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Diet composition of *Caretta caretta* (Testudines: Cheloniidae) in the Gulf of Gabès, southern Tunisia

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Abstract

Diet composition of *Caretta caretta* (Testudines: Cheloniidae) in the Gulf of Gabès, southern Tunisia. Investigating fundamental biological aspects, such as the feeding habits of long-distance migratory marine animals like sea turtles, presents significant challenges. These studies are crucial for identifying the feeding grounds and preferred prey of these turtles, thus providing valuable insights to inform habitat protection and management decisions. We analyzed the digestive tract contents of 132 *Caretta caretta* stranded and/or accidentally captured along the coast of the Gulf of Gabès from 2004 to 2010. Food items were analysed using the Relative Importance Index (IRI), the Food Index of Geistdoerfer (Q), and the Main Food Index (MFI) of Zander. We also categorized the litter and calculated its frequency of occurrence. The loggerhead diet consisted of 46 species from various zoological groups, reflecting their flexible distribution across both pelagic and benthic neritic zones. We noted a common feeding pattern for the species, with bottom-dwelling prey common in shallow environments. Molluscs, arthropods, and poriferans constituted the main prey, while tunicates and fishes were frequent secondary prey. Echinoderms and algae are accessory secondary prey and second-order additional prey, respectively. Molluscs and arthropods were ingested mainly during spring and summer, while tunicates and poriferans were ingested during autumn and winter months. Turtle size had no effect on dietary diversity or biomass percentage. This study emphasizes the value of dietary analysis in uncovering the feeding ecology and habitat use of loggerhead turtles in the Gulf of Gabès. Protecting and managing this region, and ensuring the presence of trophic resources, could be crucial for maintaining loggerhead turtle populations and enhancing their survival in Tunisian waters.

Keywords: Digestive tracts, Feeding habits, Loggerhead turtles, Mediterranean Sea.

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Resumo

Composição da dieta de *Caretta caretta* (Testudines: Cheloniidae) no Golfo de Gabès, sul da Tunísia. A investigação de aspectos biológicos fundamentais, como os hábitos alimentares de animais marinhos migratórios de longa distância, como as tartarugas marinhas, apresenta desafios significativos. Esses estudos são essenciais para identificar os locais de alimentação e as presas preferidas desses quelônios, fornecendo assim informações valiosas para embasar decisões de proteção do habitat. Analisamos o conteúdo do tubo digestivo de 132 espécimes de *Caretta caretta* encalhadas e/ou capturadas acidentalmente ao longo da costa do Golfo de Gabès, de 2004 a 2010. Os itens alimentares foram analisados usando o Índice de Importância Relativa (IRI), o Índice Alimentar de Geistdoerfer (Q) e o Índice Alimentar Principal (MFI) de Zander. Também categorizamos o lixo e calculamos sua frequência de ocorrência. A dieta da tartaruga-cabeçuda consistiu de 46 espécies de vários grupos zoológicos, refletindo sua distribuição flexível em zonas neríticas pelágicas e bentônicas. Observamos um padrão de alimentação comum para as espécies, com presas que habitam o fundo do mar, comuns em ambientes rasos. Moluscos, artrópodes e poríferos constituíram as principais presas, enquanto tunicados e peixes foram presas secundárias frequentes. Os equinodermos e as algas são presas secundárias acessórias e itens adicionais de segunda ordem, respectivamente. Moluscos e artrópodes foram ingeridos principalmente durante a primavera e o verão, enquanto tunicados e poríferos foram ingeridos durante os meses de outono e inverno. O tamanho da tartaruga não teve efeito sobre a diversidade da dieta ou a porcentagem de biomassa. Este estudo enfatiza o valor da análise da dieta para descobrir a ecologia alimentar e o uso do habitat das tartarugas-cabeçudas no Golfo de Gabès. Proteger e gerenciar essa região e garantir a presença de recursos tróficos pode ser crucial para manter as populações de tartarugas-cabeçudas e aumentar sua sobrevivência nas águas da Tunísia.

Palavras-chave: Hábitos alimentares, Mar Mediterrâneo, Tartarugas-cabeçudas, Tubos digestivos.

Introduction

Currently, all sea turtle species except the Australian Flatback, *Natator depressus* (Garman, 1880), are included in the IUCN Red List as Endangered or Vulnerable (Godfrey and Godley 2008, Wallace *et al.* 2011, IUCN 2024). The conservation of these chelonians presents a multifaceted challenge due to various factors, including their biology, life cycle, and their primarily marine habitat (Lutcavage *et al.* 1997, Rees *et al.* 2013), which limits direct observations and research opportunities, especially regarding their foraging habits and diet (Tomás *et al.* 2001). Because of this, strandings and bycatch provide scientists with a wealth of ecological and biological data on sea turtles, such as location and quality of their feeding grounds, use of trophic resources, and how human activity affects their habitats (Ullmann and Stachowitsch 2015, UNEP/MAP - SPA/RAC 2019). Comprehensive knowledge of each of these elements is crucial for effective population management (Bjorndal 1997).

Loggerhead sea turtles, *Caretta caretta* (Linnaeus, 1758), inhabit temperate and tropical regions of the Atlantic, Pacific, and Indian Oceans, and the Mediterranean Sea. As adults, this species migrates long distances between foraging regions and nesting beaches (Dodd 1988, Plotkin and Spotila 2002) with the majority of nesting occurring in the western rims of the Atlantic and Indian Oceans. In the Mediterranean, most nesting occurs in Greece, Turkey, Cyprus, and Libya (Margaritoulis *et al.* 2023). Adults and juveniles are present in the entire basin, concentrated in foraging areas along the North Adriatic and Central Mediterranean continental shelfs, with lower abundance in the southern Ionian and in the area between Sicily and Tunisia (Mancino *et al.* 2022).

The life cycle of *C. caretta* involves distinct ontogenetic habitat shifts that coincide with their growth stages (Casale *et al.* 2008). These shifts in habitat preference are related to changes in feeding strategies and diving capabilities as the turtles mature (Fouda 2021, Mariani *et al.* 2023). When hatchlings reach the sea, the oceanic phase begins, and they migrate to the open sea where they spend most of their juvenile stage. During this phase, *C. caretta* typically has a curved carapace length (CCL, notch to tip; Bolten 1999) of up to approximately 59.9 cm (Bjorndal *et al.* 2000, Tomás *et al.* 2001). Due to their limited diving capability, juvenile turtles primarily feed on pelagic prey found in the open ocean (Bolten 2003). As the turtles grow, they enter a transitional phase leading to the subadult stage (CCL range of 60–69.9 cm). During this phase, *C. caretta* utilizes both oceanic and neritic habitats (Palmer *et al.* 2021). They start to explore and inhabit more benthic environments, gradually drawing closer to neritic areas (Casale *et al.* 2008). Once they reach the adult stage and become sexually mature (CCL > 70 cm), they transit to neritic areas (Tomás *et al.* 2001, Casale and Margaritoulis 2010). In these shallower coastal areas, they predominantly feed on benthic organisms (Casale *et al.* 2011, Lazar *et al.* 2011). These habitat shifts observed throughout the life cycle reflect their changing feeding habits and adaptation to different environments as they grow and develop (Casale *et al.* 2008). Understanding these ontogenetic habitat shifts and corresponding changes in feeding preferences is crucial for conservation efforts and the management of critical habitats that are essential for the various life stages of loggerhead sea turtles.

