Research Article

Feeding Ecology and Activity Rhythms of the Critically Endangered Hawksbill Turtle

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The critically endangered hawksbill turtle (*Eretmochelys imbricata*) is a keystone species that, through its decline, has a profound effect on marine ecosystems such as coral reefs. This study aimed to characterize the activity rhythm and dietary preferences of hawksbill turtles in Martinique to develop appropriate conservation strategies at both local and global scales. Six individuals (one female and five males) were monitored using on-board cameras. Findings show that hawksbills spend more than half of their time feeding at a depth of 14.43 ± 9.72 m, especially in the morning. Video recordings revealed consumed prey, including plants and animals, and these were identified to the family level. Habitat sampling revealed potential prey from six distinct families. Video recordings (selected prey) and habitat samples (potential prey) were compared to indicate prey selection. Aplysinidae was the most frequently observed family both as consumed and potential prey. Aplysinidae and Irciniidae, both marine sponge families, represent new records in the hawksbill diet. Spongin content and brominated metabolites are proposed among the plausible factors that could define turtle food preferences and strategies. Further combined analyses could help to better define feeding strategies as an integrative and collaborative approach, which is essential for the long-term protection of this critically endangered species.

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1. Introduction

Ecologists have long understood that ecosystem diversity is the heart of its stability[1]. The hawksbill turtle (*Eretmochelys imbricata* (Linnaeus, 1766)) is a keystone species, characterized by the quality, number, and importance of its interactions with its habitat and other species[2][3][4]. Hawksbills are listed as critically endangered under criteria A2bd of the International Union for the Conservation of Nature (IUCN) Red List since 2008, with a decreasing population trend[5]. While some Regional Management Units (RMUs) show signs of recovery, others continue to face significant threats[6]. The hawksbill's worldwide population has decreased by 90% in the last century due to numerous threats such as residential and commercial development, overexploitation, pollution, energy production and mining, human intrusions and disturbance, bycatch, illegal trade, and habitat destruction, and climate change[5]. Understanding their ecological roles and trophic relationships is essential for developing effective conservation strategies to safeguard this critically endangered species[7][8].

One of a large population of hawksbills can be found in the Caribbean, namely in the French West Indies, which constitute preferential distribution areas for hawksbills[9][7]. In the French West Indies, local wildlife management, conservation structures, and a national action plan recommended studying the importance of feeding sites for hawksbills to determine the dynamics of the population and to identify the threats they face. Effective conservation of the critically endangered hawksbill is hindered by a lack of basic ecological information about its complex diet and habitat requirements[10][11][12].

Current evidence suggests that, like most sea turtles, hawksbill post-hatchlings inhabit major oceanic gyre systems, where they feed on zooplankton near the surface[13]. Once they reach a carapace length of 20–35 cm, they recruit to neritic habitats, such as coral reefs, sponge reefs, reef walls, and other hard-bottom habitats[14][9][15]. The shape of their mouths and their sharp beaks enable them to reach into reef crevices to extract food[16]. Hawksbills may feed on sponges, marine algae, seagrass, corals, mollusks, tunicates, crustaceans, sea urchins, small fish, and jellyfish[17][10][18] and are thus considered omnivorous. However, several Caribbean studies have shown that they feed almost exclusively on sponges, especially on those without chemical defenses, thus applying top-down control on sponge communities[16][19][10][20][21].

doi.org/10.32388/FKTVC0

This study focuses on the hawksbill turtle (*Eretmochelys imbricata*) population inhabiting the coastal waters of Martinique, a Caribbean island where 191 sponge species have been recorded among the 520 identified in the Caribbean[22]. While previous research has identified key marine habitats[7] and nesting sites[23] of the critically endangered hawksbill in Martinique, there is a notable lack of data on its foraging behavior, dietary preferences, activity patterns, and population size in this area. What is known, however, is that hawksbills in Martinique exhibit strong site fidelity to their foraging grounds[7]. Male hawksbills, in particular, tend to be relatively sedentary, likely due to their potential to breed annually and the proximity of nesting beaches—mainly Prêcheur, Diamant, Sainte-Luce, and Sainte-Anne along Martinique's Caribbean coast[24][7]. In northern Martinique, males and juveniles are known to share spatial foraging areas and display similar diving patterns, characterized by long, shallow dives[7]. This behavior is thought to be influenced by the spatial distribution of preferred dietary items[25][7]. The observed spatial overlap between life stages suggests that these local foraging grounds provide sufficient resources to support a multi-age population, underscoring the importance of their conservation[7].

In contrast, females undertake long-distance migrations between their nesting and foraging grounds, using specific feeding strategies to compensate for the energy costs of reproduction[26]. They may be capital or income breeders. Capital breeders rely on energy stored before reproduction and do not feed during the nesting period, whereas income breeders adjust food intake during the reproductive period. Although most sea turtles are known to be capital breeders, no conclusive evidence has confirmed this, as eating behaviors and other activities are based on pressure sensors or accelerometers without upstream validation of the signal[27][28].

Additionally, hawksbills play a crucial role in the complex ecosystem of coral reefs by eating marine sponges and macroalgae, which leaves more competitive space for coral development[20]. Their population decline may have far-reaching ecological consequences, as reduced grazing allows palatable sponges—i.e., chemically defended sponges using secondary metabolites to protect themselves from predators, competitors, or pathogens[29]—and macroalgae to proliferate, outcompeting corals[2][3]. Pre-Columbian estimates suggest that Caribbean reefs once supported up to 11 million hawksbills, contributing to effective sponge control[20]. As hawksbill populations declined due to historical human exploitation and palatable sponge abundance increased under reduced grazing pressure, the turtles increasingly fed on chemically defended sponges (Fig. 1), rendering their flesh toxic to humans. This dietary shift was documented as early as the 19th century, prior to the species becoming endangered, with accounts recorded in ship logs and historical reports[30][20]. The current imbalance—fewer hawksbills and increasing sponge and macroalgal dominance—leads to mutualistic relationships between macroalgae and sponges, where algae provide dissolved organic carbon (DOC) to sponges, and sponges supply inorganic nutrients to algae, exacerbating coral decline[31][20]. This shift limits coral and gorgonian, i.e., soft coral, recovery and undermines reef structure. Given that coral reefs support the highest levels of marine biodiversity and provide critical ecosystem services—including food security and livelihoods for hundreds of millions of people worldwide[20][32][33][34][35]—hawksbill conservation is critical. Protecting this critically endangered species is not only essential for its survival but also for safeguarding the health and resilience of these essential ecosystems.

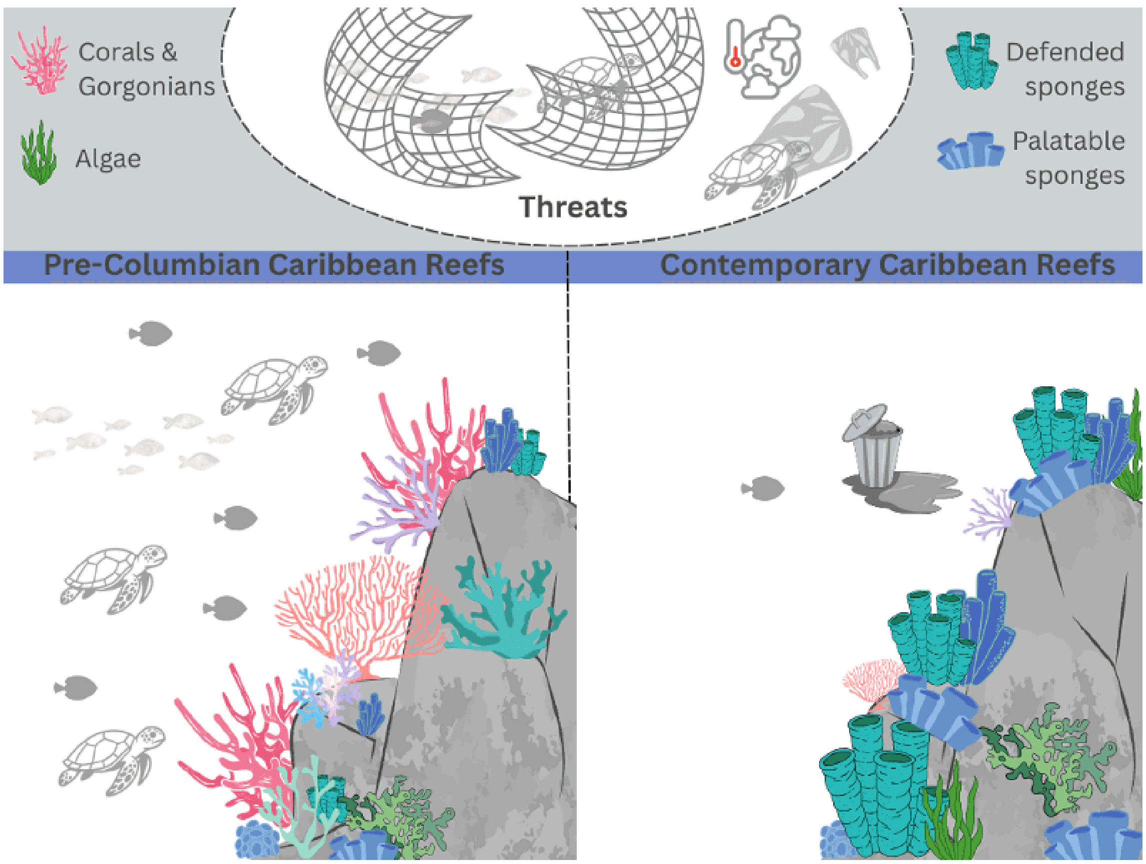

Figure 1. *Changes in sponge communities due to the decline in the hawksbill population (based on* [20]*)*

Sponges are the oldest multicellular organisms, lacking true tissues and differentiated organs[36]. During their evolutionary transition from unicellular to multicellular life, sponges developed recognition systems localized on the cell periphery or within the para- and extracellular matrix. One characteristic of

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a sponge individual is that it consists of two phases: (a) a living phase composed of different cell types, and (b) a nonliving phase which contains the matrix material, synthesized by the cells[36]. The distinct phases and characteristics of sponges make them particularly fascinating to study, as they enable sponges to interact with predators through a variety of chemical and physical defenses. Unlike other spongivores, hawksbills lack morphological adaptations to facilitate the digestion and swallowing of abrasive and copious sponge spicules[16]. Although sponges are considered the main food source in the Caribbean, the specific species consumed and the feeding strategy employed by hawksbills remain poorly understood.

Since the 1980s, researchers started studying hawksbills′ feeding ecology using techniques such as esophageal lavage, direct observation, fecal examination, stable isotope analysis (SIA), and video recordings[37]. In-water observation has proven particularly effective for determining diet composition, prey selectivity, and behavioral patterns[38][10]. However, this technique poses several challenges, including restricted study site access, limited underwater visibility, scuba-related depth constraints, and the problem of pseudo-replication due to unmarked individuals[39][38][38]. To overcome these limitations, this study employed innovative techniques previously used on green sea turtles in Martinique[27][8][40], equipping hawksbill turtles with on-board cameras to capture their behavior in situ.

This study aimed to improve knowledge of hawksbills' diet and activity rhythms in Martinique by documenting extended feeding sessions. Knowledge about their trophic ecology could enrich knowledge of hawksbills in Martinique, help identify critical foraging habitats, and support more effective conservation measures for this critically endangered species in the French West Indies.

2. Material and Methods

2.1. Ethics Statement

Hawksbill capture meets French ethical and legal requirements. The CNRS protocol was approved by the "Conseil National de la Protection de la Nature″ and the "Ministère français de l'Ecologie, du Développement Durable et de l'Energie" (permit numbers: 2013154-0037, 201710-0005, and R02-2020-08-10-006). Fieldwork was carried out under the certification of Damien Chevallier (prefectural authorizations' owner) under strict compliance with the Police of Martinique's recommendations in order to minimize animal disruption.

2.2. Capture and tag deployment

This study was conducted in Martinique, French West Indies, between “le Rocher du Diamant” and “le Sec du Diamant” (14°26.6’N, 61°2.4’W) (Fig. 2), which represents an important hotspot of biodiversity with its surrounding coral reefs and plays an important feeding and breeding area for hawksbill turtles[7].

