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Host Specificity in Sponge-Encrusting Zoanthidea (Anthozoa: Zoantharia) of Barbados, West Indies

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Abstract

Six species of common Caribbean Zoanthidea, *Parazoanthus swiftii, P. parasiticus, P. catenularis, P. puertoricense, Epizoanthus cutressi*, and *Epizoanthus* sp., are virtually restricted to living on surfaces of reef-dwelling sponges. Quantitative surveys on Barbados reefs indicate that substrate specificity is relatively high among these zoanthids with three restricted to a single primary host sponge species and three restricted to three closely related sponges. One species, *P. swiftii*, exhibits a broad range of acceptable secondary substrates, due to its unique ability to execute migrational spread in the adult polyp stage. Variations in substrate specificity have been noted between island populations within the extensive Caribbean range and appear to be due to different species compositions of local sponge communities and slight differences in zoanthid larval settling specificities.

Introduction

Tropical coral reef communities are known to support large numbers of intricate symbiotic associations. Sponges, which are major components of most coral reef communities (Reiswig, 1973), have long been known to host a variety of marine organisms (Pearse, 1949; Forbes, 1966; Long, 1968; Rutzler, 1968; Bergquist, 1978). One set of these associations, common throughout the world tropics, involves several members of the order Zoanthidea. These organisms are colonial anthozoans in which the individual polyps are connected by a basal reticulum or coenenchymal tissue strands. Six species of zoanthids live exclusively in association with sponges on reefs of the West Indies; five, *Parazoanthus swiftii* (Duchassaing and Michelotti), *P. parasiticus* (D. & M.), *P. catenularis* (D. & M.), *P. puertoricense* West and *Epizoanthus cutressi* West, have been previously reported (West, 1979) and one, *Epizoanthus* sp., is an undescribed species reported here for the first time. Previous work has suggested that in many symbiotic associations, symbionts exhibit considerable specificity in selection of hosts (Kinzie, 1974; Shoenberg and Trench, 1976; Stanton, 1977; Kinzie and Chee, 1979). The five species of sponge-encrusting zoanthids previously reported from Puerto Rico by West appear to be restricted to one or a small number of potentially available host species.

This report is limited to investigation of host specificity in these six zoanthid species at Barbados, West Indies. Field surveys along with laboratory and *in situ* experiments were conducted to determine the host preference for each zoanthid species. Patterns of host specificity and the probable mechanisms effective in host selection are discussed.

Material and Methods

Field surveys were conducted on the outer bank reef (Macintyre, 1967) from 15 to 35 m depths off the west coast of Barbados, West Indies (Lat. 13°11′N., Long. 59°39′W.) during July 1975 – January 1976. Three transects, 50 m in length by 3–8 m in width, were established perpendicular to the bank reef and surveyed using SCUBA. All sponges within the transects were recorded and identified where possible to species and all zoanthid infestations were recorded by species and extent of infestations. Transect records were augmented by observations made on excursion surveys to depths of 60 m.

Lability of host specificity in adult zoanthids was initially investigated by "proximity" experiments conducted in running sea-water aquaria at the Bellairs Research Institute. These consisted of tying a non-infested (clean) sponge to a sponge supporting an epizoic zoanthid population and monitoring the growth of the symbiont

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population. Nine laboratory proximity experiments were run for a 2 to 3-wk period, with regular inspections made daily to note whether or not spread of zoanthid colonies onto the surface of the offered host species had occurred. As a result of success in laboratory experiments, 70 *in situ* proximity experiments were carried out on the reef in the area of SCUBA transect surveys. These ran for 10 to 12 wk with inspections made at 7 to 10-d intervals.

