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Ecology of Toxicity in Marine Sponges

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Abstract

An investigation of the ecology of toxicity in marine sponges from different latitudes on the North American continent was made. Results indicated that toxicity in sponges increased with decreasing latitude. Three of the 34 species (9%) of sponges from San Juan Island, Washington, USA (48°N), were toxic to fishes. Nine of the 44 species (20%) of sponges from Santa Catalina Island, California, USA (33°N), were toxic. Seven of the 11 species (64%) of sponges from Zihuatanejo Bay, Guerrero, México (17°N), were toxic. Twenty-seven of the 36 species (75%) of sponges from La Blanquilla, Veracruz, México (19°N), were toxic. Most of these toxic sponges are openly exposed to fishes. The most common exposed sponges proved to be highly toxic to fishes. Force-feeding experiments conducted with wrasses demonstrated the effectiveness of the toxin of sponges. A hypothesis is proposed which explains the relationship between species diversity of fishes and sponge toxicity with latitude.

Introduction

The study of toxicity in marine organisms from the ecological point of view is of recent origin. In 1963, Bakus (1964) conducted research at Fanning Island, Line Islands, and postulated that grazing and browsing fishes are largely responsible for the low incidence of exposed sponges and ascidians. Many of the smaller invertebrates at Fanning Island were found to have cryptofaunistic habits. These concealed invertebrates were consumed rapidly when they were exposed to fishes. Studies at Eniwetok, Marshall Islands, by Bakus (1968) indicated that the feeding activity of fishes there was as intense as that at Fanning Island and that certain "soft-bodied" invertebrates, particularly sponges and holothurians living exposed to reef fishes, were toxic to those fishes. Koschmann (in Bakus, 1969), found that at St. John, U.S. Virgin Islands, the most common exposed species of sponges were noxious and/or toxic to fishes. These studies led Bakus to postulate a general theory on the evolution of defensive mechanisms and habits in invertebrates (see Bakus, 1969), from which the following hypothesis has been developed.

It is suggested that as species diversity in fishes increased in tropical shallow marine waters, competition for food created pressure on the evolving species to exploit energy sources, leading in many cases to more specialized feeding habits. This competitive pressure was reflected in a natural selective force operating on the prey and on grazed organisms which favored individuals with chemical defenses, retarding and, in some cases, eventually preventing predation and grazing by fishes. In this manner, toxicity in sponges may have evolved as a defensive mechanism.

In order to test the above hypothesis, research was conducted on sponges from different latitudes to study their ecology and to determine their degree of toxicity. Four study areas were chosen: one in a cold temperate zone at 48°N, San Juan Island in the San Juan Archipelago, Washington, USA; one in a warm temperate zone at 33°N, Santa Catalina Island, California, USA; and two in the tropical zone: one on the Pacific Ocean at 17°N, Zihuatanejo Bay, Guerrero, Mexico, and the other in the Gulf of Mexico at 19°N, the coral cay La Blanquilla, Veracruz, Mexico.

A review of the literature revealed that relatively few studies have been conducted on toxicity of sponges, especially with regard to ecological implications. The most significant information in this field can be found in the works of Nigrelli *et al.* (1959), Halstead (1965), Bakus (1969), Baslow (1969), Sigel *et al.* (1970), Stempien *et al.* (1970), Russell (1971), and Burkholder (1973).

Materials and Methods

The sponges used in the present work were collected by the author at depths ranging from 0 to 40 m. The use of SCUBA made possible the collection of most of the species, including those in such habitats as caves. Sponges were processed immediately after collection, or frozen in a deep freezer or on dry ice.

Carassius auratus (goldfish) was used as the test animal in laboratory experiments because it was not possible to find a marine fish common to the four study areas nor one which could be easily collected in large numbers. However, marine fishes were used in many experiments to insure that local fish species were responsive to the sponges' toxin. The goldfish proved a satisfactory test animal for these experiments.

In order to determine the toxicity of sponges in the laboratory, the following experimental technique was used for each sponge. Five grams (wet weight) of sponge were homogenized with 20 ml of each of the following solvents using a tissue homogenizer: distilled water, ethanol, acetone and chloroform. Each solvent was treated separately. The homogenate was then centrifuged at 3,000 rpm for 15 min and the supernatant evaporated at room temperature (ca. 20°C) in a 300 ml fingerbowl. On evaporation of the crude mixture, 300 ml of fresh water were added to the fingerbowl and the residue dissolved. A test fish of an average weight of 4.1 g was placed in the fingerbowl and its behavior observed and recorded for 90 min. If the fish was alive after 90 min it was transferred to a tank containing clean water and its behavior observed for the subsequent 24 h. Experimental controls were run for each test, using evaporants of the solvents.