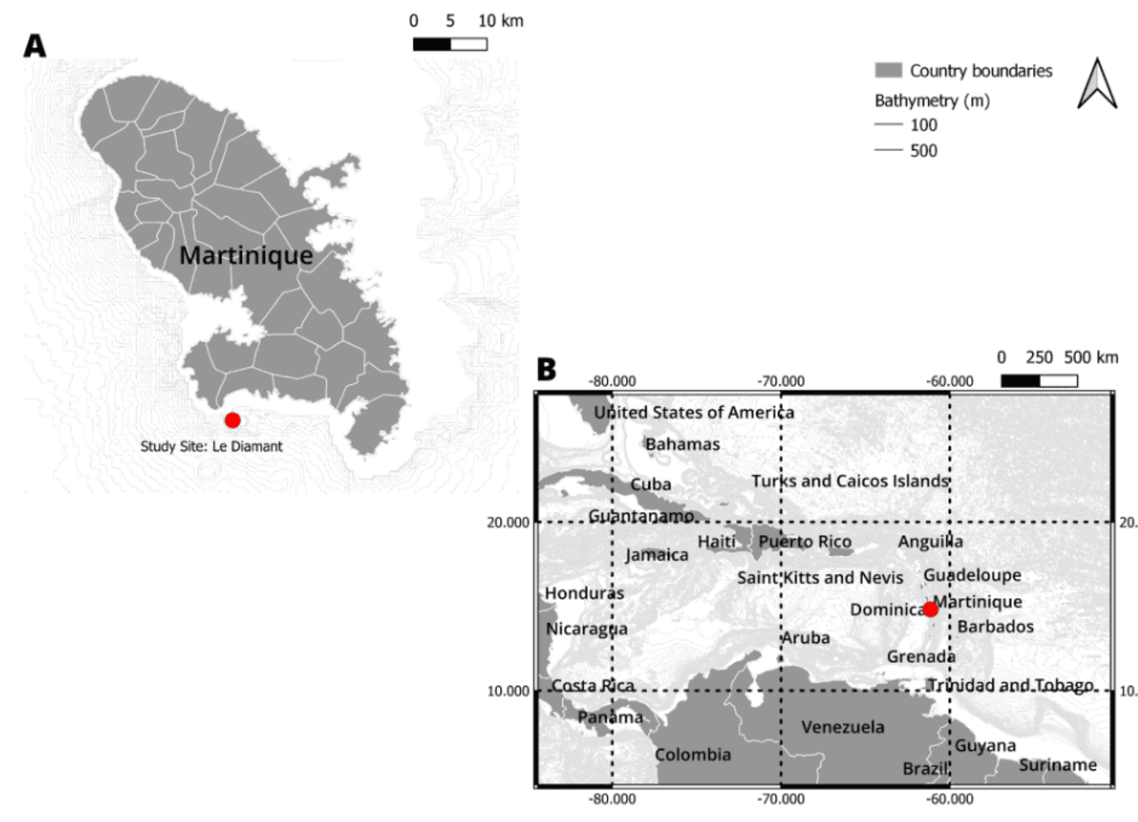

Figure 2. *Maps depicting regional views of the Eastern Caribbean and of the study site in Martinique*

Based on previous research done on food selection and habitat use patterns of green sea turtles in Martinique[27][8][41], similar techniques were applied to the hawksbills monitored. For this study, five male and one female free-ranging hawksbill turtles were equipped with onboard cameras (CATS, Customized Animal Tracking Solutions, Germany) in “Le Sec du Diamant” between November 2022 and May 2023, with each deployment lasting 48 hours. One male was equipped twice, in February and in March.

The relatively shallow depths (<20 m) of the area allowed free divers to capture the turtles manually. The capture of each turtle was performed by up to three expertly trained free divers when the turtle was static, i.e., resting or feeding at the bottom. The freediver silently dived toward the turtle to avoid detection and, once close enough and above the animal, seized the nuchal shell and pygal plate. The freediver then positioned the turtle against his chest with the hind flippers against his breastplate and rose to the surface. A second diver held the fore flippers and helped to lift the turtle onto the deck of the boat for measurements and tagging[7][42].

Each captured turtle was identified using passive integrated transponders (PIT; ID-100, TROVAN). Once an individual had been placed on a boat, the presence of a PIT was checked using a TROVAN R251 reader. If the individual was unknown (i.e., absence of PIT), a PIT was injected into the turtle's right triceps and its number was added to the database as described in Siegwalt et al.[43] and Lelong et al.[44]. Alongside individual identification, standard morphometric data were collected, e.g., curved carapace length (CCL) and curved carapace width (CCW). Additional biological data, including blood samples, tissue biopsies, photo-identification, and anomalies, were collected to support future analyses and research efforts. The CATS Cams device was attached to the top of the carapace using three galvanic timed-release systems (magnesium rings) planned to dissolve in seawater 48h later, releasing the instruments to the surface.

A CATS device included a video-recorder (1920×1080 pixels at 30 frames s^{-1}) combined with a tri-axial accelerometer, a tri-axial gyroscope, a magnetometer, a temperature sensor, a light intensity sensor, a time-depth recorder, a hydrophone, and a GPS. Depth was recorded at 1 Hz using a pressure sensor with a range from 0 to 2000 m and 0.2 m accuracy[27]. Due to low light conditions after sunset, the cameras were programmed to record from 05:00 to 18:00, but other sensors were still recording at night.

CATS were recovered using a goniometer (RXG-134, CLS, France) by geolocation of an Argos SPOT-363A tag (MK10, Wildlife Computers Redmond, WA, USA), glued to the CATS Cams device.

2.3. Time budget

Video recordings captured by the CATS devices were analyzed through visual inspection using the custom-written software TurtleCap (https://github.com/Vadym-Hadetskyi/TurtleCap) and BORIS[45] to identify behaviors. The onset and termination of each observed behavior were annotated with a temporal resolution of 0.1 seconds. A total of 44 distinct behavioral categories were identified and used to systematically label the video recordings (Table S.1); these categories, which closely mirror those previously established for green turtle behavior in Martinique[27], were further grouped into eight overarching behavioral classes (Table S.1). These categories helped us calculate the time budget, i.e., the time allocated to each behavior from 5 AM to 6 PM for hawksbills in Martinique. The time-depth dataset was associated with the corresponding observed behaviors. These were visualized and checked using R software (version 3.5.3; http://www.R-project.org/) and the *rblt* package (https://CRAN.R-project.org/package=rblt).

2.4. Diet composition

At the Diamant, the seascape is dominated by sea sponges in terms of diversity and biomass[22]. Some of the walls of the submarine caves are 100% covered by sponges, including some encrusting specimens. “Le Rocher du Diamant ″ is an area with strong current and wave action, therefore ideal for sponge development[22].

In addition to the time budget analysis, a dietary analysis was conducted using the video recordings. Individual-level diet composition was inferred from bite counts, following the methodology of Siegwalt et al.[8]. A bite was defined as a deliberate head movement directed toward a food item, with evident intent to remove and ingest all or most of the item[46]. For each foraging bout identified in the recordings, bites were counted and classified into prey categories, including marine sponges (*Porifera)*, marine algae (*Plantae)*, identifiable prey families (see Table S.2), and an ″Unknown″ category.

Twenty percent of bites could be confidently assigned to a prey category. This limitation stemmed from (1) the taxonomic complexity of sponges and algae, which often requires expert validation, and (2) the limited visibility of prey items due to the dorsal placement of the turtle-borne camera. Sponge prey (*Porifera*) were initially identified to the family level using resources such as the online Sponge Guide[47], the Caribbean Sponge Diversity field guide[22], and the *Reef Creature Identification Guide: Florida, Caribbean, Bahamas*[48].

To expand the dataset and promote local engagement, supplementary video material from regional diving centers was also collected and analyzed.

2.5. Prey selection

To define organisms to the species level to identify potential prey, samples were taken in the field. Based on the GPS coordinates of the feeding events on the video recordings, sampling along transects was performed on foraging areas of hawksbill turtles. Six scuba divers (three pairs) followed three 50 m transects, randomly distributed on Le Sec du Diamant. Samples identified on the video recordings were photographed, and a piece of approximately 10 cm^3 was sampled. To avoid contamination, prey were sampled and handled with gloves and sterile material. Each sample was put in a numbered bag and analyzed in the laboratories of Stazione Zoologica Anton Dohrn and Università Politecnica delle Marche in Italy. The taxonomy methodology is further described in Labalme et al., in prep.[49] Potential prey identified in the laboratory were compared to prey consumed as observed in video recordings to determine prey selection.

3. Results

3.1. Capture and tag deployment

The average CCL of seven hawksbills was 82 ± 2.8 cm (range = 77 to 85 cm; #1 vs. #8), and the CCW was 72.1 ± 3.1 cm (range = 68.4 to 75.4 cm; #5 vs. #6) (Table 1). One individual was captured twice (deployments #3 and #6). The camera of #5, placed on March 8, 2023, was lost. After 48 hours, no Argos signal was received, and the camera has not been recovered since. There was a technical problem with #2. The video data relating to these two deployments are therefore not included in the results presented here.

Deployments	*Individual PIT number*	*Sex*	*Capture date*	*Location*	*CCL*	*CCW*	*Tail*
#1	**#071E540D**	F	02/11/2022	Rocher du Diamant	77	/	/
#2	**#071E0C2B**	M	02/11/22	Rocher du Diamant	76	62,8	19,5
#3	**#0786CBC6**	M	01/02/2023	Sec du Diamant	82.8	75.4	24.9
#4	**#0786B33D**	M	01/02/2023	Sec du Diamant	84	74.2	21.5
#5	**#0786B3ED**	M	08/03/23	Sec du Diamant	81.7	68.4	22.5
#6	**#0786CBC6**	M	08/03/23	Sec du Diamant	see above		
#7	**#07876ED4**	M	28/03/23	Sec du Diamant	80.6	69.3	21.5
#8	**#07C7C341**	M	16/05/23	Rocher du Diamant	85	73.3	24

Table 1. *Morphological data collected from each studied individual hawksbill (n=8)*

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3.2. Time budget

3.2.1. Video analysis

In total, 70 h of multi-sensor recordings were labeled from six deployments and five individuals, and 2,914 behavioral sequences were noted (mean: 12 ± 4 h per individual, min: 6 h, max: 18 h). The predominant behavior observed in the videos was feeding, representing more than 58% (39 h) of the time budget, followed by resting (29%, 19 h) and swimming (6%, 8 h) (Fig. 3). The other behaviors were expressed in a minority (Breathing: 2 h, Gliding: 1 h, Scratching: 1 h, and Other: 0.1 h). The surfacing time is on average 2.34 min per hour, during which the hawksbills took an average of seven breaths per hour. Scratching events happened against rocks or against giant barrel sponges (*Xestospongia muta).* Interactions between individuals were noted for several seconds where the individual with the camera would (1) go to another hawksbill that was eating and chase it away or (2) rub its face with another male hawksbill.

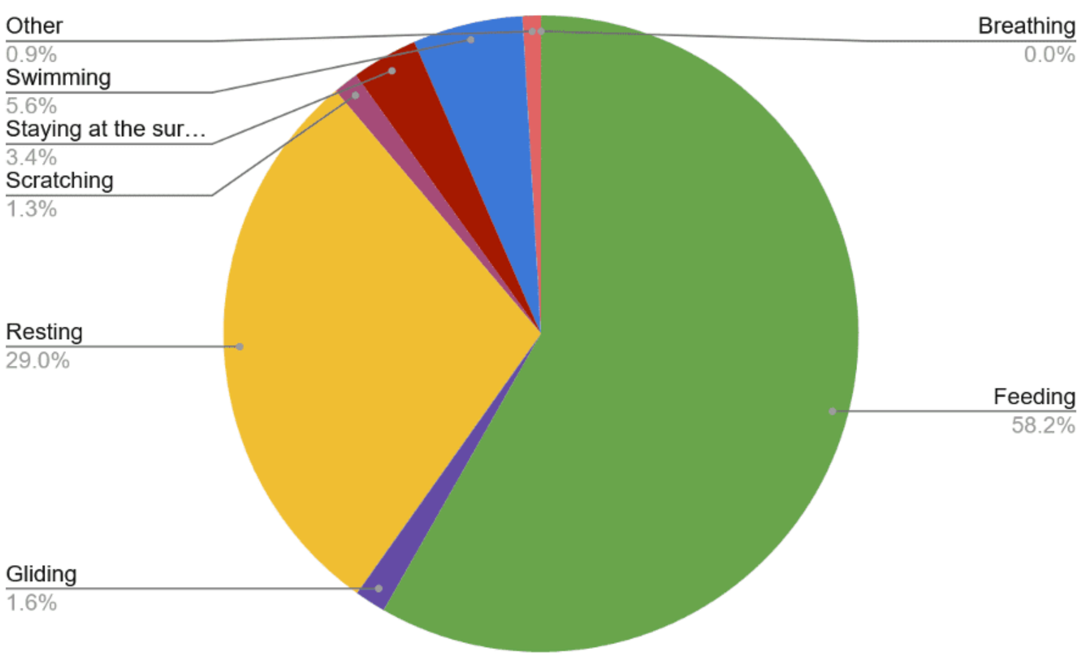

Figure 3. *Diagram representing the proportion of time allocated to the 44 behaviors grouped into eight broad categories for* E. imbricata *in Le Sec du Diamant from video analysis (n=2,914 behaviors recorded)*

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For the six individuals, all behaviors combined, the average dive depth was 15.5 ± 9.4 m, dive duration was 52.2 ± 40.9 minutes, and maximum depth was 17.8 ± 10.8 m. The deepest dive observed was 67.3 m for individual #7. At this depth range, seawater temperature records ranged from 25°C to 31°C. The behavior of the individuals differed in terms of dive duration ($p<0.001$, Kruskal-Wallis, $n=222$) and mean depth ($p<0.001$, Kruskal-Wallis, $n=222$).