Direct polyp grafting experiments were also conducted in the laboratory to assess the ability of adult zoanthid polyps to re-attach to the surface of an offered non-infested sponge. Mature polyps of all zoanthid species studied, excepting *Parazoanthus swiftii,* lie deeply and firmly embedded in the outer tissue layers of their host sponges. New polyps are developed at the colony edge by horizontal tissue extension over the sponge surface, with eventual embedment by either directional zooid growth, outward sponge growth, or a combination of these processes. Superficial coenenchymal connections may persist between polyps in some species. Polyps of *P. swiftii,* however, extend over the outer host surface, anchoring to projecting spicules or projecting spongin fiber tips, but not extending into depressions of the host surface. The polyps and connecting coenenchyme can thus be relatively easily peeled from the host surface. Whole adult polyps of the three largest species were dissected free from their natural host sponges and attached, with fine dissecting pins, to one of ten different non-infested sponge species. Control grafts, performed with *P. swiftii,* consisted of transferring polyps to uninfested individuals of its most common host sponge. All specimens used in the grafting experiments were held in running sea water for 2 to 3 wk and observations were made daily to determine the success of polyp reattachment in transplantation.

Histological examination of specimens was carried out to compare surface texture and composition of host sponges to non-infested sponges, and to examine polyp-host interfaces. Tissues, fixed in Bouin's solution, were decalcified in acetic acid, desilicified in 4% hydrofluoric acid, and embedded in paraffin. Tissue sections 5 to 20 μm were stained with Masson tetrachrome for differentiation (Humason, 1972).

Results

In transect surveys, 1 897 zoanthid-sponge associations were recorded in over 20 000 sponges examined. Data from these and excursion surveys revealed that although 21 sponge species were found to host the six species of zoanthids on Barbadian reefs, only 11 of these species were commonly found infested and can be considered primary hosts (Table 1). Sponges defined here as primary hosts are those that either support a significant portion of the local zoanthid species population (>5%), or exhibit high infestation of their own (the sponge) population (>5%). These criteria suggest that infestation is initiated through larval settlement rather than horizontal spreading of the zoanthid colony. The remaining ten species were found to host a zoanthid colony only on rare occasions and are here considered secondary hosts; they satisfy none of the criteria used to define primary hosts. More significantly, the number of primary host species represents a relatively small portion of the approximately 120 sponge species inhabiting the transect area.

Parazoanthus swiftii was observed on 11 different host sponges, but was only commonly found infesting a single primary host, *Iotrochota birotulata. P. parasiticus, P. cate-*

Table 1. Numerical abundance of zoanthid-infested sponges (N) and their represented percentage (P) of the total sponge species population in field transects of Barbados reefs. Abbreviations: *P. s.* = *Parazoanthus swiftii; P. p.* = *P. parasiticus; P. c.* = *P. catenularis; P. pr.* = *P. puertoricense; E. c.* = *Epizoanthus cutressi; E.* sp. = *Epizoanthus* sp.

Host sponge species	Zoanthid species											
	P. s.		*P. p.*		*P. c.*		*P. pr.*		*E. c.*		*E.* sp.	
	N	P	N	P	N	P	N	P	N	P	N	P
Iotrochota birotulata	48	(6%)	–	–	–	–	–	–	–	–	–	–
Gelliodes ramosa	–	–	1 098	(70%)	–	–	–	–	–	–	–	–
Cliona delitrix	–	–	182	(61%)	–	–	–	–	–	–	–	–
Callyspongia vaginalis	–	–	85	(72%)	–	–	–	–	–	–	–	–
Xestospongia muta	–	–	–	–	6	(6%)	–	–	–	–	–	–
Xestospongia sp.^{a}	–	–	–	–	22	(58%)	–	–	16	(42%)	–	–
Xestospongia sp.^{b}	–	–	–	–	62	(60%)	–	–	–	–	–	–
Agelas sp.^{a}	–	–	–	–	–	–	229	(88%)	–	–	–	–
Agelas sp.^{b}	–*	–	–	–	–	–	4	(100%)	–	–	–	–
Hymeniacidon sp.	–*	–	–	–	–	–	43	(30%)	–	–	–	–
Plakortis sp.	–	–	–	–	–	–	–	–	–	–	102	(36%)
Totals	48	(6%)	1 365	(69%)	90	(36%)	276	(67%)	16	(42%)	102	(36%)

* Noted as occasional secondary hosts in excursion surveys

Table 2. Results of host specificity proximity experiments conducted in the laboratory and *in situ*. (+ indicates spread of zoanthid polyps onto the offered uninfested sponge branch; – indicates no spread of the polyps; numerals indicate number of experiments)