The diet of *C. caretta* in the Mediterranean regions has been directly studied through analyses of feces and stomach contents (e.g. Benhardouze *et al.* 2021, Baldi *et al.* 2023, Mariani *et al.* 2023), and indirectly through stable isotope analysis (e.g. Blasi *et al.* 2018, Haywood *et al.* 2020, Cardona *et al.* 2024). This species is considered opportunistic carnivorous, and the presence of fast-moving prey, such as fish and cephalopods, has raised the question of the potential role of fishing discards in the turtle diet (Tomás *et al.* 2001, Casale *et al.* 2008, Baldi *et al.* 2023, Cardona *et al.* 2024).

The African continental shelf off Tunisia, characterized by favorable geomorphological, climatic, and oceanographic conditions, sustains one of the most productive ecosystems in the western Mediterranean Sea (Ben Salem *et al.* 2002, Hattab *et al.* 2013). This is the second widest continental shelf area in the region, and it is one of the most important neritic feeding grounds for juveniles and adults of *C. caretta* in the Mediterranean Sea (Casale and Margaritoulis 2010, Bradaï *et al.* 2020). Prior research conducted on *C. caretta* in the area had constraints such as a limited number of samples or a concentration on specific turtle size classes, which restricted a comprehensive understanding of feeding habits of these populations (Laurent and Lescure 1994, Bradaï 2000). The current study offers more recent information on the feeding habits of loggerhead sea turtles in the Gulf of Gabès using a more robust sample.

Materials and Methods

Study Area

This study was carried out in the Gulf of Gabès, located in the central Mediterranean Sea (33°–35° N and 10°–12.5° E) extending from Ras Kaboudia (Chebba) to the Tunisian–Libyan frontier (Figure 1). The region hosts one of the largest meadows of *Posidonia oceanica* (L.) Delile in the area (El Zrelli *et al.* 2020), which serves as a nursery, as well as feeding and breeding habitat for many marine species (Bradaï *et al.* 2004, Enajjar *et al.* 2015). It is considered one of the Mediterranean's most productive ecosystems (Papaconstantinou and Farrugio 2000). The seafloor is predominantly soft, resulting in the prevalence of demersal trawling (Abdou *et al.* 2018). Catches in the Gulf are dominated by cephalopods, shrimps, and demersal finfish (Sparidae and mullets) (Hattab

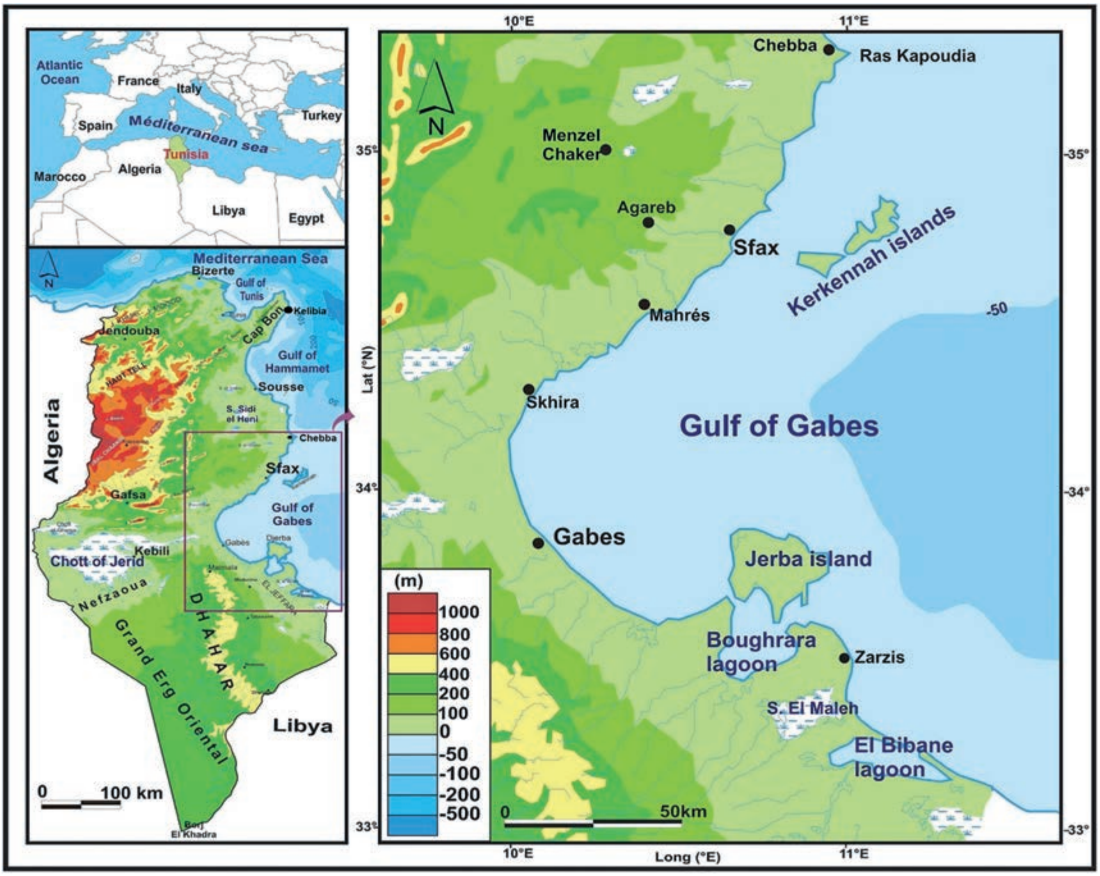

Figure 1. Localization of the Gulf of Gabès (map adapted from Béjaoui *et al.* 2019).

et al. 2013). Due to global change, non-native species are invading the Gulf of Gabès (Bradaï *et al.* 2004). Several migrants from the Red Sea and the Atlantic Ocean are either permanent residents or sporadically observed (Ben Amor *et al.* 2016, Béjaoui *et al.* 2019).

Sample Collection

In Tunisia, the National Institute of Marine Sciences and Technologies (INSTM) has monitored sea turtle and cetacean strandings since 2004 through the National Stranding Network (RNE) (Karaa *et al.* 2012). A national coordinator oversees the network, which consists of three regional monitoring groups: one covering the northern coast (from the Algerian border to Kelibia), another in the central region (from Kelibia to Chebba), and a third in the south (in the Gulf of Gabès) (Figure 1).

RNE members survey beaches and respond to information from NGOs, fisheries authorities, and coast guards in order to investigate stranded sea turtles. The network also records cases of sea turtle bycatch (UNEP/MAP - SPA/RAC 2020). All collected data, including stranding/capture date, location, and sex, are stored in a dedicated database. Each year, INSTM compiles these records into a report that is shared with RNE partner administrations and made available to the public upon request.

