SYMPOSIA SERIES FOR UNDERSEA RESEARCH
NOAA'S UNDERSEA RESEARCH PROGRAM, VOL. 1 NO.1, 1983

The Ecology of Deep and Shallow Coral Reefs

Results of a Workshop on Coral Reef Ecology held by the American Society of Zoologists, Philadelphia, Pennsylvania, December 1983

Edited by
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Washington, D.C.
December 1983

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SPONGES AS IMPORTANT SPACE COMPETITORS IN DEEP CARIBBEAN CORAL REEF COMMUNITIES[1]

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ABSTRACT

Demosponges are diverse and aggressive competitors for space in deep open-reef habitats. Sponges comprise nearly half (30/63) of all encrusting taxa recorded in this study and are significantly more diverse than corals at 90' and 120' ($p < .001$). Analyses of m^2 quadrats (total N = 111) from depths of 10', 30', 60', 90', and 120' reveal that a gorgonacean (Erythropodium) was the most frequent aggressor at 10'. Below this depth, four genera of demosponges (Chondrilla, Hemectyon, Ircinia and Verongia) were the most significant aggressors. Below 30', scleractinian corals were the taxa most frequently overgrown. Sponges should be recognized as important contributors to the organization and dynamics of open coral reef communities.

INTRODUCTION

Competition for space has gained the attention of a wide variety of investigators interested in making long-range predictions about community structure (Dayton, 1971; Lang, 1973; Jackson & Buss, 1975; Osman, 1975). In tropical coral reef communities, heavy emphasis has been placed on the transitive nature of competitive interactions between scleractinian corals and the contribution of such "competitive hierarchies" to the structure of these communities (Lang, 1973; Sheppard, 1979). Although other invertebrate groups are well-known to exist within these communities, they are known mostly from the cryptofauna (those species that inhabit the undersides of foliaceous corals or cave-like environments) where competition has been reported to be non-transitive in nature, producing "competitive networks" (Jackson & Buss, 1975; Buss & Jackson, 1979).

For "open-reef" assemblages (defined here as those reef species existing out in the open, as opposed to those in cryptic habitats) relatively little attention has been given to non-scleractinian components of the community and their contribution to reef diversity and dynamics.

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Despite this situation, it is becoming increasingly evident that non-scleractinian invertebrates such as encrusting sponges, zoanthids, ascidians, gorgonians and soft corals also compete aggressively for space in these open-reef habitats, and may often be the dominant space occupiers (Rutzler, 1970; Reiswig, 1973; Jackson & Buss, 1975; Karlson, 1980, 1983; Benayahu & Loya, 1981; Birkeland, *et al.*, 1981; Bunt, *et al.*, 1982; Sebens, 1982; Sheppard, 1982; Suchanek & Green, 1982; Sammarco, *et al.*, 1983).

Here we present a set of preliminary results from a study of such competitive interactions between scleractinian and non-scleractinian components of an open-reef habitat at a site in the U. S. Virgin Islands from depths of 10' to 120'. Specifically, we focus a) on the significant contribution made by demosponges to the species diversity of such an assemblage and b) on the quantitative and qualitative aspects of competition between demosponges and other encrusting colonial invertebrates, especially scleractinian corals.

METHODS

Data on depth distribution, species richness, percent cover and competitive interactions for encrusting colonial invertebrates were obtained with the aid of SCUBA during two NOAA NULS-1 Hydrolab Missions at Salt River Canyon, St. Croix, U.S. Virgin Islands ($17^{o}47'$N;$64^{o}45'$W): Mission I (=NOAA# 81-12) in Oct/Nov 1981 and Mission II (=NOAA# 82-12) in Aug/Sept 1982. See Suchanek (1983) for a location map. A fixed camera frame (quadrapod), outfitted with a Nikonos IV camera and 15mm lens (fully corrected for parallax), was used to photograph 0.5m^2 areas (85.75cm X 58.31cm) of coral reef substrate at 60', 90' and 120' depths. Random locations were chosen for the beginning of three contiguous transects (with 10 replicated photo-quadrats in each transect), yielding 30 possible photo-quadrats for each depth contour. Resulting color photographs (8" X 12") were analysed for percent cover of sessile organisms by tracing the outline of each species using a Houston Instuments HIPAD digitizer linked to an APPLE II computer; resolution using this technique was ca. 0.5cm of the original substrate. Because of equipment failures some quadrat-photos were lost, resulting in the following number of analysed replicate quadrats (and associated total areas) for Mission I: 29 @ 60' (=14.5m^2), 28 @ 90' (=14.0m^2), 27 @ 120' (=13.5m^2).

