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Relationship of Sponge Macrofauna with the Morphology of their Hosts in the North Aegean Sea

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Abstract

The associated macrofauna of four Aegean Sea sponge species (*Agelas oroides*, *Petrosia ficiformis*, *Ircinia variabilis* and *Aplysina aerophoba*) was compared. The total number of individuals and species was found to be related to sponge volume for all sponge species.

The associated macrofaunal weight per individual on all sponge species was negatively correlated with sponge volume. Sponge complexity, as measured by sponge surface area to biomass ratio, was not a consistent predictor of associated macrofauna abundance or diversity. Sponge macrofauna species were not host specific and their relative abundances differed among sponge species.

1. Introduction

Suggestions that habitat complexity can be quantified (HARROD & HALL 1962, DAHL 1973, VIRNSTEIN *et al.* 1984, HOEGH-GULDBERG 1988) have led many workers to investigate the effects of substrata complexity on the distribution and abundance of associated marine animals on their living hosts (EDGAR 1983, STONER & LEWIS 1985, HECK & WILSON 1987, LEWIS 1987).

Much work on habitat complexity as a predictor of the distribution and abundance of associated fauna has been done in seagrass beds (HECK & ORTH 1980, ORTH *et al.* 1984, LEWIS 1984, BELL & WESTOBY 1986, PETERSON & BLACK 1986), on macroalgae (LEWIS 1987), on sponges (WESTINGA & HOETJES 1981), on corals (McCLOSKEY 1970), and in mussel beds (JACOBI 1987). Various aspects of these substrata were used as measures of complexity: surface area (LEWIS 1987), biomass (HECK & ORTH 1980; STONER & LEWIS 1985), volume (WESTINGA & HOETJES 1981), surface area to biomass ratio (COULL & WELLS 1983, RUSSO 1989), and substrata density per sq. meter (CROWDER & COOPER 1982, STONER & LEWIS 1985, BELL & WESTOBY 1986). Work has been also done on the abundance and species composition of sponge associated fauna in general (PEARSE 1950, LONG 1968, FRITH 1975, RUTZLER 1976, COSTELLO & MYERS 1987) and specifically in the Aegean Sea (KOUKOURAS *et al.* 1985, VOULTSIADOU-KOUKOURA *et al.* 1987).

The purpose of this study was to identify and quantify the fauna associated with four sponge species *Agelas oroides* (SCHMIDT, 1984), *Petrosia ficiformis* (POIRET, 1789), *Ircinia variabilis* (SCHMIDT, 1864) and *Aplysina aerophoba* (SCHMIDT, 1862) found in the waters off the Chalkidiki Peninsula, N. Aegean Sea, Greece. The following hypotheses were tested: 1) That within a sponge species, the abundance and number of species of the associated fauna were directly related to host sponge volume, 2) that there were significant differences in the mean total abundances (per unit sponge volume) and the abun-

dances of selected abundant faunal taxa among sponge species, 3) that the species composition of associated faunal taxa is different among sponge species and 4) that among sponge species, the associated total faunal abundance and number of species were related to sponge complexity as measured by surface area to biomass ratio.

2. Methods and Materials

a) Sampling methods

The data used for this study were extracted from a complete inventory of sponge associated fauna made in 1985 by KOUKOURAS *et al.* The sponge samples were collected by diving in depths of 3 to 6 m, along the coast of Chalkidiki Peninsula (N. Aegean Sea). Sponges were removed from the bottom by covering them carefully with plastic bags underwater and detaching them with a knife. All samples were preserved in 10% formalin solution. Sponge volume was measured by sea water displacement. Sponge samples were cut into small sections (1–2 cm) along sponge canals and the fauna remaining inside the sponge was removed. The water and associated fauna remaining in the plastic bags were washed through a 1 mm sieve and macrofauna were sorted, counted, and identified to species level. Total weight (wet) was measured for each taxon.