For the feeding behaviors, the mean depth was 14.43 ± 9.72 m. The maximum dive depth during feeding was 44.4 ± 13.9 m. There was no significant difference in average feeding depth between individuals ($p>0.05$, ANOVA, $n=52$).

3.3. Diet composition

The mean bite rate was 9.01 bites/minute. The number of bites considered in the diet assessment was 3,434 over 74 hours and 45 minutes of recordings, of which 39 hours and 52 minutes of sequences with feeding activity were extracted and analyzed. From those 3,434 bites, 15% (n=531) involved Porifera. Twenty percent were categorized by the prey family (Fig. 13). Sixty-five percent (n=2,235) were noted in the category *Unknown*. The most observed prey families were Aplysinidae (27.6%), Tethyidae (15.5%), Chondrillidae (13.7%), and Sargassaceae (13.2%) (Fig. 4). Behaviors of grabbing the entire sponge or coralligenous habitat from the rock with their front flippers were observed. At the study site, most of the organisms eaten were placed under macroalgae, including *Sargassum* sp., or under giant barrel sponges (*Xestospongia muta).*

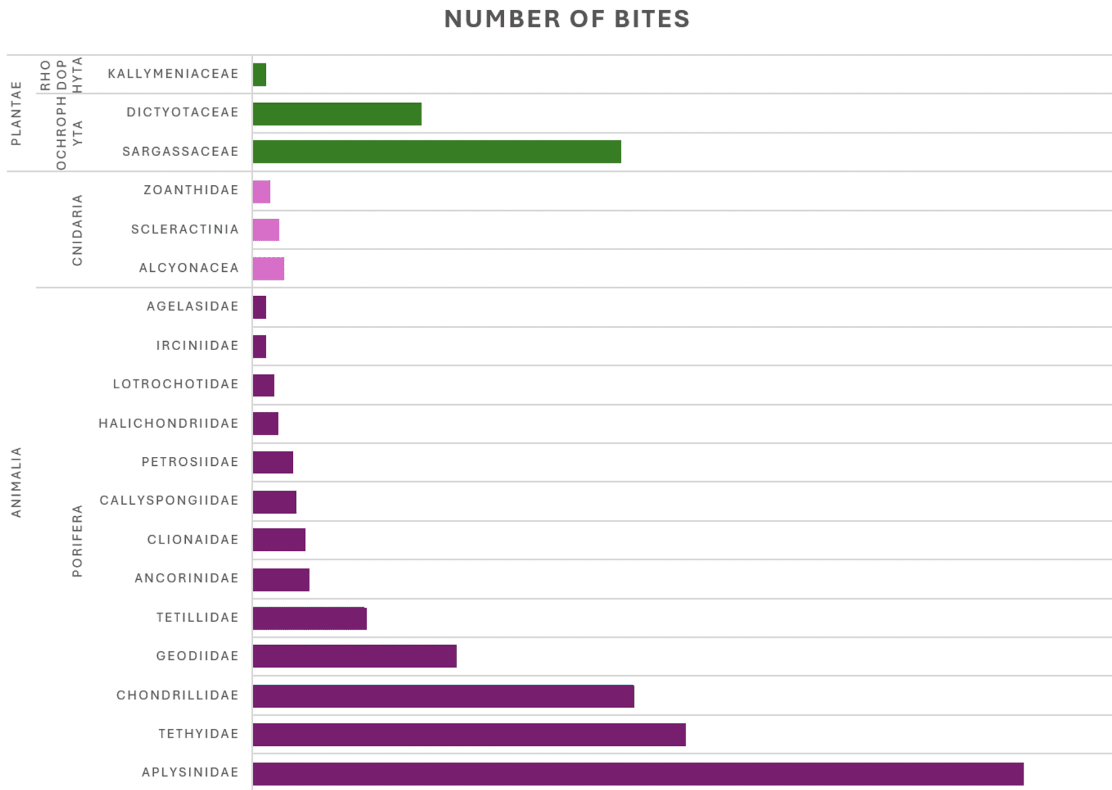

Figure 4. *Number of bites per family identified in the video analysis and attributed to a prey family (n=644)*

3.4. Prey selection

In total, 45 potential prey items were sampled, including 35 Porifera, one Cnidarian, and nine Plantae. Sixteen were sampled in the first transect, 6 in the second, and 16 again in the third transect. Some species were sampled in replicas along the different transects, such as *Xestospongia muta, Aiolochroia crassa, Verongula rigida, Ircinia felix, Hyattella cavernosa, Callyspongia vaginalis, Iotrochota birotulata,* and *Spirastrella coccinea* (Table 2). In total, 17 distinct species were identified, belonging to ten different families (Table 2). Samples were expertly analyzed through morphological analysis and DNA barcoding at Università Politecnica Delle Marche (UNIVPM) and Stazione Zoologica Anton Dohrn Napoli. Further results describing the presence of spicules, spongin fibers, and markers for DNA barcoding have been published in Labalme et al., in prep. Six families were identified both in the video recordings and in the habitat sampling: Aplysinidae, Irciniidae, Callyspongiidae, Petrosiidae, Tetillidae, and Agelasidae.

Six sponge families sampled in the study were compared to the 17 families identified as consumed prey in video recordings (hereafter referred to as consumed prey; Fig. 5). Among these, Aplysinidae was the most frequently observed family both as consumed and potential prey. Petrosiidae was sampled at least once in every transect and also recorded as consumed prey. Callyspongiidae, Iotrochotidae, Irciniidae, Agelasidae, and Tetillidae were each sampled at least once within the feeding habitat and were confirmed as consumed prey through video analysis. In contrast, Spongiidae, Niphatidae, and Spirastrellidae were identified exclusively as potential prey but were not observed being consumed. Conversely, Tethyida, Chondrillidae, Geodiidae, Halichondriidae, Clionaidae, and Ancorinidae were recorded as consumed prey but were not detected as potential prey in the habitat samples.

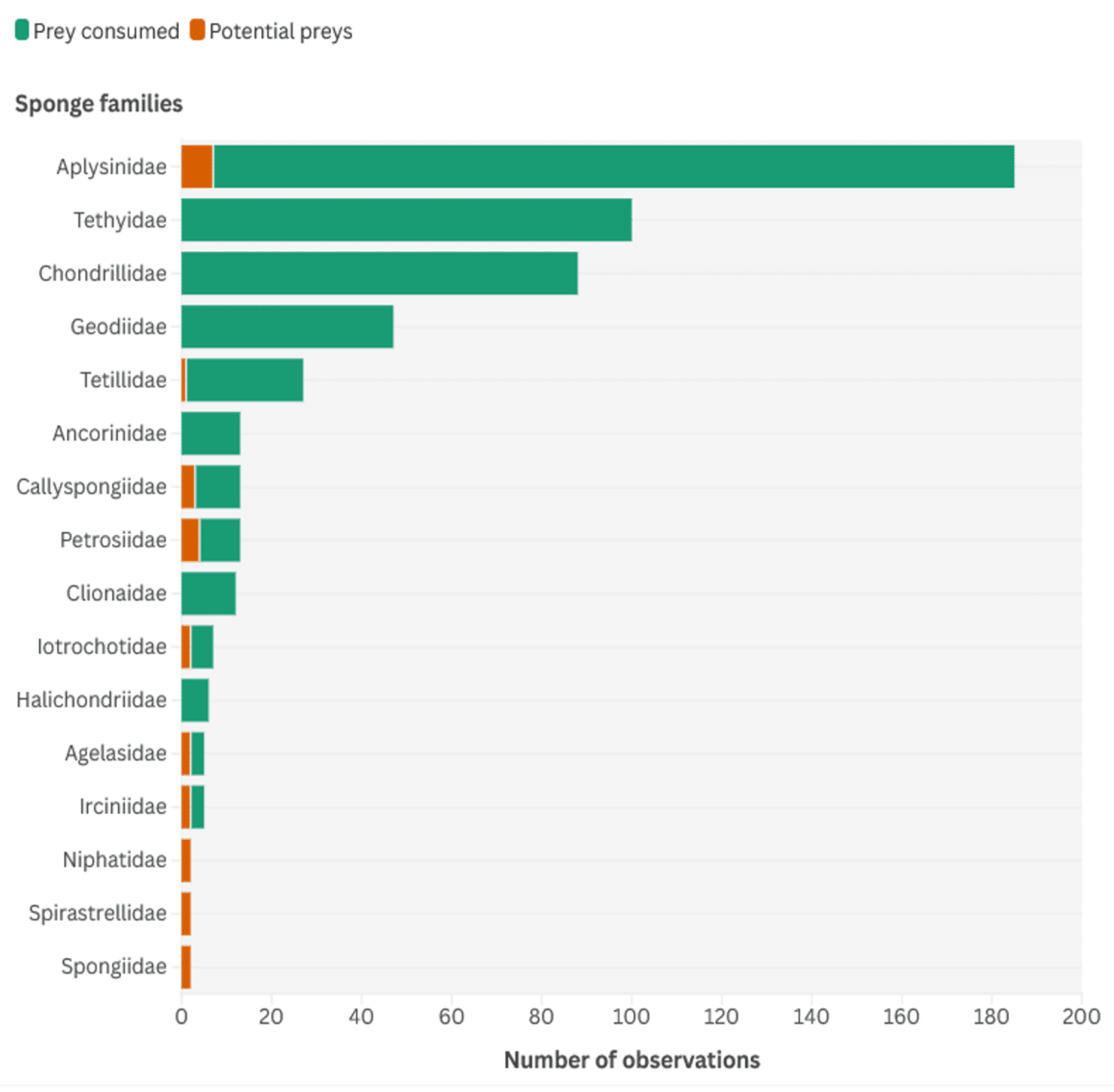

Figure 5. *Prey selection identified from prey consumed (observed in video recordings) compared to potential prey (habitat sampling)*

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Transect	Species	Family	Other
1	*Verongula rigida*	**Aplysinidae**	
	Ircinia felix	**Irciniidae**	
	Hyattela cavernosa	**Spongiidae**	
	Callyspongia vaginalis	**Callyspongiidae**	
	Callyspongia cf. pseudotoxa	Callyspongiidae	
	Neopetrosia rosariensis	**Petrosiidae**	
	Xestospongia muta	Petrosiidae	
	Cinachyrella kuekenthali	**Tetillidae**	
	Agelas clathrodes	**Agelasidae**	
	Iotrochota birotulata	**Iotrochotidae**	
	Spirastrella coccinea	**Spirastrellidae**	
			Unidentified tunicate
			Unidentified algae
2	*Aiolochroia crassa*	Aplysinidae	
	Verongula rigida	Aplysinidae	
	Ircinia felix	Irciniidae	
	Xestospongia muta	Petrosiidae	
	Agelas dispar	Agelasidae	
			Unidentified algae
3	*Aiolochroia crassa*	Aplysinidae	

Transect	Species	Family	Other
	Aplysina fulva	Aplysinidae	
	Aplysina insularis	Aplysinidae	
	Verongula rigida	Aplysinidae	
	Hyattella cavernosa	Spongiidae	
	Callyspongia vaginalis	Callyspongiidae	
	Amphimedon caribica	**Niphatidae**	
	Amphimedon compressa	Niphatidae	
	Xestospongia muta	Petrosiidae	
	Iotrochota birotulata	Iotrochotidae	
	Spirastrella coccinea	Spirastrellidae	
			Unidentified cnidarians
			Unidentified algae

Table 2. Species identified in three random transects in a foraging habitat of hawksbill turtles in Martinique.

*Items in bold are the ten family names of Porifera identified.

4. Discussion

This study highlights key findings, such as that hawksbills spend 55.4% of their time feeding and forage at depths of <20 m. In line with the initial objectives, a list of prey species was created for three distinct biogeographical regions. Food preferences were discovered in Martinique along with potential feeding strategies. This new data, never before collected, provides new insight into the feeding ecology and activity rhythm of this endangered species.