Sponge offered	*Parazoanthus swiftii*				Other Zoanthid species			
	Lab.		Field		Lab.		Field	
	+	–	+	–	+	–	+	–
Iotrochota birotulata	1	.	1	.	.	2	.	14
Verongia longissima	1	.	2	1	.	.	.	9
Verongia sp.	1	.	1	2	.	.	.	7
Hemectyon ferox	1	.	1	2	.	.	.	3
Desmapsamma anchorata	.	.	2	.	.	.	.	5
Axocielita sp.	.	.	2	.	.	1	.	.
Gelliodes ramosa	.	.	.	.	.	1	.	1
Callyspongia vaginalis	.	.	.	1	.	.	.	.
Xestospongia muta	.	.	.	1	.	1	.	1
Xestospongia sp.[b]	.	.	.	.	.	.	.	2
Agelas sp.[a]	.	.	.	.	.	.	.	2
Hymeniacidon sp.	.	.	.	.	.	.	.	3
Gelliodes sp.	.	.	.	.	.	.	.	1
Ianthella sp.	.	.	.	.	.	.	.	1
+/Total	4/4		9/16		0/5		0/49	
Percent Spreading Success	100		56		0		0	

nularis and *P. puertoricense* were each found on three primary host sponge species, with no hosts shared between these congeners. The two *Epizoanthus* spp. were each restricted to a single host sponge. *E. cutressi* was only found infesting the maroon flabellate *Xestospongia* sp.[a], which it thus shares with *P. catenularis*, while *Epizoanthus* sp. was found only on the sponge *Plakortis* sp.

Sponges not normally serving as hosts to zoanthids were rarely found with zoanthid polyps infesting their surface. In the majority of these instances, the zoanthid involved was the yellow *Parazoanthus swiftii*, most commonly found on the sponge *I. birotulata*. In virtually all of these observations, a branch of infested *Iotrochota birotulata* was either firmly attached to the rarely infested host sponge or located in close proximity. Ten different sponge species infested with *P. swiftii* were involved in this natural proximity relationship at least once: *Desmapsamma anchorata*, *Axocielita* sp., *Acarnus annominatus*, *Epipolasis* sp.[a], *Epipolasis* sp.[b], *Agelas* sp.[b], *Xytopsene* sp., *Callyspongia* sp., *Verongia longissima*, and *Hymeniacidon* sp. *P. swiftii* has rarely been encountered on coral rubble near an infested *I. birotulata* individual.

These observations suggested that mature zoanthid polyps may not be totally confined to their primary host sponges. It appeared probable that at least one zoanthid species, *Parazoanthus swiftii*, has the capability of spreading onto the surface of other sponges should opportunity occur.

Laboratory and *in situ* proximity experiments were conducted to assess the ability of adult zoanthid colonies to spread to new substrates. Results of the proximity experiments show that mature zoanthids can spread from the infested host onto the surface of the non-infested sponge (Table 2), but the only zoanthid species clearly exhibiting this capability is *Parazoanthus swiftii*. Colonization due to polyp migration was obtained in all four laboratory experiments and 9 of 16 or 56% of the field experiments involving *P. swiftii* and accessible clean sponge surfaces (Fig. 1). The other four zoanthid species examined, *P. parasiticus*, *P. catenularis*, *P. puertoricense*, and *Epizoanthus cutressi*, did not exhibit this ability in any of the 54 proximity experiments conducted on them.

Attempts to transfer zoanthids by direct grafting to uninfested sponges which do not normally host the particular zoanthid species but may host other zoanthid species resulted in no successful transfers in 14 experiments (Table 3). the grafting procedure itself was not considered to be the primary cause of surface rejection since *Parazoanthus swiftii* polyps were successfully transferred as a control graft from an individual of its major host *Iotrochota birotulata* to a non-infected individual of the same sponge species. In this laboratory experiment the polyps did attach to the sponge surface after an extended period of time in the laboratory. The negative results included attempts to graft *P. swiftii* to several sponges in which migration success was obtained in field proximity experiments.