For every sponge there was a total of 4 extracts to be tested. The minimum amount of sponge that had to be collected for a complete testing procedure was 20 g (wet weight). At times the author had considerable difficulty in collecting that amount, especially in the case of thinly encrusting species, and in some cases 20 g was not collected. In such cases, the usual procedure was to use half of the standard amount of sponge, solvent and water in the fingerbowl.

A second series of experiments was designed to test the toxicity of sponges under field conditions, forcing the marine fish *Halichoeres bivittatus* (Bloch), a wrasse, to feed on a variety of toxic sponges. These experiments were conducted only at the coral cay La Blanquilla, Veracruz, Mexico. The procedure was as follows: wrasses were collected with the aid of quinaldine. They were then force-fed with a small piece of sponge (approximately 3 mm^3). The piece of sponge was introduced with fine forceps into the stomach. The control fish was force-fed with sea urchin gonads in the same way. The behavior of the fish was observed and recorded.

A third series of experiments designed to test the palatability of sponges was conducted in each study area. Pieces of toxic and nontoxic sponges mixed with sea urchin viscera were hand-fed to fishes underwater. At first only viscera were fed, in order to attract as many fishes as possible. After a few minutes, occasional pieces of sponge mixed with sea urchin viscera were presented to the fishes. Their behavior was observed and recorded.

The last series of experiments was designed to make underwater observations on the behavior of fishes in an area where normally unexposed sponges were made available to them. Rocks with sponges attached to their unexposed surfaces were overturned. The behavior of fishes with regard to the experimentally exposed sponges was observed. In these cases no sponges were manually fed to the fishes.

A general collection of fishes was made using Chemfish in the Central part of the lagoon of La Blanquilla. The stomach contents of 196 individuals belonging to 23 species were analyzed. The sponges found in the stomachs of the collected fishes were fixed in 70% ethanol for identification.

Results

As soon as a fish is placed in a toxic sponge extract solution, it shows escape behavior (it attempts to leave the fingerbowl with violent thrashing movements). Normally, this type of behavior is accompanied by hyperventilation. Escape behavior continues until the fish loses equilibrium and its movements become slow and erratic. The loss of equilib-

Table 1. Condensed results of toxicity in sponges of San Juan Island, Washington, USA; Santa Catalina Island, California, USA; Zihuatanejo Bay, Guerrero, Mexico; and La Blanquilla, Veracruz, Mexico

Study area and depth	No. of sponge species tested	No. and (%) of toxic species	No. of highly toxic species	No. of moderately toxic species	No. of mildly toxic species	No. of very mildly toxic species
San Juan Island, Washington, USA (48°33'N; 123°01'W)						
0-50 m	34	3(9%)	3	-	-	-
Santa Catalina Island, California, USA (33°26'N; 118°29'W)						
0-40 m	44	9(20%)	5	4	-	-
Zihuatanejo Bay, Guerrero, Mexico (17°37'N; 101°34'W)						
1-20 m	11	7(64%)	1	1	-	5
La Blanquilla, Veracruz, Mexico (19°13'N; 96°06'W)						
1-15 m	36	27(75%)	12	2	5	8

rium increases, sometimes causing the fish to invert. Ventilation becomes sporadic and then ceases. This is followed by strong convulsive-like movements of the entire body, then death.

When a fish is placed in a nontoxic sponge extract solution, it shows escape behavior and, in most cases, hyperventilation for an extremely variable period of time. It then becomes calm, tending to swim slowly or remain quietly on the bottom displaying normal ventilation. Sometimes, escape behavior is resumed for a short period, after which the fish becomes calm again. In some instances, the fish shows escape behavior and hyperventilation or general hyperactivity throughout the test period. Some fish are very calm throughout the test, sitting on the bottom, or swimming slowly, displaying normal ventilation. The behavior of the control fish is similar to the behavior of the fish in a nontoxic sponge extract solution.