4.1. Size of individuals

In this study, one female was captured compared to five males. The size of the single female captured (CCL= 77 cm) was lower than those of the males found (CCL= 82.2 ± 1.76 cm); however, any further comparisons require additional research to detect any difference in size between females and males. The mean CCL of all individuals (81.9 cm) correlates with the mean CCL of males tracked in 2018 by Nivière et al.[7] (80.4 cm). However, other studies found smaller mean CCL[50][37] (Arabian Gulf: 70.8 cm, ; Eastern Pacific: 70.3 cm,). No juveniles were found during this study, contrary to our initial hypothesis. The presence of large males could be explained by the nesting beach in Le Diamant, located nearby, and the proximity of deeper waters[7].

4.2. Time-budget

This is the first study on free-ranging hawksbills showing that hawksbills express 44 different behaviors at different times of the day. Studied hawksbills allocated most of their time to feeding activity (>50%) and resting (<30%). Each individual spent on average eight hours feeding per day compared to captive hawksbills, which eat twice a day for better carapace growth and higher trypsin-specific activity[11]. This is the first study on the activity rhythm of free-ranging adult hawksbills and therefore cannot be compared with other studies. A study on captive individuals concluded that they feed twice a day with a long time interval[11]. That said, studies on green sea turtles and freshwater turtles demonstrated that nocturnal activity could be exhibited to acquire nocturnal resources that influence their survival and reproduction[51][52][53].

It is important to highlight that hawksbill turtles frequently use their forelimbs to manipulate prey, particularly when feeding in strong currents or extracting food from crevices. Additionally, they exhibit prolonged and variable foraging behavior, prospecting for food throughout the day. These behavioral nuances represent a key distinction from green sea turtles and posed a challenge in the behavioral classification process. As reported by Jeantet et al.[54], early applications of the V-Net model—originally trained on green turtle data—often misclassified hawksbill feeding events as swimming due to the overlapping use of flipper movements. However, classification accuracy improved markedly with the incorporation of transfer learning from human activity datasets, which allowed the model to better distinguish between similar motion patterns associated with different behavioral contexts.

Behavioral patterns observed in this study suggest that hawksbills exhibit distinct diel activity, with diurnal resting occurring in some individuals—particularly within the first day post-capture—followed by a full day dedicated to foraging. Importantly, the use of animal-borne video devices appears to have had minimal behavioral impact, consistent with findings in juvenile green sea turtles, which showed no significant stress response up to 90 minutes after deployment[55]. Resting areas are particularly important for reproductive females, who allocate energy toward clutch development[56][57]. Coral reefs can function as foraging habitats, resting sites, or refuges against predators, depending on the reproductive strategy employed—capital versus income breeding—particularly during the internesting period[58]. In our study, one female exhibited intense foraging activity during ten hours of monitoring, consistent with an income-breeding strategy at the end of the nesting season[26][59], while males engaged in resting behavior across both days, suggesting inter-individual variability in energy allocation.

It is interesting to note that the same male individual was recaptured twice within a one-month interval, confirming high site fidelity to feeding grounds, as previously observed in male hawksbills in Martinique, as well as in Australia and Barbados[58][7][60].

Although hawksbills are generally characterized as diurnal—active during the day and resting at night[61] —these findings highlight the need for longer-term and sex-specific behavioral tracking. Activity budgets are expected to vary in response to seasonal shifts in both biotic and abiotic factors, further emphasizing the importance of continuous monitoring during key life history stages[61]. In this context, advanced analytical tools such as V-Net offer valuable potential to bridge existing gaps in behavioral knowledge, enabling more nuanced and scalable interpretations of fine-scale animal movement and activity.

Scratching behavior, generally attributed to self-cleaning and ectoparasite removal[62], accounted for 1.1% of the total time budget in this study. This behavior was commonly observed across individuals, occurring on both hard substrates such as rocks and on giant barrel sponges (*Xestospongia muta*). Interestingly, video footage also revealed behaviors consistent with those described by Sazima et al.[63], who documented hawksbills positioning themselves at shrimp cleaning stations, potentially engaging in symbiotic interactions with barber pole shrimp (*Stenopus hispidus*). In their observations, turtles adjusted their posture to expose specific body parts—such as the hind limbs or posterior shell—under rocky ledges to facilitate cleaning.

Similar postures were recorded in the present study, particularly near *X. muta*, where shrimp were frequently noted. Although the downward-facing camera did not allow clear visualization of cleaning stations or shrimp identity, the turtles' positioning suggests that such interactions could be occurring. However, without direct visual confirmation or species-level identification of the shrimp, this remains speculative. Future studies, potentially combining behavioral observations with shrimp sampling and stationary external cameras, are needed to determine whether symbiotic cleaning interactions occur at Le Sec du Diamant.

Surfacing was observed for respiratory purposes only, with short surface intervals of 1 min 44 s ± 5 min 15 s. These values coincide with the research done on hawksbills by Storch et al.[64] at Buck Island, Caribbean. Other sea turtle species have been reported to spend considerable amounts of time at the surface for thermoregulation and the control of ectoparasites alongside gaseous exchange[65]. However, no diurnal basking was observed in the video recordings. Hawksbills are diving ectotherms, i.e., they regulate their body temperature with the environmental temperature. They rely entirely on gas exchanges at the water surface and have a time budget influenced by dive time and depth. They have high internal heat-storage capacities and therefore thermal inertia[64]. In addition, some turtles such as *Chelonia mydas* are capable of controlling heat exchange with the environment through variable blood circulation in the front flippers. It is probable that hawksbills have similar patterns, although no studies have been done[66][64]. A myriad of physiological responses to temperature have been studied, including duration of gastric and intestinal digestion, intestinal glucose transport, frequency of gastric contractions, digestive efficiency, and metabolic rate[64]. Furthermore, it has been proved that environmental temperature and gut microbial communities can have profound impacts on the digestive performance of ectothermic vertebrates. Additionally, the diversity, composition, and function of gut microbial communities themselves are influenced by temperature[67]. The synchronization of body temperature regulation and food strategies might have a strong correlation that should be taken into account when comparing diving profiles, including diurnal and nocturnal basking.

Interactions between individuals were underrepresented in the average time budget (0.13%) due to brief events. Males are known to be sedentary and to express aggressive social behavior related to resource competition, which coincides with the observations noted during this study and other studies[68]. Competition is speculated to play a role in the vertical partitioning of habitat to decrease conspecific competition and ultimately increase the carrying capacity of foraging areas[69][70]. Other social behavior observed in previous studies, such as head touching where hawksbills would rub the sides of their faces together, was observed once in this study[68]. This type of interaction has previously been shown to be a form of intraspecific communication in green sea turtles[40][71].

It should also be noted that this study provides critical supporting evidence that ghost nets and bycatch remain an active and underestimated threat in the Caribbean. Although the 'trapped in net' behavior accounted for less than 0.1% of the total observed time in this study, the presence of this behavior is not only statistically significant—it is ecologically alarming. In a sample of just six individuals, one was visually confirmed to be entangled in a ghost net in under three days. This direct observation, combined with the fact that multiple turtles required physical rescue during the course of the research, strongly suggests that such incidents may be more frequent than what behavioral data alone can capture (Delvenne & Chevallier, pers. obs.)[72]. Wallace et al.[6] echo this concern, highlighting that ghost gear continues to impact sea turtles and other marine megafauna with increasing regularity, even in areas thought to be relatively well-managed. The apparent rarity in the data likely reflects the limitations of behavioral monitoring tools in detecting brief or fatal entanglement events, rather than an absence of the threat itself. These findings underscore the urgency of improving studies on the reduction of accidental catches, ghost gear removal initiatives, enhancing in-water surveillance, and fostering region-wide collaboration to address what remains a persistent and insidious danger to marine biodiversity.

Our results support the idea that hawksbills perform shallow (0–20 m) and long dives (60–70 min), as researched by Gaos et al.[73] and Nivière et al.[7]. At these depths, sponges dominate both in terms of biomass and diversity due to the greater availability of light[22]. As hawksbills spend more than half of their time feeding, this could explain why they spend most of their time at depths from 0 to 30 m. Feeding activities were observed at various depths ranging from 5 m to 44 m (on average 14.43 ± 9.72 m). This shows that they eat a greater variety of prey, meaning that they could reach various depths or habitats depending on their opportunistic feeding. Dive durations were on average longer than 50 min, supporting the observation that hawksbills make some of the longest dives of all sea turtles[65][7]. The maximum depth recorded was 67.3 m, by a male.

The mean temperature experienced by hawksbills is similar to the mean temperature recorded in 2018 (27–32°C) in Nivière et al.[7].

4.3. Diet composition and Habitat Sampling

Understanding the dietary composition of hawksbill turtles is essential to uncovering their ecological role within coral reef ecosystems[21]. In this study, video analysis provided a rare, fine-scale perspective of hawksbill foraging behavior in Martinique, revealing that Porifera accounted for 75% of observed feeding activity. Despite some visual constraints from the dorsal camera angle, 17 prey species were successfully identified in the lab, including Aplysinidae and Irciniidae—Porifera families not previously cited as part of the hawksbill diet. These results highlight potential regional dietary variation and reinforce the value of detailed video analysis and habitat-based sampling to uncover overlooked prey and refine our understanding of hawksbill foraging ecology.

It should be noted that the species sampled and analyzed in the laboratory are not an exhaustive list of diet items. Some prey were observed in video recordings but not sampled due to diving constraints, such as strong currents and limited bottom time. Le Sec du Diamant, a high-density sponge reef, presents complex vertical structures with overlapping species, making it difficult for divers to accurately identify and collect prey in real time, unlike hawksbills, which appear adept at discriminating among them[22][74].

To complement the video data, 45 prey samples were collected from the habitat, including some species observed multiple times in the videos. Given the limited ecological knowledge of hawksbills and the difficulty in clearly identifying all prey on video, these habitat samples serve as a valuable reference and underscore the need for broader sampling[75][76][77]. Many sponge species remain hidden in crevices or caves, are difficult to access, or pose hazards such as venomous defenses[78][79].

Habitat sampling reinforced the observation that Aplysinidae sponges are abundant in hawksbill foraging grounds and were frequently recorded in the video dataset. As 17 distinct species were identified in this study, these findings could inform future studies exploring prey availability and selection in hawksbill habitats. Notably, several families were confirmed across all three datasets—video, field sampling, and laboratory identification—including Aplysinidae, Irciniidae, Callyspongiidae, Petrosiidae, Tetillidae, and Agelasidae.

Aplysinidae, part of the order Verongida, previously unreported as a hawksbill diet item, was the most prevalent family observed in both the video and habitat samples. This family, including species such as *Aplysina insularis*, is known along the Caribbean and eastern Brazilian coasts. *Verongula rigida*, another member of this family, is a known prey for spongivorous fishes like angelfishes and parrotfishes[80]. In the East Pacific Ocean, Wedemeyer-Strombel et al.[75] suggested that hawksbills may incorporate

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mangrove-associated sponges such as *Aplysina* spp. into their diets, based on stable isotope data, though direct observations were lacking. Our findings confirm for the first time that Aplysinidae sponges are indeed consumed by hawksbills in the Caribbean. Notably, this sponge family is of growing interest in biomedical research due to its production of brominated metabolites derived from tyrosine, an amino acid. These compounds exhibit a range of biological activities, including antimicrobial, enzymatic, cytotoxic, and antiparasitic effects[81]. Interestingly, Wood[82] reported that tyrosine is non-essential for hatchling green sea turtles (*Chelonia mydas*), raising new hypotheses regarding potential differences in amino acid requirements between hawksbills and other turtle species, between life stages, or possibly as an adaptive response to shifting reef ecosystems.

Irciniidae, identified in two transects, were also consumed multiple times by hawksbills. This family is ecologically and chemically diverse, with a widespread distribution and a rich associated microbiota[83][84][85]. Their high microbial diversity includes bacterial, fungal, and archaeal species, making them a target for pharmaceutical research. While never before cited as part of the hawksbill diet, our findings suggest they may be consumed for their microbial symbionts. Future work using stable isotope analysis would help confirm their role in the hawksbill diet.

Callyspongiidae were also observed as being consumed in video recordings and were later sampled and identified to the species level (*Callyspongia vaginalis, Callyspongia* cf. *pseudotoxa*). Though not previously cited in hawksbill diet studies, Lesser[86] noted that members of this family are preyed upon by a variety of reef organisms. With a global distribution and tolerance for temperatures from 5°C to 30°C, Callyspongiidae produce a wide array of bioactive compounds[87], including those with antibacterial[88], antituberculosis[89], and anti-inflammatory activities[90].