Active or potential competition between two species of zoanthids infesting the surface of a single host was rarely encountered in nature. Although *Parazoanthus catenularis* and *Epizoanthus cutressi* share *Xestospongia* sp.[a] as a primary host sponge, dual infestations were encountered on only three sponges. In each case the available sponge surface was partitioned fairly equally between the two

Table 3. Results of direct zoanthid grafting experiments conducted in the laboratory. Legend: (+) = accepted graft; (0) = rejected graft; (–) = not attempted

Recipient sponge species		Zoanthid species transferred		
		P. swiftii	*P. parasiticus*	*P. puertoricense*
Iotrochota birotulata	**	+	0	0
Xestospongia muta	**	0	–	–
Xestospongia sp.[b]	**	0	–	–
Callyspongia vaginalis	**	0	–	–
Gelliodes ramosa	**	0	–	0
Verongia longissima	*	0	0	–
Verongia sp.[a]		0	–	–
Verongia sp.[b]		0	–	–
Ircinia fasciculata		0	–	–
Agelas sp.[a]	**	–	0	0

Recipient host sponges are (**) primary or (*) secondary hosts in nature but usually not to the zoanthid species transferred; other sponges not known to host zoanthids

zoanthid colonies, with a narrow overlap area consisting of interdigitating groups of polyps at the junction. Polyp spacing appeared to be normal, with slight tentacle overlap and frequent tentacle contact between species. Although *P. swiftii* was observed sharing a minor host sponge with one of the major hosts of *P. puertoricense*, only one instance of dual colonization on *Agelas* sp.[b] was encountered. The competitive interactions between zoanthids at colony interfaces were not investigated here.

Histological sections of zoanthid-hosting sponges and non-hosting sponges suggested that two characteristics favor zoanthid colonization: (1) the surface tissues of host sponges contain large numbers of siliceous megascleres (these siliceous spicules projecting from the sponge surface penetrate the mesogleal layer of the symbiont polyps and thereby serve as attachment structures); (2) host sponges have small populations of other ectosymbionts and superficial endosymbionts (polychaetes, entoprocts, hydroids, etc.) relative to non-zoanthid hosting sponges. The presence of large populations of other symbionts is expected to inhibit initial colonization by zoanthid planulae, but until zoanthid planulae can be obtained for settlement studies, competitive inhibition must be considered speculative.

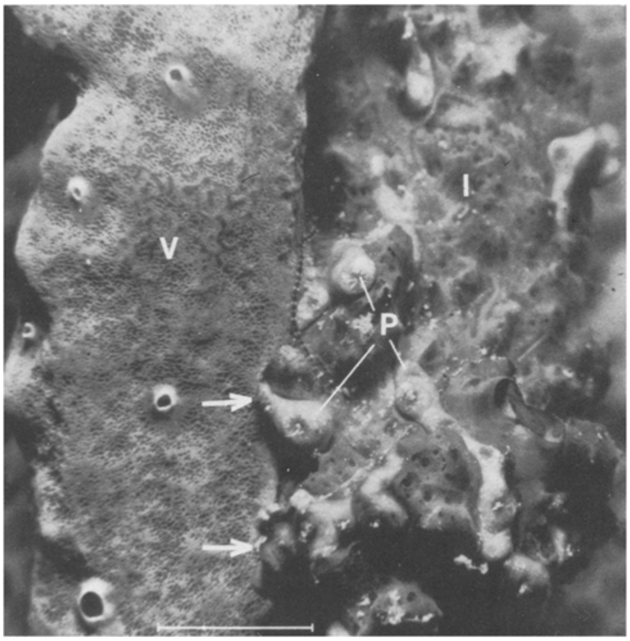

Fig. 1. Field proximity experiment showing early stages of migration of the contracted zoanthid *Parazoanthus swiftii* (P) from its primary host *Iotrochota birotulata* (I) onto the surface of a normally non-hosting sponge *Verongia longissima* (V). (Scale = 1 cm)

Discussion and Conclusions

Transect surveys, grafting experiments and *in situ* proximity experiments suggest that five of the six zoanthid species appear to have very narrow host specificities. Only *Parazoanthus swiftii* has the ability to spread onto the surface of other secondary host sponges and, more rarely, onto non-living substrates.

