water

MDPI

Article

Sponge (Porifera) Fauna Portrayal in the Foraging Area of the Hawksbill Turtle from Martinique: Applying Integrative Taxonomy

Carlotta Labalme [1], Valerio Mazzella [2,3], Barbara Calcinai [4], Cyrielle Delvenne [5,6], Damien Chevallier [5] and Laura Núñez-Pons [1,2,*]

1 Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy; carlottalabalme@gmail.com
2 NBFC—National Biodiversity Future Center, 90133 Palermo, Italy; valerio.mazzella@szn.it
3 National Institute of Marine Biology, Ecology and Biotechnology, Ischia Marine Center, Stazione Zoologica Anton Dohrn, Ischia, 80077 Naples, Italy
4 Dipartimento di Scienze della Vita e dell'Ambiente (DISVA), Università Politecnica delle Marche, Via Brecce Bianche, 60131 Ancona, Italy; b.calcinai@staff.univpm.it
5 Unité de Recherche BOREA–Biology of Aquatic Organisms and Ecosystems, MNHN, CNRS 8067, SU, IRD 207, UCN, UA, Station de Recherche Marine de Martinique, Quartier Degras, Petite Anse, Les Anses d'Arlet, 97217 Martinique, France; cyrielle.delvenne@imbrsea.eu (C.D.); damien.chevallier@cnrs.fr (D.C.)
6 Marine Biology Research Group, IMBRSea Coordination Office Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium
* Correspondence: laura.nunezpons@szn.it

Abstract

Martinique sponge fauna was largely undocumented until 2017, when the first inventory of Porifera colonizing coral reefs, mangroves and caves around the island was published. We performed an integrative classification of sponges in the foraging area of hawksbill turtle (*Eretmochelys imbricata*) in Martinique. Sponge specimens were retrieved as direct or indirect diet items consumed by hawksbill turtles after video observations, and the feeding behaviors of these predators were tracked. Morphology was supplemented with molecular identification (DNA barcoding) based on a multi-locus approach using COI, 28S and ITS genetic markers. Seventeen different species were identified, belonging to seven orders: Poecilosclerida, Dictyoceratida, Verongiida, Agelasida, Haplosclerida, Clionaida, and Tetractinellida. Haplosclerida exhibited the greatest diversity and species abundance, followed by Verongiida. The 28S marker provided the highest confidence in species identification. We provided new barcode records for *Hyattella cavernosa* and *Amphimedon caribica*. Among the cataloged sponges, only four of them had been previously reported as food items of *E. imbricata* (*Xestospongia muta*, *Iotrochota birotulata*, *Spirastrella coccinea* and *Cinachyrella kuekenthali*). The rest represent newly documented items that are potentially preyed upon by this turtle predator. The characterization of sponges as being part of the feeding habitat of hawksbill turtles underpins management and protection plans for this critically endangered species, and the benthic community on which they feed, by providing criteria for generating networks of Marine Protected Areas (MPAs) in the Caribbean regions.

Keywords: DNA barcoding; Caribbean; cytochrome c oxidase subunit 1; Internal Transcribed Spacer; morphology; sponge classification; tropical sponges; 28S rDNA C-Region

Check for updates

Academic Editors: Francesco Rendina and Valentina Perricone

Received: 26 February 2026
Revised: 22 March 2026
Accepted: 24 March 2026
Published: 2 April 2026

Copyright: © 2026 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license.

1. Introduction

Sponges (phylum Porifera) are filter-feeding animals that can outcompete other bioconstructing taxa (e.g., reef-building corals or seaweed), and they are notoriously abundant in cryptic and exposed habitats. They occur in sea and freshwater ecosystems, in shallow and deep-sea bottoms, and from the tropics to the poles [1–3]. This widespread distribution and impressive capability to dominate benthic communities are linked to their high ecological flexibility [4–6] and production of allelopathic metabolites [1]. These may act to prevent organismal settling on (antifouling) or near their surface (space out competition) or deter predators or indirect consumers, making them unpalatable (antipredation). In tropical ecosystems, predation pressure is a driving force shaping sessile benthic communities [7]. As a consequence, in Caribbean coral reefs, many sponge groups have developed an array of ways to deter predators both by means of structural elements (spicules, spongin fibers and tissue toughness) and/or by the production of toxic and noxious natural products derived by their own secondary metabolism or by their hosted endosymbionts [8–11].

Porifera are among the least consumed phyla in all oceans, due to their often undesired texture, repellent compounds, and the presence of a complex inorganic scaffold (silicon or calcareous spicules) that reduces the nutritive value of the organic component (mesohyl) [8,12]. Tropical coral reefs, especially in the face of climate changes, are transitioning from being dominated by hermatypic corals toward an overgrowth of sponges and macroalgae that could likely become future prevalent food sources [13,14]. Several opportunistic consumers in the Caribbean occasionally feed on sponges, such as hermit crabs (*Paguristes puncticeps* Benedict, 1901), sea stars (*Echinaster echinophorus* Lamarck, 1816; *Echinaster sentus* Say, 1825) and the reef fish *Thalassoma bifasciatum* Bloch, 1791 [9,10]. There are other predators with predominantly spongivorous diets, including angelfish, filefish, trunkfish and hawksbill turtles (*Eretmochelys imbricata* Linnaeus, 1766), which exert important control over sponge populations [15,16]. Sponges are associated with diverse infauna and epifauna, including zoanthidae, polychaetes, barnacles, crustaceans, mollusks, echinoderms, amphipods, hydroids, or even algae [17]. Additionally, sponges may host high densities of endosymbiotic Bacteria, Archaea, Fungi and microalgae [18,19]. In this sense, sponges may also represent an indirect source of nourishment when associated organisms supply nutritional value [17]. Several studies have demonstrated how sponge consumers, such as the opisthobranch *Tylodina perversa* Gmelin, 1791 and the parrotfish (Family: Scaridae Gmelin, 1790), target prey living in intimate association with sponges. Therefore, when it comes to studying the diet of hawksbill turtles and focusing on their preference for sponges [15,20,21], there is an open question: do turtles accidentally feed on sponges while targeting other associated fauna or endosymbionts, or are they really interested in the sponge biomass? In the literature, sponges are mostly considered the main diet for these notorious spongivorous predators (Table S1), but most works do not consider the associated biota [15,20–27].

Hawksbill turtles are distributed worldwide in tropical and, less frequently, subtropical latitudes, where rocky and coral substrates represent their main feeding grounds. According to Nivière and coauthors [28], the northernmost and southernmost regions of Martinique are the areas most frequented by these turtles. *Eretmochelys imbricata* is listed as a critically endangered species on the IUCN Red List [29,30]. Due to its spongivorous feeding habits [15,20,22–27], *E. imbricata* exerts decisive top-down control over sponge-dominated benthic communities, contributing to the local biodiversity [20,31–33]. The taxonomic characterization of sponge communities inhabiting the turtles' main feeding grounds represents the foundation for better understanding the hawksbill turtle feeding ecology [34]. Martinique is a key reservoir of hawksbill turtles due to the presence of their preferred feeding grounds, and it became one of the main catching points for *bekko*

trade (tortoiseshell trade) [35]. In 1987, the Martinican hawksbill population was declared 'gravely threatened' [36], but even now, it still represents one of the most popular foraging areas for both adult and juvenile turtles, along with Nicaragua (in the biological reserve of Cayos Miskitos), Grenada Island, Carriacou Island, St. Vincent and the Grenadines Island and the Bahamas Islands [28].

Martinique is a volcanic island located in the Lesser Antilles in the Caribbean Sea, with a heterogeneous geomorphological conformation consisting of rock/reef substrates and/or intermixed substrate where sand and rocks are interspersed [37,38]. Sponges represent a dominant component of local coral reef and rocky substrates, yet they were never thoroughly surveyed until 2017 [39]. Even though other studies dealing with Martinican Porifera fauna have been performed over the years [40–43], that of Pérez and coworkers (2017) [39], reporting 191 sponge specimens, with 134 descriptions at the species level, represents, undoubtedly, the most comprehensive work focused on sponge local taxonomy. In the inventory from Pérez and coauthors (2017) [39], Haplosclerida, Poecilosclerida, Dictyoceratida and Verongiida represented the main orders in species richness, and Aplysinidae, Niphatidae and Agelasidae the prevailing families, while genera *Agelas* spp., *Aplysina* spp., *Callyspongia* spp., and *Niphates* spp. and the species *Xestospongia muta* were the dominant taxa by biomass. Understanding hawksbill turtles' main feeding grounds is crucial for the effective protection of these habitats, contributing to the conservation of turtle populations and the overall health of the Caribbean marine ecosystem.

The aim of this study is to create a catalog of sponges in the foraging areas of *E. imbricata* turtles along the southern coast of Martinique. In our survey, we integrated morphometric observations and DNA barcoding based on three genetic markers [44–47]. This approach supported the most reliable taxonomical classification, considering the high conformational plasticity and paucity of diagnostic elements characterizing Porifera [6,48,49]. With our research, we intend to (a) enlarge the inventory of sponge prey items consumed by turtles; (b) propose potential morphological and chemical traits in the studied sponges related to their edibility as prey items; (c) submit new Porifera DNA barcodes to the public databases; and (d) enhance the previous and sole inventory of Martinican sponges compiled by Perez et al. (2017) [39]. This work lays the foundations to understand prey-selection strategies [34]; specifically, how turtles may choose and discriminate palatable and chemically defended or unpalatable species and why some species are eaten while others are completely ignored.

2. Materials and Methods

2.1. Study Site

The study area is located on the southern side of Martinique, French West Island, belonging to the Lesser Antilles in the Caribbean Sea (14°26′20.7″ N; 61°01′37.7″ W) (Figure 1), and it was defined as one of the hawksbill turtles' favorite feeding grounds [34]. This southernmost side of the island was characterized mainly by the occurrence of rock/reef substrates and/or intermixed substrate where sand and rocks are interspersed. Sponges represented the most abundant invertebrates in terms of abundance and diversity, followed by macroalgae and corals [37,39]. Male and female adults of hawksbill turtles were video tracked with CATS Cam (Camera Customized Animal Tracking Solutions, Germany; www.cats.is accessed on 13 December 2025) to record fine-scale kinematics and movement along three 50 m transects randomly distributed at depths of <20 m at "le Sec du Diamant" site. Transects were previously traced by scuba divers by laying a weighted tape marked every 5 m and delimited with buoys holding the start and end of the line. Sponge sampling was performed in successive dives specifically on specimens observed being grazed by turtles. A grazing event could be identified by biting and usage of forelimbs to handle and tear prey sponge material, occurring in repeated extended dives of over 50 min (detailed

procedures of hawksbill monitoring, time budgets and onboard camera deployments can be found in Delvenne et al. 2025 [34] and other unpublished data from the authors). Pieces of ~5 cm^3 of sponge tissue were excised underwater from each donor specimen, put in zip bags filled with seawater and transported in coolers to the BOREA Biology of Aquatic Organisms and Ecosystems Lab. Sponge samples were divided into subsamples of ~2.5 cm^3 for molecular taxonomical identification and preserved in absolute ethanol, and ~1 cm^3 fragments for molecular taxonomical identification were preserved in 70% ethanol; all were kept at 4 °C until processed.

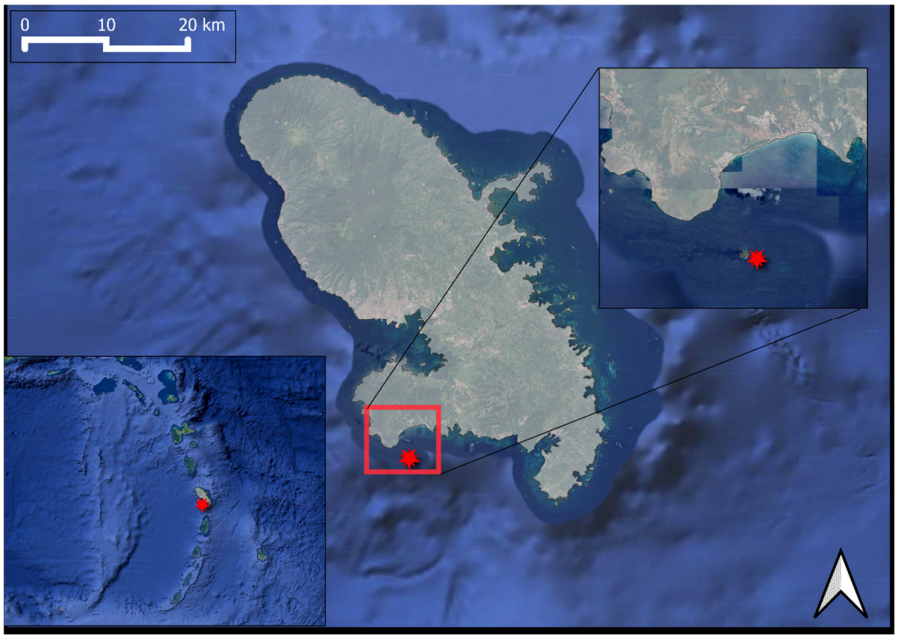


Figure 1. Map of the sampling area in "le Sec du Diamant", located in the southern side area of Martinique, French West Island. The red star indicates the precise site area of sponge collections.

2.2. Morphological Analysis

Morphological analyses required different procedures according to the different types of sponges (siliceous or horny).

2.2.1. Organic Skeleton Preparation for Horny Sponges

Horny sponges are characterized by the lack of spicules and the presence of spongin fibers. To isolate spongin fibers, sponges were cut into thin portions (~1 mm), and the organic component was removed with sodium hypochlorite (bleach). Fragments were then rinsed with distilled water and with 70% ethanol to block excessive corrosive effects of the bleach on the skeleton. The remaining organic residuals were removed with tweezers under a binocular stereo microscope (Leica EZ4, Leica Microsystems, Wetzlar, Germany). The fibers were then treated with Bio-clear®, which is a natural terpene substance with clarifying action for optimized visualization. The slides for the optical microscope were prepared and examined under a Zeiss Axioplan 2 optical microscope at Polytechnic University of Marche (Italy). During the optical microscope observation, different types of fibers were discerned as diagnostic characters using the 'Thesaurus of Sponge Morphology' [50].

2.2.2. Spicules and Skeleton Preparation for Siliceous Sponges

Siliceous sponges are characterized by siliceous spicules that can be distinguished into megascleres and microscleres. The spicular profile was studied using ~5 mm^3 sponge pieces, which were inserted inside a Pyrex® glass (Châteauroux, France) test tube. Two mL

of nitric acid was added inside the tube, and the solution was heated over a flame to accelerate the digestion of the organic components (as in Núñez-Pons et al. 2022 [51]).

Observations were performed under a Zeiss Axioplan 2 optical microscope (Oberkochen, Germany) at Polytechnic University of Marche (Italy). Spicule preparation was complemented with the skeleton examination, which shows how the spicules are organized and if they coexist with spongin fibers. The arrangement of the spicules can vary in the ectosome and choanosome, so sponge subsamples were cut into thin tangential sections of the ectosome and into transversal sections of the choanosome. Then, sponge sections were left to dry at room temperature, and Bio-Clear® (Bio-Optica, Bologna, Italy.) was applied to improve skeleton section visualization under the optical microscope. Also, in this case, different types of microscleres, macroscleres and skeletons were distinguished using the 'Thesaurus of Sponge Morphology' [50], and sponges were identified following the Systema Porifera [52]; to validate the hierarchical classification and the validity of species and genus names, we followed [53] and the World Porifera Database [54], respectively.

All the specimens are deposited in the Museum of the Dipartimento di Scienze della Vita e dell'Ambiente (UNIVPMSN), Università Politecnica delle Marche, which is under construction.

2.3. DNA Barcoding

Sponge DNA was extracted with QIAGEN DNeasy® PowerSoil® Pro Kit (Qiagen, Mo Bio Laboratories, Hilden, Germany) following the manufacturer's protocol, after providing better DNA quality than other kits and extraction procedures and for handling potential presence of chemical inhibitors in species with high microbial abundance. Extracted DNA was stored at −20 °C for downstream analyses. Quality and quantity of DNA were assessed using the Thermo ScientificTM NanodropTM 2000/2000c spectrophotometer (Wilmington, DE, USA). Three gene markers were targeted.

Cytochrome c oxidase subunit 1 (COI) marker was amplified using two pairs of primers to obtain a target fragment of approximately ~1100 bp. The standard COI partition (~640 bp) was obtained using the universal primers dgHCO2198 (5′-GGTCAACAAATCATAAAGAYATYGG-3′) and dgLCOI490 (5′-TAAACTTCAGGGTGACCAAARAAYCA-3′), designed by Folmer et al. (1994) [55]. Additionally, the alternative downstream I3-M11 partition of ~560 bp of the COI gene was amplified using the sponge-specific primers PorCOI2fwd (5′AATATGNGGGCNCCNGGNATNAC-3′) and PorCOI2rev (5′-ACTGCCCCCATNGATAAAACAT-3′) [56]. The fragment covering 18S-ITS1-5.8S-ITS2-28S (~850 bp) was amplified with the specific primers RA2_F (5′-GTCCCTGCCCTTTGTACACA-3′) and ITS2.2_R (5′-CCTGGTTAGTTTCTTTTCCTCCGC-3′) [57]. Finally, the marker gene corresponding to the 28S rDNA C-Region (430 bp) was amplified with the forward Por28S_C2_F (5′-GAAAAGAACTTTGRARAGAGAGT-3′) and reverse Por28S_D2_R (5′-TCCGTGTTTCAAGACGGG-3′) primers [58,59].

The PCR amplification was carried out using the Promega PCR kit with a Master mix prepared as follows: 5 µL of GoTaq Reaction Buffer, 2 µL of 25 Mm MgCl2 solution, 0.6 µL of forward primer, 0.6 µL of reverse primer, 0.6 µL of dNTPs (10 mM), 0.2 µL of GoTaq DNA Polymerase, 1 µL of sponge DNA template and water until the final volume of 25 µL was reached. We used the following thermal protocols: dgLCOI490—dgHCO2198: initial denaturation 95 °C 2′ (denaturation 95 °C 1′; annealing 50–54 °C 45″; extension 72 °C 1′—35 cycles), final extension 72 °C 5′, hold at 4 °C. PorCOI2fwd—PorCOI2rev: initial denaturation 95 °C 5′ (denaturation 94 °C 30″; annealing 52.2–57 °C 45″; extension 70 °C 90″—40 cycles), final extension 72 °C 10′, and hold at 4 °C. RA2_F—ITS2.2_R: initial denaturation 95 °C 5′ (denaturation 94 °C 30″; annealing 52.8 °C 45″; extension 72 °C 60″—38 cycles), final extension 72° C 10′, hold at 4 °C. Por28S_C2_F—Por28S_D2_R: initial

denaturation 95° C 2′ (denaturation 95 °C 30″; annealing 54–55 °C 30″; extension 72 °C 60″—38 cycles), final extension 72 °C 5′, plus hold at 4 °C (Table S2).