We analysed the diet of *C. caretta* in the Gulf of Gabès between October 2004 and June 2010. During this period, we examined the digestive tracts of 132 turtles. Seasonal sampling included 24 turtles in winter and fall (N = 10 and 14, respectively) and 108 turtles in spring and summer (N = 72 and 36, respectively). The highest number of turtles sampled was in May (56 turtles).

The sampled turtles included 111 dead stranded turtles from different locations (57 in Gabès, 22 in Jerba Island, 20 in Zarzis, five in Kerkennah Island, six in Sfax, and one in Chebba; Figure 1) as well as 21 individuals accidentally caught in benthic trawls off Sfax and discovered dead upon arrival at INSTM. We performed necropsies at the INSTM Center in Sfax following the protocol described by Work (2000). During necropsies, we isolated the contents of the esophagus, stomach, and intestines, rinsed them with fresh water, and sieved them using a 1 mm mesh.

Data Collection

We identified prey items to the lowest possible taxonomic level and estimated their numbers when feasible. After drying samples at approximately 60°C for 24 hours, we measured their dry weight to the nearest tenth of a gram. For consistency, we limited our analysis to macroscopic items (> 1 mm). Prey identification relied on distinguishable remains such as fish bones, cephalopod beaks, prosobranch gastropod opercula, and decapod chelipeds.

To classify the digestive contents, we used a binocular magnifying glass and referred to multiple identification guides (Riedl 1963, Fischer *et al.* 1987). When digestion was too advanced for precise species identification, we assigned prey items to broader taxonomic categories, such as Family, Order, or Class.

We categorized digestive contents of the turtles into three categories based on their origin and state: (1) prey, which includes the remains of organisms that turtles have captured either alive or dead; (2) remains that were likely inadvertently captured by the turtles while they were foraging for food (non-prey remains); and (3) debris.

Data Analysis

The quantitative analysis of prey included estimates of the following parameters usually used in diet studies and involving the following coefficients:

*Percentage of prey item in number (%*N*).*—This metric represents the percentage ratio between the number of individuals of a prey item i (Ni) and the total number of prey (Nt): $\%N = 100 \times (Ni / Nt)$.

Percentage of prey item in weight (%W).—Percentage ratio of the weight of individuals_of prey item i (wi) and the total weight of prey (Wt): $\%W = 100 \times (wi / Wt)$.

Food coefficient or prey (Q) (Geistedoerfer 1975).—$Q = \%N \times \%W$ where: $\%N$ and %W represent the percentage of prey in number and in weight, respectively.

*Frequency of occurrence of prey item (%*F*).*—This measure represents the ratio, expressed in percentage, of the number of observations of a specific prey item i (Ni) and the total number of full digestive tracts analyzed (Nt): $\%F = Ni / Nt$.

Main Food Index (MFI) (Zander 1982).—The MFI for each food item integrates three indices: $\%N$, $\%F$, and %W and is calculated using the formula: $MFI = [\%W \times (\%N + \%F) / 2]^{1/2}$.

Index of relative importance (IRI).—This index was calculated to indicate the importance of each prey (Pinkas *et al.* 1971): $IRI = \%Fi\ (\%Wi + \%Ni)$, where i represents a specific prey item, %*F* is its frequency of occurrence, and %W and %*N* represent its proportion of contents in the digestive tracts by weight and by number, respectively. The IRI values were converted to a percentage to facilitate comparisons between prey items (Cortés 1997).

Percent index of relative importance (%IRI).—This index provides a standardized measure for dietary analysis. It is calculated using the following equation: %IRIi = 100 × (IRIi/IRIt), where %IRIi is the Percent Index of Relative Importance for prey item *i*, and IRIt represents the total of all Indexes of Relative Importance values for prey.

The methods of Geistdoerfer (1975) and Zander (1982) are used to categorize prey. According to Zander (1982), prey are classified into four groups: essential prey (MFI > 75), primary prey (51 ≤ MFI ≤ 75), secondary prey (26 ≤ MFI ≤ 50), and accessory prey (MFI < 26). The dietary coefficient of Geistdoerfer (1975) divides the prey into three categories, each subdivided into two sub-categories using both food coefficient Q and frequency index %*F* as following: (1) Main prey Q > 100, preferential %*F* > 30, occasional %*F* < 30; (2) Secondary prey: 10 < Q < 100, frequent %*F* > 10, accessory %*F* <10; and (3) Additional prey: Q <10, first order %*F* >10, second order *F* % <10.

Diet Shifts

We used a non-parametric MANOVA to analyze feeding variation. We applied a two-factor design to test the null hypothesis that diet did not differ between sexes and predator size (CCL).

We conducted statistical analyses based on the prey categories. To evaluate potential dietary differences with size, we divided the turtles into two size classes according to their life stages (Casale *et al.* 2008): class I: post-pelagic juveniles (PPJ) (CCL > 35 cm) and class II: adults (CCL ≥ 70 cm).

We considered the number of prey in each category as the dependent variables, and defined sex (Female or Male) and size class (I, II) as factors. To test differences in diet, we applied the multivariate *F* value (Wilks' lambda), which compares the error variance/covariance matrix with the effect variance/covariance matrix.

Results

Sample Collection

We examined the diet of loggerhead turtles in the Gulf of Gabès from October 2004 to June 2010. During this period, we analyzed 132 digestive tracts, of which 91 contained feeding remains. Of these turtles, 70 turtles were found stranded, while 21 were accidentally captured dead by bottom trawls. Among the stranded turtles, one showed signs of boat strike, three had hooks in their intestines, and 66 exhibited no apparent cause of mortality.

The turtles studied (*N* = 91; mean = 58.32 cm; SD = 9.14) varied in size, with the smallest with a CCL of 28 cm, while the majority (*N* = 90; 99%), had a CCL greater than 35 cm. Of these, 76 turtles (83.52%) were classified as post-pelagic juveniles (PPJ), and 14 (15.38%) were adults. The largest turtle recorded had a CCL of 77.5 cm. Most of these turtles were sampled in spring and summer and were predominantly found in early decomposition (*N* = 37; 40.65%) or decomposed (*N* = 20; 21.97%); 34 turtles (37.36%) were found freshly dead (Figures 2 and 3).

Dietary Composition

Dietary analyses showed that *C. caretta* feed on a variety of prey (Figure 4). Of analyzed turtles, 66% (*N* = 60) consumed up to 20 different prey items (Figure 5).

Undigested organic matter.—Loggerhead turtles showed a high dietary diversity, with 46 species of various zoological groups (Table 1). The total weight of the 2520 prey items was

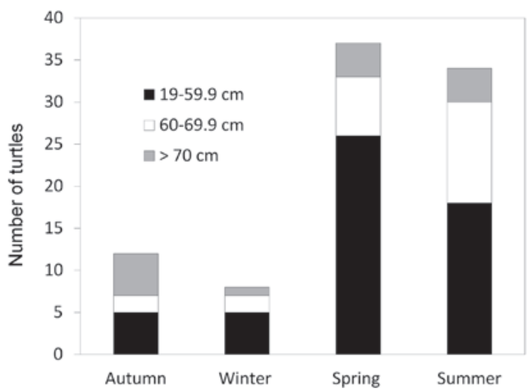

Figure 2. Curved Carapace Length (CCL) frequency histogram of the sampled turtles according to the seasons.