Quantitative and qualitative data on competitive interactions between encrusting colonial fauna and flora were taken at 10', 30', 60', 90' and 120' using a 1.0m^2 quadrat. A random point was chosen for the start at each depth and replicate quadrats were then placed contiguously along that depth contour (number of replicates at each depth = 30 @ 10', 30 @ 30', 20 @ 60', 14 @ 90' and 17 @ 120'). Each interaction was scored as a) an overgrowth encounter or b) a standoff.

RESULTS

Digitized photographs from Mission I demonstrate that sponges comprise the most diverse taxonomic group, representing nearly half (30/63) of all species recorded, as well as dominating the total species richness (SR) values at each depth (Fig. 1). The mean SR of sponges and corals in the photo-quadrats was not significantly different at 60', but sponges were significantly more diverse on the

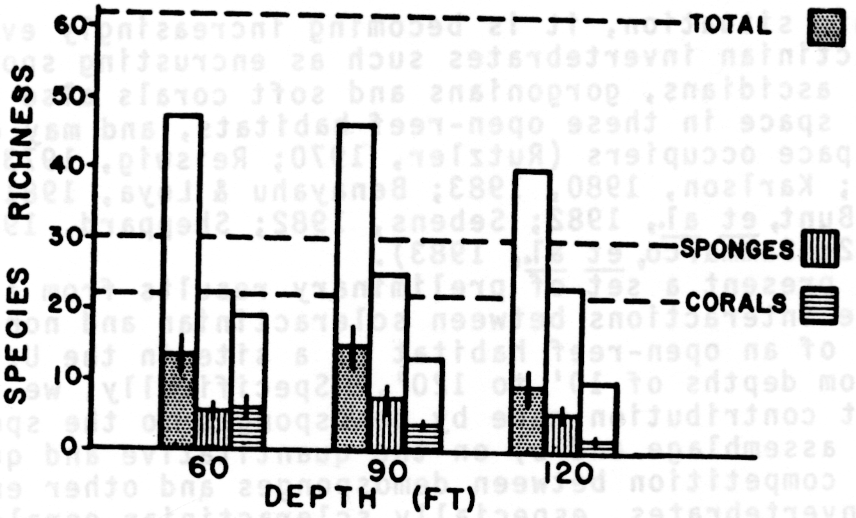

Figure 1. Species richness (SR) values obtained from digitized photo-quadrats of Mission I. Dashed lines = SR values pooled over all depths. Open histogram bars = SR values pooled for each depth. Shaded bars = mean SR values for $0.5m^2$ quadrats ± S.D. line.

deeper reefs (t-test: $p < .001$ at 90' (df=27) and 120' (df=26)). Interestingly, although the percent cover of sponges (8.0 ± 4.9 at 60', 19.1 ± 12.5 at 90' and 12.3 ± 9.5 at 120') and corals (18.3 ± 10.6 at 60', 23.8 ± 13.2 at 90' and 39.1 ± 23.1 at 120') was not significantly different at 90', corals occupy considerably more area than sponges at both 60' and 120' (t-test: $p < .001$).

The greatest number of both total interactions and overgrowths (per m^2) occurred at the 120' depth (Fig. 2). While the frequency of standoffs was relatively consistent over all depths, overgrowths increased to a mean of 9.0 ± 5.4 at 120'. The frequencies of overgrowths at 10', 60' and 90' were not significantly different from each other, but at 120' were much greater than at all other depths (t-test: $p < .01$ for 30'; $p < .001$ for 10', 60' and 90').

