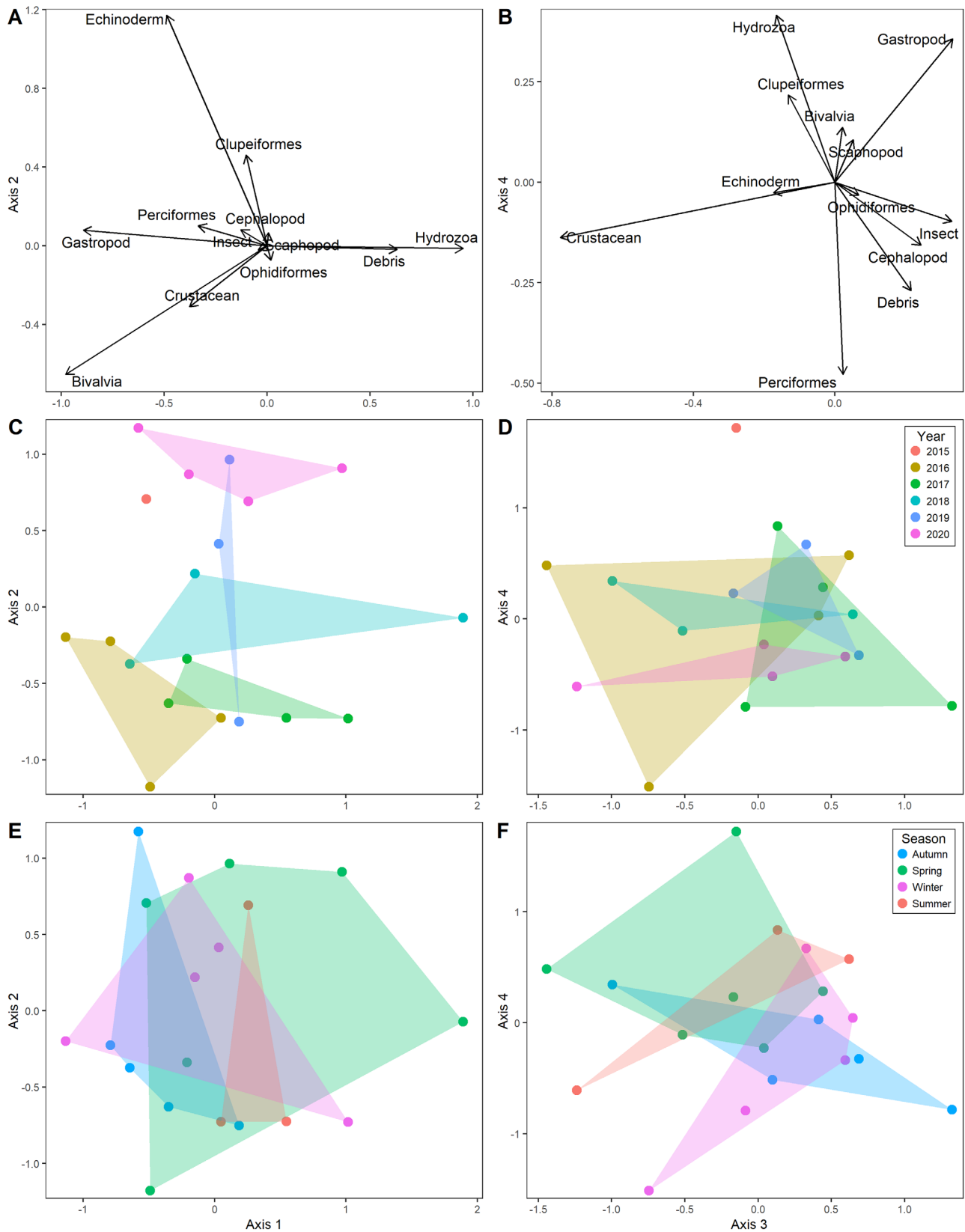


Fig. 7. PCA showing animal prey consumption tendencies of green turtles *Chelonia mydas* (n = 142) in Paraná, southern Brazil, at high taxonomic resolution, based on (A,C,E) Axes 1 and 2 and (B,D,F) Axes 3 and 4. Interannual diet tendencies (2015–2020) (C,D) and diet tendencies by seasons (E,F) are also shown. Shaded regions: multivariate subspaces