Amplified PCR products were checked and visualized on a 1% agarose gel pre-stained with GelRed™ (Nucleic Acid Gel Stain, 10,000× (Biotium™, Fremont, CA, USA) through the ChemiDoc™MP Imaging System (Bio-Rad Laboratories, Inc., Hercules, CA, USA). Successful amplicons were purified from exceeding reagents and salts with a purifying step based on magnetic beads (Beckman Coulter™ Agencourt AMPure XP, Indianapolis, IN, USA) as described by Núñez-Pons and coauthors (2022) [51]. Purified PCR products were sequenced in double sense (forward and reverse) with Sanger sequencing method by means of 3730xl DNA Analyzer (Applied Biosystem, Carlsbad, CA, USA) Sanger sequencer. Visualization and quality control of DNA chromatograms, assemblage of forward and reverse sequences and sequence editing were performed on Geneious Prime 2025.0.3 (https://www.geneious.com accessed on 13 December 2025). Good quality and assembled sequences were aligned against reference sequences from public database Genbank (https://www.ncbi.nlm.nih.gov/genbank/ accessed on 13 December 2025) through BLAST ® (Basic Local Alignment Search Tool; https://blast.ncbi.nlm.nih.gov/ accessed on 13 December 2025) in order to confirm Porifera origin of the sequences and compare the morphological versus the molecular identification of each sample. Sequences and specimen descriptions were deposited in GenBank. (Accession numbers: COI entries: PQ849445-PQ849461, PQ896986-PQ896987; 28S entries: PV034580-PV034604; ITS entries: PV035853-PV035869; Table S3).

2.4. Species Delimitation Analysis

When possible, three conspecific and three congeneric reference sequences were downloaded from GenBank, and for query species with no reference data available, the best-matching records according to BLAST searches [60] were retrieved for the analysis. Reference sequences were aligned with our sponge sequences, and the resulting alignments were trimmed to a position at which more than 50% of the sequences had nucleotides, and missing positions at the ends were coded as missing data (Ns).

To delimitate candidate species based on molecular distinctiveness in the COI dataset, we used Automatic Barcoding Gap Discovery (ABGD) and ASAP (Assemble Species by Automatic Partitioning) species delimitation algorithms [61,62], applying Kimura 2-parameter (K80 or K2p) pairwise genetic distances [63] for identification and assignment of sequence clusters into hypothetical groups (species). COI alignments in fasta format were used as input files on the Spart explorer webpage (https://spartexplorer.mnhn.fr accessed on 23 January 2026), and the tests showed concordant species delimitation results with the parameters set as follows: Pmin = 0.001, Pmax = 0.1, Steps = 10, X = 1, and Nb bins = 20 (28 January 2026 version).

Due to the conspicuous gap position variability in both the ribosomal 28S and 18S–ITS1–5.8S–ITS2–28S markers, we divided the datasets by genera or similarity clusters and then ran GBlocks 0.91b independently via web interface (https://ngphylogeny.fr/tools/tool/276/form accessed on 23 January 2026) to identify and exclude blocks of ambiguous single, non-codifying gene alignments, applying relaxed settings [64,65].

Distance matrices were built in MEGA 12 [66,67]. For COI alignments, pairwise distances were calculated applying the K2p+G model (Kimura 2-parameter and Gamma distribution –shape parameter = 1) [63], running the bootstrap method (1000 replicates) and handling gaps with partial deletion option (5% cutoff), following standard barcoding practice. Uncorrected p distances were instead calculated for nuclear markers (curated 28S and 18S–ITS1–5.8S–ITS2–28S alignments from GBlocks) to deal with alignment sensitivity

and substitution saturation. The resulting distances were used as additional estimates for species delimitation.

3. Results

A total of 36 specimens were collected along the three transects traced at the study site. The morphological and molecular analysis revealed that 63% of the sponges were characterized by the presence of spicules (megasclere and/or microsclere), while the remaining 37% revealed only spongin fibers (Figure 2A). Seventeen different species were identified, belonging to seven orders: Poecilosclerida, Dictyoceratida, Verongiida, Agelasida, Haplosclerida, Clionaida, and Tetractinellida (see Table 1). The order harboring the largest diversity and abundance was Haplosclerida, followed by Verongiida (Figure 2B). Several species were redundant along the three transects. A total of five *Xestospongia muta* occurred along all three transects. *Verongula rigida* (three specimens) and *Ircinia felix* (three specimens) occurred at least once along all the transects, while *Iotrochota birotulata* (two specimens), *Agelas clathrodes* (two specimens), *Aiolochroia crassa* (two specimens), *Callyspongia aculeata* (two specimens), *Hyattella cavernosa* (three specimens) and *Spirastrella coccinea* (four specimens) were observed at least along two transects. The remaining sponges were observed only once (*Aplysina fulva*, *Aplysina insularis*, *Agelas dispar*, *Callyspongia* cf. *pseudotoxa*, *Amphimedon caribica*, *Amphimedon compressa*, and *Cinachyrella kuekenthali*) (Table 1).

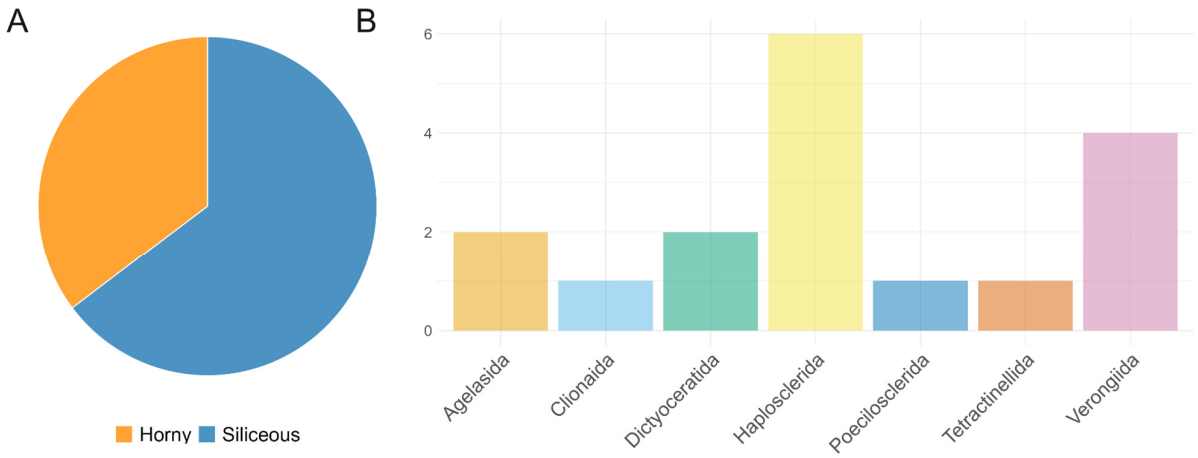


Figure 2. (**A**) Pie chart representing the percentage of sponge samples with siliceous spicules and horny sponges with only spongin fibers among the analyzed specimens. (**B**) Sponge diversity in terms of number of species per order observed along the three transects.

From the DNA barcoding analysis, we obtained at least one marker for each sample, except for one specimen of *Spirastrella coccinea*, *Callyspongia aculeata*, and *Cinachyrella kuekenthali*, for which no markers were obtained. The failure in sponge DNA amplification is probably due to the presence of inhibitors or bad DNA preservation in absolute ethanol for some species. Among the 36 sponge samples, 33% were amplified with three markers, 36% with two markers and 30% with only one marker. The 5′ end Folmer partition of the COI gene recurrently amplified non-targeted DNA (Alpha-proteobacteria, Gamma-proteobacteria, polychaetes, and crustaceans).

Table 1. Classification of sponge specimens of the present study, reporting the transect of collection.

Order	Family	Genus	Species	Transect
Verongiida	Aplysinidae	*Aiolochroia*	*Aiolochroia crassa* Hyatt, 1875	2, 3
Dictyoceratida	Irciniidae	*Aplysina*	*Aplysina fulva* Pallas,1766	3
			Aplysina insularis Duchassaing and Michelotti, 1864	3
		Verongula	*Verongula rigida* Esper, 1794	1, 2, 3
		Ircinia	*Ircinia felix* Duchassaing and Michelotti, 1864	1, 2
	Spongiidae	*Hyattella*	*Hyattella cavernosa* Pallas, 1766	1, 3
Haplosclerida	Callyspongiidae	*Callyspongia*	*Callyspongia aculeata* Linnaeus, 1759	1, 3
			Callyspongia cf. *pseudotoxa* Muricy and Ribeiro, 1999	1
	Niphatidae	*Amphimedon*	*Amphimedon caribica* Pulitzer-Finali, 1986	3
			Amphimedon compressa Duchassaing and Michelotti, 1864	3
	Petrosiidae	*Neopetrosia*	*Neopetrosia rosariensis* Zea and Rützler, 1983	1
		Xestospongia	*Xestospongia muta* Schmidt, 1870	1, 2, 3
Tetractinellida	Tetillidae	*Cinachyrella*	*Cinachyrella kuekenthali* Uliczka, 1929	1
Agelasida	Agelasidae	*Agelas*	*Agelas clathrodes* Schmidt, 1870	1
			Agelas dispar Duchassaing and Michelotti, 1864	2
Poecilosclerida	Iotrochotidae	*Iotrochota*	*Iotrochota birotulata* Higgin, 1877	1, 3
Clionaida	Spirastrellidae	*Spirastrella*	*Spirastrella coccinea* Duchassaing and Michelotti, 1864	1, 3

By contrast, we achieved 50% successful sequences for the COI extension region (I3-M11), 63% for the 28S rDNA C-Region and 45% for the whole ITS region. Samples belonging to *Xestospongia muta* (five specimens), *Iotrochota birotulata* (two specimens), *Ircinia felix* (three specimens), *Agelas dispar*, *Aiolochroia crassa* (two specimens) and *Amphimedon compressa* exhibited conformity among the morphological and molecular diagnosis, whereas the taxonomical annotation for the remaining sponges majorly relied on morphological re-examinations.

Genetic analysis with ASAP based on the COI marker (622 bp alignment covering only the Erpenbeck I3-M11 partition), comprising 79 sequences and 34 presumed species from our sponge dataset and reference sequences, identified 18 and 19 groups in the most reliable partitions with threshold distances of 0.0006 and 0.003, respectively, in accordance with the lowest ASAP score values (Table S4, Figure S1). The recursive ABGD analysis, however, recovered 19–33 groups across a wide range of prior intraspecific divergence values (P = 0.001–0.0599), with the initial partition of 19 taxa yielding strong stability and coinciding with the ASAP grouping (Table S5, Figure S2).

The best-supported delimitation of 19 groups in the COI marker underestimated the putative species representation of the dataset (34) and only discriminated seven out of the nine assumed query species from our survey submitted through the COI gene. In genera *Spirastrella* and *Amphimedon*, we could discriminate species consistent with our designated morphospecies, notwithstanding that genetic conspecific representation was low. *Xestospongia* formed a unique uniform grouping with no intraspecific differentiation, whereas in *Agelas*, intrageneric group detection existed but was inconsistent across species. The molecular taxonomic delimitation for *Aplysina*, *Aiolochroia*, *Hyattella* and *Verongula* was poorly resolutive and often mixed sponges belonging to other genera (Figures S1 and S2), reflecting the low resolution of universal COI barcoding genes in these genera and the need to apply multi-locus approaches. The taxonomic groups representing our dataset exhibited

intraspecific distances ranging from 0% to 9.1% and congeneric interspecific distances from 0% to 13%.

The mean K80 Kimura intraspecific distances were: 0.1% *Agelas dispar*, 0% *Aiolochroia crassa*, 0% *Amphimedon compressa*, 0% *Aplysina fulva*, 9% *Aplysina insularis*, 0% *Hyattella cavernosa*, 0.3% *Spirastrella coccinea*, 0.6% *Verongula rigida*, and 0.3% *Xestospongia muta*. The mean congeneric interspecific Kimura distances were: 0.04% for *Agelas*, 11% for *Aplysina*, 4% for *Spirastrella*, 0.4% for *Verongula* and 0.5 for % *Xestospongia*. For genera *Amphimedon*, *Aiolochroia* and *Hyattella*, there were no reference congeneric nucleotide entries, so distance estimations were not possible.

Together with the ABGD and ASAP groupings, the MEGA 12 K2p+G distance matrix for the COI alignment and the p distance matrices from the 28S and ITS were used to support species annotations and congruence with morphological identifications (see Tables S3–S5 for pairwise distance matrices).

Systematic information for each specimen of this collection with detailed morphological and spicule descriptions and with DNA-barcoding remarks is provided in the next sections. The classification used followed the Systema Porifera [52] and the recent revision proposed by Morrow and Cárdenas [53].

Systematic Description

Class Demospongiae Sollas, 1885

Subclass Verongimorpha Erpenbeck, Sutcliffe, De Cook, Dietzel, Maldonado, van Soest, Hooper and Wörheide, 2012

Order Verongiida Bergquist, 1978

Family Aplysinidae Carter, 1875

Genus *Aiolochroia* Wiedenmayer, 1977

Species *Aiolochroia crassa* Hyatt, 1875

Material. T2_20 and T3_01 (Figure 3) from transects 2 and 3 in Le Sec du Diamant.

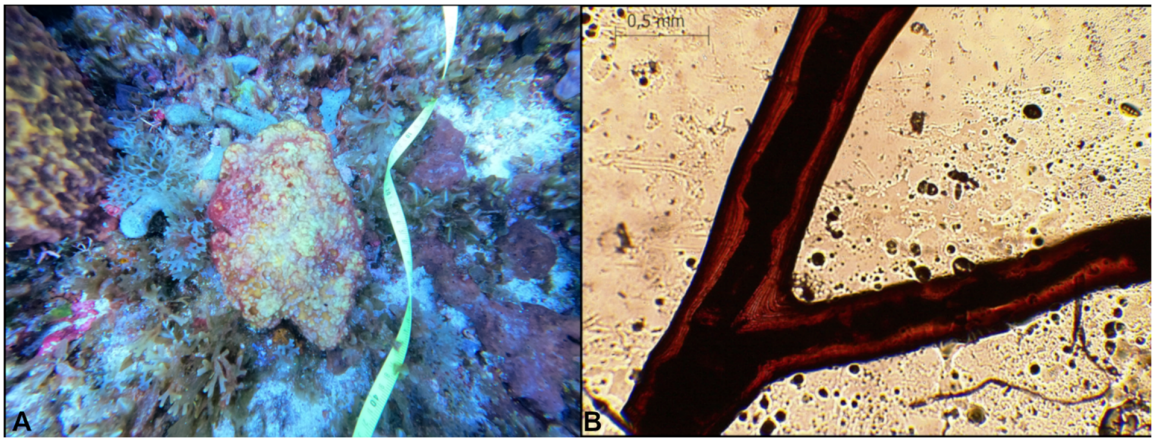


Figure 3. (**A**) Specimen of *Aiolochroia crassa* collected in situ on transects 1 and 2. (**B**) Spongin fiber with irregular pith that occupies up to 60% of the fiber thickness in *A. crassa*.

Description. The specimen is massive in shape. In situ, it is yellow/pinkish in color (Figure 3A), while it becomes black in alcohol due to the presence of aerophobic pigments. The surface is irregularly verrucose, with rounded tubercles, while the consistency is resilient. Only spongin fibers organized in a dendritic way occur, and they are characterized by the presence of quite irregular pith that occupies from 50% to 60% of the width of the fiber (Figure 3B). The fiber diameter of the samples ranges from 220 to 470 µm.

Remarks. This is a common shallow-water Caribbean sponge [68], widely spread in the Caribbean region, and it is reported in the sponge species list of Martinique by

Pérez et al. 2017 [39]. The morphological features of the analyzed specimens fit with those described in the literature in external morphology (yellow massive specimens with irregularly conulose surface) and in the size and organization of the fibers (fiber diameter 150–560 [69]). The COI and ITS sequences exhibited >99% similarity to *A. crassa* reference sequences from Florida (USA), Brazil and Bermuda, while the closest reference for the 28S marker, with 96% resemblance, coincided with *Suberea creba* and *Suberea* spp. from French Polynesia, Vanuatu, and New Caledonia [70]. Morphological inspection and COI and ITS barcoding confirmed the classification of *A. crassa*. To date, there is no specific mention of *A. crassa* being part of the hawksbill turtle diet in the literature reviewed.

Genus *Aplysina* Nardo, 1834

Species *Aplysina insularis* Duchassaing and Michelotti, 1864

Material. T3_09 (Figure 4) from transect 3 in Le Sec du Diamant.

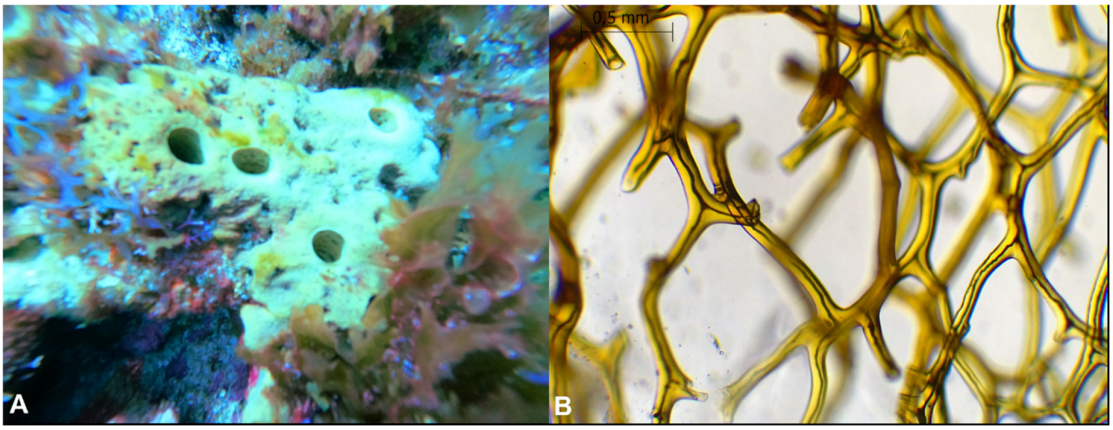


Figure 4. (**A**) Specimen of *Aplysina insularis* collected on transect 3. (**B**) Spongin fibers with very thin pith that occupies less than 50% of the fiber thickness.

Description. Group of four low tubes with apical oscula approximately 1 cm in diameter (Figure 4A). It is yellow in color and becomes black in alcohol due to aerophobic pigments. The surface is smooth in situ and becomes microconulose upon preservation in alcohol. Only spongin fibers occur by forming quite irregular, rounded and ovoid meshes about 100–800 µm wide (Figure 4B). The fibers have pith. The latter occupies less than 50%. The diameter of the fibers ranges from 40 to 120 µm.