The results of the experiments on toxicity in sponges from the four study areas are shown in Tables 1 and 2. An arbitrary classification of the different degrees of toxicity found in sponge extracts was adopted to facilitate simplification of results. On the basis that at least one of the four solvent extracts caused death, the classification is as follows: highly toxic sponges, caused death of a fish within 60 min; moderately toxic sponges, caused death of a fish within 61 to 120 min; mildly toxic sponges, caused death of a fish within 121 to 720 min; very mildly toxic sponges, caused death of a fish within 721 to 960 min.

In the force-feeding experiments, immediately after the wrasse is force-fed a piece of toxic sponge it swims to the bottom of the aquarium. A few minutes later it shows paralysis-like signs in the anterior part of the body. During this period, the dorsal and pectoral fins sometimes vibrate erratically for a few seconds. The paralysis-like signs then extend over the entire body, with loss of equilibrium. Shortly thereafter, the wrasse shows strong sporadic convulsive-like movements of the entire body followed by death.

The wrasse which is force-fed a piece of nontoxic sponge swims to the bottom of the aquarium and remains on the bottom ventilating rapidly for several minutes. It then resumes normal behavior and ventilation, either swimming or sitting on the bottom. The behavior of the control fish is similar to the behavior of the wrasse which is force-fed a piece of nontoxic sponge.

The results of the force-feeding experiments with wrasses and sponges of La Blanquilla, Veracruz, Mexico, are shown in Table 3.

Palatability experiments were conducted underwater in all four areas of study, at the depth in which the sponges

Table 2. Toxicity in sponges of San Juan Island, Washington, USA; Santa Catalina Island, California, USA; Zihuatanejo Bay, Guerrero, Mexico; and La Blanquilla, Veracruz, Mexico

Sponge code no.[a]	Sponge species	Exposed and/or unexposed[b]	Non-toxic	Toxic	Time of death (min) and (solvent)[c]
FH1	Unidentified sponge	E	X		
FH2	*Haliclona* sp.	E	X		
FH3	*Myxilla incrustans* (Esper)	E	X		
FH4	*Haliclona permollis* (Bowerbank)	E	X		
FH5	*Halichondria panicea* (Pallas)	E		X	25(a)
FH6	*Terpios* sp.	E	X		
FH7	*Syringella amphispicula* De Laubenfels	E	X		
FH8	*Mycale adhaerens* (Lambe)	E	X		
FH9	*Halisarca sacra* De Laubenfels	E+U	X		
FH10	*Esperiopsis originalis* De Laubenfels	E	X		
FH11	*Iophon pattersoni* (Bowerbank)	E	X		
FH12	*Haliclona* sp.	E	X		
FH13	*Scypha* sp.	E	X		
FH14	Unidentified sponge	E	X		
FH15	*Lissodendoryx* aff. *kyma* (De Laubenfels)	E		X	34(d)
FH16	*Haliclona* sp.	E	X		
FH17	*Haliclona* sp.	E	X		
FH18	*Polymastia pachymastia* De Laubenfels	E	X		
FH21	*Hymeniacidon* sp.	E	X		
FH22	*Tethya aurantia* (Pallas)	E	X		
FH23	*Suberites ficus* Nardo	E	X		
FH24	*Tetilla* sp.	E	X		
FH25	*Isodictya* sp.	E	X		
FH26	*Stylissa stipitata* De Laubenfels	E	X		
FH28	Unidentified sponge	E	X		
FH29	Unidentified sponge	E	X		
FH30	*Biemna rhadia* De Laubenfels	E+U	X		
FH31	*Cliona celata* Grant	E+U	X		
FH32	*Aphrocallistes vastus* Schulze	E	X		
FH33	*Poecillastra* sp.	E	X		
FH34	Unidentified sponge	E	X		
FH35	Unidentified sponge	E	X		
FH36	*Sigmadocia* sp.	E+U	X		
FH37	*Mycale lingua* (Bowerbank)	E		X	57(a)
SC1	*Verongia* sp.	E	X		
SC2	Unidentified sponge	E	X		
SC3	*Stelletta* sp.	E	X		
SC4	Unidentified sponge	E		X	55(a)
SC5	Unidentified sponge	E+U	X		
SC6	Unidentified sponge	E	X		
SC7	*Isociona lithophoenix* (De Laubenfels)	E	X		
SC10	Keratose sponge (Dendroceratida)	E		X	72(d)
SC11	*Sigmadocia* sp.	E		X	60(c)
SC13	*Cliona celata* Grant	E+U	X		
SC14	*Tethya aurantia* (Pallas)	E	X		
SC17	*Microciona parthena* De Laubenfels	E		X	75(d)
SC20	Unidentified sponge	E	X		
SC21	*Hymeniacidon* sp.	E	X		
SC22	Unidentified sponge	E	X		
SC24	*Hymeniacidon sinapium* De Laubenfels	E	X		
SC25	Unidentified sponge	E	X		
SC26	Unidentified sponge	E	X		
SC27	*Haliclona* sp.	E+U		X	30(c)
SC28	Unidentified sponge	E	X		
SC29	Keratose sponge (Dendroceratida)	E		X	55(a)
SC30	*Hymenamphiastra cyanocrypta* De Laubenfels	E+U	X		
SC31	*Timea authia* De Laubenfels	E+U	X		
SC32	Unidentified sponge	U	X		
SC33	*Dysidea* sp.	E	X		
SC34	Unidentified sponge	E	X		
SC35	*Penares cortius* De Laubenfels	E	X		
SC36	Unidentified sponge	E	X		
SC37	Unidentified sponge	E	X		
SC43	*Suberites ficus* Nardo	E	X		
SC44	Unidentified sponge	E	X		
SC46	Unidentified sponge	E+U	X		
SC47	*Haliclona* sp.	E	X		
SC49	Unidentified sponge	U	X		