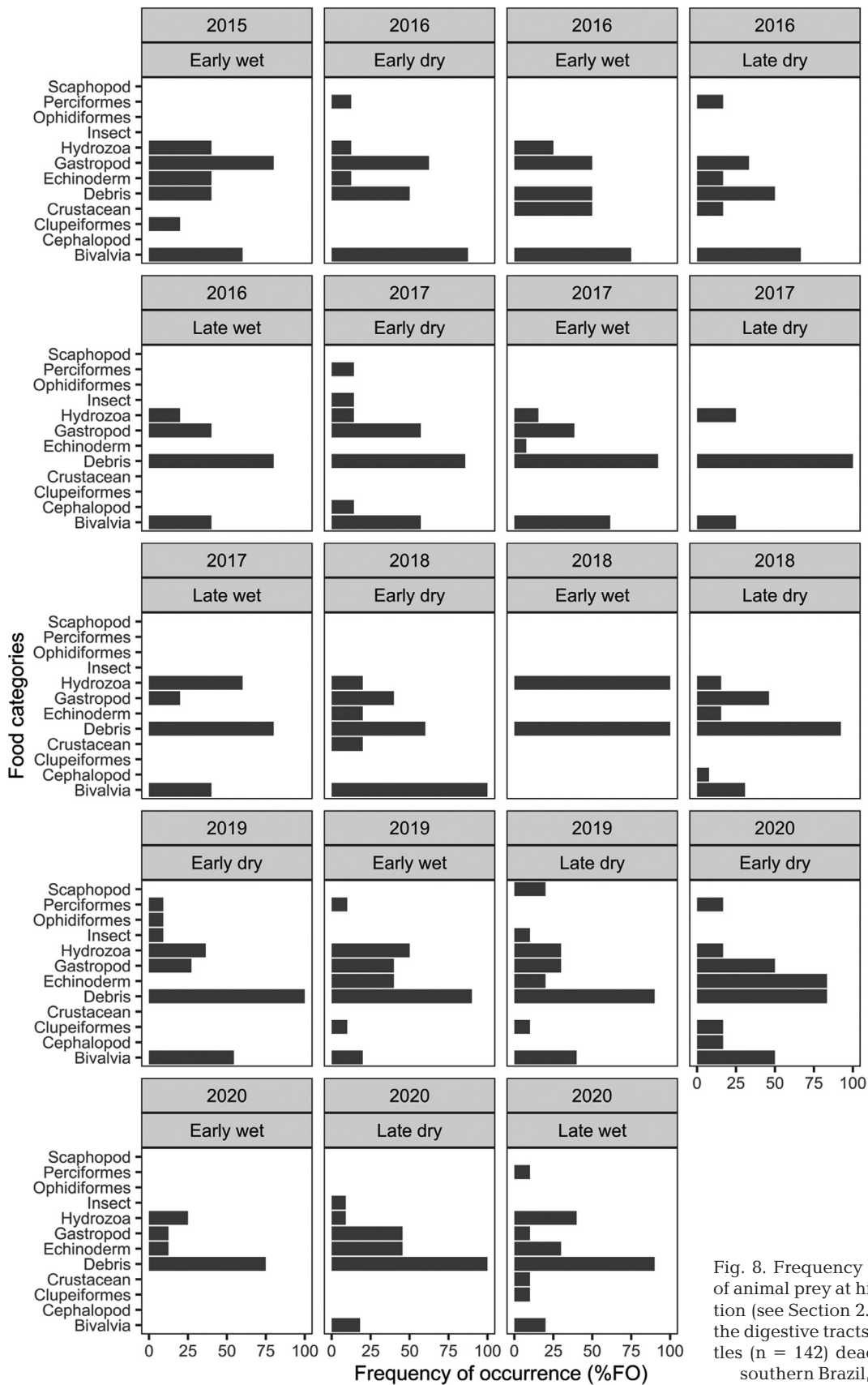


Fig. 8. Frequency of occurrence (%FO) of animal prey at high taxonomic resolution (see Section 2.3 for details) found in the digestive tracts of juvenile green turtles (n = 142) dead-stranded in Paraná, southern Brazil, from 2015 to 2020

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). The positive portion of Axis 4 confirmed the exploitation of Hydrozoa (a.s. = 0.29), Cyanobacteria (0.31), and Rhodophyta (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 & 4).