Remarks. This species is widely distributed from the east Brazilian coasts to the Caribbean [71,72]. The morphological description fits with that of Zea (1987) [73] and Pinheiro et al. (2007) [74] in terms of external morphology (general shape and color) and the skeleton (fiber and mesh size and shape). The COI segment revealed a similarity of 91% to a conspecific sequence *A. insularis* from Florida (USA) and 8–13% dissimilarity to other Caribbean *Aplysina* spp., which disagrees with the low variability reported in the COI marker for genus *Aplysina* [75]. Unfortunately, nuclear ribosomal barcodes could not be retrieved to further support the molecular identification. Specific mentions of *Aplysina insularis* in the diet of hawksbill turtles are not explicitly described in the literature, but this species is described in the inventory of Pérez et al. (2017) [39].

Species *Aplysina fulva* Pallas, 1766

Material. T3_15 (Figure 5) from transect 3 in Le Sec du Diamant.

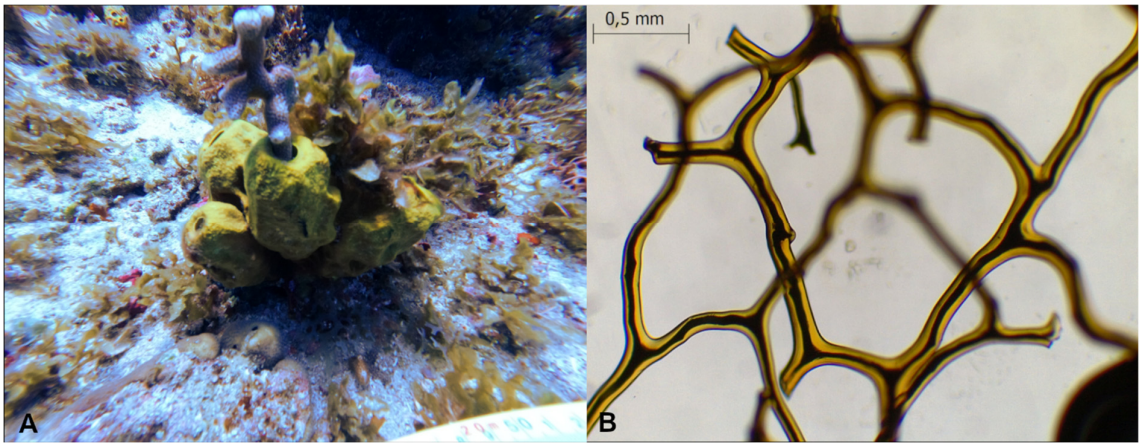


Figure 5. (**A**) *Aplysina fulva* collected along transect 3. (**B**) Spongin fibers with pith that occupies around 50% of fiber's diameter.

Description. It is an aggregate of cylindrical tubes with apical oscules (Figure 5A). It is yellow in situ, while it becomes black in alcohol due to the presence of aerophobic pigments. The surface is microconulose due to the presence of protruding fibers. The fibers range from 40 to 110 µm in width and form a reticulated skeleton with ovoid, rounded meshes of about 300–1000 µm (Figure 5B). The pith occupies around 50% of the fiber's thickness.

Remarks. *Aplysina fulva* is widely distributed in the Caribbean, especially in the southern, western and eastern Caribbean; the Greater Antilles; and the Bahamas [54], and it is reported in the inventory of Pérez et al. (2017) [39] in the reef habitats of Martinique. This species is characterized by huge morphological plasticity, especially in Brazil [74]; nevertheless, the general shape (erect, finger-like tubes) and the characteristics of the skeleton (size of fibers and meshes) agree with those described by Van Soest (1978) [69] and Zea (1987) [73] from the Caribbean. The molecular analysis for the three markers (COI, 28S and ITS) revealed 99–100% identity with *A. fulva* from Atlantic Panamá (Bocas del Toro) and the Bahamas, and up to 1.8% distance from other Caribbean *Aplysina* spp., congruent with what is described in other surveys [75]. There are no mentions in the literature that document *A. fulva* as part of *E. imbricata*'s diet items, yet there are records of green turtles rubbing themselves against these sponges for minutes, hypothetically getting anointed with allelochemical compounds to prevent epibiosis (personal observations). Actually, this sponge species is documented to concentrate large amounts of antipredatory chemical defenses and precursors of bioactive compounds (e.g., brominated tyrosine derivatives) in the outer layers as a means of protection [76].

Genus *Verongula* Verrill, 1907

Species *Verongula rigida* Esper, 1794

Material. T1_07 (Figure 6A), T2_18 (Figure 6B) and T3_13 (Figure 6C) from transects 1, 2, and 3, respectively, in Le Sec du Diamant.

Description. It comprises a group of low oscular mound-tubes that are yellow and yellow-purplish in color when they are in their habitat (Figure 6A,B) but become black in alcohol due to pigment oxidation. It presents a 'honeycomb' surface. The skeleton is reticulated, made up of spongin fibers with pith occupying up to 80% the fiber's thickness (Figure 6D). The skeleton is characterized by elongated polygonal meshes (470–640 µm) (Figure 6D). The diameter of the fibers ranges from 80 to 200 µm.

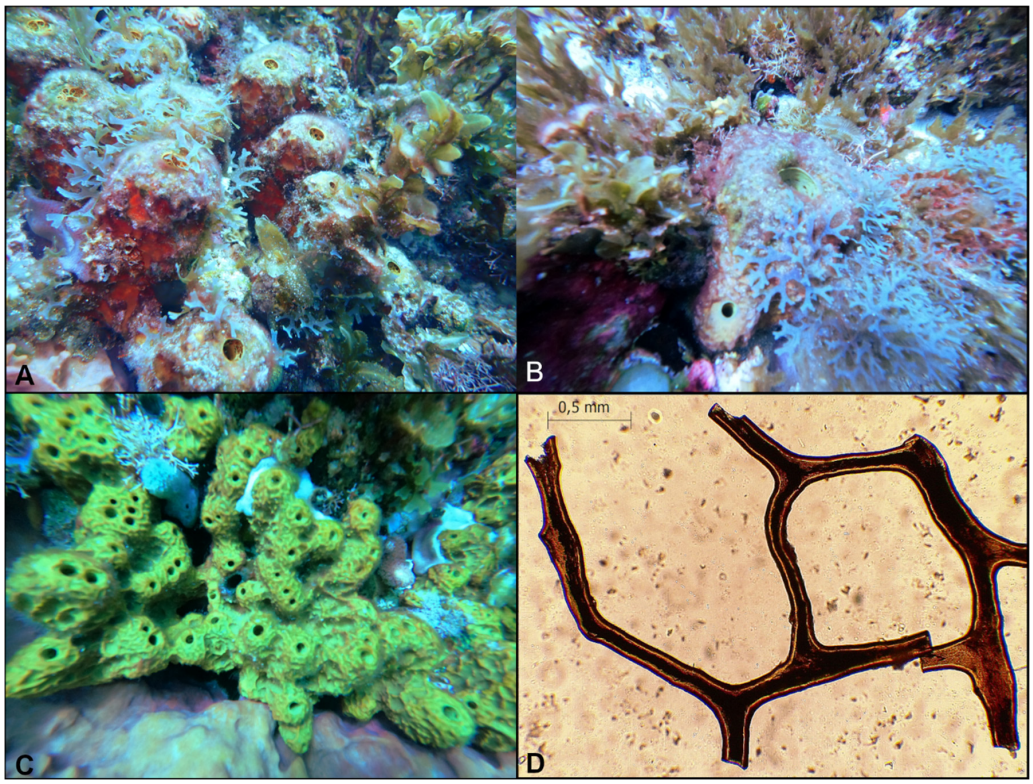


Figure 6. (**A**) Specimen of *Verongula rigida* sampled from transect 1. (**B**) *V. rigida* from transect 2. (**C**) *V. rigida* collected on transect 3. (**D**) Reticulated skeleton of spongin fibers with pith that occupies more than 50% of fiber's width.

Remarks. *Verongula rigida* is widely distributed in the Caribbean, and it was already recorded in Martinique in reef habitats [39,43,77]. The 28S barcode retrieved 99% identity with a *V. rigida* from Bocas del Toro (Panamá), and the COI segments matched *Verogula* sp. and *V. gigantea* deposited sequences from Belize and the Bahamas, with similarities >99%. The ITS sequences exhibited 1% distance from references of *Aplysina lacunosa* and 16% from a congeneric *V. gigantea*, both from the Bahamas. The collected specimens belong to Aplysinidae and to the genus *Verongula*, having an anastomosing skeleton of polygonal meshes and a honeycomb-like surface [68]. They fit the descriptions provided by Zea (1987) [73], who described the species as yellow groups of tubes protruding from a basal mass with apical pseudooscules and a surface with ridges; the fibers are 77–220 µm in diameter, with the medulla occupying 54–60%. *V. rigida* was never recorded as a hawksbill diet item in the literature; by contrast, it was found to be consistently preyed upon by several Caribbean spongivore fish: angelfishes, parrotfishes and trunkfishes [78].

Subclass Keratosa Grant, 1861

Order Dictyoceratida Minchin, 1900

Family Irciniidae Gray, 1867

Genus *Ircinia* Nardo, 1833

Species *Ircinia felix* Duchassaing and Michelotti, 1864

Material. T1_05, T2_02, and T3_04 on transects 1 (Figure 7A), 2 (Figure 7B) and 3 (Figure 7C), respectively, in Le Sec du Diamant.

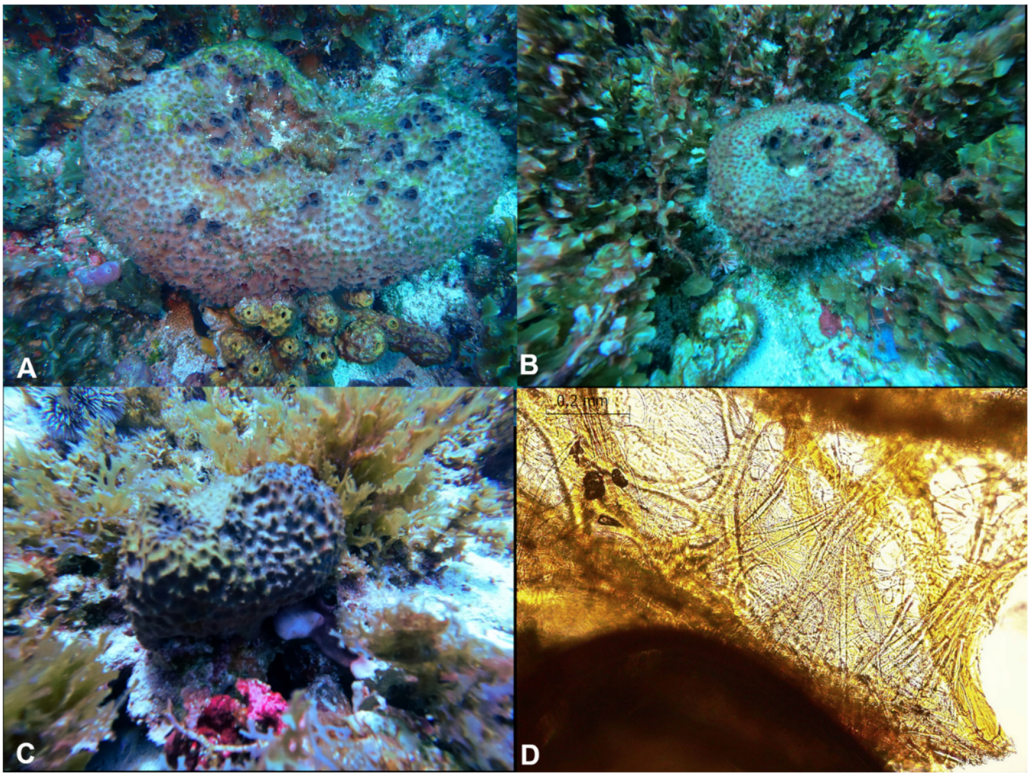


Figure 7. (**A**) Specimen of *Ircinia felix* collected on transect 1. (**B**) *I. felix* in situ from transect 2. (**C**) *I. felix* from transect 3. (**D**) Spongin fibers arranged into fibrofascicles in *I. felix*.

Description. It has a massive shape with a strongly conulose surface (Figure 7A–C). It is gray and cream in color. The consistency is soft and resilient. Numerous oscules occur in quite delimited and depressed regions at the top of the sponge and are slightly covered by sediment; oscules are darker than the rest of the sponge surface. Spongin fibers are present and arranged into fibrofascicles (Figure 7D). Some foreign spicules and sediments are embedded inside the fibers. Irciniid filaments range from 2.5 to 10 µm. The width of the primary fibers ranges from 70 to 220 µm; the diameter of secondary fibers ranges from 10 to 40 µm.

Remarks. *Ircinia felix* is widely distributed from the Brazilian coast to Florida (USA), including the Caribbean regions [54]. It is reported in the species list of Martinique by Pérez et al. (2017) [39] as dwellers of reefs. This species is, according to Zea (1987) [73], characterized by its low conules and clear or dark oscule edges that contrast with the general sponge color; the fibers are fasciculate and with detritus. We obtained sequences of the ITS marker matching *I. felix* reference sequences from Bermuda with >99% similarity, while the 28S sequence revealed a 99% match with a reference of *I. camapana* collected in Bocas del Toro (Panamá). There is no specific literature documenting *I. felix* within the hawksbill diet, but the high concentration of antipredator compounds in the inner tissue of the sponge may be considered a response to high predator pressure in the past [76].

Family Spongiidae Gray, 1867

Genus *Hyattella* Lendenfeld, 1888

Species *Hyattella cavernosa* Pallas, 1766

Material. T1_08C (Figure 8A), T1_13 (Figure 8B) and T3_20 (Figure 8C) on transects 1 and 3 in Le Sec du Diamant.

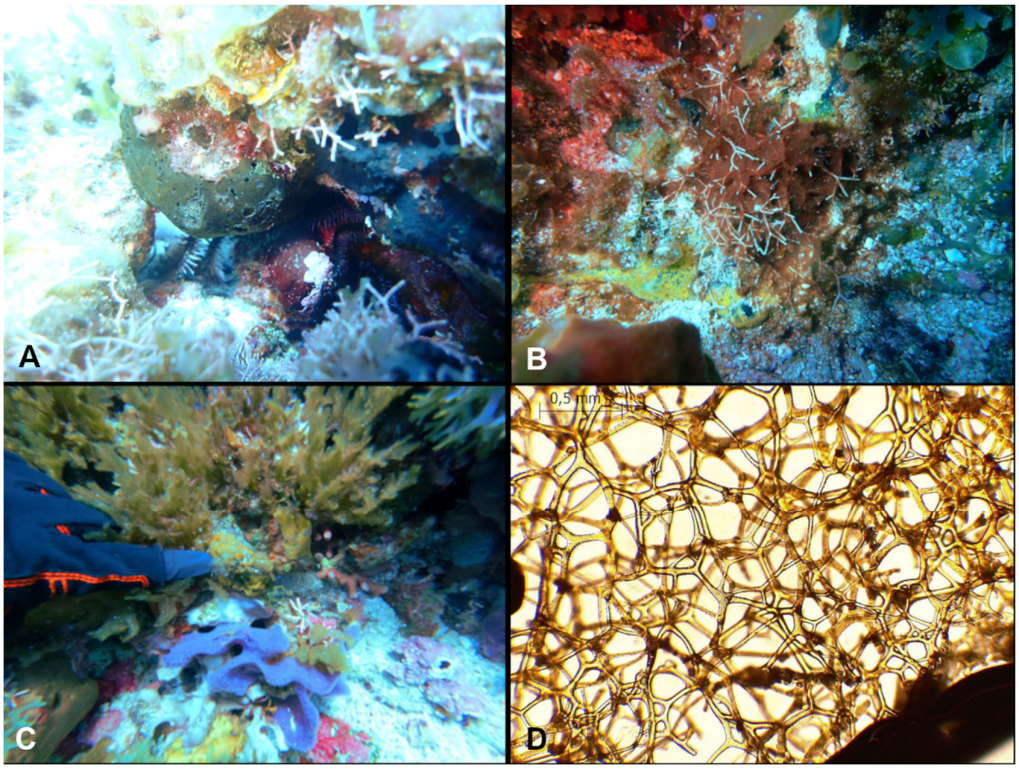


Figure 8. (**A**,**B**) *Hyattella cavernosa* photographed in situ on transect 1. (**C**) Sample collected along transect 3. (**D**) Reticulated skeleton made up of secondary spongin, amber fibers of *H. cavernosa*.

Description. It is a sponge with a variable, amorphous shape and is cream in color (Figure 8A–C); it is frequently covered by encrusting organisms and algae. The consistency is soft. The choanosome is very cavernous. Spicules are absent, while homogeneous amber fibers are present, forming a reticulated skeleton with rounded meshes of about 80–400 µm (Figure 8D). Primary fibers, in general, are free from inclusion, rarely with exogenous spicules; they are about 100 µm in diameter and sometimes fasciculated; secondary fibers are free of inclusion; their diameters range from 20 to 50 µm. It is difficult to distinguish the primary fibers from the secondary ones.

Remarks. *Hyattella cavernosa* is geographically distributed from the Brazilian coasts to the Gulf of Mexico, thus including Caribbean regions. Until now, it has never been recorded in Martinique, and so this constitutes a new record in the Martinique sponge catalog, according to the inventory from Pérez et al. (2017) [39]. The morphological character described above fits with those of the species *Hyattella cavernosa* reported by Sandes and Pinheiro [79], although a certain variability in the size of the fibrous skeleton is reported by the authors. In their paper, they describe the species as having fasciculated primary and secondary fibers free of inclusions that are 40–60 and 20–30 µm wide, respectively, while the meshes are 150–400 µm in diameter. Nevertheless, these differences are considered by the authors to be intraspecific variations. Our specimens fit the description by Muricy and coworkers [80], who reported fasciculated primary spongin fibers with debris and secondary fibers free of debris, even if the size of the primary fibers (62–210 µm) and of the meshes (90–350–720 µm) is slightly larger. There was no precedent nucleotide data available for this species on GenBank. The COI barcode revealed >99% similarity to reference records of *Aiolochroia* and *Aplysina* spp., indicating the poor resolution of this marker in this taxon. The ITS sequences, however, matched with *Spongia* spp. from Vietnam and France, with similarities over 87%. We, hence, determined these samples to be *Hyattella cavernosa* based on the morphological identifications. There are no previous references of hawksbill turtles feeding on *H. cavernosa*.

Subclass Heteroscleromorpha Cárdenas, Pérez and Boury-Esnault, 2012
Order Haplosclerida Topsent, 1928
Family Callyspongiidae Laubenfels, 1936
Genus *Callyspongia* Duchassaing and Michelotti, 1864
Subgenus *Callyspongia* (*Cladochalina*) Schmidt, 1870
Species *Callyspongia* (*Cladochalina*) *aculeata* Linnaeus, 1759

Material. T1_11 (Figure 9A) and T3_06 (Figure 9B) on transects 1 and 3 in Le Sec du Diamant.