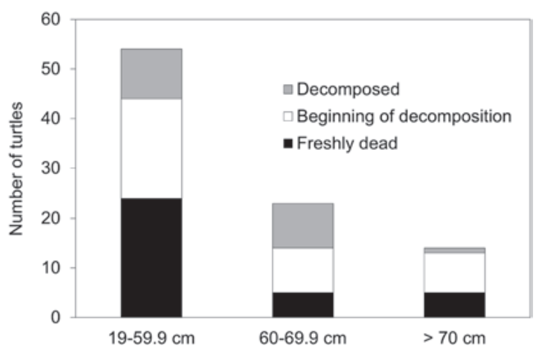

Figure 3. Curved Carapace Length (CCL) frequency histogram of the sampled turtles according to their stages of decomposition.

17.28218 kg, with an average of 27.7 prey items per digestive tract. Notably, two adult turtles had 313 and 278 individuals of the sponge *Chondrosia reniformis* Nardo, 1847, each weighing over 2 kg, in their digestive tracts. These turtles had carapace lengths (CCL) of 77.5 cm and 72 cm and were stranded in May and November 2008, respectively.

Molluscs and arthropods served as preferred primary prey (Q > 100 and *F*% > 30%), while porifera were occasional prey (Q > 100 and *F*% < 30%) (Table 1). As secondary prey (10 < Q < 100), we found tunicates, fish, and echinoderms at the following frequencies: 12.1 (*N* = 11), 18.7 (*N* = 17), and 7.7 (*N* = 7) (Table 1), respectively. Molluscs and arthropods represented the primary food sources, with average masses of 27.7 g and 43.59 g, corresponding frequencies of 60.4% and 49.5%, and %IRI of 39.4% and 30.5%. Those taxa were primary represented by the cuttlefish, *Sepia officinalis* Linnaeus, 1758, (%*F* = 33), the gastropod, *Hexaplex trunculus* (Linnaeus, 1758) (%*F* = 22), the crab, *Eucrate crenata* (de Haan, 1835) (%*F* = 19.8), and the spot-tail mantis shrimp, *Squilla mantis* (Linnaeus, 1758) (%*F*= 15.4).

The most recorded species of molluscs was the cuttlefish, *Sepia officinalis.* This species served as food source for 30 turtles (CCL ranged from 28 cm to 73 cm; mean = 54.94; SD = 10.06). The sample included two mature turtles (CCl = 72 cm and 73 cm), which stranded in Gabès in September 2007 and August 2008, respectively, and two juveniles (CCL = 28 cm and 37 cm). The first juvenile turtle was stranded in Gabès in July 2008 and had a cuttlefish beak weighing 3.15 g in its stomach. The second turtle, which stranded in Chebba in June 2008, was found to have the remains of two cuttlefish totaling 30.5 g in its tract. The second most recorded molluscs, the gastropod, *H. trunculus,* was recorded from 20 turtles across various seasons of the year (4 in autumn, 2 in winter, 8 in spring, and 6 in summer). Concerning the two turtles sampled during winter, one was a subadult (CCL = 58 cm) stranded in January 2005; the other one was an adult female (SCCL = 77 cm) stranded in December 2007. The gastropod, *H. trunculus,* was associated with marine phanerogams, *Posidonia oceanica* or *Cymodocea nodosa* (Ucria) Asch., in both cases (subadult and adult female *C. caretta*).

Several fish species with distinct habitat preferences were identified: *C. caretta* fed on benthic prey [e.g., Signatidae, *Hypocampus hippocampus* (Linnaeus, 1758) and Mullidae, *Mullus* sp.], pelagic prey (e.g., Clupeidae, *Sardinella aurita* Valenciennes, 1847) and prey

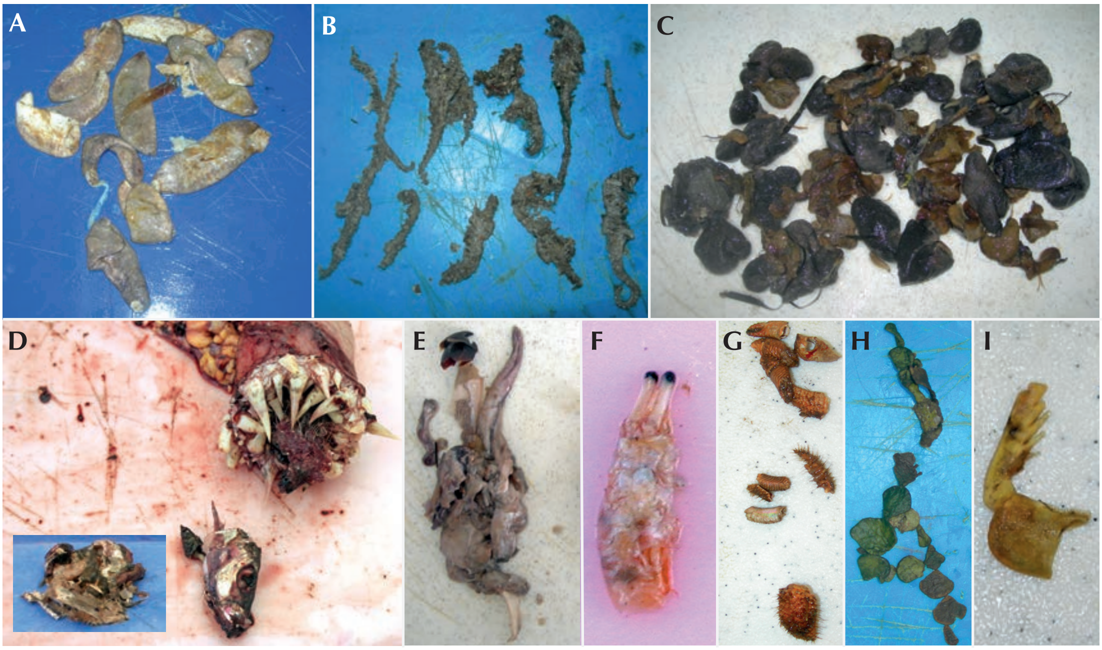

Figure 4. Examples of prey ingested by *Caretta caretta* in the Gulf of Gabès: (**A**) *Holothuria polii* (white spot cucumber); (**B**) *Hypocampus hypocampus* (Short snouted seahorse); (**C**) *Chondrosia reniformis* (Leather-Sponge); (**D**) *Sardinella aurita* (Gilt sardine); (**E**) *Sepia officinalis* (Common cuttlefish)*;* (**F**) *Pagurus* sp. (Hermit crabs); (**G**) *Pilumnus hirtellus* (bristly crab); (**H**) *Halimeda tuna* (sea cactus); (**I**) Chela of *Squilla mantis* (Spot-tail Mantis Shrimp).

with a demersal distribution [e.g., Sparidae, *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817)]. In our samples, syngnathid fish were rare, found in the digestive tract of only two turtles stranded during the spring season—one subadult (CCL = 59 cm) and one adult female (CCL = 70 cm)—both of which had 10 and 12 individuals of *H. hippocampus* in their diet, respectively.

