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THE ROLE OF SPONGE COLLAGENS IN THE DIET OF THE HAWKSBILL TURTLE (ERETMOCHELYS IMBRICATA)

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INTRODUCTION

Sponges are an important component of many hard-substrate marine communities. This is particularly true on coral reefs, where the contribution of sponges to the reef biomass frequently exceeds that of hermatypic corals[1]. Despite their widespread distribution and abundance, however, sponges have few significant predators[2]. Certain species of dorid nudibranch mollusks, echinoid and asteroid echinoderms, and fish are notable exceptions. This relative immunity to predation has been variously attributed to the mechanical protection provided by skeletal components such as siliceous spicules and tough, organic fibers, and to the chemical protection provided by toxic or noxious secondary compounds[3,4]. The defensive utility of these attributes of sponges against potential predators, however, remains largely inferential.

The hawksbill turtle (Eretmochelys imbricata), a marine turtle associated with coral reefs, has recently been discovered to be a sponge specialist in the Caribbean[5]. Adults of this species average approximately 50 kg in weight and thus are the largest known sponge specialist. Patterns in the hawksbill's diet appear to be correlated with some, but not all, of the proposed defensive mechanisms of sponges. The importance of siliceous spicules and of the biochemical composition of sponges to diet choice will be discussed elsewhere. The present paper describes patterns in the composition and structure of the collagenous, organic skeleton of sponges, and discusses the relevance of these attributes to predation by hawksbills.

MATERIALS AND METHODS

Food items contained in the partial or entire digestive tracts of 64 hawksbills (23-88 cm straight carapace length) were identified, dried to a constant weight and weighed. Because of the progressive state of digestion of food items along the digestive tract, only sponges contained in the stomach were fully identified and included in quantitative analyses. Digestive tract contents were obtained from turtles captured by subsistence fishermen in Caribbean Panama, and at seven islands in the West Indies. Sponge identifications were made with the assistance of a sponge specialist, and follow the classification system of Lévi[6].

RESULTS AND DISCUSSION

Digesta of the hawksbills examined consisted predominantly, and in many cases exclusively, of sponges. All but one of the 64 turtles contained sponges in the digestive tract. A total of 31 species of sponges, all belonging to the Class Demospongea, were identified. Twenty-two of these (13 genera) contributed 98.2% of the total dry weight of all sponges identified in the stomachs. These 22 species, all representatives of the subclass Tetractinomorpha, belong to three of the 13 orders of Demospongea. The orders were represented by the following genera: (Order Astrophorida) Geodia, Ancorina, Myriastra and Ecionemia; (Order Hadromerida) Suberites, Placospongia, Tethya, Spheciospongia, Aaptos and Timea; and (Order Spirophorida) Cinachyra. Chondrosia and Chondrilla, which are also included in the above percentage, are listed as incertae sedis by Lévi[6], but their affinities with either the Hadromerida or the Astrophorida are widely recognized[6,7]. Detailed analyses of the digestive tract contents will be presented elsewhere[5].

The predominance of these three orders in the digestive tract contents reflects a remarkable degree of selectivity on the part of the turtles. Some orders are missing from the diet for obvious reasons, such as their occurrence in inappropriate habitats, or a stony composition. However, four orders (Axinellida, Poecilosclerida, Haplosclerida, Dictyoceratida), are abundantly represented on coral reefs in the Caribbean[7]. Their poor representation in the sample is more puzzling.

The types of sponges identified from the digestive tracts of hawksbills show distinctive properties with respect to spongin and collagen fibrils, the two collagenous constituents of the well developed intercellular matrix. Spongin (the spongin B of Gross et al.[8]), a type of collagen unique to sponges, forms the macroscopic organic skeleton of many species, and is a component of a number of specialized structures. Collagen fibrils (the spongin A of Gross et al.[8]), which are visible only with the electron microscope, are similar, if not identical, to those found in connective tissue throughout the animal kingdom. Although universally present in the phylum Porifera, the fibrils vary in their density in the interstitial stroma of various species[9,10].

Spongin

The three orders of sponges that predominated in the gut contents apparently contain no spongin in the form of fibers (spiculated spongin fibers or horny fibers), and little, if any, spongin in other forms. Table 1 summarizes information available in the literature concerning the systematic distribution of the five types of spongin within the class Demospongea. As the table indicates, the orders of sponges that are important in the hawksbill's diet—Astrophorida, Spirophorida and Hadromerida—are three of six that lack spongin fibers. With the exception of the small and primitive group Homosclerophorida, these are the only orders of sponges that lack spongin fibers and are possible food sources, the Desmophorida and Tabulospongida being unsuitable because of their stony consistency. One explanation that is consistent with such a pattern in the diet is that spongin fibers serve as a feeding deterrent. Additional data are needed to substantiate this hypothesis.

Spongin, with its various reinforcements, provides strength and elasticity to a sponge[6], but the apparent avoidance of it by hawksbills is difficult to explain on the basis of mechanical deterrence to ingestion. Hawksbills have very powerful jaws, as evidenced by their ability to feed on sponges with a high silica content such as Geodia and Placospongia, and on

Table 1. Systematic distribution of spongin in the Class Demospongea. Categories of spongin types are defined by Garrone[9]. The symbol "+" indicates the presence of spongin in at least some representatives of the order. The "-" symbol indicates the absence of spongin in all representatives, based on available data. Sources: Lévi[6], Garrone[9].