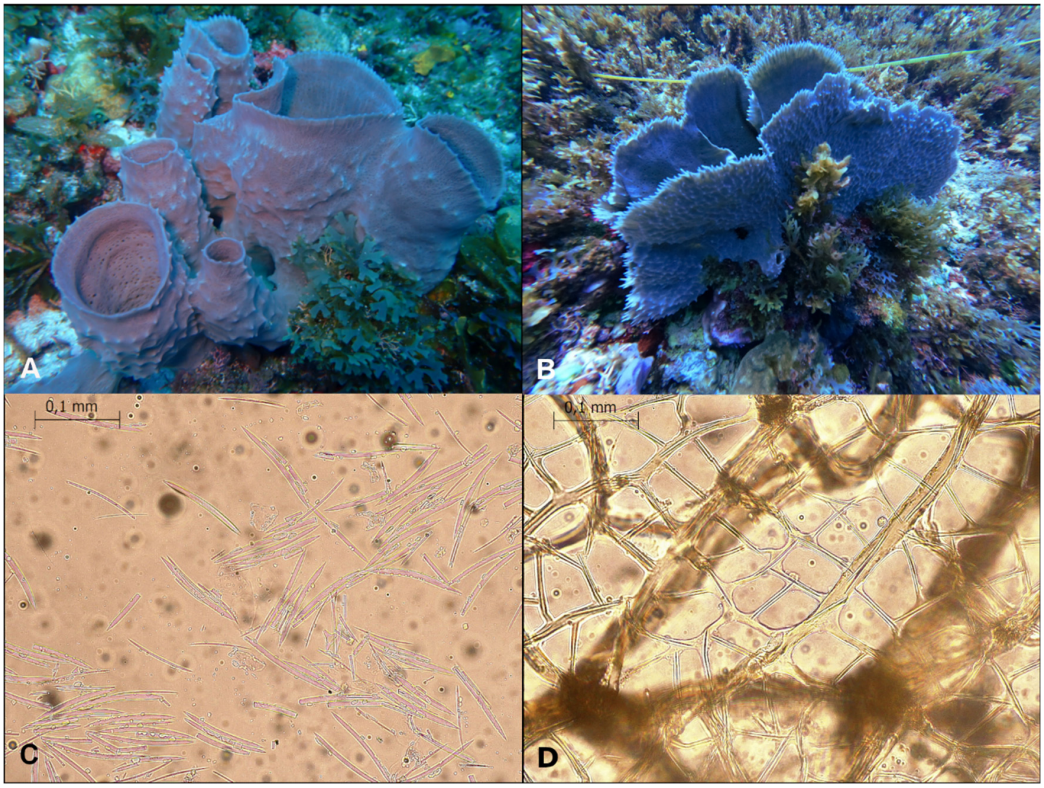


Figure 9. Pictures in situ of *Callyspongia* (*Cladochalina*) *aculeata*: (**A**) tubular morphotype of *C.* (*C.*) *aculeata* on transect 1; (**B**) *C.* (*C.*) *aculeata* on transect 3, fan morphotype. Skeleton and spicules under the optical microscope of *C.* (*C.*) *aculeata*: (**C**) blunt and curved oxeas; (**D**) plurispiculate primary and secondary spongin fibers plus the unispiculate tertiary fibers.

Description. Violet tubes and fan morph with spiny surface (Figure 9A,B). The consistency is tough. The ectosome is a regular web of triangular meshes (50–100 µm in size) made up of primary and secondary fibers of about 18–30 µm and 5–12 µm, respectively. The fibers are unispicular. The choanosome (Figure 9D) is characterized by a reticulation of fasciculated primary and secondary fibers that are plurispicular and by tertiary unispicular fibers. The fibers form small meshes of 50–100 µm within larger polygonal meshes of 200–350 µm. Fibers I range from 40 to 80 µm; fibers II range from 20 to 60 µm; and fibers III range from 10 to 20 µm. Spicules are curved oxeas (Figure 9C), mainly with blunt extremities. The length of the spicules ranges from 80 to 120 µm (mean: 94 µm; S.D.: ≈8.94), while the average width is around 10 µm.

Remarks. *Callyspongia aculeata* frequently occurs on Caribbean coral reefs. It represents one of the most frequent sponges in Martinique's reef habitats [32,39]. It can present great phenotypic plasticity both in morph and color [81]. The definitive classification as *C. aculeata* was determined from the morphological observations only, as there was no reliable molecular data. The morphological description fits precisely with that reported by Van Soest (1980) [82] in terms of the general external morphology (cluster of long erect tubes

and fun-shaped) and in the characteristics of the skeleton. Previous preying behaviors on *C. aculeata* have not been mentioned in *E. imbricata*. By contrast, it is preyed upon by many Caribbean fish [83,84].

Subgenus *Callyspongia* (*Toxochalina*) Ridley, 1884

Species *Callyspongia* (*Toxochalina*) cf. *pseudotoxa* Muricy and Ribeiro, 1999

Material. T1_10, transect 1 in Le Sec du Diamant.

Description. It has a massive, lobate shape (Figure 10A) and is light blue in color in living organisms. The surface is smooth, and three oscules are evident on one lobe. The consistency is slightly elastic but resistant. The ectosomal tangential skeleton is made up of unispicular primary, secondary and tertiary fibers forming quadrangular meshes up to 500 µm (Figure 10B). The primary fibers are about 80–100 µm, the secondary fibers are about 60 µm, and the tertiary fibers are from 10 to 20 µm. The choanosomal skeleton is made up of paucispicular ascending fibers of about 80 µm in diameter, supporting the ectosomal skeleton, and by unipaucispicular secondary fibers of 40–50 µm in diameter. Spicules are oxeas and range from 50 to 90 µm in length (mean: 66 µm; S.D.: ≈15.17) and have very thin toxas of about 20–25 µm (Figure 10C,D).

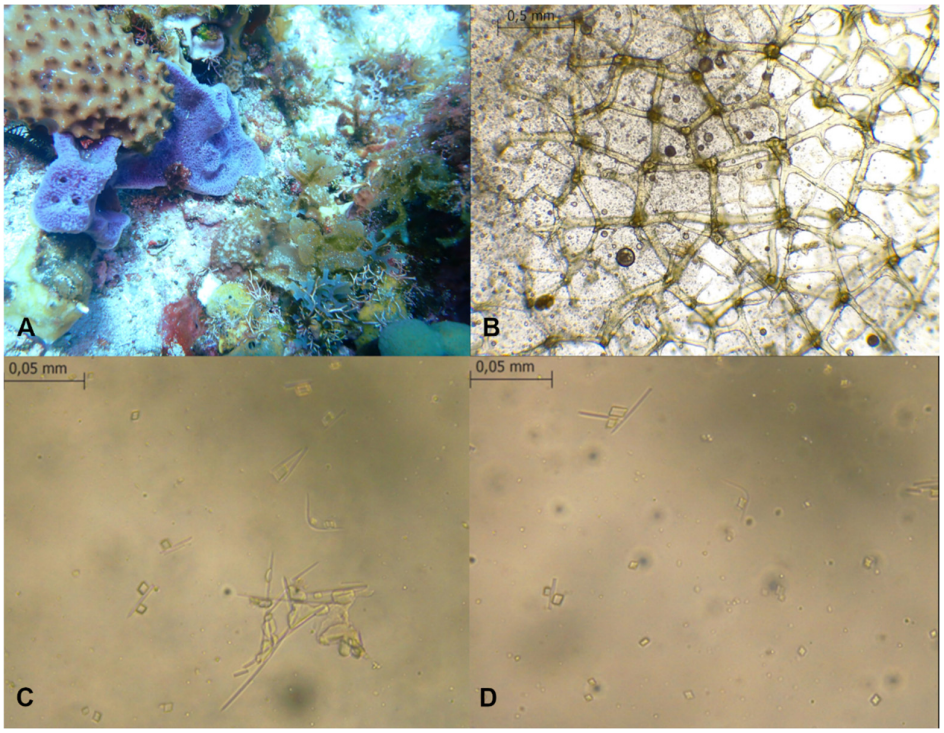


Figure 10. (**A**) Specimen of the sponge *Callyspongia* (*Toxochalina*) cf. *pseudotoxa* collected on transect 1. (**B**) Picture taken under the optical microscope of the ectosomal skeleton. (**C**,**D**) Pictures taken under the optical microscope of toxas belonging to *C.* (*T.*) cf. *pseudotoxa*.

Remarks. *Callyspongia* (*Toxochalina*) *pseudotoxa* is mainly distributed along the Brazilian coasts (de Voogd et al. 2025). This represents the first record for Martinique. The only successful marker obtained was the 28S, which matched with a *C. pseudotoxa* reference sequence from Brazil with a similarity of 98%. The morphological description in part corresponds to that of *C.* (*T.*) *pseudotoxa* described by Muricy and Ribeiro (1999) [85] in terms of the general shape and skeleton organization. We could classify down to the genus level (*Toxochalina*) thanks to the presence of toxas (Figure 10C,D), but these spicules and the oxeas are thinner than those described for *C.* (*T.*) *pseudotoxa*. There is no evidence of the presence of *C. pseudotoxa* in the hawksbill diet in the literature.

Family Niphatidae van Soest, 1980

Genus *Amphimedon* Duchassaing and Michelotti, 1864
Species *Amphimedon compressa* Duchassaing and Michelotti, 1864

Material. T3_12, transect 3 in Le Sec du Diamant.

Description. It has a massive, flabellate morph (Figure 11A). It is brown in color and has a tough and resilient consistency. The surface is microconulose. Ridges and more flattened regions occur, with evident oscules mainly concentrated on the rims of the ridges (Figure 11A). The ectosomal skeleton is a network of multispicular spicule tracts forming ovoid meshes up to 400 µm (Figure 11C). The choanosomal skeleton is reticulated, with ascending fibers made up of numerous compacted spicules connected by thinner transversal tracts (Figure 11D). The primary fibers range from 50 to 80 µm and are plurispiculate; the secondary fibers range from 20 to 50 µm and are paucispicular. The mesh width is 100–300 µm. The spicules are curved, blunt or acerate oxeas (Figure 11B) whose length ranges from 150 to 180 µm (mean: 162 µm; S.D.: ≈13.04), while they have an average width of 10 µm.

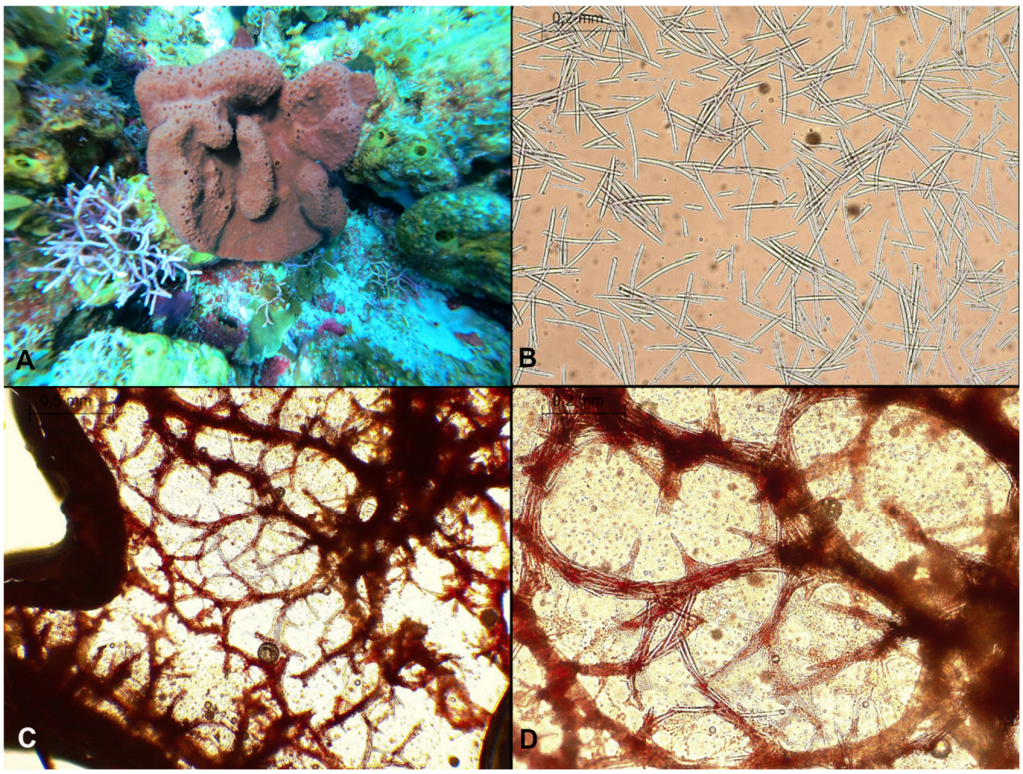


Figure 11. (**A**) Underwater photograph of *Amphimedon compressa* from transect 3. Skeleton and spicules under optical microscope of *A. compressa*: (**B**) oxeas (blunt, acerate and curved). (**C**) Ectosomal skeleton of multispicular spicule tracts. (**D**) Reticulated, choanosomal skeleton with ascending and multispiculated primary fibers.

Remarks. The distribution area of *A. compressa* ranges from the northeastern Brazilian coast to the Gulf of Mexico, including the Caribbean regions [54]. It has already been recorded on Martinique's reef by Pérez et al. 2017 [39]. The specimen characteristics fit with the morphological description by Van Soest (1980) [82] in terms of the general external characteristics (dark brown, flabelliform sponge, with rows of oscules) and the skeletal organization (ascending fibers 50–80 µm in diameter, secondary fibers 20–30 µm in diameter and oxeas with dimensions of 140–167 µm × 3.5–5.5 µm). The COI and 28S barcodes revealed over 100% and 98% identities, respectively, with *Amphimedon compressa* references from Florida and Brazil, thus confirming the taxonomical examination. This sponge species does not seem to be preferred by *E. imbricata*, because it has never been

recalled in the literature as being among its diet items. Additionally, *A. compressa* appears to be chemically defended by the production of bioactive sesterterpenes and amphitoxins, with potential antipredatory properties [86].

Species *Amphimedon caribica* Pulitzer-Finali, 1986

Material. T3_07, transect 3 in Le Sec du Diamant.

Description. It has an irregular fan shape (Figure 12A) and is blue-violet, with a smooth surface. No visible oscula arranged on one face are observable from the pictures taken in situ or from the samples. The consistency is rubbery. The skeleton is anisotropic, with primary and secondary spicule tracts rich in spongin, creating irregular, elongated meshes (Figure 12B) with a diameter of 210–650 µm. The diameter of the primary fibers ranges from 50 to 90 µm, while the diameter of the secondary fibers is about 140–200 µm. The spicular type was represented by slightly curved oxeas that ranged from 210 to 250 µm in length (mean: 222 µm; S.D.: ≈14.72) and had an average width of 10 µm.

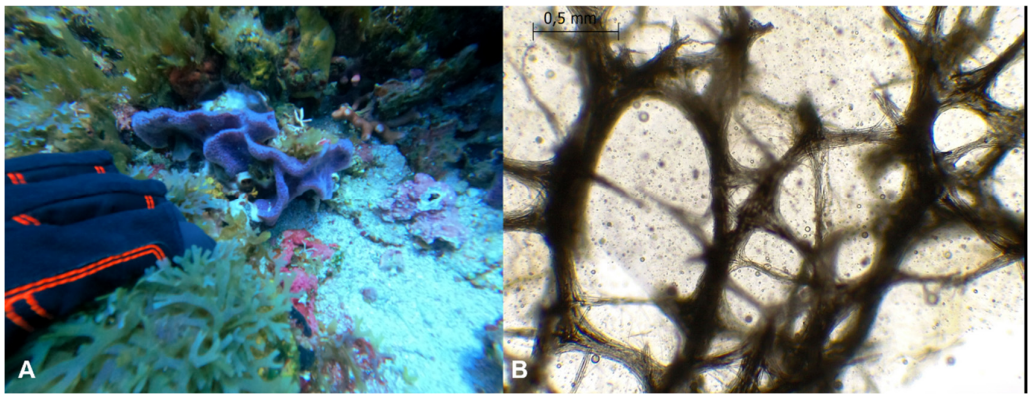


Figure 12. (**A**) *Amphimedon caribica* photographed in situ along transect 3. (**B**) Picture taken under the optical microscope of a portion of the anisotropic skeleton of *A. caribica*.

Remarks. *Amphimedon caribica* is mainly recorded along Brazilian coasts, the eastern Caribbean and the Greater Antilles [54]. It has also been recorded on the reefs of Martinique [39]. The morphological features led us to univocally identify this sponge as *A. caribica* because the external morphological characteristics (violet, gray palmate sponge) and the characteristics of the skeleton (fibers up to 100 µm and meshes of 150–400 µm) fit with the description of the type by Pulitzer-Finali (1986) [87]. Our 28S and ITS barcodes represent the first molecular data for this species, revealing 80% similarity with *Haliclona* and *Amphimedon* spp. available records. According to the literature, these sponges do not appear to be part of the hawksbill turtle diet.

Family Petrosiidae van Soest, 1980

Genus *Neopetrosia* de Laubenfels, 1949

Species *Neopetrosia rosariensis* Zea and Rützler, 1983

Material. T1_08D and T1_08B, transect 1 in Le Sec du Diamant.

Description. It has a massively encrusting, lobate shape and is black in color (Figure 13A,B). The consistency is tough. The surface is smooth, with evident oscules. The ectosome is an isodictyal network with triangular meshes (Figure 13D); the choanosome is more confused, with irregular meshes (Figure 13C). Spicules are acerate, blunt and curved oxeas (Figure 13C). The length of spicules ranges from 150 to 170 µm (mean: 160 µm; S.D.: ≈7.91), and the average width is 10 µm.

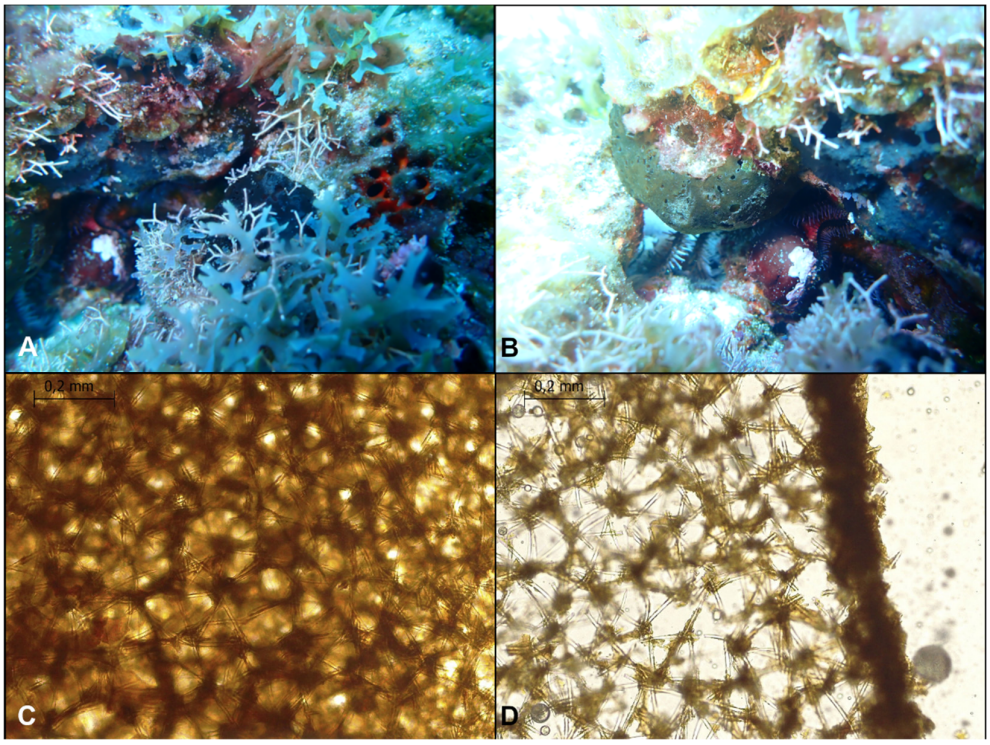


Figure 13. *Neopetrosia rosariensis:* (**A**) specimen (sample T1_08D) collected in situ along transect 1. (**B**) Fresh specimen (sample T1_08B) collected in situ along transect 1. (**C**) Choanosome. (**D**) Ectosome.