Plant remains mainly consisted of the green algae, *Halimeda tuna* (J. Ellis & Solander) J. V. Lamouroux, *C. nodosa,* and *P. oceanica.* These algae, found in the digestive tract of 25 turtles (%*F* = 27.5; Table 1), were still pigmented and appeared undigested. Similarly, porifera, *C. reniformis* and *Tethya* sp., were found predominantly intact within the gastrointestinal

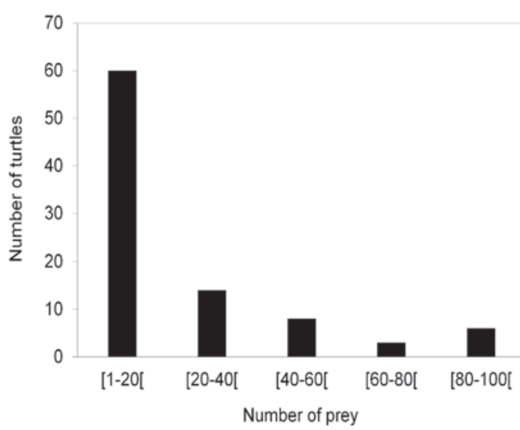

Figure 5. Frequency distribution of number of prey items versus number of turtles presenting food in their digestive tract.

Table 1. Classification of prey of *Caretta caretta* (Loggerhead Sea Turtle) in the Gulf of Gabès in categories according to Zander (1982) and Geistdoerfer (1975); *one ovisac of Rajidae was found in the stomach of a subadult turtle (CCL = 58 cm) in spring 2005 in Sfax region; %*F*: Frequency of occurrence of prey item; %W: Percentage of prey item in weight; %*N*: Percentage of prey item in number; %IRI: Percentage index of relative importance: %Q: food coefficient; MFI: Main Food Index.

Taxon/Prey types and their frequencies of occurrence	%F	%W	%N	%IRI	%Q	MFI	Prey categories (Zander 1982)	Prey categories (Geistdoerfer 1975)
Molluscs	60.4	14.6	25.6	39.4	372.76	67.63	Main prey	Preferred main prey
Gastropoda: *Hexaplex trunculus* (22), *Turritella* sp. (1.1), *Turritella communis* (1.1), *Cerithium scabridum* (3.3), *Cerithium vulgatum, Bittium reticulatum* (1.1), Unidentified gastropods (8.79); Bivalvia: *Pinctada radiata* (5.49), *Mactra corallina* (1.1), *Cerastoderma glaucum* (1.1), *Cardium* sp. (1.1), *Ostreola stentina* (1.1), *Ostreola* sp. (1.1), *Cerithium vulgatum* (1.1), unidentified Bivalvia (3.3); Cephalopoda: *Octopus vulgaris* (1.1), *Sepia officinalis* (33), unidentified Cephalopoda (6.58)								
Arthropoda	49.5	23	15.1	30.5	347.3	92.20	Essential prey	Preferred main prey
Crabs: *Eucrates crenata* (19.8), *Maja squinado* (5.49), *Libinia dubia* (1.1), *Maja* sp. (8.79), *Parthenope anguilifrons* (3.3), *Pilumnus hirtellus* (1.1), unidentified crab (7.69); Shrimps: *Metapenaeus monoceros* (1.1); *Melicertus kerathurus* (3.3), *Squilla mantis* (15.4); Hermit crab: *Pagurus* sp. (2.2); Balanomorph cirriped: *Balanus perforatus* (2.2)								
Porifera	16.5	43.2	38	21.7	1641.6	159.4	Essential prey	Occasional main prey
Chondrosia reniformis (12.1), *Tetya* sp. (7.69)								
Bony fishes	18.7	3.5	3.2	2	11.2	8.27	Accessory prey	Frequent secondary prey
Diplodus vulgaris (1.1), *Sardinella aurita* (3.3), *Mullus* sp. (1.1), *Hypocampus hippocampus* (2.2), unidentified fish (13.2)								
Tunicates	12.1	7.5	7.3	2.9	54.75	16.48	Accessory prey	Frequent secondary prey
Pyura dura (6.59), *Microcosmus vulgaris* (8.79)								
Echinodermata	7.7	5.4	4.6	1.3	24.84	9.51	Accessory prey	Accessory secondary prey
Paracentrotus lividus (2.2), *Holothuria polii* (3.3), unidentified echinoderms (2.2)								
Nemathelminthes	2.2	0.1	2	0.1	0.2	0.07	Accessory prey	Second-order additional prey
Tonaudia tonaudia (1.1), *Kathlania leptura* (1.1)								
Platyhelminthes	2.2	0.01	1.79	0.1	0.018	0.007	Accessory prey	Second-order additional prey
Diaschistorchis pandus (2.2)								
Algae	27.5	2.14	1.79	1.7	3.83	5.77	Accessory prey	Second-order additional prey
Caulerpa prolifera (1.1), *Coduim bursa* (1.1), *Lithophyllum racemus* (2.2), *Phymatolithon calcareum* (1.1), *Halimeda tuna* (7.69), *unidentified algues* (2.2), *Cymodocea nodosa* (13.2), *Posidonia oceanica* (13.2)								
Elasmobranchs*	1,1	0.01	0.04	0	0	0.004	Accessory prey	Second-order additional prey
Ovisac of *Raja* sp. (1.1)								

system of the necropsied turtles. Fifteen turtles (%F = 16.5; Table 1) had sponges in their diet.

This study detected 3 non-native species in the digestive contents of *C. caretta:* the pearl oyster, *Pinctada radiata* (Leach, 1814); the spider crab, *Libinia dubia* H. Milne-Edwards, 1834; and the blunt-spined euryplacid crab, *Eucrate crenata*. Additionally, two balanomorph barnacles (*Balanus perforates* Bruguière, 1789), one of which was affixed to a pearl oyster (*P. radiata*), were found in the undigested organic remains of two turtles: one subadult (CCL = 66 cm) and one adult (CCL = 72 cm).

Non-organic matter (Debris).—Thirteen of the 132 turtles analyzed (9.85%) had anthropogenic debris, such as soft plastics, ropes, wood, and fish hooks, while three turtles (2.32%) had sandy debris (Tables 2 and 3) in their digestive tracts. With the exception of fish hooks,

Table 2. Type and occurrence of marine debris ingested by *Caretta caretta* (*N* = 13) in the Gulf of Gabès; *N*d: number of debris; *N*t: number of turtles for which debris was found.