Table 2 (continued)

Sponge code no.[a]	Sponge species	Exposed and/or unexposed[b]	Non-toxic	Toxic	Time of death (min) and (solvent)[c]
SC50	*Stelletta estrella* De Laubenfels	E	X		
SC52	Unidentified sponge	E		X	80(c)
SC53	Unidentified sponge	U	X		
SC55	*Haliclona* sp.	E	X		
SC56	Unidentified sponge	U	X		
SC57	*Verongia thiona* De Laubenfels	U	X		
SC59	*Haliclona* sp.	E		X	18(a)
SC60	*Haliclona* sp.	E		X	70(a)
SC61	Unidentified sponge	E	X		
SC62	Unidentified sponge	E	X		
Z1	*Haliclona* sp.	E		X	50(c)
Z2	Unidentified sponge	U	X		
Z3	Unidentified sponge	U		X	721-960(a)
Z4	Unidentified sponge	U	X		
Z5	Unidentified sponge	U	X		
Z7	Unidentified sponge	U		X	721-960(a)
Z8	Unidentified sponge	U	X		
Z9	Unidentified sponge	U		X	721-960(d)
Z10	Unidentified sponge	U		X	721-960(d)
Z11	*Ridleia* sp.	U		X	80(a)
Z12	Unidentified sponge	U		X	721-960(a)
V1	*Haliclona rubens* (Pallas)	E		X	20(c)
V2	*Verongia* sp.	E		X	721-960(d)
V3	*Callyspongia fallax* Duchassaing and Michelotti	E		X	721-960(d)
V4	*Haliclona doria* De Laubenfels	E		X	721-960(d)
V5	*Thalyseurypon* sp.	E		X	34(d)
V6	*Ianthella* sp.	E		X	721-960(d)
V7	*Neopetrosia longleyi* De Laubenfels	E		X	721-960(d)
V8	*Gelliodes areolata* (Wilson)	E		X	721-960(d)
V10	*Haliclona viridis* (Duchassaing and Michelotti)	E		X	37(a)
V11	*Halichondria* sp.	E+U		X	30(d)
V12	*Tethya actinia* De Laubenfels	E+U		X	120(a)
V13	*Haliclona* sp.	U	X		
V14	*Placospongia carinata* (Bowerbank)	U	X		
V15	*Geodia gibberosa* Lamarck	E+U		X	350(d)
V16	*Haliclona* sp.	E+U		X	21(d)
V17	*Chondrilla nucula* Schmidt	E+U		X	40(d)
V18	*Acarnus* sp.	U	X		
V19	Adociidae	U	X		
V20	*Halichondria* sp.	U	X		
V21	Callyspongidae	U	X		
V22	*Haliclona* sp.	E+U		X	42(c)
V23	*Adocia* sp.	E		X	50(d)
V24	*Ircinia fasciculata* (Pallas)	E		X	55(d)
V25	*Callyspongia* sp.	E		X	180-240(d)
V26	*Iotrochota birotulata* (Higgin)	E	X		
V30	*Callyspongia* sp.	E	X		
V31	*Ircinia strobilina* (Lamarck)	E		X	90(a)
V32	*Agelas sparsus* (Gray)	E		X	721-960(d)
V33	*Ianthella ardis* De Laubenfels	E		X	721-960(d)
V34	*Dysidea etheria* De Laubenfels	E		X	121-160(c)
V36	*Cliona* sp.	E+U	X		
V37	Myxillidae	E		X	25(c)
V38	*Mycale* sp.	E		X	240-300(a)
V39	*Geodia* sp.	E		X	180-240(d)
V40	*Ircinia* sp.	E		X	721-960(d)
V41	*Haliclona* sp.	E		X	35(d)