Petrosiidae sponges, particularly *Xestospongia muta*—the giant barrel sponge—are dominant and ecologically important components of Caribbean reef ecosystems. They have been widely studied for their large size, structural role in the reef, and sensitivity to bleaching events[91][92][93]. In this study, *X. muta* was identified in laboratory samples, and hawksbills were observed foraging near these sponges in the video recordings. As *X. muta* supports diverse microbial communities that play a critical role in nutrient cycling[94], prey species living in its proximity may be particularly appealing to hawksbills due to this enriched microhabitat.

Baumbach et al.[76] explored the nutritional value of *X. muta*, comparing it with prey species actually consumed by hawksbills, such as *Geodia neptuni* and *Kallymenia limminghi*. In our video data, Geodiidae

doi.org/10.32388/FKTVC0

appeared as part of the hawksbill diet, yet were absent from habitat samples—suggesting they may occur in deeper or inaccessible microhabitats at Le Sec du Diamant, beyond the scope of our transects. Despite their structural defenses—such as high spongin and collagen content that gives Geodiidae a dense, rubbery texture[95][96][97])—these sponges may still be preferred for their rich biochemical profile, including glycoproteins, acid polysaccharides, and carbohydrate-rich matrices[36][98]. The Aplysinidae family has similar characteristics and was also observed as prey during video recordings. These nutritional benefits could outweigh the physical challenges of ingestion, explaining why hawksbills invest substantial foraging time on them. Indeed, Baumbach et al.[76] showed that hawksbills prioritize prey with higher nutritional value and availability—such as *G. neptuni* and *K. limminghi*—over less nutritious or harder-to-access options like *X. muta* or *Halimeda opuntia*. This selective behavior supports the idea that hawksbills may establish home ranges where high-energy prey is concentrated, optimizing their foraging efficiency.

Additionally, Chondrillidae and Tethyidae, the second most observed family in the video recordings, are part of the most diverse environment on Earth due to their High Microbial Abundance (HMA)[99]. Three of the most recorded sponges, namely *Geodia* sp., *Chondrilla nucula*, and *Chondrosia* sp., have a high HMA. These sponges can derive up to 60% of their heterotrophic diet from their bacterial symbiosis, whereas Low Microbial Abundance (LMA) sponges can only obtain <1% of their diet from their bacterial symbiosis[100][101]. The LMA species cited as prey in the literature but not observed during video recording is *Placospongia* sp.[102]. Unlike scleractinian corals that can associate with a particular *Symbiodinium* species[103][104]), sponges can host extremely complex and diverse symbiont communities that are not strictly pairwise or even endosymbiotic[105]. Microbial communities associated with prey organisms could bring additional nutritional value to hawksbills.

Tetillidae were previously reported as hawksbill prey in several regions, including Honduras, Costa Rica, Puerto Rico, and Turks & Caicos[106][107][108][4]. In this study, *Cinachyrella kuekenthali* was identified from both video and lab analyses, consistent with past reports citing other *Cinachyrella* species and *Craniella* spp. as diet items. Agelasidae were also documented in our dataset and have been previously cited as hawksbill prey[109], further confirming their relevance in hawksbill foraging ecology.

Sargassum sp., a recurrent component of the diet of hawksbills both in the video analysis and in the literature, has started invading the Martinique coast in recent years[110]. This invasion has had a huge impact on the entire marine ecosystem. Macroalgae have been reported as an overall threat to reefs

doi.org/10.32388/FKTVC0

throughout the Mesoamerican Reef, as coral health continues to degrade and algae outcompete corals for space[111]. This was noted during video analysis, as Le Sec du Diamant is covered by growing macroalgae, including *Sargassum* sp. This could lead to a change in habitat composition and in the ecosystem. The result would be a change in food selection or even a change of habitat, making them move to other locations or die if they do not have the ability to find other resources.

Sargassaceae, Dictyotaceae, and Kallymeniaceae were identified during the video analysis. These were largely cited in the literature as part of hawksbills′ diet along with other plant organisms (Chlorophyta, Tracheophyta, Phaeophyta, and Rhodophyta). Sargassum sp., a macroalga from the Sargassaceae family, was a recurrent component observed in the hawksbills’ diet and is increasingly invading the Martinique coast, significantly impacting the marine ecosystem[110]. This proliferation, also noted at le Sec du Diamant, threatens coral health by outcompeting them for space[111], potentially altering habitat composition and food availability. Consequently, hawksbills may need to adapt their feeding strategies, relocate, or face survival challenges. The selection of plants by hawksbills could be explained by the fact that they are easily digestible and that they might help to facilitate the passage of copious sponge spicules[16]. It has been studied that brown and green algae have high lipid and polysaccharide content that could have lubrication properties[112][113]. Some red algae have less lipid and polysaccharide content[114]. However, some red algae, e.g., *K. limminghii*, which is part of hawksbills’ diet in Honduras, have a lipopolysaccharide mucus content that can protect against damage to the gastrointestinal tract by sponge spicules[76]. Unfortunately, only 0.001% of plants were observed in the video analysis, but it is likely the actual percentage is larger. It should be noted that 75% of bites were categorized under ″Unknown″ as no clear image could be observed due to the tilt of the camera.

4.4. Recommendations for future studies

To enhance our understanding of hawksbill turtle feeding strategies, we recommend the implementation of a multidisciplinary methodological framework in future research. This approach should combine video recordings with complementary analytical techniques to enable a more comprehensive and ecologically relevant interpretation of foraging behavior. Stable isotope analysis will allow for the inference of long-term dietary patterns and habitat use across ontogenetic stages[75], while chemical profiling of prey can reveal bioactive compounds that may influence prey selection[115]. Quantitative assessments of protein and nutrient content are necessary to evaluate the energetic value of consumed items, e.g., bomb calorimetry[76], and microbial and symbiosis studies are essential to understanding how

doi.org/10.32388/FKTVC0

sponge-associated microbiomes may alter prey nutritional properties, particularly through modifications of carbon-to-nitrogen ratios[101]. Notably, sponge species such as *Haliclona* sp. may utilize dissolved organic matter (DOM) via specialized microbial symbionts, making them especially valuable to hawksbills and supporting optimal foraging theory[116], whereby individuals select energetically rewarding prey even at higher handling costs—a pattern also observed in bird species[117]. To assess prey availability and its influence on foraging choices, habitat assessments using standardized benthic transects should be conducted in key feeding areas such as Le Sec du Diamant, following the methodology proposed by Baumbach et al.[76]. These ecological data, when interpreted alongside behavioral observations and dietary analysis, will provide a more nuanced understanding of hawksbill foraging ecology.

In parallel, the development and application of technological innovations are critical. The continued refinement of machine learning models such as the V-Net[54], which enables automated detection of hawksbill behaviors from video footage, is particularly promising. Once trained and validated, V-Net will facilitate the deployment of advanced biologgers—including tri-axial accelerometers, gyroscopes, and magnetometers—over extended periods ranging from one week to several months. These tools will improve our capacity to monitor individual movements and habitat use, thereby contributing to the delineation of important feeding zones both in Martinique and in international waters. One of the main threats in Martinique's waters is accidental bycatch (ghost nets and gillnets)[6][71]. Efforts to reduce existing threats in Martinique and international waters should be embedded within a framework of international scientific collaboration, drawing on expertise across laboratories to co-develop conservation strategies that integrate novel technologies, rigorous diet analysis, and local ecological knowledge[75][118].

Finally, it is crucial to recognize that scientific insights alone are not sufficient for effective conservation. Translating research into impact requires clear and compelling science communication, ranging from peer-reviewed articles and public engagement through documentaries and social media to direct dialogue with policymakers and coastal communities. Collaborations with communication professionals can help ensure that complex findings are conveyed accurately and persuasively. Furthermore, the adoption of standardized, open-access data-sharing protocols will support coordinated international research and conservation actions, particularly for migratory marine species like hawksbill turtles that traverse multiple geopolitical jurisdictions. This integrative and collaborative model is essential for the long-term protection of this critically endangered species.

Supplementary Materials

Category	*Behavior*	*Definition*	
Breathing	Turtle is breathing one time at the surface		
Feeding	Chewing on movement	Turtle is chewing and keeps swimming	
	Chewing stationary	Turtle is chewing while landing at the bottom	
	Chewing in the flow	Turtle is chewing in the flow, leading to passive movement	
	Grabbing on movement	Turtle is grabbing prey at the bottom and keeps swimming	
	Grabbing stationary	Turtle is grabbing prey while landing at the bottom	
	Grabbing in the flow	Turtle is grabbing prey in the flow, leading to passive movement	
	Feeding	Turtle is eating	
	Feeding stationary	Turtle is eating at the bottom	
	Feeding on movement	Turtle is eating while swimming	
	Feeding in the flow	Turtle is eating in the flow, leading to passive movement	
	Holding with flippers	Turtle is holding prey with two front flippers	
	Looking for prey	Turtle is actively looking for prey	
	Moving head forward into crevices	Turtle is moving its head into crevices	
Gliding	Gliding ascent	Turtle is swimming passively without a flipper beat toward the surface	
	Gliding descent	Turtle is swimming passively without a flipper beat toward the bottom	
Resting	Resting	Turtle is resting at the bottom without moving	

doi.org/10.32388/FKTVC0

Category	*Behavior*	*Definition*	
	Resting active	Turtle is resting at the bottom but is agitated and moves its head	
	Resting in flow	Turtle is resting in the flow, leading to passive body movement	
	Resting watching	Turtle is resting at the bottom, watching behind it	
Scratching	Scratching	Turtle is scratching its shell	
	Scratching head	Turtle is scratching its head	
	Scratching camera	Turtle is scratching, and the camera touches a rock or other element	
Staying at the surface	Turtle is breathing several times at the surface		
Swimming	Stepping back	Turtle is moving backward at the bottom	
	Swimming horizontally	Turtle is swimming horizontally	
	Swimming ascent	Turtle is swimming toward the surface	
	Swimming descent	Turtle is swimming toward the bottom	
	Swimming fast ascent	Turtle is swimming fast toward the surface	
	Swimming fast descent	Turtle is swimming toward the bottom	
	Swimming fast horizontally	Turtle is swimming fast horizontally	
	Swimming in place	Turtle is swimming but stays in place	
	Swimming on the seafloor	Turtle is moving while landing at the bottom	
	Prospection	Turtle is swimming slowly, prospecting to the right and to the left	
	Watching	Turtle is swimming, watching behind it	
	Left U-turn	Turtle is turning to the left	
	Right U-turn	Turtle is turning to the right	
Unknown	Escape	Turtle is escaping to avoid aggression from another turtle	

Category	*Behavior*	*Definition*
	Touching	Turtle is touching a second turtle
	Foraging	Turtle is touching the bottom to search for something
	Landing	Turtle is abruptly landing at the bottom
	Obstacle	Turtle is encountering an obstacle
	Pursuit	Turtle is pursuing a second turtle
	Trapped in net	Turtle got caught in a net while swimming underwater

Table S.1. Detailed definition of each behavior and its repartition into broader categories

Kingdom	Phylum	Class	Order	Family
Animalia	Cnidaria	Anthozoa	Alcyonacea	
			Zoantharia	Zoanthidae
			Scleractinia	
	Porifera	Demospongiae	Agelasida	Agelasidae
			Chondrosida	Chondrillidae
			Dictyoceratida	Irciniidae
			Hadromerida	Clionaidae
				Tethyidae
			Haplosclerida	Petrosiidae
				Callyspongiidae
			Poecilosclerida	Iotrochotidae
			Suberitida	Halichondriidae
			Tetractinellida	Tetillidae
				Geodiidae
				Ancorinidae
			Verongiida	Aplysinidae
Plantae	Phaeophyta	Phaeophyceae	Fucales	Sargassaceae
			Dictyotales	Dictyotaceae
	Rhodophyta	Florideophyceae	Gigartinales	Kallymeniaceae

Table S.2. Prey families identified during video analysis

Statements and Declarations

Conflicts of Interest

The author certifies that there is no conflict of interest over this article.

Funding

Funding Open access funding provided by Université des Antilles. The Program BEPHYTES of the Centre National de la Recherche Scientifique (CNRS) was co-funded by the FEDER Martinique (Fonds Européen de Développement Régional PO/FEDER/FSE 2014–2020, Conventions 246239), Collectivité Territoriale de Martinique (CTM, convention 258342), the Direction de l'Environnement, de l'Aménagement et du Logement (DEAL, Martinique, France (Convention N°2017/164894), the Office De l'Eau (ODE) Martinique, France (Convention n°180126) and the Office Français de la Biodiversité (OFB, Parc Naturel Marin de Martinique, OFB-23-0563), the town of Les Anses d'Arlet and ANSLO'S. The Program TOPASE of the CNRS was funded by Fonds Européen pour les affaires maritimes et la pêche (FEAMP), the Minister of Agriculture and FranceAgriMer.