Marine debris type	*N*d	*N*t	Occurrence (%)
Soft plastics	6	4	30.77
Ropes	11	4	30.77
Wood	5	2	15.38
Fish hooks	3	3	23.08

Table 3. Frequency of occurrence of anthropogenic marine debris ingestion in *Coretta caretta* in the central Mediterranean Sea (CCL, Curved Carapace Length; *N*, number of individuals included in the study).

Locality	*N*	CCL range (cm)	Occurrence (%)	References
Western Mediterranean (Spain)	54	34.0–69.0	79.63	Tomás *et al.* 2001
Western Mediterranean (Valencia region, East Spain)	155	11.0–80.0	78.1	Domènech *et al.* 2019
Tyrrhenian Sea (Sardinia, Tuscany, Lazio Campania, Italy)	150	21.0–82.7	85	Matiddi *et al.* 2017
Tyrrhenian Sea (Gulf of Naples, Italy)	54	-	1.6	Bentivegna *et al.* 2003
Tyrrhenian Sea (Lazio and Campania regions, Italy)	61	22.0–81.8	91.5	Mariani *et al.* 2023
Adriatic Sea (Slovenia and Croatia)	54	25.0–79.2	35.2	Lazar and Gracan (2011)
Adriatic Sea (Abruzzo and Molise regions, Italy)	89	19.2–107.0	43.83	Mariani *et al.* 2023
Adriatic Sea (Gulf of Manfredonia, Italy)	76	32.3–81.7	35.1	Baldi *et al.* 2023
Central Mediterranean Sea (Lampedusa Island, Italy)	79	25.0–80.3	48.1	Casale *et al.* 2008
Central Mediterranean Sea (Lampedusa Island and Sicily, Italy)	567	18.2–82.0	35.4	Casale *et al.* 2016
Central Mediterranean Sea (Malta)	99	20.0–69.5	20.2	Gramentz (1988)
Central Mediterranean Sea (Gulf of Gabès, Tunisia)	132	28–77.5	9.85	Present Study
Eastern Mediterranean (North Cyprus)	135	-	42.7	Duncan *et al.* 2024

all anthropogenic materials were small and seemingly not problematic for the turtles examined. Plastic debris, specifically soft plastic and ropes were ingested by eight turtles across various seasons of the year (2 in autumn, 1 in winter, 1 in spring, and 4 in summer).

Diet Shifts

The results of the MANOVA showed that there was no difference in the loggerhead diet on body size and sex (Table 4). The relative significance index (%IRI) of some prey items varied seasonally, indicating that molluscs and arthropods were ingested more frequently in spring and summer, whereas tunicates and poriferans were ingested more frequently in fall and winter; fish consumption was only recorded in spring and summer (Figure 6).

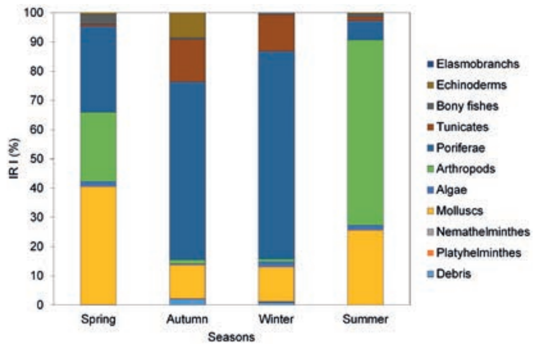

Figure 6. Seasonal variation in % IRI percentages of different items in *Caretta caretta* in the Gulf of Gabès; %IRI: Percentage index of relative importance.

Discussion

Dietary Composition

The analysis of digestive contents of *Caretta caretta* in the Gulf of Gabès revealed a diverse array of prey items, non-prey remains and debris, as detailed below:

Prey.—Forty-six prey items were discovered in the digestive tracts of 132 *C. caretta,* 20 of which were in 66% of the animals studied. This finding supports the loggerhead turtles' opportunistic and predatory feeding patterns already suggested in other regions in the Mediterranean Sea (Godley *et al.* 1997, Tomás *et al.* 2001, Bentivegna *et al.* 2003, Casale *et al.* 2008, Hochscheid *et al.* 2013). Additionally, based on the frequency and mass, benthic organisms such as porifera, arthropods, and molluscs seemed to be the preferred prey of loggerhead sea turtles in the Gulf of Gabès. According to Zander's classification (1982), these items are categorized as essential prey (porifera and arthropods) and main prey (molluscs). These findings align with studies from other Mediterranean regions, which demonstrates that *C. caretta* mostly feed on benthic molluscs and crustaceans (Godley *et al.* 1997, Casale *et al.* 2008, Lazar *et al.* 2011, Baldi *et al.* 2023, Mariani *et al.* 2023).

The frequency of identifiable remains in the turtles' digestive tracts may be influenced not only by the types of prey consumed but also by the structural attributes of the prey that affect their retention within the turtles' digestive systems. Soft-bodied prey, such as cnidarians,

Table 4. Multivariate analysis of variance (MANOVA) table of Wilks' lambda. (*df,* degrees of freedom; W.L, value of Wilks lambda; *F*, approximate *F* value; H.*df*, hypothesis *df*; E.*df*, error *df;* Sig, significant.

Effect	*df*	W.L	F	H.*df*	E.*df*	Sig.
Size	1	0.85	1.85	10	103	0.06
Sex	1	0.79	1.28	20	206	0.19
Size * Sex	1	0.77	1.46	20	206	0.10

are less likely to be observed, whereas more robust prey, such as gastropods or crabs, are more likely to be detected. The abundance of various prey items found in the digestive tract of *C. caretta,* including the sea cucumber, *Holothuria polii* Delle Chiaje, 1824, the gastropod, *H. trunculus,* and the crab, *E. crenata,* aligns with their presence and distribution in the infralittoral and circalittoral bottoms of southern Tunisia (Bradaï 2000, Elhasni *et al.* 2010, El Lakhrach *et al.* 2012).

Sponges, *Chondrosia reniformis* and *Tethya* sp., were found in 12.1% and 7.69% of the cases, respectively. They were completely undigested in all instances, suggesting that *C. caretta* is incapable of digesting sponges, unlike hawksbill turtles, *Eretmochelys imbricate* (Linnaeus, 1766) (Bjorndal 1997). Possible explanations have been proposed for the ingestion of sponges: (1) mistaken prey identity (Steuer 1905, Acevedo *et al.* 1984); (2) sponges are a source of bacterial fauna or oligoelements (Laurent and Lescure 1994); and (3) accidental ingestion while targeting other prey (Casale *et al.* 2008). The significant weight of sponges in the dataset, largely due to two samples containing over 2 kg of *C. reniformis* each, inflated their IRI% value but may not accurately reflect their dietary importance at the population level. The substantial amount of *C. reniformis* supports the hypothesis of accidental ingestion of sponges. Notably, *C. reniformis* was the most frequently identified sponge and has been previously reported in the diet of trawl bycaught and in stranded turtles in the Mediterranean Sea (Casale *et al.* 2008, Palmer *et al.* 2021, Baldi *et al.* 2023).