Remarks. It is mainly distributed around the Greater Antilles and the eastern and southwestern Caribbean [69,73]. This species is a new record to be added to the sponge inventory of Martinique, and it was not mentioned in the work of Pérez et al. (2017) [39]. Only the 28S molecular marker was obtained, and the sequence was matched with 100% identity to a *Neopetrosia rosariensis* reference entry from Martinique, and it had 98% similarity with a conspecific from Bocas del Toro (Panamá). The morphological features of our sample are close to those described for the reference species reported by Zea et al. (2026) [88]. The species is described as having a variable shape consisting of dark black tubes or with a basal mass from which low tubes protrude, and spicules vary according to the geographic distribution (in the Bahamas, 120–170 by 2–5.5 µm, and in Colombia, 100–212 by 0.8–11.6). The black color is characteristic of the species and can be confused with the congeneric *N. carbonaria* (Lamarck, 1814), characterized by black color but also by larger spicules.

Genus *Xestospongia* de Laubenfels, 1932

Species *Xestospongia muta* Schmidt, 1870

Material. T1_01, T1_03, T2_03, T3_02, and T3_10 from transects 1, 2 and 3 in Le Sec du Diamant.

Description. *Xestospongia muta* is also called 'the giant barrel sponge' for its characteristic vase or barrel shape (Figure 14A–E). The color is cinnamon-tan, pink-lilac. The consistency is crumbly and incompressible, while the surface structure is ribbed. The skeleton is isotropic, without distinction between primary and secondary fibers (Figure 14G); the spicules prevail on spongin fibers. The ectosome consists of an isotropic reticulation of spicule tracts surrounding single large meshes (up to 200 µm in diameter). The choanosome is a reticulation of spicule tracts that form rounded meshes 200–400 um in diameter. The megascleres are represented by curved and acerate oxeas, often becoming strongyloxeas (Figure 14F). Their length ranges from 380 to 400 µm (mean: 391 µm; S.D.: ≈9.83), while the width ranges from 10 to 15 µm. Microscleres are absent.

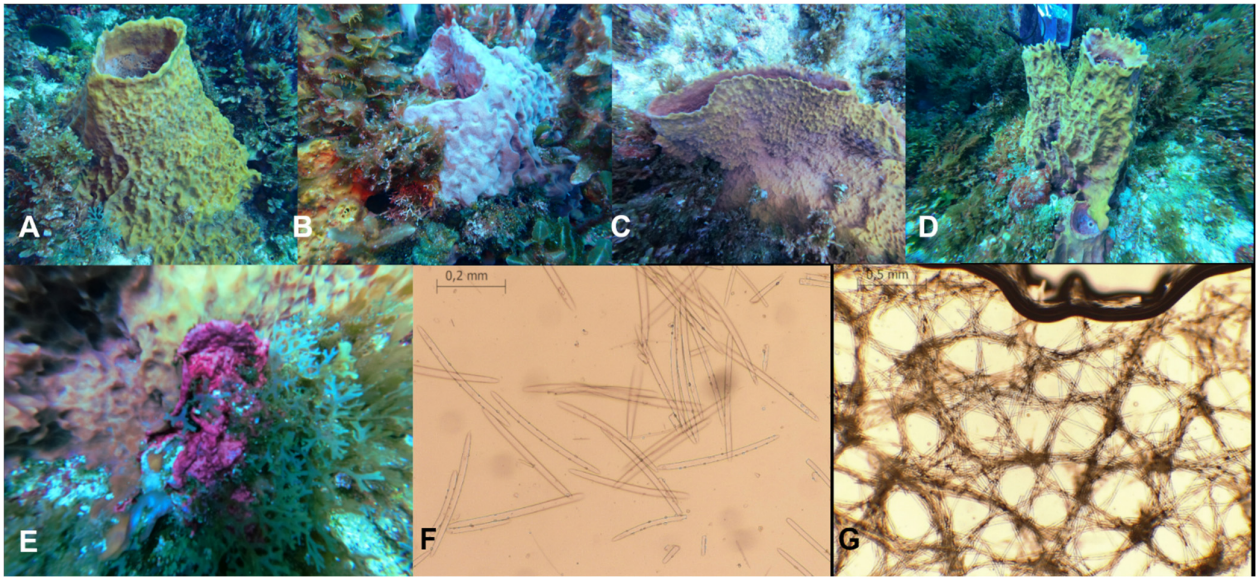


Figure 14. (**A**,**B**) The giant barrel sponges *Xestospongia muta* occurring in transect 1; in B is shown the bleached morphotype. (**C**) The only specimen of *X. muta* collected from transect 2. (**D**,**E**) Two specimens found in transect 3. Pictures taken under the optical microscope of *X. muta* skeleton and spicules: (**F**) oxeas; (**G**) aggregates of siliceous spicules forming an isotropic skeleton.

Remarks. *Xestospongia muta* represents an important and dominant habitat-forming organism in Caribbean waters [82]. It is widely distributed and abundant in Caribbean regions [39,82] and in our study site; it is strongly characterized by its characteristic large size and shape in the adult state; our specimens fit with the descriptions of the species in terms of the general shape and skeleton organization; the spicules are reported by Zea (1987) [73] as quite variable according the geographic locality, but our specimens show a range of sizes within the described values. The barcodes obtained for the COI partition matched with *X. muta*, *X. bergquisita*, *X. proxima* and *X. testudinaria* reference sequences with >99% similarity, demonstrating a low resolutive power of this marker in species delimitation in *Xestospongia*. This species was reported as being a prey item in the *E. imbricata* diet by Baumbach and coauthors (2022) [25]. This sponge does not seem to have high organic or energy content due to its high hash residue [25], but it hosts large quantities of endosymbionts and epifauna, which could enhance its nutritional value.

Order Tetractinellida Marshall, 1876

Suborder Spirophorina Bergquist and Hogg, 1969

Family Tetillidae Sollas, 1886

Genus *Cinachyrella* Wilson, 1925

Species *Cinachyrella kuekenthali* Uliczka, 1929

Material. T1_04, transect 1 in Le Sec du Diamant.

Description. This sponge is characterized by a subspherical shape (Figure 15A) and is orange to brownish in color. The surface is slightly hispid and usually covered by algae and epiphytes. The porocalices are high in density on the top of the sponge. The consistency is elastic but firm. It is characterized by a radial skeleton mainly composed of oxeas (Figure 15B). The spicule types are oxeas, anatriaenes (rare in the specimen), protriaenes (Figure 15D), and large sigmaspires (Figure 15C). The oxeas length is around 2–5 mm; that of protriaene rhabds is 1.7–3 mm; that of anatriaenes is not measured; that of sigmaspires is around 16.3 µm on average.

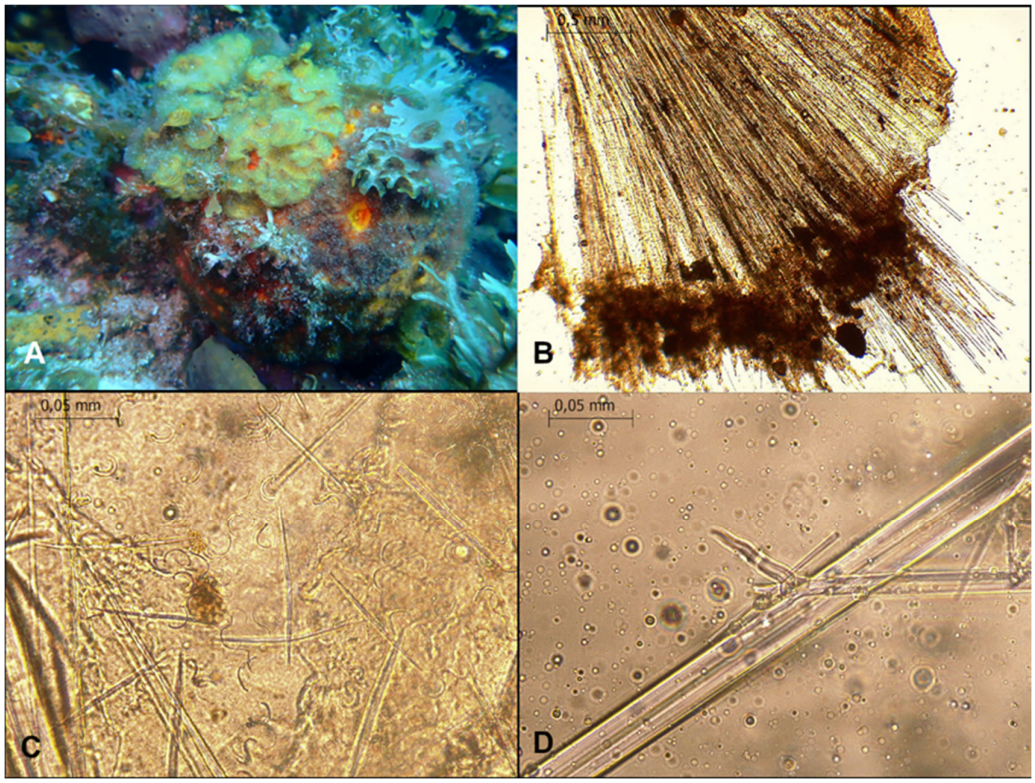


Figure 15. (**A**) Fresh sample of *Cinachyrella kuekenthali* collected on transect 1. Skeleton and spicules of *C. kuekenthali* observed under the optical microscope: (**B**) radiated skeleton made up of oxeas; (**C**) sigmaspires and oxeas; (**D**) extremity of a protriaene.

Remarks. *Cinachyrella kuekenthali* spreads from the Brazilian coasts to those of the Carolinas (USA), passing through Caribbean regions [54]. In Martinique, this species was recorded on coral reef habitats [39,89]. The morphological characteristics such as the shape, color, skeleton architecture and spicule types and dimensions fit the description of the species *Cinachyrella kuekenthali*. No molecular data was retrieved; thus, the taxonomical identification was fully supported by the morphological examination. Sponges in the genus *Cinachyrella* were found among the diet contents of hawksbills on the Mona and Monito Islands in Puerto Rico, but the authors suggested a low feeding preference for this species [22].

Order Agelasida Hartman, 1980

Family Agelasidae Verrill, 1907

Genus *Agelas* Duchassaing and Michelotti, 1864

Species *Agelas dispar* Duchassaing and Michelotti, 1864

Material. T2-01, transect 2 in Le Sec du Diamant.

Description. It is a massive and lobate sponge with a slightly smooth surface; the color is purplish-brown (Figure 16A), while the consistency is tough but resilient. Its skeleton is reticulated, consisting of primary and secondary fibers (Figure 16B,C). The diameter of the primary fibers ranges from 50 to 120 µm, while those of the secondary fibers range from 40 to 60 µm. Spicules are cored inside the primary spongin fibers that are also echinated (Figure 16C,D). Spicules are verticillate acanthostyles with dimensions of 160–200 µm × 10–15 µm (mean: 175 µm; S.D.: ≈13.42). The number of whorls varies between 11 and 12.

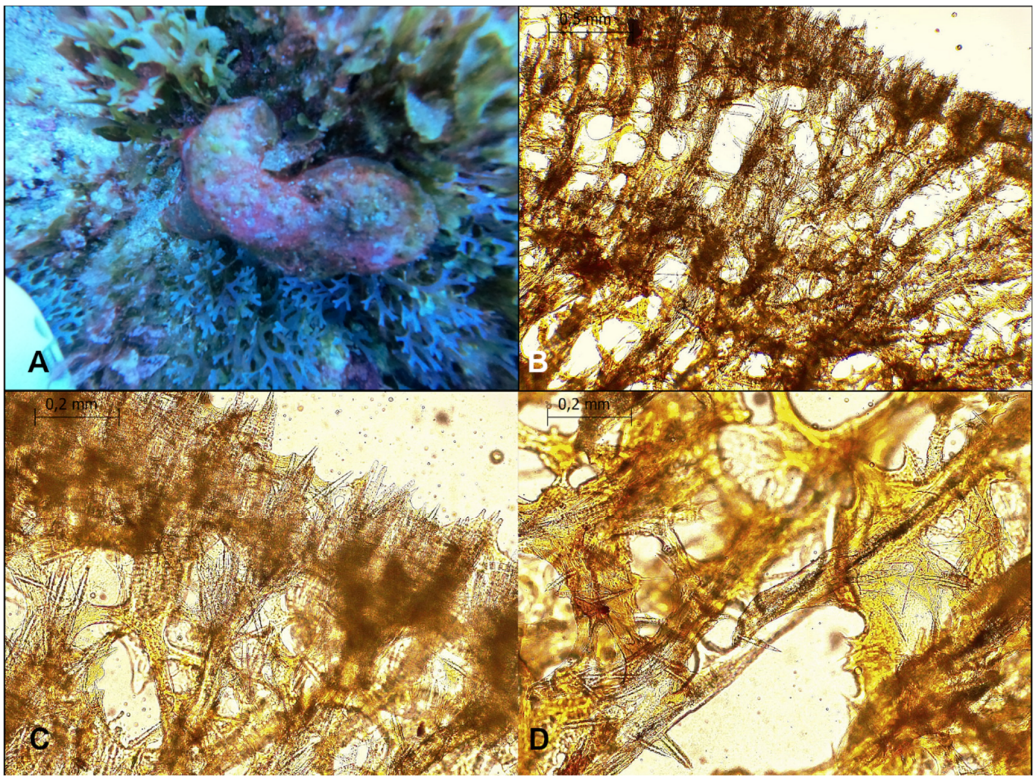


Figure 16. (**A**) *Agelas dispar* photographed in situ along transect 2. Pictures taken under optical microscope of the skeleton, fibers and spicules of *A. dispar*: (**B**,**C**) the reticulated skeleton is made up of primary multispiculated fibers and secondary fibers; (**D**) spongin fibers appear cored and echinated by verticillate megascleres.

Remarks. *Agelas dispar* can be found on the Brazilian coasts up to the Bahamian region [54]. The morphological description fits with that reported by Duchassaing and Michelotti (1864) [71], according to the authors, in terms of the size and organization of the primary fibers (cored and echinated, 32–130 µm in diameter) and secondary fibers (rarely echinated, 20–80 µm) [73]. All three genetic markers—COI, 28S and ITS—revealed barcodes with >99% similarity to reference sequences of *Agelas dispar* from Venezuela and several regions in the Caribbean Sea. However, for all markers, there were other congeneric specimens exhibiting highly matching entries. For COI, *A. schmidti*, *A. wiedenmayeri* and *A. dispar* sequences had 100 to 99% identities, which differed by 2% distance from *A conifera*, *A* cf. *tubulata* and *A.* cf. *cerebrum* and by 8% from *A. sventres*, *A. citrina* and *A. clathrodes*. The 28S barcodes from *A. dispar* were 1% distant from *A conifera* and 2% dissimilar to *A. oroides*, *A mauritiana* and *A. clathrodes*. For the ITS marker, *A. dispar* barcodes were >99% matching with *A. schmidti*, *A. wiedenmayeri* and *A. cervicornis*; between 2 and 3% dissimilar to entries of *A. nemoechinata*, *A. mauritiana*, *A. cerebrum*, *A dilatata*, *A. repens*, *A. sceptrum*, *A. arborescens*, *A. conifera*, *A. novaecaledoniae* and *A. ceylonica*; and 4–6% distant from *A. sventres*, *A. citrina*, *A. oroides*, *A. clathrodes* and *Agelas* sp. These outcomes suggest low genetic variability in the barcoding loci in genus *Agelas* and align with the incongruent, and likely overestimated, morphospecies designations when correlated with phylogenomic and population genetic analyses [90]. There is no specific evidence for the presence of *Agelas dispar* in the diet of the hawksbill turtle. Genus *Agelas* is characterized by the production of secondary metabolites [91] and by siliceous structural elements. On the one hand, these features could make the sponge less palatable, but on the other, the rich presence of endosymbionts with high nutritional supply—typical of *Agelas* spp. [90]—could turn these sponges into more attractive prey for hawksbill turtles.

Species *Agelas clathrodes* Schmidt, 1870

Material. T1_06 and T1_08, transect 1 in Le Sec du Diamant.

Description. It has an encrusting, lobate shape and is orange in color. The uppermost surface is smooth and characterized by areas of oscules and holes (Figure 17A–D). The consistency is tough but also slightly resilient. The skeleton is reticulated, with evident primary and secondary echinated fibers (Figure 17C,E,F). Spicules are verticillate acanthostyles presenting a number of whorls that range from 6 to 10 (Figure 17B). The length of spicules ranges from 100 to 220 µm (mean: 171 µm; S.D.: ≈39.83), while the average width is 10 µm. The diameter of the fibers ranges from 20 to 70 µm.

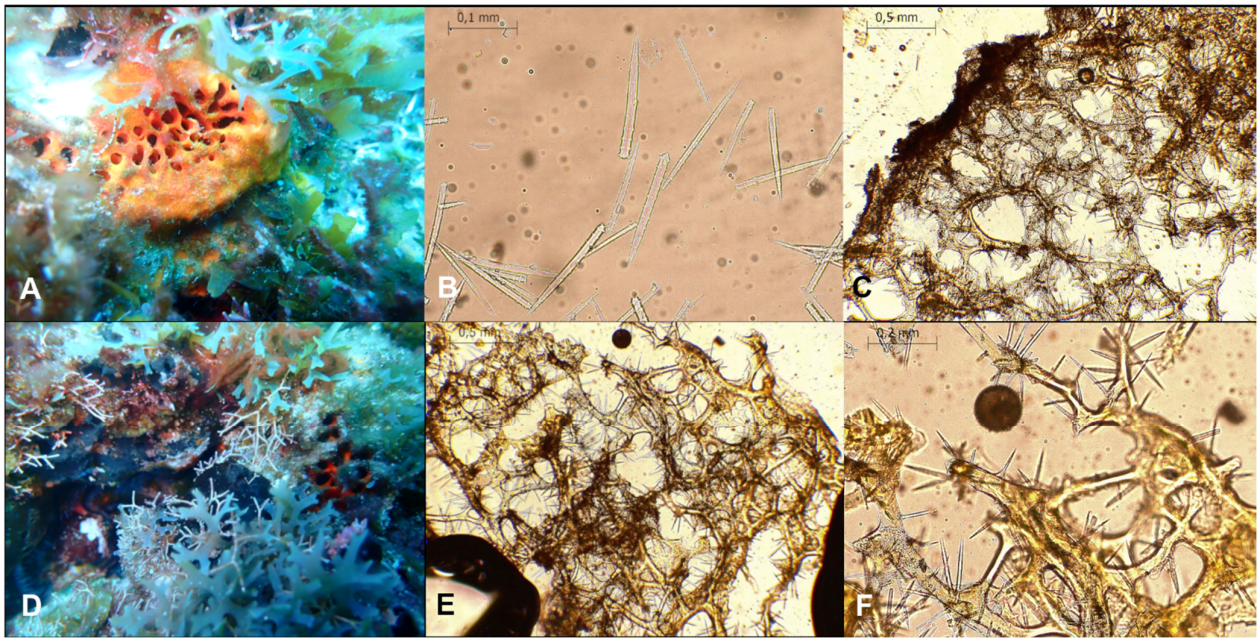


Figure 17. (**A**,**D**) Specimens of *Agelas clathrodes*. Spicules and skeleton of *A. clathrodes* under optical microscope: (**B**) verticillate acanthostyles; (**C**,**E**,**F**) reticulated skeleton with echinating spicules.