### 3.5. Seasonal diet variation

Although no significant seasonal difference was found in the HTM analysis regarding macroalgae consumption, only 6 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 cyanobacterium *Lyngbya majuscula* Harvey ex Gomont, 1892 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%) (Fig. 6).

Concerning seasonal variation in food consumption based on the HTA analysis, there was a significant difference (PERMOVA,  $F_3 = 1.9586$ ;  $p = 0.0292$ ) (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. 30.00–34.09% in the remaining seasons), and from 39.02 to 45.95% (vs. 20.00–36.36%), 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) was mainly ingested in winter (88.64%) and summer (85.00%) (Figs. 7 & 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%) (Figs. 7 & 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%) (Figs. 7 & 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 remaining seasons) (Figs. 7 & 8).

## 4. DISCUSSION

Green turtles found stranded along the coast of Paraná 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 data sets on green turtle diet in the SWAO and underscores the substantial temporal variation in SWAO green turtle diet. 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 yr of this study (2008–2020). We observed that green turtles presented a more diverse diet than in previous studies (Guebert-Bartholo et al. 2011, Gama et al. 2016), with higher consumption of invertebrates and fish, which is similar to the findings of Vélez-Rubio et al. (2016), Piovano et al. (2020), and 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 in the future to evaluate ecological theories, such as understanding how density-dependence and competition can affect green turtle foraging decisions.

The juveniles analyzed herein 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 inverte-

brate 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 coast of Paraná, 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, consumption of Mollusca 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 coast of Paraná foraged mostly on invertebrates, highlighting the unique dietary tendencies for the species in this estuarine complex (Gama et al. 2021). However, 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 the rapid digestion of this prey type (González Carman et al. 2014, Hays et al. 2018), which suggests that 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 greatest occurrence from 2017 to 2020, especially in 2018; these are mostly LN years (data obtained from <http://enos.cptec.inpe.br/>; accessed August 2021) that presented low temperature and low rainfall rates. 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 (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 it 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 avail-

ability 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 Benedetto & 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 of 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 6 species of macroalgae being consumed. This is consistent with the findings of Pellizzari et al. (2014), who reported higher species richness and higher biomass along the coast of Paraná 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, the former of which improves the metabolism of turtles during these seasons (Bjorndal 1980, Brand-Gardner et al. 1999). It is important to consider that both the dietary transit times and turtle metabolism are slower at 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 presence of prey species throughout the year in some islands along the coast of Paraná (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

plant matter, as both the intake passage time and digestion are faster (Amorocho & Reina 2008). However, as shown by Quiñones et al. (2022), it is possible that some of the juveniles analyzed herein do not possess the gut specialization to digest vegetal matter items, therefore consuming more prey of animal origin. Also, as verified by Meylan et al. (2022), turtles may adapt to changes in prey availability, which impacts foraging effort and areas, and perhaps survival. Some of the turtles foraging in this area may be recent recruits that were previously foraging at 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 bycatch of trawler fisheries (Cattani et al. 2011), which occur in Paraná 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, 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 (2008–2020) are likely related to the climatic variation resulting from the onset of EN 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 *Sargassum 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 the result of such 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 SST, 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 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 the capacity of green turtles 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 good body condition, we cannot say their diet reflects the items consumed only by healthy individuals that use the coast of Paraná 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 isotope analysis (Gama et al. 2021), which, similar to our findings, showed invertebrates and green algae as the most consumed and important prey items. Despite the current 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 along the coast of Paraná, including islands, rocky shores, meadows, and mangroves. Thus, recording diet changes across years and how the species responds to climate variability helps understand the foraging habits of the species over time and individual variability in terms of habitat use and exposure to threats. This helps identify changes in food resources and track the impacts on both the foraging habitat and the species itself. Hence, this study contains data that may help to delimit areas to be protected and managed in the SWAO, and to inform and prioritize further conservation actions based on the distribution of foraging resources used by the species.

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#### LITERATURE CITED

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