Fish were the fourth most frequent taxon in the diet of *C. caretta* (18.7% *F*; 3.5% W). Apart from syngnathids, whose slow movement makes them easier prey (Brongersma 1972, Burke *et al.* 1993, Kleiber *et al.* 2010), other prey like cephalopods are generally not considered part of the loggerhead's natural diet (Plotkin *et al.* 1993, Laurent and Lescure 1994). Loggerhead turtles have limited capability to capture fast-moving and highly maneuverable prey (Plotkin *et al.* 1993, Tomás *et al.* 2001); however, maneuverable species are frequently caught by fishing gears, particularly trawlers, and become part of their discard (Sánchez *et al.* 2007), making them more easily accessible to turtles.

Two possible origins could be attributed to the fish sampled in our study. The first hypothesis proposes that turtles might opportunistically consume fish when caught and placed on the deck of fishing boats (Laurent and Lescure 1994, Seney 2003). The second and more plausible hypothesis suggests that the fish might be discarded by trawlers and later scavenged from the seafloor by turtles (Tomás *et al.* 2001, Seney and Musick 2007, Casale *et al.* 2008, Benhardouze *et al.* 2021, Palmer *et al.* 2021). This argument is supported by the presence of *Mullus* sp. and *D. vulgaris* in the turtle's diet, two species commonly targeted by trawlers in our study area (Jarboui *et al.* 2005, El Lakhrach *et al.* 2019).

Similarly, Cardona *et al.* (2024) suggested that the decline in fish consumption by *C. caretta* along the Spanish Mediterranean coast could be linked to a reduction in the fishing fleet in that area. In the Mediterranean, trawlers target multiple species and produce substantial discards (Tsagarakis *et al.* 2014), making it available for turtle consumption (Mariani *et al.* 2023). This has important conservation implications, since *C. caretta* are also scavengers and may be attracted to areas with intense fishing activity due to the availability of discards, which increases their probability of incidental capture (Baldi *et al.* 2023).

The opportunistic carnivorous diet of *C. caretta* is supported by the presence of tunicates such as *Pyura dura* (Heller, 1877) and *Microcosmus* sp. reported in this study. To date, tunicates are rarely reported in the diet of loggerhead turtles. Pelagic tunicates, such as *Pyrosoma atlanticum* (Péron, 1804), have only been documented in early pelagic juveniles from the western Mediterranean Sea and the North Atlantic (Brongersma 1972, Van Nierop and Den

Hartog 1984, Tomás *et al.* 2001). Among benthic tunicates, the only species previously identified in the diet of *C. caretta* was *Molgula manhattensis* (De Kay, 1843) found in Chesapeake Bay, Virginia, USA (Seney and Musick 2007).

Echinoderms were found only seven times in our study (%*F* = 7.7% and *N*% = 4.6), whereas in the research conducted by Casale *et al.* (2008), they were part of the diet of over 25% of loggerhead turtles. This discrepancy is probably attributed to differences in substrate composition. Frequenting trawled areas could expose turtles to habitats with diminished biodiversity, as repeated trawling activity often leads to the decline of some taxa (Handley *et al.* 2014, Baldi *et al.* 2023) and the replacement of native species by more opportunistic or scavenging species.

Algae and plants were part of the diet of 25 turtles (%*F* = 27.5). The presence of algae in the digestive contents of *C. caretta* has been reported in the Mediterranean (Basso and Cocco 1986, Tomás *et al.* 2001, Casale *el al.* 2008) and the Atlantic (Acevedo *et al.* 1984, Frick *et al.* 2009), where turtles likely ingest algae incidentally among the floating debris. In this study, the algae recovered could also originate from the seafloor of the Gulf of Gabès, where these species are commonly found (Zaouali 1993, Hattour and Ben Mustapha 2013). Notably, these algae were also undigested, corroborating the strictly carnivorous behavior of the studied species. Unable to digest plant matter, the turtles probably ingested the algae accidentally while preying on animal species (Casale *et al.* 2008). However, their presence suggests that loggerhead turtles might use shallow marine areas with ample light penetration, particularly regions abundant in *Posidonia* and *Cymodocea* seagrass beds. These shallow benthic environments, characterized by extensive seagrass beds, serve as habitats for a highly diverse set of species and are commonly utilized by loggerheads for foraging (Godley *et al.* 1997, Houghton *et al.* 2000, Casale *et al.* 2008, Lazar *et al.* 2011, Patel *et al.* 2016).

Three non-indigenous species previously reported in the Gulf of Gabès were observed in the diet of the sampled turtles: the bivalve, *Pinctada radiata,* and the crab, *E. crenata,* both originating from the Indo-Pacific, and the West Atlantic crab, *Libinia dubia* (Ben Amor *et al.* 2016). Since the sampling period occurred before 2014, when the blue crab, *Portunus segnis* (Forskål, 1775), was first report in Tunisian waters (Rabaoui *et al.* 2015), this species was not reported as part of the diet of the necropsied turtles. In recent years, the species has been reported in the diet of these turtles (Bradaï *et al.* 2017), suggesting that loggerhead sea turtles can serve as a tool for monitoring potential new invasive species.

Non-prey remains.—Barnacles of the species *Balanus perforatus* Bruguière, 1789 were identified among the remains. Sea turtles epibionts, such as amphipods and cirripeds, have been previously documented in the diet *of C. caretta* sampled in the Atlantic (Frick *et al.* 2009). These organisms are likely ingested while attached to anthropogenic debris floating on the surface (Frick *et al.* 2009). As one of the most common fouling organisms (Christie and Dalley 1987), barnacles can be consumed by sea turtles indirectly through their association with organisms such as crabs (Karaa *et al.* 2018) or pearl oysters (Abdelsalam and Elebiary 2023).

Non-organic matter (Debris).—Anthropogenic debris was present in 9.85% of the turtles. This proportion is higher than reported for *C. caretta* sampled in the Gulf of Naples between 1991 and 2001 (only 1.6% of 40 turtles examined) but lower than values recorded in other regions of the central Mediterranean. These differences suggest a spatial and temporal variability in the distribution of debris or its consumption by turtles (Table 3). Several factors may influence these findings, including turtle recovery method, the age of the turtles, and the approach used to characterize marine debris ingestion. Differences in the frequency of debris consumption may provide insight about the pollution level in those areas. In our study, debris were more frequently observed in the summer, coinciding with increased turtle activity at the water's surface. During this period, turtles often need to surface for air, making them more vulnerable to capture and recapture. This can result in stress and lead to buoyancy issues, prompting them to accidently ingest floating debris while foraging on surface-associated organisms.