A number of separate specimens ($n=7,8,13$ and 10) of four sponge species (*Agelas oroides*, *Petrosia ficiformis*, *Aplysina aerophoba* and *Ircinia variabilis*) were oven dried for 24 hrs at 90 °C. Immediately after removal from the oven, the samples were weighed and then immersed very quickly (1 to 2 secs) into a high viscosity liquid detergent. Quick immersion prevented the viscous liquid from entering the small pores of the sponge but allowed coverage of the external surface and internal surfaces of large canals. To measure sponge surface area the methods of HARROD & HALL (1977) as modified by COULL & WELLS (1983) were used. The difference in weight before and after detergent treatment was related to surface area by a linear algorithm calculated using known plastic card surface areas and weight differences before and after detergent treatment. The sponge surface area to biomass ratio was considered as complexity among sponge species. Within sponge species complexity was defined as volume.

b) Statistical Analysis

All data were tested for normality (Kolmogorov-Smirnov test) and oneway analysis of variance (ANOVA) was used to test for significant differences in means of selected variables among sponge species. All data were tested for homogeneity of variances (F max test) prior to analysis and, when necessary, corrections to heterogeneous variances were made by data transformation. Following ANOVA, comparisons of means among groups (sponge species) were tested with the Scheffe F -test (SOKAL & ROHLF 1981).

For each sponge species the relationships between the abundance (NI) and biomass (B) of associated fauna vs. sponge volume were estimated by linear regression. When regressions were significant, the slopes of the regression lines were compared using the Tukey method (SOKAL & ROHLF 1981). The degree of association among the variables was found using Pearson's product moment correlation coefficient.

Since the relationship between number of associated species (NS) and sponge volume (V) is curvilinear and of the form $Y = aX^b$, linear regression and correlation analysis were performed on the log transformed variables NS and V and best fit curves were estimated for each sponge species.

For each sponge species, surface area was related to biomass (SA vs. B) by linear regression. Slopes of the lines and mean SA/B ratios were tested for differences among sponge species and used as a complexity measure.

An overall comparison of associated faunal species composition among sponge species was made using cluster analysis (PIELOU 1984) using the Bray-Curtis similarity index. The Shannon-Weaver evenness index (J) was calculated to estimate the degree of equitability of species abundance.

3. Results

All data were normally distributed. There were significant differences in mean faunal abundance per unit sponge volume (NI/V) among sponge species ($F = 18.87$, $df = 55$, $p < 0.001$) (Figure 1). The sponge species pair *Ircinia variabilis* (*I.v.*) and *Aplysina aerophoba* (*A.a.*) were similar in mean NI/V . The sponge species pair *Petrosia ficiformis* (*P.f.*) and *Agelas oroides* (*A.o.*) were also similar in NI/V . The sponge pair *I.v.*-*A.a.* had significantly higher mean NI/V values than the sponge pair *P.f.*-*A.o.*. There were no significant differences in mean faunal biomass per unit sponge volume (B/V) among sponge species (Figure 2).