[a] Letter prefix indicates area of study: FH, San Juan Island, Washington, USA; SC, Santa Catalina Island, California, USA; Z, Zihuatanejo Bay, Guerrero, Mexico; V, La Blanquilla, Veracruz, Mexico.

[b] In the natural habitat.

[c] Time of death of a fish in the extract of the solvent that produced death most rapidly. For practical purposes in this work, a fish is considered dead when the apparent vital functions have ceased and the fish does not respond to any kind of tactile stimulation. Solvents: a, acetone; c, ethanol; d, distilled water.

Table 3. Results of force-feeding experiments with wrasses (*Halichoeres bivittatus*) and sponges of La Blanquilla, Veracruz, Mexico

Sponge code no.	Sponge species[a]	Non-toxic	Toxic	Time of death (min)	Observations on fish
V1	*Haliclona rubens* (Pallas)		X	7	Paralysis-like signs within 3 min. Spasmodic convulsive-like movements within 4 min.
V5	*Thalyseurypon* sp.		X	9	Paralysis-like signs within 4 min. Convulsive-like movements within 6 min.
V10	*Haliclona viridis* (Duchassaing and Michelotti)		X	8	Paralysis-like signs within 3 min. Convulsive-like movements within 5 min.
V11	*Halichondria* sp.		X	8	Paralysis-like signs within 4 min. Convulsive-like movements within 5 min.
V16	*Haliclona* sp.		X	10	Paralysis-like signs within 5 min. Convulsive-like movements within 7 min.
V17	*Chondrilla nucula* Schmidt		X	10	Paralysis-like signs within 7 min. Convulsive-like movements within 8 min.
V30	*Callyspongia* sp.	X			Fish normal 24 and 48 h after force-feeding.
V36	*Cliona* sp.	X			Fish normal 24 and 48 h after force-feeding.
V37	Myxillidae		X	12	Paralysis-like signs within 5 min. Convulsive-like movements within 7 min.

[a] Total = 9 species.

were collected and with the fishes at that depth. Fishes did not eat the sponges which were offered them. There were a few instances with nontoxic and mildly toxic sponges where fish took a bite of sponge, but they released it immediately.

During the underwater observations in all four areas, no fishes were seen eating exposed sponges or unexposed sponges that had been made available to them by turning over rocks, in strong contrast to the data reported for Fanning Island by Bakus (1964).

In the analysis of the stomach contents of 23 species of fishes collected at La Blanquilla, Veracruz, Mexico, sponges (both toxic and nontoxic) were found in the stomach of only one species, *Pomacanthus paru* (Bloch), in which, in the one specimen examined, they comprised approximately 75% of the stomach content. The species of sponges found were *Adocia* sp., *Callyspongia* sp., *Geodia gibberosa* Lamarck, *Halichondria* sp., *Haliclona* sp., *Lissodendoryx* sp., *Myxilla* sp., and *Neopetrosia longleyi* De Laubenfels.

Discussion

The results of the experiments on the toxicity of sponges shown in Table 1 indicate a clear and definite trend: as latitude decreases, toxicity increases. At San Juan Island, Washington (48°N), of the 34 species tested only 3 (9%) were toxic. At Santa Catalina Island, California (33°N), of the 44 species tested 9 (20%) were toxic. In Zihuatanejo Bay, Guerrero, Mexico (17°N), of 11 species tested 7 (64%) were toxic. At La Blanquilla, Veracruz, Mexico (19°N), of the 36 species tested 27 (75%) were toxic. It is of interest to note that the 3 toxic sponges found at San Juan Island, Washington, are not endemic to that region. Two of them, *Halichondria panicea* and *Mycale lingua*, have a world-wide distribution and the other, *Lissodendoryx* aff. *kyma*, is also found on the coast of California. Similar species of this genus are reported from all parts of the world (De Laubenfels, 1932). In addition, the author found that some sponge genera were consistently toxic in the different

areas of study. These were species of *Haliclona* and *Halichondria*, which were also among the most toxic sponges studied.