Remarks. *Agelas clathrodes* is widely distributed in the Caribbean and also in Martinique's reefs [39,43,77]. Due to the great morphological similarity at the skeleton level and in terms of spicules and external appearance between *Agelas clathrodes* and *Agelas sventres* [92], the molecular analysis in this sample was essential to support a correct taxonomical identification. Only the 28S barcode was retrieved, which was matched with >99% identity to *Agelas clathrodes* and reported distances ranging from 2 to 3% with other congeneric reference sequences like *A. conifera*, *A. oroides*, *A. mauritiana*, *A. dispar*, and *Agelas* sp. There is no literature reporting the regular consumption of *Agelas clathrodes* by *E. imbricata*.

Order Poecilosclerida Topsent, 1928

Family Iotrochotidae Dendy, 1922

Genus *Iotrochota* Ridley, 1884

Species *Iotrochota birotulata* Higgin, 1877

Material. T1_02 and T3_08, transects 1 and 3 in Le Sec du Diamant.

Description. It has a black, yellow branching shape (Figure 18A,B). It stains the preservation alcohol with purple tones, as well as the fingers upon touching, and it releases dark exudate and mucus when squeezed. The consistency is quite tough but resilient. The surface is slightly irregular and microconulose. Oscules occur along the branches. The base from which the branches depart is encrusting. Spicular types are represented by strongyles, styles (Figure 18C) and birotulas (Figure 18D). The length of strongyles ranges from 185 to 200 µm (mean: 195 µm; S.D.: ≈8.66), while their width ranges from 5 to 10 µm. The length

of styles ranges from 170 to 250 µm (mean: 226 µm; S.D.: ≈39.01), with the width ranging between 5 and 10 µm. Birotula microscleres are 10–12.5 µm (Figure 18D).

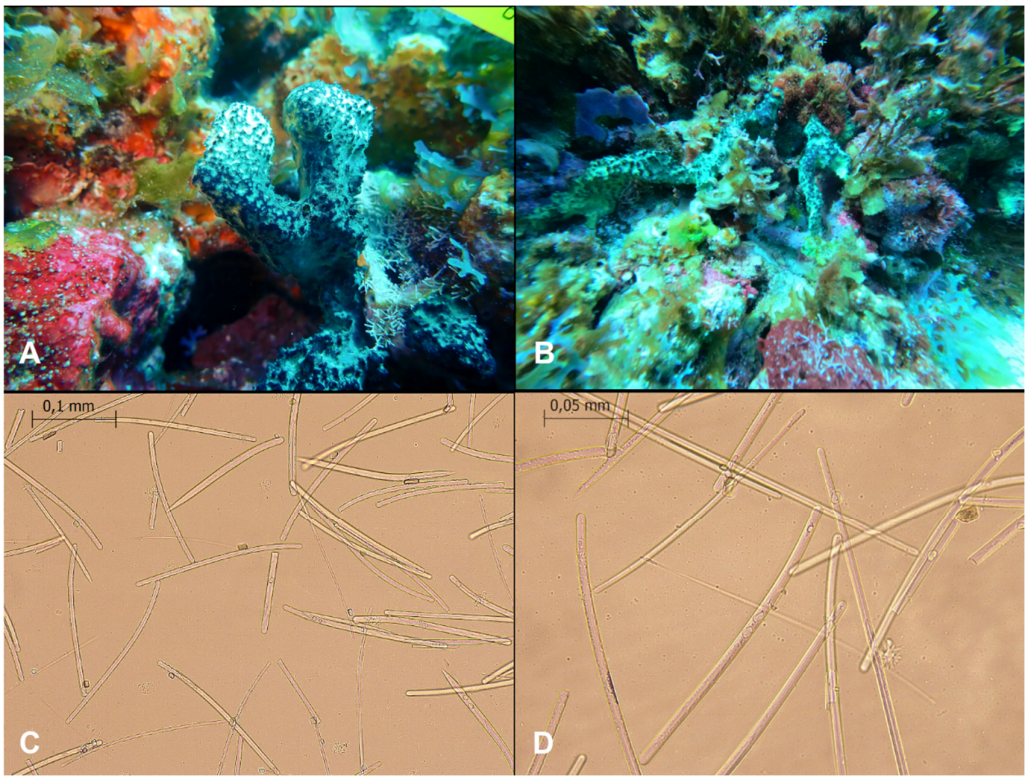


Figure 18. Two specimens collected on transects 1 and 3 of branching *Iotrochota birotulata*: (**A**) black morphotype; (**B**) yellow morphotype. Spicules of *I. birotulata* under the optical microscope: (**C**) strongyles and styles; (**D**) macroscleres and birotula microsclere in the center.

Remarks. *Iotrochota birotulata* is widely distributed from Brazil to Florida, passing through the Caribbean, Fernando de Noronha and Atol das Rocas, the Greater Antilles, and Guianan Guyana [54]. The morphological shape, color, spicule-types, surface structure and consistency fit with those of *I. birotulata*. The 28S barcodes matched with a *I. birotulata* sequence from the Caribbean with >99% similarity and differed by over 3% distance values from *I.* cf. *baculifera* and *Iotrochota* sp. references and by 8–9% from *I. protea* entries. It is probable that the 28S could be more discriminant for species delimitation in this genus than what has been reported in other surveys using the COI [93]. *Iotrochota birotulata* was reported in the stomach contents of hawksbill turtles sampled in Cuba [26].

Order Clionaida Morrow and Cárdenas, 2015

Family Spirastrellidae Ridley and Dendy, 1886

Genus *Spirastrella* Schmidt, 1868

Species *Spirastrella coccinea* Duchassaing and Michelotti, 1864

Material. T1_09, T1_12, T3_03, and T3_11, transects 1 and 3 in Le Sec du Diamant.

Description. It has a leathery encrusting shape (Figure 19A–D) and is orange in color with a tough consistency. The surface is smooth, with slightly elevated oscules that are highlighted by a lighter edge. The spicules are tylostyles (146–680 µm × 5–18 µm) (Figure 19E) and spirasters (29–50 µm) (Figure 19F). The ectosome is packed with the spirasters, while the choanosome contains some microscleres but chiefly tylostyles in confusion.

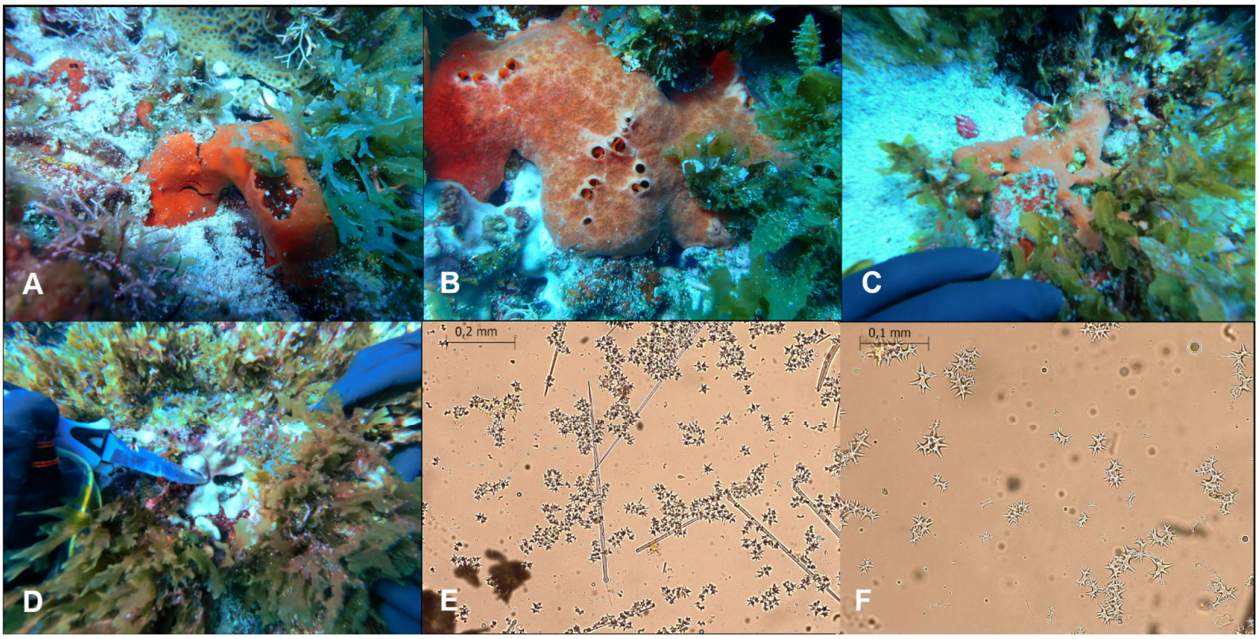


Figure 19. Fresh specimens of *Spirastrella coccinea*: (**A**,**B**) specimens collected on transect 1; (**C**,**D**) specimens collected on transect 3. Pictures under optical microscope of microscleres and megascleres in *S. coccinea*: (**E**) tylostyles and spirasters; (**F**) spirasters.

Remarks. It is widely distributed in the Caribbean and Bermuda, and along the Bahamian, Floridian, and Brazilian coasts [54]. The morphological shape, color, consistency and spicule-shape and size (especially the microscleres) fit with the description of *Spirastrella coccinea* (e.g., Pulitzer-Finali (1986) [87]), with tylostyles of 340–685 µm and spirasters with an average size of 25 µm. The molecular validation afforded sequences from 28S matching with Caribbean *S. hartmani* and *S. sabogae* and with *S. cunctatrix* from Israel (Mediterranean) with 99% similarity and recording distances of 8–10% from unidentified *Spirastrella* spp. and *Spheciospongia incrostans* and *Spheciospongia solida* from Hawai'i. Seemingly, the ITS sequences matched with >99% similarity to Caribbean references of *S. hartmani* and *S. sabogae* and reported 13% distance from a *S. hartmani* entry from Australia. There were no available conspecific sequences covering the loci used to compare with our dataset. *Spirastrella coccinea* and *S. hartmani* may be easily confused *de visu*, but the first is "bright vermillion or dull red, more leathery, and has a stouter category of spiraster spicules" [88]. After morphological re-examination, the identification of *Spirastrella coccinea* was confirmed by relying on the morphology of spirasters, which are quite distinctive between these two species. *Spirastrella coccinea* was recorded for the first time in the *E. imbricata* diet by León and Bjorndal (2002) [20]. This sponge turned out to be positively selected by the turtle, despite its low nutrient value and chemical defense [9].

4. Discussion

The majority of the sponges investigated in this study were previously cited in the inventory carried out by Pèrez et al. (2017) [39], with the exception of two species: *H. cavernosa* and *N. rosariensis*. These latter entries represent two new geographical records in Martinique. Additionally, we also retrieved the first sequence records from the species *H. cavernosa* and *A. caribica*, both novel barcode nucleotide entries in the GenBank database (*H. cavernosa*—COI entries: PQ849451; ITS entries: PV035855, PV035858 and PV035869; 28S entries: PV034604; *A. caribica*—28S entries: PV034597). Among the sponge species investigated here, only four of them have already been recorded in the literature as diet items of hawksbill turtles. These were *X. muta* [25], *C. kuekenthali* [22], *I. birotulata* [26]

and *S. coccinea* [20]. The remaining 13 species identified have never been mentioned in the literature as being part of the diet of *E. imbricata* [15,20,22–27] (Table S1). Among the above-mentioned sponges, *X. muta* and *C. kuekenthali* are not particularly preferred by the hawksbill turtle due to the remarkable concentration of siliceous spicules, which reflects low nutritional and energy value [22,25]. According to Chanas and Pawlik (1995) [8], the nutritional value of sponges is negatively correlated with the presence of spicules, while their palatability is reduced by the presence of repellent chemical compounds. Due to the high ash content and low nutritive value of *X. muta* and *C. kuekenthali* [22,25], we hypothesized that the microorganisms associated with these sponges (e.g., Cyanobacteria, Bacillota or Firmicutes, Actinomycetota or Actinobacteria, and Spirochaetota) in *X. muta* [94], or fouling biota in the case of *C. kuekenthali*, contribute to raising their nutritive value and palatability. By contrast, *I. birotulata* and *S. coccinea* seem to be positively selected by hawksbill turtles [20,26]. This positive selection of *I. birotulata* could be linked to the concentration of palatable compounds in the sponge flesh [9] and the conspicuous mucous secretions that characterize this species [95], which we hypothesized could provide lubrication to favor the transit through the gastrointestinal tract of siliceous spicules. The esophagus of *E. imbricata* presents a strong keratinized epithelium that has a mechanical function, and it lacks esophageal glands and mucus-producing cells, which has been proposed as being an adaptation to tough spongivorous diets [96]. Thus, the ingestion of slimy prey may afford alleviation against the abrasion of ingested spicules and facilitate the digestion of certain sponges. Instead, *S. coccinea* seems to be frequently preyed upon by fishes (mainly angelfishes belonging to genera *Holacanthus* and *Pomacanthus* and the filefish, *Cantherhines macrocerus*) and by the hawksbill turtle, despite its reported chemical arsenal and its low nutritional value [9,16,83].

Meylan and coworkers (1990) [97] claimed that although some sponges may have low energy content and incidence of chemical defenses, they could still be preferred by turtles, suggesting that they may contain critical nutrients. On this line, León and coworkers [20] suggested the possible assimilation of essential nutrients by turtle consumers when feeding on *S. coccinea*, the second most frequent sponge recorded in this study after *X. muta*.

Among the new 13 records of sponges potentially preyed upon by *E. imbricata* in Martinique, the species *I. felix*, *H. cavernosa*, *A. crassa*, *V. rigida*, *A. insularis* and *A. fulva* belong to the aspiculate subclass Keratosa. These sponges are characterized by skeletons made up of solely organic spongin fibers, lacking spicules, and, in the case of *I. felix*, skeletons also contain collagen filaments. According to Meylan (1985) [12], these structural elements may represent an important protein source for turtles, while the lack of spicules (and consequent increased nutritious content) is generally balanced with the production of bioactive compounds with antipredatory activities. This agrees with Duffy and Paul's work (1992) [98], who experimentally proved that chemical defenses are more effective in prey with poor nutritional quality, likely because the repellent properties dilute as the energy content increases. Consequently, sponges with high nutritional value, which are more attractive to predators, tend to protect themselves by harboring larger amounts, or more powerful chemical defenses.

We suggest that these sponges (i.e., *I. felix*, *H. cavernosa*, *A. crassa*, *V. rigida*, *A. insularis* and *A. fulva*) may have high nutritional quality or may contain critical nutrients. *Eretmochelys imbricata* was also observed to feed more than once on *C. aculeata* [34], one of the most abundant sponges in Martinique and Caribbean reefs [39]. This sponge has been reported to be profusely preyed upon by several fish species in the Caribbean [9] and to possess proteinaceous fibers and spongin B [83]. This said, it is possible that *E. imbricata* may find this sponge to be an attractive source of nourishment. *Neopetrosia rosariensis* and *Agelas clathrodes* are new records in the diet of the hawksbill turtle. Both are encrusting and

lobate species that contain abundant siliceous structural elements (spongin and spongin with echinated fibers with cored spicules, respectively). From the pictures taken in the field (Figures 13 and 17), we noted that the sampled specimens were covered by algae and epiphytes. So, in this case, it could be acknowledged that algae might represent the main food target and that the sponges were accidentally bitten while grazing. Both Chlorophyceae and Phaeophyceae are rich in lipopolysaccharide mucus content [99,100], which may add lubricative properties for digesting spongy tissues along the turtles' gastrointestinal tract [25,96]. *Agelas clathrodes* is known to produce a series of bioactive molecules, such as clathrodin (2,3 debromoroidin), which has anti-cholinergic and anti-serotonergic activity [101]. Crude extracts of *A. clathrodes* were found to be significant deterrents against Pomacanthinae angelfishes [102]. Among all the above-mentioned, *A. clathrodes* and *N. rosariensis* could constitute incidental and indirect prey items of *E. imbricata*. Other items like *A. compressa* and *A. caribica* were never recorded as part of the usual prey of *E. imbricata*. *Amphimedon* spp. are known to synthesize bioactive alkaloids, ceramides and cerebrosides, as well as fatty acids, and the origin of some of these compounds is suspected to rely on the associated endosymbiont community [103,104]. Indeed, a number of nutritious metabolites and essential fatty acids within aquatic food webs seem to derive from microorganismal biosynthesis [105–107]. Therefore, certain sponge prey with rich associated microbial communities represent sources of fatty acids of crucial importance for energy storage, cell membrane composition and signaling [104].

Sponge species preyed with higher incidence (sampled at least twice) were often those that were most abundant and, hence, more available (*X. muta*, *S. coccinea*, *V. rigida*, *A. crassa*, *I. birotulata*, *C. aculeata*, *H. cavernosa*, and *I. felix*), even if some of these may have lower nutritional value [25]. Instead, the reasons why other less conspicuous sponges were preyed upon with lower incidence, like *C. kuekenthali*, *A. caribica*, *A. compressa*, *C. pseudotoxa*, *A. dispar*, *A. fulva and A. insularis*, *A. clathrodes* and *N. rosariensis*, could have multiple explanations: (1) lower availability at the study site; (2) structural elements and secondary metabolites acting synergistically, making these sponges less palatable; (3) incidental feeding for having similar characteristics (i.e., similar shape and color) [34,108]; and (4) the target feeding items are represented by the associated organisms. In order to create a reliable catalog of sponges preyed upon by hawksbill turtles, future efforts should consider complementary approaches, including stable isotopic analysis [109], to confirm effective assimilation of the sponge preyed upon.