Acknowledgments

This study was carried out within the framework of the Plan National d'Action Tortues Marines Antilles. We are grateful to the numerous volunteers and free divers for their participation in the field operations.

References

1. ^*McKeever A (2022). "What are keystone species?" National Geographic.*
2. a, b*Paine RT (1966). "Food Web Complexity and Species Diversity." The American Naturalist.* ***100****(910):65–75. http://www.jstor.org/stable/2459379.*
3. a, b*Hamann M, Godfrey MH, Seminoff JA, Arthur K, Barata PCR, Bjorndal KA, et al. (2010). "Global research priorities for sea turtles: Informing management and conservation in the 21st century." Endangered Species Research.* ***11****(3):245–269. doi:10.3354/esr00279.*
4. a, b*Stringell TB, Clerveaux WV, Godley BJ, Kent FEA, Lewis EDG, Marsh JE, Phillips Q, Richardson PB, Sanghera A, Broderick AC (2016). "Taxonomic distinctness in the diet of two sympatric marine turtle species." Marine Ecology.* ***37****(5):1036–1049. doi:10.1111/MAEC.12349.*

5. [a, b] *Mortimer JA, Donnelly M (IUCN SSC Marine Turtle Specialist Group) (2008). "Eretmochelys imbricata." The IUCN Red List of Threatened Species 2008: e.T8005A12881238. doi:10.2305/IUCN.UK.2008.RLTS.T8005A12881238.en.*

6. [a, b, c] *Wallace B, Bandimere A, Abreu-Grobois F, Acosta H, Akiti J, Akomedi M, Alfaro-Shigueto J, Allen C, Angenda D, Ayissi I, Azanza Ricardo J, Barrientos-Muñoz K, Barrios-Garrido H, Bjorndal K, Bretón Vargas E, Broderick A, Calderón Peña R, Carreras C, Ceriani S, Mast R (2025). "Updated global conservation status and priorities for marine turtles." Endangered Species Research.* ***56****:247–276. doi:10.3354/esr01385.*

7. [a, b, c, d, e, f, g, h, i, j, k, l, m, n, o, p] *Nivière M, Chambault P, Pérez T, Etienne D, Bonola M, Martin J, et al. (2018). "Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle." Biological Conservation.* ***223****:170–180. doi:10.1016/J.BIOCON.2018.05.002.*

8. [a, b, c, d] *Siegwalt F, Jeantet L, Lelong P, Martin J, Girondot M, Bustamante P, Benhalilou A, Murgale C, Andreani L, Jacaria F, Campistron G, Lathière A, Barotin C, Buret-Rochas G, Barre P, Hielard G, Arqué A, Régis S, Lecerf N, Chevallier D (2022). "Food selection and habitat use patterns of immature green turtles (Chelonia mydas) on Caribbean seagrass beds dominated by the alien species Halophila stipulacea." Global Ecology and Conservation.* ***37****:e02169. doi:10.1016/J.GECCO.2022.E02169.*

9. [a, b] *Meylan AB (1999). "Status of the Hawksbill Turtle (Eretmochelys imbricata) in the Caribbean Region." Chelonian Conservation and Biology.* ***3****(2):177–184.*

10. [a, b, c, d] *von Brandis RG, Mortimer J, Reilly BK, van Soest R, Branch G (2014). "Diet Composition of Hawksbill Turtles (Eretmochelys imbricata) in the Republic of Seychelles." Western Indian Ocean J. Mar. Sci. https://www.researchgate.net/publication/281086919_Diet_Composition_of_Hawksbill_Turtles_Eretmochelys_imbricata_in_the_Republic_of_Seychelles.*

11. [a, b, c] *Jualaong S, Kanghae H, Thongprajukaew K, Saekhow S, Amartiratana N, Sotong P (2021). "Optimal feeding frequency for captive hawksbill sea turtle (Eretmochelys imbricata)." Animals.* ***11****(5):1252. doi:10.3390/ANI11051252.*

12. [^] *Clyde-Brockway CE, Heidemeyer M, Paladino FV, Flaherty EA (2022). "Diet and foraging niche flexibility in green and hawksbill turtles." Marine Biology.* ***169****(8):108. doi:10.1007/S00227-022-04092-1.*

13. [^] *Reich KJ, Bjorndal KA, Bolten AB (2007). "The lost years of green turtles: using stable isotopes to study cryptic lifestages." Biology Letters.* ***3****(6):712–714. doi:10.1098/RSBL.2007.0394.*

14. [^] *Bjorndal KA (1997). "Foraging ecology and nutrition of sea turtles." The Biology of Sea Turtles.* ***1****(1):199–231.*

15. ^Bolten AB (2003). "Variation in sea turtle life history patterns: Neritic vs. oceanic developmental stages." The Biology of Sea Turtles. **2**:243–257.

16. a, b, c, dMeylan A (1988). "Spongivory in Hawksbill Turtles: A Diet of Glass." Science. **239**(4838):393–395. https://www.jstor.org/stable/1700236?seq=1#metadata_info_tab_contents.

17. ^Bjorndal KA, Bolten AB (2010). "Hawksbill sea turtles in seagrass pastures: Success in a peripheral habitat." Marine Biology. **157**(1):135–145. https://doi.org/10.1007/S00227-009-1304-0/FIGURES/8.

18. ^Martínez-Estévez L, Steller DL, Zilliacus KM, Cuevas Amador JP, Amador FC, Szuta D, Miller SD, Dayton GH, Tershy BR, Croll DA (2022). "Foraging ecology of critically endangered Eastern Pacific hawksbill sea turtles (Eretmochelys imbricata) in the Gulf of California, Mexico." Marine Environmental Research. **174**:105532. doi:10.1016/j.marenvres.2021.105532.

19. ^Van Dam RP, Diez CE (1997). "Surfacing Behavior of the Marine Turtle Eretmochelys imbricata." Journal of Herpetology. https://www.widecast.org/What/Country/PuertoRico/Docs/vanDam&Diez_(1997)_Hawksbill_surfacing_behavior.pdf.

20. a, b, c, d, e, f, gPawlik JR, Loh TL, McMurray SE (2018). "A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: What's old, what's new, and future directions." PeerJ. **2018**(1):e4343. doi:10.7717/PEERJ.4343/FIG-4.

21. a, bLeón YM, Bjorndal KA (2002). "Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems." Marine Ecology Progress Series. **245**:249–258. doi:10.3354/MEPS245249.

22. a, b, c, d, e, fPérez T, Díaz MC, Ruiz C, Cóndor-Luján B, Klautau M, Hajdu E, et al. (2017). "How a collaborative integrated taxonomic effort has trained new spongiologists and improved knowledge of Martinique Island (French Antilles, eastern Caribbean Sea) marine biodiversity." PLOS ONE. **12**(3):e0173859. doi:10.1371/JOURNAL.PONE.0173859.

23. ^Rossi M, Safi M, de Montgolfier B (2025). "First Characterization of Nesting Behaviors of Leatherback Turtles (Dermochelys coriacea) and Hawksbill Turtles (Eretmochelys imbricata) in Martinique and Inter-Species Comparison." Wild. **2**(2):12. doi:10.3390/wild2020012.

24. ^Ferreira RL, Ceia FR, Borges TC, Ramos JA, Bolten AB (2018). "Foraging niche segregation between juvenile and adult hawksbill turtles (Eretmochelys imbricata) at Príncipe Island, West Africa." Journal of Experimental Marine Biology and Ecology. **498**:1–7. doi:10.1016/J.JEMBE.2017.10.005.

25. ^Hays G, Hobson V, Metcalfe J, Righton D, Sims D (2006). "Flexible foraging movements of leatherback turtles across the North Atlantic Ocean." Ecology. **87**(10):2647–2656. https://doi.org/10.1890/0012-9658(2006)87[2647:FFMOLT]2.0.CO;2.

26. [a, b]*Plot V, Jenkins T, Robin JP, Fossette S, Georges JY (2013). "Leatherback Turtles Are Capital Breeders: Morphometric and Physiological Evidence from Longitudinal Monitoring." Physiological and Biochemical Zoology.* ***86****(4):385–397. doi:10.1086/671127.*

27. [a, b, c, d, e]*Jeantet L, Planas-Bielsa V, Benhamou S, Geiger S, Martin J, Siegwalt F, et al. (2020). "Behavioural inference from signal processing using animal-borne multi-sensor loggers: A novel solution to extend the knowledge of sea turtle ecology." Royal Society Open Science.* ***7****(5):200139. doi:10.1098/rsos.200139.*

28. [^]*Jeantet L, Vigon V, Geiger S, Chevallier D (2021). "Fully Convolutional Neural Network: A solution to infer animal behaviours from multi-sensor data." Ecological Modelling.* ***450****:109555. doi:10.1016/j.ecolmodel.2021.109555.*

29. [^]*Pawlik JR (2011). "The Chemical Ecology of Sponges on Caribbean Reefs: Natural Products Shape Natural Systems." BioScience.* ***61****(11):888–898. doi:10.1525/bio.2011.61.11.8.*

30. [^]*McClenachan L, Jackson JBC, Newman MJH (2006). "Conservation implications of historic sea turtle nesting beach loss." Frontiers in Ecology and the Environment.* ***4****(6):290–296. https://doi.org/10.1890/1540-9295(2006)4[290:CIOHST]2.0.CO;2.*

31. [^]*Pawlik JR, Burkepile DE, Thurber RV (2016). "A Vicious Circle? Altered Carbon and Nutrient Cycling May Explain the Low Resilience of Caribbean Coral Reefs." BioScience.* ***66****(6):470–476. doi:10.1093/BIOSCI/BIW047.*

32. [^]*Crabbe MJC (2008). "Climate change, global warming and coral reefs: Modelling the effects of temperature." Computational Biology and Chemistry.* ***32****(5):311–314. doi:10.1016/j.compbiolchem.2008.04.001.*

33. [^]*Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011). "Projecting Coral Reef Futures Under Global Warming and Ocean Acidification." Science.* ***333****(6041):418–422. doi:10.1126/science.1204794.*

34. [^]*de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, Hussain S, Kumar P, McVittie A, Portela R, Rodriguez LC, ten Brink P, van Beukering P (2012). "Global estimates of the value of ecosystems and their services in monetary units." Ecosystem Services.* ***1****(1):50–61. doi:10.1016/j.ecoser.2012.07.005.*

35. [^]*Harvey BJ, Nash KL, Blanchard JL, Edwards DP (2018). "Ecosystem-based management of coral reefs under climate change." Ecology and Evolution.* ***8****(12):6354–6368. doi:10.1002/ece3.4146.*

36. [a, b, c]*Müller WEG (1982). "Cell Membranes in Sponges." International Review of Cytology.* ***77****(C):129–181. doi:10.1016/S0074-7696(08)62466-3.*

37. [a, b]*Méndez-Salgado E, Chacón-Chaverri D, Fonseca LG, Seminoff JA (2020). "Trophic ecology of hawksbill turtles (Eretmochelys imbricata) in Golfo Dulce, Costa Rica: integrating esophageal lavage and stable isotop*

e (δ13C, δ15N) analysis." Latin American Journal of Aquatic Research. ***48****(1):114–130. doi:*[*10.3856/VOL48-ISSUE1-FULLTEXT-2230*]*.*

38. ^a, b, c^ *von Brandis RG, Mortimer JA, Reilly BK (2010). "In-water observations of the diving behaviour of immature hawksbill turtles, Eretmochelys imbricata, on a coral reef at D'Arros Island, Republic of Seychelles." Chelonian Conservation and Biology.* ***9****(1):26–32. doi:10.2744/CCB-0815.1.*

39. ^ *Hooker SK, Baird RW (2001). "Diving and ranging behaviour of odontocetes: a methodological review and critique." Mammal Review.* ***31****(1):81–105. doi:10.1046/J.1365-2907.2001.00080.X.*

40. ^a, b^ *Charrier I, Jeantet L, Maucourt L, Régis S, Lecerf N, Benhalilou A, Chevallier D (2022). "First evidence of underwater vocalizations in green sea turtles Chelonia mydas." Endangered Species Research.* ***48****:31–41. doi:10.3354/ESR01185.*

41. ^ *Jeantet L, Hadetskyi V, Vigon V, Korysko F, Paranthoen N, Chevallier D (2022). "Estimation of the Maternal Investment of Sea Turtles by Automatic Identification of Nesting Behavior and Number of Eggs Laid from a Tri-Axial Accelerometer." Animals: An Open Access Journal from MDPI.* ***12****(4):520. doi:10.3390/ANI12040520.*