	Spiculated spongin fibers	Horny fibers	Filaments	Spiculoids	Gemmules
Subclass Homoscleromorpha					
Order Homosclerophorida	- (?)	-	-	-	-
Subclass Tetractinomorpha					
Order Astrophorida	-	-	-	-	-
Order Spirophorida	-	-	-	-	-
Order Desmophorida	-	-	-	-	-
Order Hadromerida	-	-	-	-	Suberitidae
Order Axinellida	+	-	-	-	-
Subclass Ceractinomorpha					
Order Poecilosclerida	+	-	-	-	-
Order Halichondrida	+	-	-	-	-
Order Haplosclerida	+	-	-	-	Spongillidae
Order Dictyoceratida	-	+	Ircinia	-	-
Order Dendroceratida	-	+ (except Halisarcidae)	-	Darwinella Igernella	-
Subclass Sclerospongia					
Order Ceratoporellida	+ (?)	-	-	-	-
Order Tabulospongida	- (?)	-	-	-	-

very rubbery, cartilagenous species like Chondrosia. The jaws of hawksbills are certainly more powerful than those of the various angelfish that are known to feed on fibrous sponges, such as Callyspongia[3].

Collagen Fibrils

The types of sponges that were found in the digestive tract contents of hawksbills are rich in collagen fibrils. Sponges of the subclass Tetractinomorpha tend to have a higher density of collagen fibrils in the intercellular matrix than do those of the subclass Ceractinomorpha[9]. By contrast, loose-textured sponges are characterized by extracellular spaces poor in fibrillar components. The tetractinellid tetractinomorphs (Astrophorida, Spirophorida and Desmophorida), in particular, are rich in collagen fibrils[6].

There is considerable documentation in the literature of a high collagen fibril content in several genera that are consumed by hawksbills. Tethya and Chondrosia are singled out by Garrone[9] as examples of dense-textured sponges. In the latter, fibrils constitute the only skeletal framework of the sponge[11]. A high collagen fibril content has been observed in Jaspis stellifera[10] and in Stelletta grubii (Simpson, pers. comm.). The latter is a member of the Stellettidae, which includes Myriastra, Ancorina and Ecionemia—all of which are well represented in the turtles. Fibrillar bundles, formed by the association of several hundred collagen fibrils, have been observed in Chondrosia, Tethya and Suberites[9].

The amount of collagen fibrils present in the digestive tract contents is high, not only because of the particular species of sponges present, but also because large amounts of fibril-rich ectosome or cortex had been eaten. Densely-packed collagen fibrils form the cortex of Chondrosia, Chondrilla and Tethya and the thickened ectosome of Jaspis stellifera and Suberites massa[9,10]. Collagen fibril content is also high in the external, asexual buds that occur in some sponges, such as Tethya lyncurium[12]. A large number of buds of Tethya cf. actinia were present in the digesta.

A high collagen fibril content imparts a dense, rubbery consistency to a sponge. This is particularly apparent in species that contain little or no silica, such as Chondrilla or Chondrosia. This consistency may serve as a mechanical feeding deterrent to some predators, but it does not appear to discourage predation by hawksbills.

A high collagen fibril content in sponges may represent a positive attribute from the standpoint of predators because of the nutritional value they impart. The fibrils have been found to be among the most highly glycosylated in the animal kingdom[9]. Data are available[8,9,11,13] on the amino acid composition, nitrogen content and carbohydrate content of fibrils of several sponge species.

Carbohydrate-rich compounds (glycoproteins and acid mucopolysaccharides) that are associated with the fibrils[14] may represent a more substantial and accessible source of nutrition than the fibrils themselves.

Various studies on the intercellular matrix of sponges have revealed the presence of uronic acid, hexosamines, acid polysaccharides, glycoproteins, and several sugars, such as glucose, galactose, mannose, xylose, fucose and arabinose[9]. Although these compounds have been isolated from sponges of diverse taxonomic groups—not all of which can be considered rich in collagen fibrils—some are known to be intimately linked to the fibrils, and thus would impart additional nutritional value to fibril-rich sponges.

Collagen in Coelenterates

Collagen is also an important structural component of coelenterates (Cnidaria and Ctenophora), which are common food items for marine turtles. Nearly all the species feed opportunistically on coelenterates, chiefly medusoid forms, such as jellyfish (Scyphozoa), siphonophores (Hydrozoa) and comb jellies (Ctenophora). Leatherbacks (*Dermochelys coriacea*), the largest of all living turtles, weigh up to 644 kg and are thought to subsist largely, if not exclusively, on such a diet[15]. They are known to feed on scyphozoans including *Cyanea*, *Rhizostoma*, *Stomolophus* and *Catostylus*, and on the siphonophores *Apolemia* and the Portuguese man-of-war, *Physalia*.

The coelenterates consumed by the leatherback and other marine turtles characteristically contain large amounts of thick, gelatinous mesoglea. Although this mesoglea may contain cells, it is essentially a collagenous intercellular matrix[16,17]. Kimura et al.[18] showed the quantitative importance of collagen as a constituent of jellyfish. These authors determined that 70% of the ash-free dry weight of the umbrella (main body) of a 37.6 kg *Stomolophus nomurai* consisted of protein, and of this, 80-90% was collagen. Piez and Gross[13] reported a high collagen content in the medusa-like float of the siphonophore *Physalia*. The amount of collagen in comb jellies is apparently significantly smaller[17]. Little is known about the nutritional requirements or digestive physiology of *Dermochelys*, and thus the nutritional value of jellyfish collagen to this species is unknown. Given the status of collagen as the quantitatively dominant macromolecular constituent of jellyfish—the primary item in the diet—its possible role in their nutrition deserves investigation.

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