The relatively broad host range of *Parazoanthus swiftii* may result from its unique method of host infestation. As noted earlier polyps of *P. swiftii*, unlike the other zoanthid species, do not extend into the sponge surface tissues, but instead spread over the surface of their host, anchoring to projecting spicules or fiber tips. In contrast, the other five zoanthid species all lie deeply embedded in the surface tissue of their host sponge. The basic difference in host specificity patterns between these two groups appears to be related to the ability of *P. swiftii* to spread across continuity barriers to new substrate surfaces and the inability of the other five zoanthid species to spread from colonized hosts.

The restriction of a particular zoanthid species to one or a few primary host sponges is probably a result of specificity of site selection by the zoanthid larvae. Recognition of the appropriate substrate probably involves both tactile and chemosensory response (Wilson, 1952; Crisp, 1979), but experimental studies of behavior and taxes of larvae of the sponge-dwelling zoanthids have not yet been done.

Strong support for existence of larval chemoreceptive site selection is provided by the relatively narrow primary host specificity of each of the six species. Three species, *Parazoanthus swiftii, Epizoanthus cutressi,* and *Epizoanthus* sp., are each apparently restricted to a single primary host sponge species as an acceptable settling surface. Each of these host sponges are members of different orders: *Iotrochota birotulata* (Poecilosclerida), *Xestospongia* sp.[a] (Haplosclerida), and *Plakortis* sp. (Homosclerophorida). The other three zoanthids each apparently settle successfully on three host sponges, one restricted to members of the order Axinellida and Halichondrida, one restricted to three species of the genus *Xestospongia* (order Haplosclerida) and the remaining zoanthid to two different species of the Haplosclerida and a single species of the Hadromerida. The large numbers of non-spiculate keratose sponges in Barbadian waters appear to have been bypassed as hosts in evolution of the settling specificity, probably due to their lack of attachment spicules and the relatively common presence of other symbionts on or just below the surfaces of this group of sponges.

Host specificity reported here in the Barbadian zoanthids is clearly similar to host occurrence reported for five of these zoanthid species in Puerto Rico (West, 1979). Where host sponge species do occur in both areas, colonization by respective zoanthid species is generally similar, indicating wide geographic concordance of host specificity. In both locations, for example, *Epizoanthus cutressi* and *Parazoanthus catenularis* primarily inhabit species of *Xestospongia,* presumably the same species: *P. puertoricense* occurs on species of *Agelas* in both areas, but species-level identification of this genus is uncertain at present; *P. parasiticus* infests *Gelliodes ramosa* and *Callyspongia vaginalis* in both sites. Some differences between geographic regions are indicated by the colonization of *Speciospongia* sp. (probably *S. vesparia*) in Puerto Rico by *P. parasiticus* and the absence of colonization of this species in Barbados. Preliminary surveys (unpublished data) carried out at Jamaica suggest that significant differences in host specificity do exist between those zoanthid populations and the Barbadian populations, probably attributable in large part to differences in species composition of available host sponge populations in the two regions.

The ability of certain members of the Zoanthidea to exhibit a substrate preference for sponges and the narrow specificity of this preference are adaptations that have contributed to the survival and perpetuation of this group in a community widely recognized as being substrate-limited (Connell, 1961, 1973; Dayton, 1971; Glynn, 1973; Paine, 1974; Jackson, 1977). While the external surface of sponges presents a relatively hostile substrate for most sessile organisms (Frost, 1976), the advantage of successful colonization of this under-utilized resource is obvious. The zoanthids which have been able to exploit this specific substrate are relatively free from competition with other benthic invertebrates for this potentially limiting resource. The pattern of coloniality of these zoanthids differs from that of "associative settlement" discussed by Crisp (1979) in that these colonies are essentially clones derived from single larval settlement on a host. The major features of the colonial system are similar, however, with species specific substrate recognition, regular spacing (territoriality) of colony members and the major benefit being ability to survive on unstable, isolated habitats (Crisp, 1979), their host sponge surfaces.

The narrow host specificity shown by each of these sponge-inhabiting zoanthid species in turn reduces interspecific competition between species to near zero and enhances the long term survival of each species through niche separation. Direct investigation of settling preferences by zoanthid larvae is still required to substantiate the strong but circumstantial evidence for host specificity reported here.

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