Integrative taxonomy combining DNA barcoding with morphological analysis is the most appropriate approach to classifying organisms, discriminating between species, and discovering new species [44,45,47,110,111]. Furthermore, for those organisms characterized by great plasticity—like sponges, whose genetic database is currently underpopulated—and with still many gaps in the nucleotide entries, additional integrated analyses could be useful to avoid misidentification, such as chemotaxonomy [112,113] or microbiome characterization [114]. Addressing molecular taxonomy in sponges is often difficult due to the poor DNA quality and quantity, especially when surveys take place at remote sites with limited access to reagent shipping and freezing protocols for nucleic acid preservation. Furthermore, sponges are habitat-forming species that can host great diversities of micro- and macro-organisms as epiphytes (on the surface) or endophytes (within their tissues and cells) and whose DNA is often co-extracted and co-amplified during PCR. Indeed, amplifying clean sponge sequences is challenging due to the lack of sponge-specific primers, while an additional issue is the scarcity of accurate annotation in the public databases. This has led to frequent misidentifications and ambiguous matches in the existing entries, particularly for the universal metazoan COI marker [45,115,116]. The low resolutive capability of the COI barcodes in delimitating species in many Porifera groups was corroborated in our

ABGD and ASAP analyses, which highlights the need to include additional, more variable loci, like ribosomal nuclear markers, and the necessity of repopulating our reference sequencing data. From our findings, we propose the primary usage of the more resolutive 28S marker in combination with morphological validation for future sponge–turtle interaction studies. Secondarily, support with the ITS and COI barcoding fragments and with chemical profiling could help in determining sponge diet characterization. Thanks to the 'Barcoding of life' initiative and to the Sponge Barcoding Project (www.spongebarcoding.org), sponge identification at the species level is becoming more efficient and reliable [45,117–119].

The present work intends to lay a baseline for upcoming studies describing the diet of *E. imbricata* in Martinique in order to determine: (1) if sponges are preyed upon, digested and assimilated by this species; (2) if and how the hawksbill turtles select their main diet items; and (3) which are the strategies used to discriminate palatable sponges from unpalatable ones. Our study also represents an important step toward future investigations into the ecology of the *E. imbricata* and the development of effective conservation measures to protect their foraging habitats.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w18070850/s1, Supplementary_data_Labalme_et_aliii.docx: Table S1 Spongivorous diets of *E. imbricata* recorded in several Carib-bean regions, Costa Rica and Republic of Seychelles, Table S2 Primers used for the amplification and sequencing, Table S3 Accession numbers, sample codes and taxonomy of the sponge samples from this study, Table S4 ASAP table, Figure S1 ASAP partitions showing proposed species delimitation, Table S5 ABGD table, Figure S2 AABGD partitions showing proposed species delimitation; Table S6 Estimates of evolutionary divergence between sequences for COI aligned data.xlsx; Table S7 Estimates of evolutionary divergence between sequences for 28S aligned data.xlsx; Table S8 Estimates of evolutionary divergence between sequences for ITS aligned data.xlsx.

Author Contributions: Conceptualization: L.N.-P., B.C., C.D. and D.C.; sample material and pictures: C.D. and D.C.; morphological analysis: B.C. and C.L.; molecular analysis: C.L. and V.M.; sequence editing, C.L. and L.N.-P.; data analysis, C.L., V.M. and L.N.-P.; writing—original draft, C.L. and L.N.-P.; writing—review and editing, L.N.-P., B.C., V.M., C.D. and D.C.; funding acquisition: L.N.-P. and D.C. All authors have read and agreed to the published version of the manuscript.

Funding: This project was partially funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4—Call for tender No. 3138 of 16 December 2021, rectified by Decree No. 3175 of 18 December 2021 of the Italian Ministry of University and Research funded by the European Union—NextGenerationEU: Award Number: Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022, adopted by the Italian Ministry of University and Research, CUP C63C22000520001, Project title "National Biodiversity Future Center—NBFC". The BEPHYTES Project (BEhavioral and PHYsiological responses of marine Turtles to Environmental Stress—CNRS) was co-financed by the FEDER Martinique and DEAL Martinique (European Union, Conventions 246239, 2012/DEAL/0010/4-4/31882, 2014/DEAL/0008/4-4/32947 and 2017/164894), ODE Martinique (Conventions 014-03-2015 and 180126), the Collectivité Territoriale of Martinique (CTM, 258342) and the Office Français de la Biodiversité/Parc Naturel Marin de Martinique (OFB-23-0563).

Data Availability Statement: Sequences and specimen descriptions were deposited in GenBank (accession numbers: COI entries: PQ849445-PQ849461, PQ896986-PQ896987; 28S entries: PV034580-PV034604; ITS entries: PV035853-PV035869) and Sponge Barcoding Project databases for public access.

Acknowledgments: Thanks are due to Luigi Maria Cusano for assisting in the laboratory. Special acknowledgments are given to Elvira Mauriello, Pasquale De Luca and Raimondo Pannone Servizio di Biologia Molecolare from the Marine Resources Department of the Zoological station of Naples (RIMAR-SZN) for the special support in the sequencing optimization.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Wulff, J.L. Ecological Interactions of Marine Sponges. *Can. J. Zool.* **2006**, *84*, 146–166. [CrossRef]
2. Becerro, M.A. Quantitative Trends in Sponge Ecology Research. *Mar. Ecol.* **2008**, *29*, 167–177. [CrossRef]
3. Bell, J.J. The Functional Roles of Marine Sponges. *Estuar. Coast. Shelf Sci.* **2008**, *79*, 341–353. [CrossRef]
4. Rützler, K. Sponges in Coral Reefs. In *Coral Reefs: Research Methods: Monographs on Oceanographic Methodology*; Stoddart, D.R., Johannes, R.E., Eds.; UNESCO: Paris, France, 1978; pp. 299–314. Available online: https://repository.si.edu/handle/10088/7849 (accessed on 13 July 2025).
5. Diaz, M.C.; Rützler, K. Sponges: An Essential Component of Caribbean Coral Reefs. *Bull. Mar. Sci.* **2001**, *69*, 535–546.
6. Rützler, K. Sponges on Coral Reefs: A Community Shaped By Competitive Cooperation. *Boll. Mus. Ist. Biol.* **2004**, *68*, 85–148.
7. Freestone, A.L.; Osman, R.W.; Ruiz, G.M.; Torchin, M.E. Stronger Predation in the Tropics Shapes Species Richness Patterns in Marine Communities. *Ecology* **2011**, *92*, 983–993. [CrossRef]
8. Chanas, B.; Pawlik, J. Defenses of Caribbean Sponges against Predatory Reef Fish. II. Spicules, Tissue Toughness, and Nutritional Quality. *Mar. Ecol. Prog. Ser.* **1995**, *127*, 195–211. [CrossRef]
9. Pawlik, J.; Chanas, B.; Toonen, R.; Fenical, W. Defenses of Caribbean Sponges against Predatory Reef Fish. I. Chemical Deterrency. *Mar. Ecol. Prog. Ser.* **1995**, *127*, 183–194. [CrossRef]
10. Waddell, B.; Pawlik, J. Defenses of Caribbean Sponges against Invertebrate Predators. I. Assays with Hermit Crabs. *Mar. Ecol. Prog. Ser.* **2000**, *195*, 125–132. [CrossRef]
11. Loh, T.-L.; Pawlik, J.R. Chemical Defenses and Resource Trade-Offs Structure Sponge Communities on Caribbean Coral Reefs. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 4151–4156. [CrossRef]
12. Meylan, A. The Role of Sponge Collagens in the Diet of the Hawksbill Turtle (*Eretmochelys imbricata*). In *Biology of Invertebrate and Lower Vertebrate Collagens*; Bairati, A., Garrone, R., Eds.; Springer: Boston, MA, USA, 1985; pp. 191–196.
13. Bell, J.J.; Davy, S.K.; Jones, T.; Taylor, M.W.; Webster, N.S. Could Some Coral Reefs Become Sponge Reefs as Our Climate Changes? *Glob. Change Biol.* **2013**, *19*, 2613–2624. [CrossRef] [PubMed]
14. Campana, S.; Arts, M.G.I.; Díez-Vives, C.; Mueller, B.; Bang, C.; Riesgo, A.; Haas, A.F.; Muyzer, G.; De Goeij, J.M. Sponges on Shifting Reefs: Holobionts Show Similar Molecular and Physiological Responses to Coral versus Macroalgal Food. *Front. Mar. Sci.* **2024**, *11*, 1298922. [CrossRef]
15. Meylan, A. Spongivory in Hawksbill Turtles: A Diet of Glass. *Science* **1988**, *239*, 393–395. [CrossRef] [PubMed]
16. Wulff, J.L. Sponge Feeding by Caribbean Angelfishes, Trunkfishes, and Filefishes. In *Sponges in Time and Space Biology, Chemistry, Paleontology*; Van Soest, R.W.M., van Kempen, T.M.G., Braekman, J.C., Eds.; Balkema: Rotterdam, The Netherlands, 1994; pp. 265–271.
17. Kiran, G.S.; Sekar, S.; Ramasamy, P.; Thinesh, T.; Hassan, S.; Lipton, A.N.; Ninawe, A.S.; Selvin, J. Marine Sponge Microbial Association: Towards Disclosing Unique Symbiotic Interactions. *Mar. Environ. Res.* **2018**, *140*, 169–179. [CrossRef]
18. Taylor, M.W.; Radax, R.; Steger, D.; Wagner, M. Sponge-Associated Microorganisms: Evolution, Ecology, and Biotechnological Potential. *Microbiol. Mol. Biol. Rev.* **2007**, *71*, 295–347. [CrossRef]
19. Webster, N.S.; Taylor, M.W. Marine Sponges and Their Microbial Symbionts: Love and Other Relationships. *Environ. Microbiol.* **2012**, *14*, 335–346. [CrossRef]
20. León, Y.; Bjorndal, K. Selective Feeding in the Hawksbill Turtle, an Important Predator in Coral Reef Ecosystems. *Mar. Ecol. Prog. Ser.* **2002**, *245*, 249–258. [CrossRef]
21. Bjorndal, K.A. Nutritional Ecology of Sea Turtles. *Copeia* **1985**, *3*, 736–751. [CrossRef]
22. Rincon-Diaz, M.P.; Diez, C.E.; Van Dam, R.P.; Sabat, A.M. Foraging Selectivity of the Hawksbill Sea Turtle (*Eretmochelys imbricata*) in the Culebra Archipelago, Puerto Rico. *J. Herpetol.* **2011**, *45*, 277–282. [CrossRef]
23. Stringell, T.B.; Clerveaux, W.V.; Godley, B.J.; Kent, F.E.A.; Lewis, E.D.G.; Marsh, J.E.; Phillips, Q.; Richardson, P.B.; Sanghera, A.; Broderick, A.C. Taxonomic Distinctness in the Diet of Two Sympatric Marine Turtle Species. *Mar. Ecol.* **2016**, *37*, 1036–1049. [CrossRef]
24. Méndez-Salgado, E.; Chacón-Chaverri, D.; Fonseca, L.G.; Seminoff, J.A. Trophic Ecology of Hawksbill Turtles (*Eretmochelys imbricata*) in Golfo Dulce, Costa Rica: Integrating Esophageal Lavage and Stable Isotope (δ13C, δ15N) Analysis. *Lat. Am. J. Aquat. Res.* **2020**, *48*, 114–130. [CrossRef]
25. Baumbach, D.S.; Zhang, R.; Hayes, C.T.; Wright, M.K.; Dunbar, S.G. Strategic Foraging: Understanding Hawksbill (*Eretmochelys imbricata*) Prey Item Energy Values and Distribution within a Marine Protected Area. *Mar. Ecol.* **2022**, *43*, e12703. [CrossRef]
26. Abreu-Grobois, F.A.; Briseño-Dueñas, R.; Márquez-Millán, R.; Sarti-Martínez, L. In Proceedings of the Eighteenth International Sea Turtle Symposium, Mazatlán, México, 3–7 March 1998. Available online: https://repository.library.noaa.gov/view/noaa/30887 (accessed on 13 July 2025).
27. Brandis, R.; Mortimer, J.; Reilly, B.; Soest, R.; Branch, G. Diet Composition of Hawksbill Turtles (*Eretmochelys imbricata*) in the Republic of Seychelles. Available online: https://www.semanticscholar.org/paper/Diet-Composition-of-Hawksbill-Turtles-(Eretmochelys-Brandis-Mortimer/1796c75c3221347b611e6148537897842d56ecdf (accessed on 18 February 2026).

28. Nivière, M.; Chambault, P.; Pérez, T.; Etienne, D.; Bonola, M.; Martin, J.; Barnérias, C.; Védie, F.; Mailles, J.; Dumont-Dayot, É.; et al. Identification of Marine Key Areas across the Caribbean to Ensure the Conservation of the Critically Endangered Hawksbill Turtle. *Biol. Conserv.* **2018**, *223*, 170–180. [CrossRef]
29. Meylan, A.; Donnelly, M. Status Justification for Listing the Hawksbill Turtle (*Eretmochelys imbricata*) as Critically Endangered on the 1996 IUCN Red List of Threatened Animals. *Chelonian Conserv. Biol.* **1999**, *3*, 200–224.
30. Louis-Jean, L.; Lenfant, P.; Galzin, R.; Marechal, J.-P. Crossing Fishery Statistics with Marine Turtle Bycatch Data and Habitat Mapping in Martinique. In *FWI Proceedings of the Gulf and Caribbean Fisheries Institute*; University of Miami: Miami, FL, USA, 2009; Volume 61, pp. 375–379.
31. Hill, M.S. Spongivory on Caribbean Reefs Releases Corals from Competition with Sponges. *Oecologia* **1998**, *117*, 143–150. [CrossRef]
32. Loh, T.-L.; McMurray, S.E.; Henkel, T.P.; Vicente, J.; Pawlik, J.R. Indirect Effects of Overfishing on Caribbean Reefs: Sponges Overgrow Reef-Building Corals. *PeerJ* **2015**, *3*, e901. [CrossRef]
33. Pawlik, J.R.; Loh, T.-L.; McMurray, S.E. 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**, *6*, e4343. [CrossRef]
34. Delvenne, C.; Martin, J.; Jeantet, L.; Lelong, P.; Bourgeois, O.; Lecerf, N.; Lefebvre, F.; Aubert, N.; Flora, F.; Régis, S.; et al. Feeding Ecology and Activity Rhythms of the Critically Endangered Hawksbill Turtle. *Qeios* **2025**. [CrossRef]
35. Ogren, L.H.; Berry, F.H.; Bjorndal, K.A.; Kumpf, H.E.; Mast, R.; Medina, G.; Reichart, H.A.; Witham, R. In Proceedings of the Second Western Atlantic Turtle Symposium, Mayaguez, Puerto Rico, 12–16 October 1987. Available online: https://repository.library.noaa.gov/view/noaa/5886 (accessed on 13 July 2025).
36. Lescure, J. Tortues Maritimes de l'Atlantique Ouest. In Proceedings of the Second Western Atlantic Turtle Symposium, Mayaguez, Puerto Rico, 12–16 October 1987.
37. Legrand, H.; Lenfant, P.; Sotheran, I.S.; Foster-Smith, R.L.; Galzin, R.; Maréchal, J.-P. Mapping Marine Benthic Habitats in Martinique (French West Indies). *Caribb. J. Sci.* **2010**, *46*, 267–282. [CrossRef]
38. Failler, P.; Pètre, É.; Binet, T.; Maréchal, J.-P. Valuation of Marine and Coastal Ecosystem Services as a Tool for Conservation: The Case of Martinique in the Caribbean. *Ecosyst. Serv.* **2015**, *11*, 67–75. [CrossRef]
39. Pérez, T.; Díaz, M.-C.; Ruiz, C.; Cóndor-Luján, B.; Klautau, M.; Hajdu, E.; Lobo-Hajdu, G.; Zea, S.; Pomponi, S.A.; Thacker, R.W.; et al. 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* **2017**, *12*, e0173859. [CrossRef] [PubMed]
40. Ereskovsky, A.V.; Lavrov, D.V.; Willenz, P. Five New Species of Homoscleromorpha (Porifera) from the Caribbean Sea and Re-Description of *Plakina jamaicensis*. *J. Mar. Biol. Ass.* **2014**, *94*, 285–307. [CrossRef]
41. Fontana, T.; Cóndor-Luján, B.; Azevedo, F.; Pérez, T.; Klautau, M. Diversity and Distribution Patterns of Calcareous Sponges (Subclass Calcinea) from Martinique. *Zootaxa* **2018**, *4410*, 331–369. [CrossRef] [PubMed]
42. Grenier, M.; Ruiz, C.; Lage, A.; Perez, T. New Cave-Dwelling *Plakina* (Plakinidae, Homoscleromorpha, Porifera) from Martinique Island (French Antilles). *Zootaxa* **2020**, *4729*, 92–104. [CrossRef]
43. Piron, J.; Pastour, J.; Tysklind, N.; Smith-Ravin, J.; Priam, F. Screening of the Antimicrobial Activity of Marine Sponge Extracts from Martinique. *BioRxiv* **2021**. [CrossRef]
44. Hebert, P.D.N.; Cywinska, A.; Ball, S.L.; deWaard, J.R. Biological Identifications through DNA Barcodes. *Proc. R. Soc. Lond. B* **2003**, *270*, 313–321. [CrossRef]
45. Wörheide, G.; Erpenbeck, D. DNA Taxonomy of Sponges—Progress and Perspectives. *J. Mar. Biol. Ass.* **2007**, *87*, 1629–1633. [CrossRef]
46. Pires, A.C.; Marinoni, L. DNA Barcoding and Traditional Taxonomy Unified through Integrative Taxonomy: A View That Challenges the Debate Questioning Both Methodologies. *Biota Neotrop.* **2010**, *10*, 339–346. [CrossRef]
47. Miralles, A.; Puillandre, N.; Vences, M. DNA Barcoding in Species Delimitation: From Genetic Distances to Integrative Taxonomy. In *DNA Barcoding*; DeSalle, R., Ed.; Methods in Molecular Biology; Springer: New York, NY, USA, 2024; Volume 2744, pp. 77–104.
48. Duran, S.; Rützler, K. Ecological Speciation in a Caribbean Marine Sponge. *Mol. Phylogenet. Evol.* **2006**, *40*, 292–297. [CrossRef]
49. Wulff, J. Parallel Phenotypic Plasticity and Divergent Ecological Strategies in Morphologically and Molecularly Similar Sympatric Sponge Species. *Biol. J. Linn. Soc.* **2024**, *142*, 424–440. [CrossRef]
50. Boury-Esnault, N.; Rützler, K. Thesaurus of Sponge Morphology. In *Smithsonian Contributions to Zoology*; Smithsonian Libraries and Archives: Washington, DC, USA, 1997; pp. 1–55. [CrossRef]
51. Núñez Pons, L.; Mazzella, V.; Rispo, F.; Efremova, J.; Calcinai, B. DNA Barcoding Procedures for Taxonomical and Phylogenetic Studies in Marine Animals: Porifera as a Case Study. In *Marine Genomics*; Verde, C., Giordano, D., Eds.; Methods in Molecular Biology; Humana: New York, NY, USA, 2022; Volume 2498, pp. 195–223.
52. Hooper, J.N.A.; Van Soest, R.W.M.; Willenz, P. *Systema Porifera*; Springer: Boston, MA, USA, 2002.
53. Morrow, C.; Cárdenas, P. Proposal for a Revised Classification of the Demospongiae (Porifera). *Front. Zool.* **2015**, *12*, 7. [CrossRef]