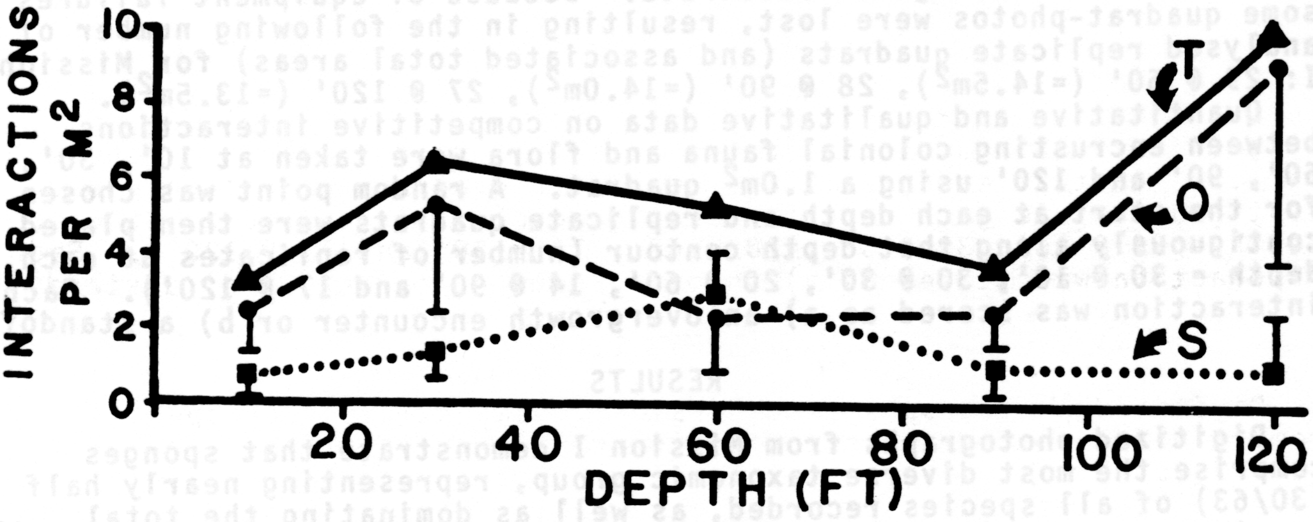

Figure 2. Number of interactions per m^2 (+ or - S.D. lines) versus depth. T = total number of interactions, O = overgrowths, S = standoffs.

The relative contribution of the three most frequent interactors is given in Figs. 3A & 3B. Clearly sponges were the most common aggressors, monotonically increasing both the frequency of their overgrowths and their relative standing as aggressors with depth (Fig. 3A). Corals on the other hand were by far the most frequently overgrown species, especially at depth (Fig. 3B). Several other taxonomic groups were also frequently involved in these overgrowth interactions. Their relative contributions are given below as the (% of all interactions as aggressors)/(% of all interactions as subordinates) for depths of 10', 30', 60', 90' and 120' respectively for each taxonomic group: millepore corals - 12/34, 16/5, 0/0, 0/0, 0/0; zoanthids - 12/0, 4/0, 0/0, 0/0, 2/0; ascidians - 1/1, 10/1, 6/0, 0/0, 1/3.

With increasing depth the relative importance of various aggressors changed substantially. At the shallowest depth studied, 10', the gorgonacean Erythropodium was the most dominant aggressor, but was never recorded as an aggressor in any observations below this depth. At 30' the demosponge Agelus was the most influential aggressor, initiating 25% of all aggressive interactions at that depth. Similarly, at 60', 90' and 120', those species that initiated 10% or greater of all overgrowths were demosponges; these genera are listed below with the percentage of the total overgrowth that they themselves initiated at each depth: 60' = Chondrilla (34%), Hemectyon (23%), Ircinia (11%); 90' = Chondrilla (40%), Hemectyon (23%), Verongia (11%); 120' = Verongia (34%), Chondrilla (26%).