A direct relationship was found between exposed sponges in their natural habitat and the presence of toxicity in these species. Most toxic sponges were found living either entirely exposed or both exposed and unexposed to fishes, with the exception of the very mildly toxic sponges from Zihuatanejo, which were entirely unexposed. Zihuatanejo appears to have a relatively low diversity of sponges. Most of the sponges collected there (10 of 11 species) were small and encrusting and found under rocks. In Zihuatanejo and Veracruz most nontoxic sponges were unexposed, and in the few exposure cases the sponges, such as *Iotrochota birotulata*, have a colored, strong-smelling exudate which when released in water is avoided by fishes. However, at San Juan Island and Santa Catalina Island most nontoxic sponges were living exposed. It is important to note that in the tropical areas studied, the most common exposed sponges were found to be highly toxic. This confirms the observation by Bakus (1969) who reported similar findings for St. John and the Eniwetok Atoll.

Stempien *et al.* (1970) reported on the ichthyotoxic activity of 125 species of Caribbean sponges. They found that only 24 sponges (20%) were toxic. Their extracts were prepared with 1.0 g of the sponge per 10 ml of distilled water. The test animal, the marine killifish *Fundulus heteroclitus*, was placed in 200 ml of sea water with 2 ml of the sponge extract. It is clear that differences in materials and methods between the work of Stempien *et al.* (1970) and the present research are likely to yield discrepancies. Furthermore, Stempien and his colleagues did not note data on the collection of sponges such as degree of exposure and habitat characteristics. Of the 24 toxic species reported, only 4 are identified to species, 6 are identified to genus, and 14 are unidentified.

Another interesting phenomenon related with changes in latitude is that of species diversity in marine fishes. As latitude decreases there is a marked increase in the diversity of fish species. On the Pacific coast of Canada (48° - 55°N), Clemens and Wilby (1946) reported 227 species of fishes from nearshore and deep waters. In southern California (Point Conception to Mexico, 32° - 34°N), Lavenberg (*in* Bakus, 1969) reported 180 species of fishes from depths of 0 to 30 m. At Alligator Reef, Florida (25°N), Starck (1968) reported 517 species of fishes from nearshore and deep waters, 389 of which occur on coral reefs at depths of 0 to 45 m. In the Dry Tortugas (in the Gulf of Mexico, 24°N), the number of fish species reported in nearshore and deep waters was 442, of which 300 are found on coral reefs (Longley and Hildebrand, *in* Starck, 1968). Gosline and Brock (1960) reported 448 species of inshore fishes for the Hawaiian Islands (17° - 28°N). Finally, Scott (1962) and Marshall (1964) reported that in Queensland, Australia (10° - 28°S) there are over 1,000 species of nearshore and deep-water fishes (see Bakus, 1969). There are no similar reports for the Zihuatanejo and Veracruz areas. However, extrapolating from the available information, one would expect a moderately high species diversity of fishes there, although the precise number of species may not be as great as that of the tropical regions previously mentioned, since Zihuatanejo has no coral reefs and La Blanquilla is situated near the northernmost development of coastal coral cays in the Gulf of Mexico.

In shallow marine tropical ecosystems of hard bottoms, the most important predators and grazers are fishes. This is not characteristic of cold-water marine ecosystems, in which this role is played predominantly by invertebrates, resulting in a different pattern of energy flow (Bakus, 1969). From the present research, the author believes that as species diversity in fishes increased in tropical shallow marine waters, competition for food put pressure on the evolving species to exploit any source of energy available to them, leading in many cases to more specialized feeding habits. This competitive pressure was reflected in a natural selective force operating on the prey and on grazed organisms, resulting in the evolution of defensive mechanisms by certain invertebrates and their avoidance by fishes. Sponges, relatively vulnerable organisms with sessile habits and frequently soft bodies, presumably evolved toxicity as a defensive mechanism. Perhaps in a similar manner they evolved cryptofaunistic habits (e.g. unexposed habitats where they are not easily reached by predators).