In addition, three turtles ingested natural debris, such as sand, likely while foraging on the seabed. As part of their feeding behaviour, *C. caretta* often search the ocean floor for food, which can result in incidental sand ingestion (Preen 1996). All of the anthropogenic debris, except for fishhooks, consisted of small fragments. This observation, combined with the absence of apparent pathologies linked to debris ingestion, suggest that it was not a direct cause of death. However, the long-term effects of plastic consumption, especially from repeated intake over time, remain poorly understood. Non-lethal ingestion of debris has been documented in several studies (e.g., Tomás *et al.* 2002, Revelles *et al.* 2007, Casale *et al.* 2008, 2016, Lazar and Gracan 2011). Plastic debris retained in the digestive tract can increase the risk of internal injuries and cause sub-lethal effects such as reduced stomach capacity, inappetence, buoyancy issues, and chemical contamination. Over time, these consequences can harm turtles' health, reducing their fitness and potentially leading to death (Nelms *et al.* 2016).

Regional Variability in Diet

Loggerhead turtles' diets in the Mediterranean vary according to feeding habitats and availability of prey species. In the Balearic Islands, they primarily feed on the Mediterranean jellyfish, *Cotylorhiza tuberculate* (Macri, 1778) (Revelles *et al.* 2007). In the central Mediterranean, hermit crabs serve as a major food source (Casale *et al.* 2008). Along the Greek coast, they target Mediterranean mussels (*Mytilus galloprovincialis*, Lamarck, 1819) (Houghton *et al.* 2000), while in the Adriatic Sea, they feed on European clams (*Corbula gibba* Olivi, 1792), and crabs (*Liocarcinus* sp.; and *Goneplax rhomboids* Linnaeus, 1758) (Lazar *et al.* 2011, Mariani *et al.* 2023).

In the Gulf of Gabès, loggerheads predominantly consume the Blunt-spined euryplacid crab (*E. crenata*), the cuttlefish (*S. officinalis*), the Banded murex (*H. trunculus*), and the Spot-tail Mantis Shrimp (*S. mantis*). This study expanded the data on the phyla and species preyed on by the loggerhead sea turtles in the Tunisian Plateau (Central Mediterranean Sea). It also emphasizes the use of dietary analysis, which offers insights into marine biodiversity and the distribution of non-native species in the area.

Relationship Between Diet and Used Marine Habitats

Caretta caretta in the Gulf of Gabès primarily feed on prey from benthic neritic zones, as their dietary data revealed. They commonly consumed the crab, *E. crenata,* the cephalopod, *S. officinalis,* and the gastropod, *H. trunculus,* which inhabit the sublittoral zone at depths of 1030 meters (Zaouali 1993, Elhasni *et al.* 2010, El Lakhrach *et al.* 2012). Additionally, these turtles also exhibited pelagic feeding behavior. They ingested floating debris, such as wood and plastic, and pelagic prey like Clupeidae (*S. aurita*). The alternate use between benthic and pelagic habitats has been supported by numerous studies that documented the bycatch of juvenile turtles by surface and bottom longlines in the study area (Jribi *et al.* 2008, Echwikhi *et al.* 2011). The natural characteristics of Gulf of Gabès, including its shallow depth (less than 50 m) and wide continental shelf, enable loggerhead turtles to forage across the entire water column. This habitat structure allows turtles to alternate between pelagic and benthic zones with minimal energy expenditure. Our findings support previous research showing that both juvenile and adult loggerhead turtles adopt an opportunistic amphi-habitat feeding strategy. As they mature, however, they increasingly prefer benthic prey (Casale *et al.* 2004, 2007a,b).

Diet Shifts

Diet and turtle size.—Turtle size does not appear to affect food preferences. Studies on *C. caretta* from the western Mediterranean Sea, the Tyrrhenian Sea and the Adriatic Sea show similar feeding behavior regardless of size (Haywood *et al.* 2020, Baldi *et al.* 2023, Mariani *et al.* 2023). The absence of evidence for a size-related habitat shift may be explained by an intermediate neritic transition phase for juvenile turtles (Casale *et al.* 2018, Haywood *et al.* 2020). Conversely, other authors suggest that the number and diversity of prey species (mostly benthic) increased with turtle size (Tomás *et al.* 2001, Youngkin 2001). In a study conducted in thesoutheast US, researchers found that adult turtles consume more gastropods, while subadults consume more fish, indicating that the size of the turtles might influence the proportions of certain prey (Molter *et al.* 2022). Given that most of the turtles sampled in the current study were primarily PPJ, further investigation and a larger sample size are needed to better understand the impact of turtle size on diet in the Gulf of Gabès.

Seasonal changes in diet.—The seasonal variation in the relative prey importance index (%IRI) reveals shifts in the types of prey ingested across different seasons. Molluscs, arthropods, algae, tunicates, and porifera were consumed throughout the year. Molluscs and arthropods were more frequently consumed in spring and summer, whereas tunicates and poriferans were more frequently consumed in fall and winter. This seasonal shift in prey types may relate to reduced activity in *C. caretta* during colder seasons (Hochscheid *et al.* 2005). Additionally, opportunistic feeding behavior may explain the consumption of teleosts (fish) during the warm months.

Even during the colder months, loggerhead turtles in the Gulf of Gabès continue feeding on benthic organisms such as sponges, gastropods, and bivalves. Similar behavior has been observed in other locations in the Mediterranean (Hochscheid *et al.* 2005), in South Africa (Hughes 1974), and in the United States, particularly the Gulf of Mexico (Plotkin *et al.* 1993). These findings highlight the adaptability and resilience of *C. caretta,* enabling them to sustain feeding habits year-round, even during the winter. By adopting a “sit-and-wait” overwintering strategy with infrequent surfacing, these chelonians sufficiently reduce the metabolic costs of overwintering (Hochscheid *et al.* 2005). Satellite tracking data from the Mediterranean demonstrated that these turtles are not obligate hibernators (Hochscheid *et al.* 2007). Wintering strategies differ within the Mediterranean basin, as warmer temperatures in the eastern region may allow turtles to remain active, continue feeding, and take fewer rest periods during winter (Hochscheid *et al.* 2007).

Conclusion

This study highlights the value of diet analysis in revealing the feeding ecology and habitat use of loggerhead turtles in the Gulf of Gabès. The majority of *Caretta caretta* in this region are post-pelagic juveniles and exhibit opportunistic feeding behaviour, consuming trophic resources from both pelagic and benthic environments. Their diet changes with the seasons, and they remain active during the winter without hibernating.

The Gulf of Gabès, which has the most productive marine habitats in Tunisian waters, is likely to be one of the most important areas for loggerhead turtles in the Mediterranean (Casale and Margaritoulis 2010). Satellite telemetry and flipper tagging data suggest that the region is home to 28 to 44.4% of the females nesting in western Greece (Patel *et al.* 2015). Efforts to protect and manage this area, ensuring the availability of diverse and healthy trophic resources in both pelagic and benthic zones, could be pivotal for supporting populations of *C. caretta* and promoting their survival in Tunisian waters. The importance of the Tunisian plateau for loggerhead turtles in the Mediterranean highlights the need for sustained, long-term monitoring efforts to assess the conservation status of these chelonian populations in the region (Karaa *et al.* 2016 a,b). Future efforts should prioritize analyzing gastrointestinal contents as an ecological indicator and biodiversity markers to enhance our understanding and protection of marine turtles in the region.

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