54. de Voogd, N.; Alvarez, B.; Boury-Esnault, N.; Cárdenas, P.; Díaz, M.-C.; Dohrmann, M.; Downey, R.; Goodwin, C.; Hajdu, E.; Hooper, J.; et al. World Porifera Database. Available online: https://www.marinespecies.org/Porifera (accessed on 15 December 2025).
55. Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA Primers for Amplification of Mitochondrial Cytochrome c Oxidase Subunit I from Diverse Metazoan Invertebrates. *Mol. Mar. Biol. Biotechnol.* **1994**, *3*, 294–299. [CrossRef]
56. Xavier, J.R.; Rachello-Dolmen, P.G.; Parra-Velandia, F.; Schönberg, C.H.L.; Breeuwer, J.A.J.; van Soest, R.W.M. Molecular Evidence of Cryptic Speciation in the "Cosmopolitan" Excavating Sponge *Cliona celata* (Porifera, Clionaidae). *Mol. Phylogenet. Evol.* **2010**, *79*, 119–129. [CrossRef] [PubMed]
57. Wörheide, G.; Nichols, S.A.; Goldberg, J. Intragenomic Variation of the rDNA Internal Transcribed Spacers in Sponges (Phylum Porifera): Implications for Phylogenetic Studies. *Mol. Phylogen. Evol.* **2004**, *33*, 816–830. [CrossRef] [PubMed]
58. Chombard, C.; Boury-Esnault, N.; Tillier, S. Reassessment of Homology of Morphological Characters in Tetractinellid Sponges Based on Molecular Data. *Syst. Biol.* **1998**, *47*, 351–366. [CrossRef] [PubMed]
59. Erpenbeck, D.; Ekins, M.; Enghuber, N.; Hooper, J.N.A.; Lehnert, H.; Poliseno, A.; Schuster, A.; Setiawan, E.; De Voogd, N.J.; Wörheide, G.; et al. Nothing in (Sponge) Biology Makes Sense—Except When Based on Holotypes. *J. Mar. Biol. Ass.* **2016**, *96*, 305–311. [CrossRef]
60. Altschul, S.F.; Gish, W.; Miller, W.; Myers, E.W.; Lipman, D.J. Basic Local Alignment Search Tool. *J. Mol. Biol.* **1990**, *215*, 403–410. [CrossRef]
61. Puillandre, N.; Lambert, A.; Brouillet, S.; Achaz, G. ABGD, Automatic Barcode Gap Discovery for Primary Species Delimitation. *Mol. Ecol.* **2012**, *21*, 1864–1877. [CrossRef]
62. Puillandre, N.; Brouillet, S.; Achaz, G. ASAP: Assemble Species by Automatic Partitioning. *Mol. Ecol. Res.* **2021**, *21*, 609–620. [CrossRef]
63. Kimura, M. A Simple Method for Estimating Evolutionary Rates of Base Substitutions through Comparative Studies of Nucleotide Sequences. *J. Mol. Evol.* **1980**, *16*, 111–120. [CrossRef]
64. Castresana, J. Selection of Conserved Blocks from Multiple Alignments for Their Use in Phylogenetic Analysis. *Mol. Biol. Evol.* **2000**, *17*, 540–552. [CrossRef]
65. Talavera, G.; Castresana, J. Improvement of Phylogenies after Removing Divergent and Ambiguously Aligned Blocks from Protein Sequence Alignments. *Syst. Biol.* **2007**, *56*, 564–577. [CrossRef]
66. Stecher, G.; Tamura, K.; Kumar, S. Molecular Evolutionary Genetics Analysis (MEGA) for macOS. *Mol. Biol. Evol.* **2020**, *37*, 1237–1239. [CrossRef] [PubMed]
67. Stecher, G.; Suleski, M.; Tao, Q.; Tamura, K.; Kumar, S. MEGA 12.1: Cross-Platform Release for macOS and Linux Operating Systems. *J. Mol. Evol.* **2026**, *94*, 14–18. [CrossRef] [PubMed]
68. Bergquist, P.R.; De Cook, S.C. Family Aplysinellidae Bergquist, 1980. In *Systema Porifera*; Hooper, J.N.A., Van Soest, R.W.M., Willenz, P., Eds.; Springer: Boston, MA, USA, 2002; pp. 1094–1096.
69. van Soest, R. Marine Sponges from Curaçao and Other Caribbean Localities Part I. Keratosa. *Stud. Fauna Curaçao Other Caribb. Isl.* **1978**, *56*, 1–94.
70. Bergquist, P.R. Dictyoceratida, Dendroceratida and Verongida from the New Caledonia Lagoon (Porifera: Demospongiae). *Mem. Qld. Mus.* **1995**, *38*, 1–51.
71. Duchassaing de Fonbressin, P.; Michelotti, G. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem*; De Erven Loosjes: Haarlem, The Netherlands, 1864; Volume 21, p. 124.
72. Muricy, G.; Lopes, D.A.; Hajdu, E.; Carvalho, M.S.; Moraes, F.C.; Klautau, M.; Menegola, C.; Pinheiro, U. *Catalogue of Brazilian Porifera*; Museu Nacional Série Livros; Museu Nacional: Rio de Janeiro, Brazil, 2011; pp. 253–300.
73. Zea, S. Esponjas Del Caribe Colombiano. In *Dictyoceratida, Dendroceratida, Verongida, Haplosclerida, Poecilosclerida, Halichondrida, Axinellida, Desmophorida y Homosclerophorida*; Editorial Catálogo Cientifico: Bogotá, Colombia, 1987; p. 286.
74. Pinheiro, U.D.S.; Hajdu, E.; Custódio, M.R. *Aplysina nardo* (Porifera, Verongida, Aplysinidae) from the Brazilian Coast with Description of Eight New Species. *Zootaxa* **2007**, *1609*, 1–51. [CrossRef]
75. Cruz-Barraza, J.A.; Carballo, J.L.; Rocha-Olivares, A.; Ehrlich, H.; Hog, M. Integrative Taxonomy and Molecular Phylogeny of Genus Aplysina (Demospongiae: Verongida) from Mexican Pacific. *PLoS ONE* **2012**, *7*, e42049. [CrossRef]
76. Freeman, C.J.; Gleason, D.F. Chemical Defenses, Nutritional Quality, and Structural Components in Three Sponge Species: *Ircinia felix*, *I. campana*, and *Aplysina fulva*. *Mar. Biol.* **2010**, *157*, 1083–1093. [CrossRef]
77. Piron, J.; Betzi, S.; Pastour, J.; Restouin, A.; Castellano, R.; Collette, Y.; Tysklind, N.; Smith-Ravin, J.; Priam, F. Antimicrobial and Cytotoxic Effects of Marine Sponge Extracts *Agelas clathrodes*, *Desmapsamma anchorata* and *Verongula rigida* from a Caribbean Island. *PeerJ* **2022**, *10*, e13955. [CrossRef]
78. Wulff, J.L. Targeted Predator Defenses of Sponges Shape Community Organization and Tropical Marine Ecosystem Function. *Ecol. Monog.* **2021**, *91*, e01438. [CrossRef]

79. Sandes, J.; Bispo, A.; Pinheiro, U. Two New Species of *Haliclona* Grant, 1836 (Haplosclerida: Chalinidae) from Sergipe State, Brazil. *Zootaxa* **2014**, *3793*, 273–280. [CrossRef] [PubMed]
80. Muricy, G.; Esteves, E.L.; Moraes, F.C.; Santos, J.P.; da Silva, S.M.; Klautau, M.; Lanna, E. *Biodiversidade marinha da Bacia Potiguar*; Museu Nacional Série Livros; Museu Nacional: Rio de Janeiro, Brazil, 2008; Volume 29.
81. López-Legentil, S.; Erwin, P.M.; Henkel, T.P.; Loh, T.-L.; Pawlik, J.R. Phenotypic Plasticity in the Caribbean Sponge *Callyspongia vaginalis* (Porifera: Haplosclerida). *Sci. Mar.* **2010**, *74*, 445–453. [CrossRef]
82. van Soest, R. Marine Sponges from Curaçao and Other Caribbean Localities Part II. *Haplosclerida. Stud. Fauna Curaçao Other Caribb. Isl.* **1980**, *62*, 1–173.
83. Randall, J.E.; Hartman, W.D. Sponge-Feeding Fishes of the West Indies. *Mar. Biol.* **1968**, *1*, 216–225. [CrossRef]
84. Lesser, M.P.; Slattery, M. Ecology of Caribbean Sponges: Are Top-Down or Bottom-Up Processes More Important? *PLoS ONE* **2013**, *8*, e79799. [CrossRef]
85. Muricy, G.; Ribeiro, S.M. Shallow-Water Haplosclerida (Porifera, Demospongiae) from Rio de Janeiro State, Brazil (Southwestern Atlantic). *Beaufortia* **1999**, *49*, 83–108.
86. Albrizio, S.; Ciminiello, P.; Fattorusso, E.; Magno, S.; Pawlik, J.R. Amphitoxin, a New High Molecular Weight Antifeedant Pyridinium Salt from the Caribbean Sponge *Amphimedon compressa*. *J. Nat. Prod.* **1995**, *58*, 647–652. [CrossRef]
87. Pulitzer-Finali, G. A Collection of West Indian Demospongiae (Porifera) In appendix, a list of Demospongiae hitherto recorded from the West Indies. *Ann. Mus. Civ. Stor. Nat. Giacomo Doria* **1987**, *86*, 65–216.
88. Zea, S.; Henkel, T.P.; Pawlik, J.R. *The Sponge Guide: A Picture Guide to Caribbean Sponges*, 4th ed.; University of North Carolina Wilmington (UNCW), Center for Marine Science: Wilmington, NC, USA, 2026. Available online: https://spongeguide.uncw.edu/ (accessed on 18 February 2026).
89. Cleary, D.F.R.; De Voogd, N.J. The Impact of Space, Host Dissimilitude, and Environment on Prokaryotic Communities of Golf Ball Sponges. *Mar. Ecol.* **2024**, *45*, e12815. [CrossRef]
90. Pankey, M.S.; Gochfeld, D.J.; Gastaldi, M.; Macartney, K.J.; Clayshulte Abraham, A.; Slattery, M.; Lesser, M.P. Phylosymbiosis and Metabolomics Resolve Phenotypically Plastic and Cryptic Sponge Species in the Genus *Agelas* across the Caribbean Basin. *Mol. Ecol.* **2024**, *33*, e17321. [CrossRef]
91. Van Soest, R.W.M.; Braekman, J.C. Chemosystematics of Porifera: A Review. *Mem. Qld. Mus.* **1999**, *44*, 569–589.
92. Parra-Velandia, F.J.; Zea, S.; Van Soest, R.W.M. Reef Sponges of the Genus *Agelas* (Porifera: Demospongiae) from the Greater Caribbean. *Zootaxa* **2014**, *3794*, 301–343. [CrossRef] [PubMed]
93. Núñez-Pons, L.; Calcinai, B.; Gates, R.D. Who's There?—First Morphological and DNA Barcoding Catalogue of the Shallow Hawai'ian Sponge Fauna. *PLoS ONE* **2017**, *12*, e0189357. [CrossRef] [PubMed]
94. Bayona, L.M.; Kim, M.-S.; Swierts, T.; Hwang, G.-S.; De Voogd, N.J.; Choi, Y.H. Metabolic Variation in Caribbean Giant Barrel Sponges: Influence of Age and Sea-Depth. *Mar. Environ. Res.* **2021**, *172*, 105503. [CrossRef] [PubMed]
95. Pastrana Franco, O.J.; Santafe Patiño, G.G.; Sánchez Romero, E.L. Perfil Lipídico y Ensayos de Las Actividades Antioxidante, Insecticida y Antialimentaria de La Esponja Marina *Iotrochota birotulata* (Iotrochotidae: Demospongiae). *Rev. Biol. Trop.* **2019**, *67*, 213–223. [CrossRef]
96. Oliveira, R.E.M.D.; Attademo, F.L.N.; Sousa, A.C.F.C.D.; Gurgel, J.V.D.O.; Magalhães, M.D.S.; Moura, C.E.B.D.; Fragoso, A.B.L.; Silva, F.J.L.; Oliveira, M.F.D. Morphological characterization of the digestive tube of hawksbill sea turtle (*Eretmochelys imbricata*) hatchlings. *Microsc. Microanal.* **2022**, *28*, 2138–2149. [CrossRef]
97. Meylan, A. Nutritional Characteristics of the Sponges in the Diet of the Hawksbill Turtle. In *New Perspectives in Sponge Biology*; Ruetzler, K., Ed.; Smithsonian Institution Press: Washington, DC, USA, 1990; pp. 191–196.
98. Duffy, J.E.; Paul, V.J. Prey Nutritional Quality and the Effectiveness of Chemical Defenses against Tropical Reef Fishes. *Oecologia* **1992**, *90*, 333–339. [CrossRef]
99. Kraan, S. Algal Polysaccharides, Novel Applications and Outlook. In *Carbohydrates—Comprehensive Studies on Glycobiology and Glycotechnology*; Chang, C.-F., Ed.; InTech: London, UK, 2012.
100. Bayu, A.; Handayani, T. High-Value Chemicals from Marine Macroalgae: Opportunities and Challenges for Marine-Based Bioenergy Development. *IOP Conf. Ser. Earth Environ. Sci.* **2018**, *209*, 012046. [CrossRef]
101. Fathima, A.; Arafath, Y.; Hassan, S.; Bramhachari, P.V.; Kiran, G.S.; Selvin, J. Novel Insights into Environmental Niche Adaptations and Secondary Metabolite Biosynthesis Potential of Marine Sponge Microbiome. In *Understanding the Microbiome Interactions in Agriculture and the Environment*; Veera Bramhachari, P., Ed.; Springer Nature: Singapore, 2022; pp. 113–137.
102. Hoppe, W. Growth, Regeneration and Predation in Three Species of Large Coral Reef Sponges. *Mar. Ecol. Prog. Ser.* **1988**, *50*, 117–125. [CrossRef]
103. Shady, N.H.; Fouad, M.A.; Salah Kamel, M.; Schirmeister, T.; Abdelmohsen, U.R. Natural Product Repertoire of the Genus Amphimedon. *Mar. Drugs* **2018**, *17*, 19. [CrossRef]
104. Parrish, C.C. Essential Fatty Acids in Aquatic Food Webs. In *Lipids in Aquatic Ecosystems*; Kainz, M., Brett, M.T., Arts, M.T., Eds.; Springer: New York, NY, USA, 2009; pp. 309–326.

105. Gillan, F.T.; Stoilov, I.L.; Thompson, J.E.; Hogg, R.W.; Wilkinson, C.R.; Djerassi, C. Fatty Acids as Biological Markers for Bacterial Symbionts in Sponges. *Lipids* **1988**, *23*, 1139–1145. [CrossRef]
106. De Kluijver, A.; Nierop, K.G.J.; Morganti, T.M.; Bart, M.C.; Slaby, B.M.; Hanz, U.; De Goeij, J.M.; Mienis, F.; Middelburg, J.J. Bacterial Precursors and Unsaturated Long-Chain Fatty Acids Are Biomarkers of North-Atlantic Deep-Sea Demosponges. *PLoS ONE* **2021**, *16*, e0241095. [CrossRef] [PubMed]
107. Zhang, S.; Song, W.; Nothias, L.F.; Couvillion, S.P.; Webster, N.; Thomas, T. Comparative Metabolomic Analysis Reveals Shared and Unique Chemical Interactions in Sponge Holobionts. *Microbiome* **2022**, *10*, 22. [CrossRef] [PubMed]
108. Schuyler, Q.A.; Wilcox, C.; Townsend, K.; Hardesty, B.; Marshall, N. Mistaken Identity? Visual Similarities of Marine Debris to Natural Prey Items of Sea Turtles. *BMC Ecol.* **2014**, *14*, 14. [CrossRef] [PubMed]
109. Peterson, B.J.; Fry, B. Stable Isotopes in Ecosystem Studies. *Annu. Rev. Ecol. Syst.* **1987**, *18*, 293–320. [CrossRef]
110. Hebert, P.D.N.; Stoeckle, M.Y.; Zemlak, T.S.; Francis, C.M. Identification of Birds through DNA Barcodes. *PLOS Biol.* **2004**, *2*, e312. [CrossRef]
111. Bucklin, A.; Steinke, D.; Blanco-Bercial, L. DNA Barcoding of Marine Metazoa. *Annu. Rev. Mar. Sci.* **2011**, *3*, 471–508. [CrossRef]
112. Erpenbeck, D.; Van Soest, R.W.M. Status and Perspective of Sponge Chemosystematics. *Mar. Biotechnol.* **2007**, *9*, 2–19. [CrossRef]
113. Padial, J.M.; Miralles, A.; De La Riva, I.; Vences, M. The Integrative Future of Taxonomy. *Front. Zool.* **2010**, *7*, 16. [CrossRef]
114. Díez-Vives, C.; Taboada, S.; Leiva, C.; Busch, K.; Hentschel, U.; Riesgo, A. On the Way to Specificity—Microbiome Reflects Sponge Genetic Cluster Primarily in Highly Structured Populations. *Mol. Ecol.* **2020**, *29*, 4412–4427. [CrossRef]
115. Erpenbeck, D.; Hooper, J.N.A.; Wörheide, G. CO1 Phylogenies in Diploblasts and the "Barcoding of Life"—Are We Sequencing a Suboptimal Partition? *Mol. Ecol. Notes* **2006**, *6*, 550–553. [CrossRef]
116. Solé-Cava, A.M.; Wörheide, G. *The Perils and Merits (or the Good, the Bad and the Ugly) of DNA Barcoding of Sponges—A Controversial Discussion*; Museu Nacional Série Livros; Museu Nacional: Rio de Janeiro, Brazil, 2007; pp. 603–612. [CrossRef]
117. Stoeckle, M.Y.; Hebert, P.D.N. Barcode of Life. *Sci. Am.* **2008**, *299*, 82–89. [CrossRef]
118. Vargas, S.; Schuster, A.; Sacher, K.; Büttner, G.; Schätzle, S.; Läuchli, B.; Hall, K.; Hooper, J.N.A.; Erpenbeck, D.; Wörheide, G. Barcoding Sponges: An Overview Based on Comprehensive Sampling. *PLoS ONE* **2012**, *7*, e39345. [CrossRef]
119. Yang, Q.; Franco, C.M.M.; Sorokin, S.J.; Zhang, W. Development of a Multilocus-Based Approach for Sponge (Phylum Porifera) Identification: Refinement and Limitations. *Sci. Rep.* **2017**, *7*, 41422. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.