42. ^ *Bonola M, Girondot M, Robin JP, Martin J, Siegwalt F, Jeantet L, Lelong P, Grand C, Chambault P, Etienne D, Gresser J, Hielard G, Arqué A, Régis S, Lecerf N, Frouin C, Lefebvre F, Sutter E, Vedie F, Barnerias C, Laurent T, Bordes R, Guimera C, Aubert N, Bouaziz M, Pinson A, Frédéric F, Duru M, Benhalilou A, Murgale C, Maillet T, Andreani L, Campistron G, Sikora M, Rateau F, Francis G, Eggenspieler J, Woignier T, Allenou JP, Louis-Jean L, Chanteur B, Béranger C, Crillon J, Brador A, Habold C, Le Maho Y, Chevallier D (2019). "Fine scale geographic residence and annual primary production drive body condition of wild immature green turtles (Chelonia mydas) in Martinique Island (Lesser Antilles)." Biology Open.* ***8****(12). doi:10.1242/bio.048058.*

43. ^ *Siegwalt F, Benhamou S, Girondot M, Jeantet L, Martin J, Bonola M, Lelong P, Grand C, Chambault P, Benhalilou A, Murgale C, Maillet T, Andreani L, Campistron G, Jacaria F, Hielard G, Arqué A, Etienne D, Gresser J, Régis S, Lecerf N, Frouin C, Lefebvre F, Aubert N, Vedie F, Barnerias C, Thieulle L, Guimera C, Bouaziz M, Pinson A, Flora F, George F, Eggenspieler J, Woignier T, Allenou JP, Louis-Jean L, Chanteur B, Béranger C, Crillon J, Brador A, Habold C, Le Maho Y, Robin JP, Chevallier D (2020). "High fidelity of sea turtles to their foraging grounds revealed by satellite tracking and capture-mark-recapture: New insights for the establishment of key marine conservation areas." Biological Conservation.* ***250****:108742. doi:10.1016/J.BIOCON.2020.108742.*

44. ^ *Lelong P, Besnard A, Girondot M, Habold C, Priam F, Giraudeau M, Le Loc'h G, Le Loc'h A, Fournier P, Fournier-Chambrillon C, Bustamante P, Dupont SM, Vincze O, Gros-Desormeaux J-R, Martin J, Bourgeois O, Lepori M, Régis S, Lecerf N, Lefebvre F, Aubert N, Frouin C, Flora F, Pimentel E, Pimentel M, Siegwalt F, Jeantet L, Chambault P, Hielard G, Arqué A, Arthus M, Louis-Jean L, Brador A, Giannasi P, Etienne D, Lecerf N, Chevallier*

P, Chevallier T, Meslier S, Landreau A, Maceno M, Larcher E, Le Maho Y, Chevallier D (2024). "Demography of endangered juvenile green turtles in face of environmental changes: 10 years of capture-mark-recapture efforts in Martinique." Biological Conservation. **291**:110471. doi:10.1016/j.biocon.2024.110471.

45. ^Friard O, Gamba M (2016). "BORIS: A free, versatile open-source event-logging software for video-audio coding and live observations." Methods in Ecology and Evolution. **7**:1325–1330. doi:10.1111/2041-210X.12584.
46. ^Thomson JA, Whitman ER, Garcia-Rojas MI, Bellgrove A, Ekins M, Hays GC, Heithaus MR (2018). "Individual specialization in a migratory grazer reflects long-term diet selectivity on a foraging ground: implications for isotope-based tracking." Oecologia. **188**(2):429–439. doi:10.1007/S00442-018-4218-Z.
47. ^Zea S, Henkel TP, Pawlik JR (2014). The Sponge Guide: a picture guide to Caribbean sponges. 3rd ed. www.spongeguide.org. www.spongeguide.org.
48. ^Humann P, Deloach N, Wilk L (2018). Créatures du Récif. Identification. Florida, Caraïbes, Bahamas. PLB Editions.
49. ^Labalme C, Mazzella V, Calcinai B, Delvenne C, Chevallier D, Núñez-Pons L (2025). "Sponge fauna portrayal in the foraging area of the hawksbill turtle from Martinique applying integrative taxonomy." In prep.
50. ^Chatting M, Smyth D, Al-Maslamani I, Obbard J, Al-Ansi M, Hamza S, et al. (2018). "Nesting ecology of hawksbill turtles, Eretmochelys imbricata, in an extreme environmental setting." PLoS ONE. **13**(9):e0203257. doi:10.1371/JOURNAL.PONE.0203257.
51. ^Green D (1997). "Basking in Galapagos Green Turtles." In: Espey H, Espey A, editors. Proceedings 17th Annual Sea Turtle Symposium, 4-8 March 1997, Orlando, Florida. https://www.test.ists40perth.com.au/wp-content/uploads/2021/02/17-turtle-1.pdf#page=8.
52. ^Jessop TS, Limpus CJ, Whittier JM (2002). "Nocturnal Activity in the Green Sea Turtle Alters Daily Profiles of Melatonin and Corticosterone." Hormones and Behavior. **41**(3):342–350. doi:10.1006/hbeh.2002.1775.
53. ^McKnight DT, Ard K, Auguste RJ, Barhadiya G, Benard MF, Boban P, et al. (2023). "Nocturnal basking in freshwater turtles: A global assessment." Global Ecology and Conservation. **43**:e02444. doi:10.1016/J.GECCO.2023.E02444.
54. a, bJeantet L, Zondo K, Delvenne C, Martin J, Chevallier D, Dufourq E (2024). "Automatic identification of the endangered hawksbill sea turtle behavior using deep learning and cross-species transfer learning." Journal of Experimental Biology. **227**(24). doi:10.1242/jeb.249232.
55. ^Robinson NJ, Doñate-Ordóñez R, Chatzievangelou D, Brooks AML, Cuffley J, Fields CYA, Hoefer S, Pinou T, Smith A, Mills S (2024). "Short-Term Effects of Attaching Animal-Borne Devices on the Behavior of Juvenile Green Turtles." Ecology and Evolution. **14**(12). doi:10.1002/ece3.70707.

56. ^Fossette S, Schofield G, Lilley MKS, Gleiss AC, Hays GC (2012). "Acceleration data reveal the energy management strategy of a marine ectotherm during reproduction." Functional Ecology. **26**(2):324–333. doi:10.1111/j.1365-2435.2011.01960.x.

57. ^Wallace BP, Zolkewitz M, James MC (2015). "Fine-scale foraging ecology of leatherback turtles." Frontiers in Ecology and Evolution. **3**(FEB):15. doi:10.3389/FEVO.2015.00015/BIBTEX.

58. a, bWalcott J, Eckert S, Horrocks JA (2012). "Tracking hawksbill sea turtles (Eretmochelys imbricata) during inter-nesting intervals around Barbados." Marine Biology. **159**:927–938. doi:10.1007/s00227-011-1870-9.

59. ^Bonnet X, Bradshaw D, Shine R (1998). "Capital versus income breeding: An ectothermic perspective." Oikos. **83**(2):333–342. doi:10.2307/3546846.

60. ^Shimada T, Limpus CJ, Hamann M, Bell I, Esteban N, Groom R, Hays GC (2020). "Fidelity to foraging sites after long migrations." Journal of Animal Ecology. **89**(4):1008–1016. doi:10.1111/1365-2656.13157.

61. a, bKataoka K, Okuyama J, Kobayashi M, Abe O, Yoseda K, Yasuda T, Arai N (2009). "Comparison of the activity budget between wild and reared juvenile hawksbill turtles." Proceedings of the 4th International Symposium on SEASTAR2000 and Asian Bio-Logging Science. 19–22.

62. ^Siegfried TR, Reimer J, Roberto E, Noren C, Vidal A, Dixon K, DuBois M, Piacenza SE (2023). "Size-Mediated Sea Turtle Behavioral Responses at Artificial Habitats in the Northern Gulf of Mexico." Animals. **13**(1). doi:10.3390/ANI13010114/S1.

63. ^Sazima I, Grossman A, Sazima C (2004). "Hawksbill turtles visit moustached barbers: cleaning symbiosis between Eretmochelys imbricata and the shrimp Stenopus hispidus." Biota Neotropica. **4**(1):1–6. doi:10.1590/S1676-06032004000100011.

64. a, b, c, dStorch S, Wilson RP, Hillis-Starr ZM, Adelung D (2005). "Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle Eretmochelys imbricata." Marine Ecology Progress Series. **293**:263–271.

65. a, bWalcott J, Eckert S, Horrocks JA (2013). "Diving behaviour of hawksbill turtles during the inter-nesting interval: Strategies to conserve energy." Journal of Experimental Marine Biology and Ecology. **448**:171–178. doi:10.1016/J.JEMBE.2013.07.007.

66. ^Hochscheid S, Bentivegna F, Speakman JR (2002). "Regional Blood Flow in Sea Turtles: Implications for Heat Exchange in an Aquatic Ectotherm." Physiological and Biochemical Zoology. **75**(1):66–76. doi:10.1086/339050.

67. ^Fontaine SS, Novarro AJ, Kohl KD (2018). "Environmental temperature alters the digestive performance and gut microbiota of a terrestrial amphibian." The Journal of Experimental Biology. **221**(Pt 20). doi:10.1242/J

EB.187559.

68. a, b *Gaos AR, Johnson CE, McLeish DB, King CS, Senko JF (2021). "Interactions among Hawaiian Hawksbills Suggest Prevalence of Social Behaviors in Marine Turtles." Chelonian Conservation and Biology.* ***20****(2):167–172. doi:10.2744/CCB-1481.1*.
69. ^ *Blumenthal JM, Austin TJ, Bothwell JB, Broderick AC, Ebanks-Petrie G, Olynik JR, et al. (2009). "Diving behavior and movements of juvenile hawksbill turtles Eretmochelys imbricata on a Caribbean coral reef." Coral Reefs.* ***28****:55–65. doi:10.1007/s00338-008-0416-1*.
70. ^ *Matley JK, Johansen LK, Klinard NV, Eanes ST, Jobsis PD (2021). "Habitat selection and 3D space use partitioning of resident juvenile hawksbill sea turtles in a small Caribbean bay." Marine Biology.* ***168****(8):1–15. https://doi.org/10.1007/S00227-021-03912-0/FIGURES/7*.
71. a, b *Chevallier D, Maucourt L, Charrier I, Lelong P, le Gall Y, Menut E, Wallace B, Delvenne C, Vincze O, Jeantet L, Girondot M, Martin J, Bourgeois O, Lepori M, Fournier P, Fournier-Chambrillon C, Régis S, Lecerf N, Lefebvre F, Aubert N, Arthus M, Pujol M, Nalovic MA, Nicolas M, Burg M-C, Chevallier P, Chevallier T, Landreau A, Meslier S, Larcher E, Le Maho Y (2024). "The response of sea turtles to vocalizations opens new perspectives to reduce their bycatch." Scientific Reports.* ***14****(1):16519. doi:10.1038/s41598-024-67501-z*.
72. ^ *Delvenne C, Chevallier D (2024). "Tortue imbriquée prise dans un filet de pêche (Martinique)." https://www.youtube.com/watch?v=FS5nB6jR5RY*.
73. ^ *Gaos AR, Lewison RR, Wallace BP, Yañez IL, Liles MJ, Baquero A, Seminoff JA (2012). "Dive behaviour of adult hawksbills (Eretmochelys imbricata, Linnaeus 1766) in the eastern Pacific Ocean highlights shallow depth use by the species." Journal of Experimental Marine Biology and Ecology.* ***432–433****:171–178. doi:10.1016/J.JEMBE.2012.07.006*.
74. ^ *Wood LD, Milton SL, Maple TL (2017). "Foraging Behavior of Wild Hawksbill Turtles (Eretmochelys imbricata) in Palm Beach County, Florida, USA." Chelonian Conservation and Biology.* ***16****(1):70–75. doi:10.2744/ccb-1242.1*.
75. a, b, c, d *Wedemeyer-Strombel KR, Seminoff JA, Liles MJ, Sánchez RN, Chavarría S, Valle M, Altamirano E, Gadea V, Hernandez N, Peterson MJ, Smith KJ, Trueman CN, Peterson TR, Newsome SD (2021). "Fishers' Ecological Knowledge and Stable Isotope Analysis Reveal Mangrove Estuaries as Key Developmental Habitats for Critically Endangered Sea Turtles." Frontiers in Conservation Science.* ***2****. doi:10.3389/fcosc.2021.796868*.
76. a, b, c, d, e, f *Baumbach DS, Zhang R, Hayes CT, Wright MK, Dunbar SG (2022). "Strategic foraging: Understanding hawksbill (Eretmochelys imbricata) prey item energy values and distribution within a marine protected area." Marine Ecology.* ***43****(2):e12703. doi:10.1111/MAEC.12703*.