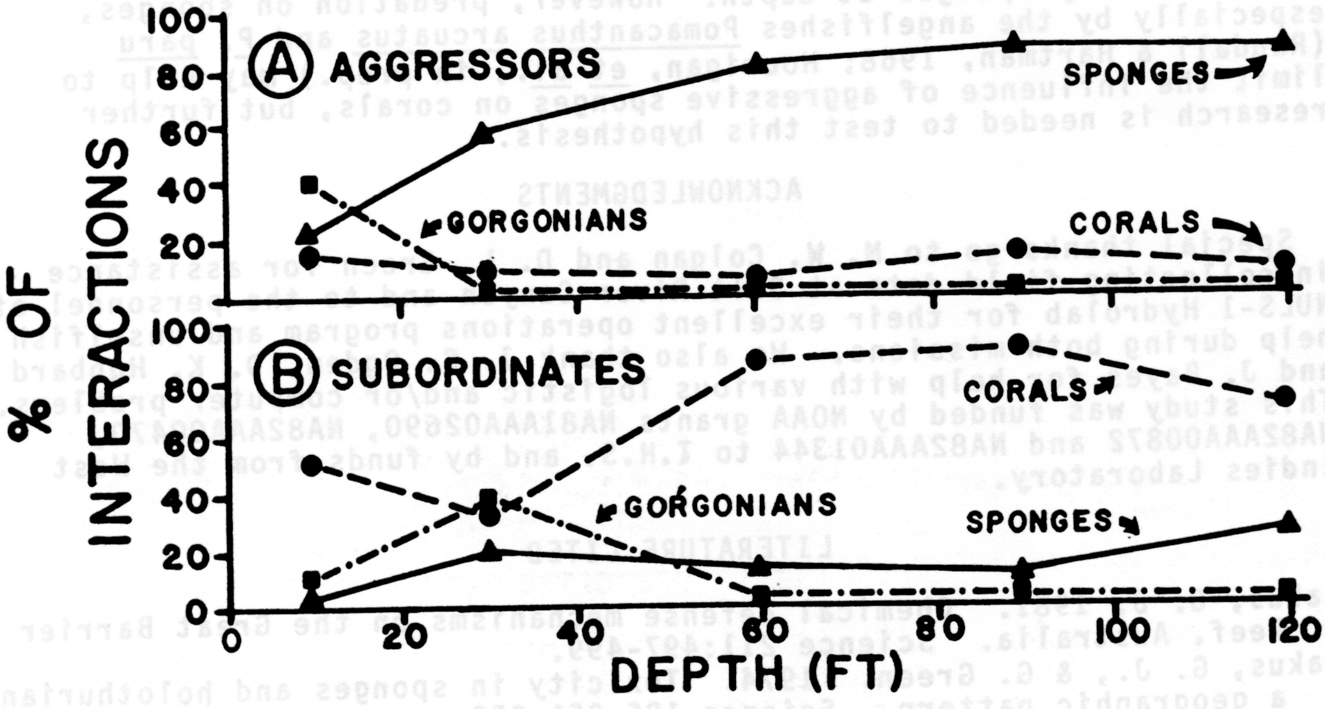

Figure 3. Percent of all interactions versus depth. Each taxonomic group was scored as either A) an aggressor (was overgrowing another species) or B) a subordinate (was being overgrown).

DISCUSSION

We present evidence here that demosponges play an important role in open-reef communities of the Caribbean, not only in terms of species richness, but also with respect to the intense competition for space that occurs in these environments. Demosponges are known from open-reef habitats (Reiswig, 1973), but until now virtually no quantitative data have been available on sponge/coral interactions from these communities. Although the relative aggressiveness of demosponges appears to be correlated with depth, reaching a maximum in our study at 90' and 120', it is interesting to note that coral cover increases from a mean of 18.3% at 60' to 39.1% at 120'. Nevertheless, the total species richness of sponges clearly overwhelms that of corals at 90' and 120'. The processes that permit both a high diversity of sponges and a high frequency of aggressive overgrowths on corals, while allowing such a high % coral cover, remain obscure at this time.

Mechanisms by which sponges can acquire, maintain and expand their space are likely to involve rapid growth rates and/or allelochemicals. Some sponges are known to possess virulent toxins (Bakus & Green, 1974), although these have typically been considered antipredatory in nature (Bakus, 1981). The use of allelochemicals by sponges for aggressive growth over corals has been suspected (Bryan, 1973; Jackson & Buss, 1975), but only recently has a sponge toxin that inhibits coral growth been identified (Sullivan, *et al.*, 1983).

Whether corals themselves use allelochemicals to ward off attacking sponges is uncertain, but this seems unlikely (or at least ineffective) because of the high frequency of aggressive overgrowths by sponges at depth. However, predation on sponges, especially by the angelfishes *Pomacanthus arcuatus* and *P. paru* (Randall & Hartman, 1968; Hourigan, *et al.*, in prep.) may help to limit the influence of aggressive sponges on corals, but further research is needed to test this hypothesis.

ACKNOWLEDGMENTS

Special thanks go to M. W. Colgan and D. L. Green for assistance in collecting field data at Salt River Canyon and to the personnel of NULS-1 Hydrolab for their excellent operations program and unselfish help during both missions. We also thank J. C. Ogden, D. K. Hubbard and J. Bayes for help with various logistic and/or computer problems. This study was funded by NOAA grants NA81AAA02690, NA82AAA00470, NA82AAA00872 and NA82AAA01344 to T.H.S. and by funds from the West Indies Laboratory.

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