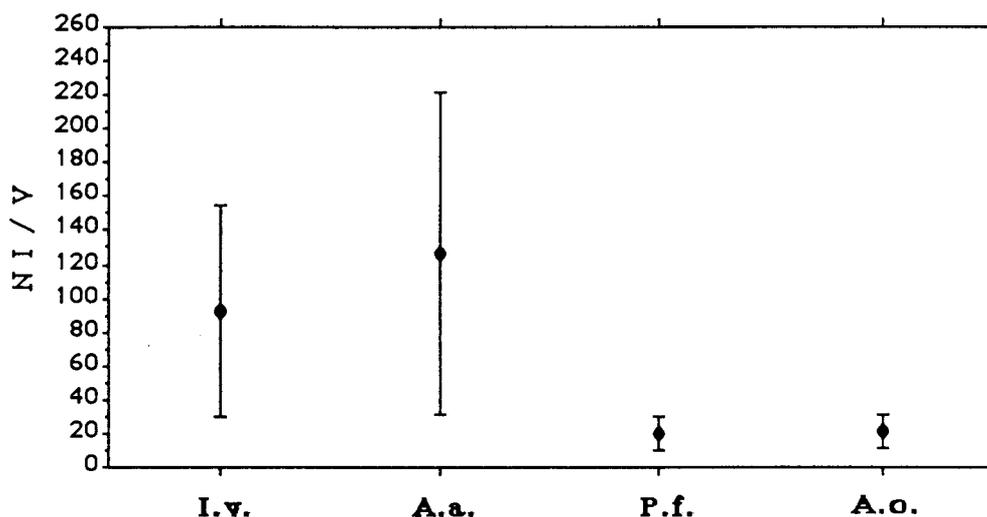


Figure 1. Mean faunal abundance (NI) per unit sponge volume (V) among sponge species (*I.v.* = *Ircinia variabilis*, *A.a.* = *Aplysina aerophoba*, *P.f.* = *Petrosia ficiformis*, *A.o.* = *Agelas oroides*). (± 1 S.D.)

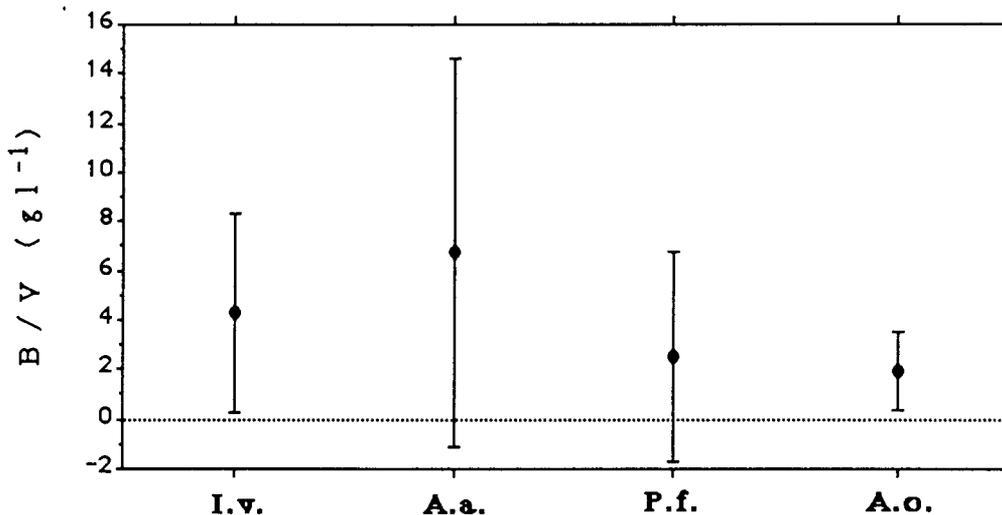


Figure 2. Mean faunal biomass per unit sponge volume (B/V) among sponge species. (± 1 S.D.)

All the correlations between NI and V among the four sponge species were significant ($p < .05$) and positive (Figure 3). Within each sponge species the number of individuals was directly related to sponge volume. There were significant ($p < .05$) differences in