The present research indicates that mildly and very mildly toxic sponges exist only in the tropical areas studied. In the temperate zones the toxic sponges were highly toxic or moderately toxic. One could speculate that perhaps there are several stages in the evolutionary process of sponges in acquiring toxicity. Possibly the first stages evolved with the production of mildly noxious substances, followed by the production of

more highly noxious substances, with increasing degrees of toxicity.

Sponges have been very successful in their use of defensive mechanisms. For example, in the shallow waters of the Caribbean Sea and the Gulf of Mexico, sponges are very abundant and diverse. The results of the force-feeding experiments from La Blanquilla, Veracruz, presented in Table 3, conducted with the wrasse *Halichoeres bivittatus*, are a strong indication of the effectiveness of these sponges' toxin. The author observed that wrasses died in a matter of minutes following the forced ingestion of small pieces of highly toxic sponges. Wrasses were not affected when force-fed with nontoxic sponges under the same circumstances.

There are, nevertheless, species of fishes that do feed on sponges. Randall and Hartman (1968) reported on the analysis of the stomach content of 212 species of West Indian reef and inshore fishes. They found sponge remains in 21 species. Of these, 11 fed on sponges and had sponges comprising from 6 to 97.1% of their stomach contents. In the author's analysis of the stomach contents of the most common fishes in the lagoon of La Blanquilla, sponge remains were found in only one species, the angelfish *Pomacanthus paru*. Sponges comprised 75% of the stomach contents of this one specimen. According to Randall and Hartman (1968), the sponge-feeding fishes belong to highly specialized teleost families, suggesting that this habit has evolved in geologically late time, perhaps in response to increased competition for energy sources on coral reefs. It is of interest that sponge-feeding fishes in which sponges constitute the main source of food tend to ingest a large number of sponge species. For example, Randall and Hartman (1968) found that specimens of *Holacanthus ciliaris* may consume as many as 40 species of sponges, with up to 9 species of sponges per fish. The highly toxic sponges, such as *Haliclona rubens*, if consumed, were eaten in very small amounts. Randall and Hartman suggest that this is the mechanism by which these fishes avoid the absorption of large quantities of toxin. Thus, even though toxic sponges are ingested by a small number of fishes, toxicity as a defensive mechanism is successful, since the sponges are eaten in only small amounts, thus preventing their rapid and total depletion.

The type of highly specialized feeding habit in fishes mentioned above suggests the existence of an adaptation to sponge toxin. There are nudibranchs that feed exclusively on sponges, toxic and nontoxic according to the concept used here, without apparent detrimental effects (Graham, 1955). Moreover, a number of annelids, mollusks, bryozoans and crustaceans are found closely associated with toxic and nontoxic sponges (i.e., living within them).

There is very little information available on sponges consumed by fishes in temperate latitudes. McCleneghan (*in* Bakus, 1969) found that only one specimen of the fish *Pimelometopon pulchrum* contained sponges in its stomach from a total of 22 species (144 specimens) of kelp forest fishes in southern California. Bakus (1969) reported that *Hypsypops rubicunda* (3 specimens) and *P. pulchrum* (1 specimen) consumed sponges, out of a total of 53 inshore species (477 specimens) of fishes in southern California waters. Quast (1968) reported that of 45 species of kelp forest fishes (approximately 2,200 specimens) in southern California only *Medialuna californiensis* consumed sponges. The question arises: why are sponges in higher latitudes almost free of fish predation? This may be attributed to the fact that species diversity of fishes in shallow marine waters is considerably lower in higher latitudes than in the tropics. Consequently, fishes in higher latitudes are not under as strong competitive pressure for exploitation of the food resources available as are fishes in tropical shallow marine waters. Another answer might be the food preference of fishes in higher latitudes. Underwater and laboratory observations and experiments with a number of fish species have led the author to believe that many sponges (toxic and nontoxic) are not palatable to fishes. Perhaps this is because most sponges have either mineralized sclerites (spicules) or tough fibrous components (spongin), both sclerites and spongin, or in certain cases, noxious chemical compounds.

There is insufficient experimental evidence to determine specific physiological effects of sponge toxin on organisms naturally occurring in the sponges' environment. The author suggests that the toxic material produced by sponges may be constantly released into the surrounding water, serving as a warning to approaching predators. There is no evidence to confirm this. However, Bakus (1973) suggested a similar phenomenon for holothurians, based on the feeding behavior of fishes and steroid saponin production in seastars (see Feder, 1972).

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