77. ^Bjorndal KA, Wetherall JA, Bolten AB, Mortimer JA (1999). "Twenty-Six Years of Green Turtle Nesting at Tortuguero, Costa Rica: An Encouraging Trend." Conservation Biology. **13**(1):126–134. doi:10.1046/j.1523-1739.1999.97329.x.

78. ^Rützler K (2004). "Sponges in coral reefs: a community of considerable complexity (examples from the Caribbean)." Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova. **68**:85–148.

79. ^Chanas B, Pawlik JR (1995). "Defenses of Caribbean sponges against predatory reef fish. II. Spicules, tissue toughness, and nutritional quality." Marine Ecology Progress Series. **127**(1–3):195–211. doi:10.3354/meps127195.

80. ^Wulff JL (2021). "Targeted predator defenses of sponges shape community organization and tropical marine ecosystem function." Ecological Monographs. **91**(2). doi:10.1002/ecm.1438.

81. ^Galeano E, Martínez A, Thomas OP, Robledo S, Munoz D (2012). "Antiparasitic bromotyrosine derivatives from the Caribbean marine sponge Aiolochroia crassa." Química Nova. **35**(6):1189–1193. doi:10.1590/S0100-40422012000600023.

82. ^Wood JR (1974). "Amino acids essential for the growth of the hatchling green sea turtle (Chelonia mydas)." Proceedings of the World Mariculture Society. **5**:233–248.

83. ^de Voogd NJ, Alvarez B, Boury-Esnault N, Cárdenas P, Díaz M-C, Dohrmann M, et al. (2025). "World Porifera Database." https://www.marinespecies.org/porifera. doi:10.14284/359.

84. ^OBIS (2025). "Distribution records of Irciniidae (Gray, 1867)." Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. https://obis.org.

85. ^Hardoim C, Costa R (2014). "Microbial Communities and Bioactive Compounds in Marine Sponges of the Family Irciniidae—A Review." Marine Drugs. **12**(10):5089–5122. doi:10.3390/md12105089.

86. ^Lesser MP (2006). "Benthic–pelagic coupling on coral reefs: Feeding and growth of Caribbean sponges." Journal of Experimental Marine Biology and Ecology. **328**(2):277–288. doi:10.1016/J.JEMBE.2005.07.010.

87. ^de Sousa LHN, de Araújo RD, Sousa-Fontoura D, Menezes FG, Araújo RM (2021). "Metabolites from Marine Sponges of the Genus Callyspongia: Occurrence, Biological Activity, and NMR Data." Marine Drugs. **19**(12):663. doi:10.3390/md19120663.

88. ^El-Hawary SS, Sayed AM, Mohammed R, Hassan HM, Rateb ME, Amin E, et al. (2019). "Bioactive Brominated Oxindole Alkaloids from the Red Sea Sponge Callyspongia siphonella." Marine Drugs. **17**(8):465. doi:10.3390/md17080465.

89. ^Daletos G, Kalscheuer R, Koliwer-Brandl H, Hartmann R, de Voogd NJ, Wray V, et al. (2015). "Callyaerins from the marine sponge Callyspongia aerizusa: Cyclic peptides with antitubercular activity." Journal of Natur

al Products. ***78****(8):1910–1925.*

90. ^*Youssef DT, Ibrahim AK, Khalifa SI, Mesbah MK, Mayer AM, van Soest RW (2010). "New antiinflammatory sterols from the Red Sea sponges Scalarispongia aqabaensis and Callyspongia siphonella." Natural Product Communications.* ***5****(1):1934578X1000500107.*
91. ^*McMurray SE, Blum JE, Pawlik JR (2008). "Redwood of the reef: growth and age of the giant barrel sponge Xestospongia muta in the Florida Keys." Marine Biology.* ***155****(2):159–171. doi:10.1007/s00227-008-1014-z.*
92. ^*McMurray SE, Blum JE, Leichter JJ, Pawlik JR (2011). "Bleaching of the giant barrel sponge Xestospongia muta in the Florida Keys." Limnology and Oceanography.* ***56****(6):2243–2250. doi:10.4319/lo.2011.56.6.2243.*
93. ^*García-Hernández J, Tuohy E, Toledo-Rodríguez D, Sherman C, Schizas N, Weil E (2021). "Detrimental conditions affecting Xestospongia muta across shallow and mesophotic coral reefs off the southwest coast of Puerto Rico." Diseases of Aquatic Organisms.* ***147****:47–61. doi:10.3354/dao03633.*
94. ^*Fiore CL, Baker DM, Lesser MP (2013). "Nitrogen Biogeochemistry in the Caribbean Sponge, Xestospongia muta: A Source or Sink of Dissolved Inorganic Nitrogen?" PLoS ONE.* ***8****(8):e72961. doi:10.1371/journal.pone.0072961.*
95. ^*Meylan A (1985). Feeding Ecology of the Hawksbill Turtle (Eretmochelys Imbricata): Spongivory as a Feeding Niche in the Coral Reef Community (Silica, Collagen, Chemical Ecology). https://www.proquest.com/openview/b96467135275c0fc05c0814d494d4471/1?pq-origsite=gscholar&cbl=18750&diss=y.*
96. ^*Waddell B, Pawlik JR (2000). "Defenses of Caribbean sponges against invertebrate predators. II. Assays with sea stars."*
97. ^*Wörheide G, Dohrmann M, Erpenbeck D, Larroux C, Maldonado M, Voigt O, Borchiellini C, Lavrov DV (2012). "Deep Phylogeny and Evolution of Sponges (Phylum Porifera)." Advances in Marine Biology.* ***61****:1–78. doi:10.1016/B978-0-12-387787-1.00007-6.*
98. ^*Wecker P, Fournier A, Bosserelle P, Debitus C, Lecellier G, Berteaux-Lecellier V (2015). "Dinoflagellate diversity among nudibranchs and sponges from French Polynesia: Insights into associations and transfer." Comptes Rendus Biologies.* ***338****(4):278–283. doi:10.1016/j.crvi.2015.01.005.*
99. ^*Hentschel U, Usher KM, Taylor MW (2006). "Marine sponges as microbial fermenters." FEMS Microbiology Ecology.* ***55****(2):167–177. doi:10.1111/J.1574-6941.2005.00046.X.*
100. ^*Rix L, Ribes M, Coma R, Jahn MT, de Goeij JM, van Oevelen D, Escrig S, Meibom A, Hentschel U (2020). "Heterotrophy in the earliest gut: a single-cell view of heterotrophic carbon and nitrogen assimilation in sponge-microbe symbioses." The ISME Journal.* ***14****(10):2554–2567. doi:10.1038/s41396-020-0706-3.*

101. ^a, b^ Hudspith M, van der Sprong J, Rix L, Víg D, Schoorl J, de Goeij JM (2021). "Quantifying sponge host and microbial symbiont contribution to dissolved organic matter uptake through cell separation." Marine Ecology Progress Series. **670**:1–13. doi:10.3354/MEPS13789.

102. ^ Ramirez MD, Avens L, Meylan AB, Shaver DJ, Stahl AR, Meylan PA, et al. (2023). "Dietary plasticity linked to divergent growth trajectories in a critically endangered sea turtle." Frontiers in Ecology and Evolution. **11**. doi:10.3389/fevo.2023.1050582.

103. ^ Abrego D, Ulstrup KE, Willis BL, van Oppen MJH (2008). "Species–specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress." Proceedings of the Royal Society B: Biological Sciences. **275**(1648):2273–2282. doi:10.1098/RSPB.2008.0180.

104. ^ Baker AC (2003). "Flexibility and Specificity in coral-algal symbiosis: Diversity, Ecology and Biogeography of Symbiodinium." Annu. Rev. Ecol. Evol. Syst.. **34**:661–689. doi:10.1146/annurev.ecolsys.34.011802.132417.

105. ^ Ferrier-Pagès C, Leal MC (2018). "Stable isotopes as tracers of trophic interactions in marine mutualistic symbioses." Ecology and Evolution. **9**(1):723–740. doi:10.1002/ECE3.4712.

106. ^ Carr A, Stancyk S (1975). "Observations on the ecology and survival outlook of the hawksbill turtle." Biological Conservation. **8**(3):161–172. doi:10.1016/0006-3207(75)90060-9.

107. ^ Rincon-Diaz MP, Diez CE, van Dam RP, Sabat AM (2011). "Foraging selectivity of the Hawksbill Sea Turtle (Eretmochelys imbricata) in the Culebra Archipelago, Puerto Rico." Journal of Herpetology. **45**(3):277–282. doi:10.1670/10-120.1.

108. ^ Berube MD, Dunbar SG, Rützler K, Hayes WK (2012). "Home Range and Foraging Ecology of Juvenile Hawksbill Sea Turtles (Eretmochelys imbricata) on Inshore Reefs of Honduras." Chelonian Conservation and Biology. **11**(1):33–43. doi:10.2744/CCB-0898.1.

109. ^ Rincon-Diaz MP, Rodriguez-Zarate CJ (2004). "Characterization of nesting beaches and feeding areas of marine turtles at the San Bernardo Archipelago, Colombian Caribbean." Bol. Invest. Mar. Cost. **33**(1):137-158.

110. ^a, b^ Resiere D, Valentino R, Nevière R, Banydeen R, Gueye P, Florentin J, Cabié A, Lebrun T, Mégarbane B, Guerrier G, Mehdaoui H (2018). "Sargassum seaweed on Caribbean islands: an international public health concern." The Lancet. **392**(10165):2691. doi:10.1016/S0140-6736(18)32777-6.

111. ^a, b^ Pawlik JR, Loh TL, McMurray SE, Finelli CM (2013). "Sponge Communities on Caribbean Coral Reefs Are Structured by Factors That Are Top-Down, Not Bottom-Up." PLoS ONE. **8**(5):e62573. doi:10.1371/JOURNAL.PONE.0062573.

112. ^ Bayu A, Handayani T (2018). "High-value chemicals from marine macroalgae: Opportunities and challenges for marine-based bioenergy development." IOP Conference Series: Earth and Environmental Science. **20**

9(1):012046. doi:10.1088/1755-1315/209/1/012046.

113. ^Kraan S (2012). *Algal Polysaccharides, Novel Applications and Outlook. In: Carbohydrates - Comprehensive Studies on Glycobiology and Glycotechnology.* doi:10.5772/51572.
114. ^Cian R, Drago S, de Medina F, Martínez-Augustin O (2015). "Proteins and Carbohydrates from Red Seaweeds: Evidence for Beneficial Effects on Gut Function and Microbiota." *Marine Drugs.* **13**(8):5358. doi:10.3390/MD13085358.
115. ^Esposito R, Federico S, Glaviano F, Somma E, Zupo V, Costantini M (2022). "Bioactive Compounds from Marine Sponges and Algae: Effects on Cancer Cell Metabolome and Chemical Structures." *International Journal of Molecular Sciences.* **23**(18):10680. doi:10.3390/ijms231810680.
116. ^Stephens D, Krebs J (1986). *Foraging Therory.* 1st ed. Princeton: Princeton University Press.
117. ^Chevallier D, Baillon F, Robin JP, le Maho Y, Massemin-Challet S (2008). "Prey selection of the black stork in the African wintering area." *Journal of Zoology.* **276**(3):276–284. doi:10.1111/J.1469-7998.2008.00488.X.
118. ^European Marine Board (2024). *Navigating the Future VI: Placing the Ocean within the wider Earth system.* Ostend, Belgium: European Marine Board. 116 pp. doi:10.5281/zenodo.13329469.

Declarations

Funding: Funding Open access funding provided by Université des Antilles. The Program BEPHYTES of the Centre National de la Recherche Scientifique (CNRS) was co-funded by the FEDER Martinique (Fonds Européen de Développement Régional PO/FEDER/FSE 2014– 2020, Conventions 246239), Collectivité Territoriale de Martinique (CTM, convention 258342), the Direction de l'Environnement, de l'Aménagement et du Logement (DEAL, Martinique, France (Convention N°2017/164894), the Office De l'Eau (ODE) Martinique, France (Convention n°180126) and the Office Français de la Biodiversité (OFB, Parc Naturel Marin de Martinique, OFB-23-0563), the town of Les Anses d'Arlet and ANSLO'S. The Program TOPASE of the CNRS was funded by Fonds Européen pour les affaires maritimes et la pêche (FEAMP), the Minister of Agriculture and FranceAgriMer.

Potential competing interests: No potential competing interests to declare.