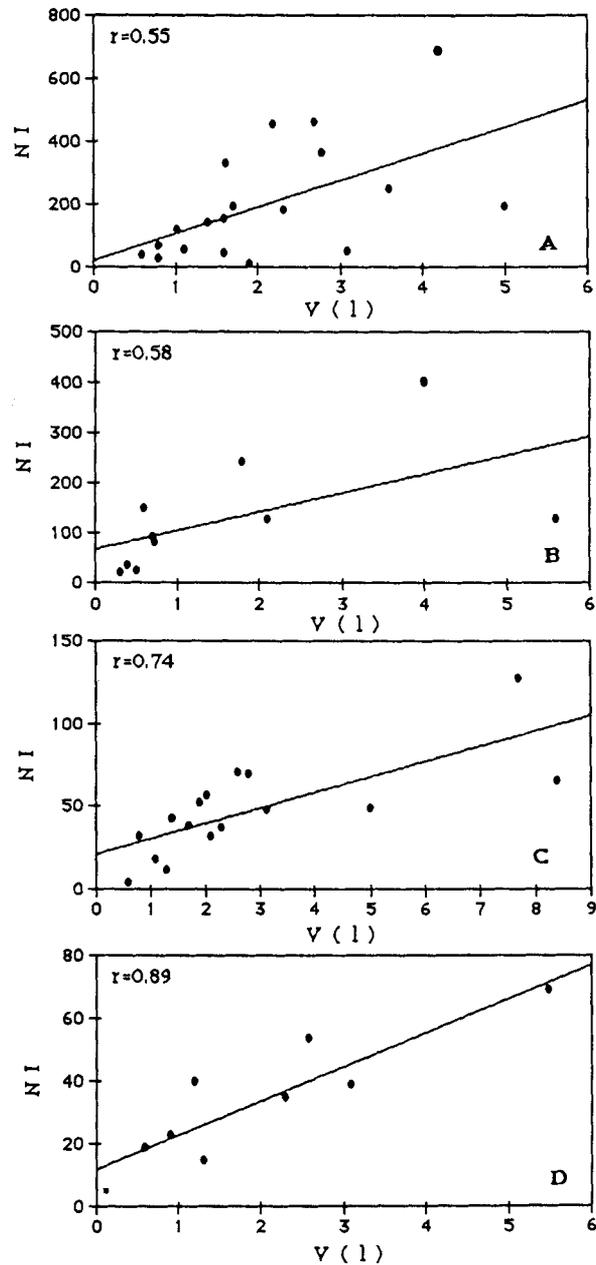


Figure 3. Regression of associated faunal abundance (NI) with sponge volume (V) for: *Ircinia variabilis* (A), *Aplysina aerophoba* (B), *Petrosia ficiformis* (C), *Agelas oroides* (D).

slopes of regression lines (NI vs. V) among sponge species. The slopes of the lines for $I.v.$ and $A.a.$ were similar, as were those for $P.f.$ and $A.o.$. The regression lines for sponge pair $I.v.-A.a.$ had significantly greater slopes than those for the sponge pair $P.f.-A.o.$. The associated faunal abundance (NI) increases faster with change in sponge volume (V) for the sponge pair $I.v.-A.a.$ than for $P.f.-A.o.$.

All regression lines and correlations of $\log NS$ vs. $\log V$ for all four sponge species were significant ($p < .05$). The number of associated faunal species was proportional to sponge volume. Slopes of regression lines were significantly different ($p < 0.05$). The sponge species $I.v.$ and $A.a.$ which had similar slopes supported more faunal species per unit volume, than the sponge species $P.f.$ and $A.o.$ (Figure 4).

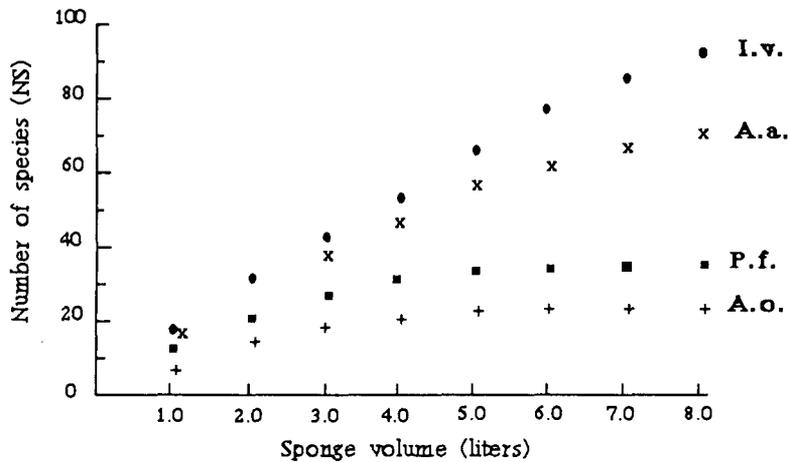


Figure 4. Number of faunal species associated with the four sponge species (best fit curves to the data).

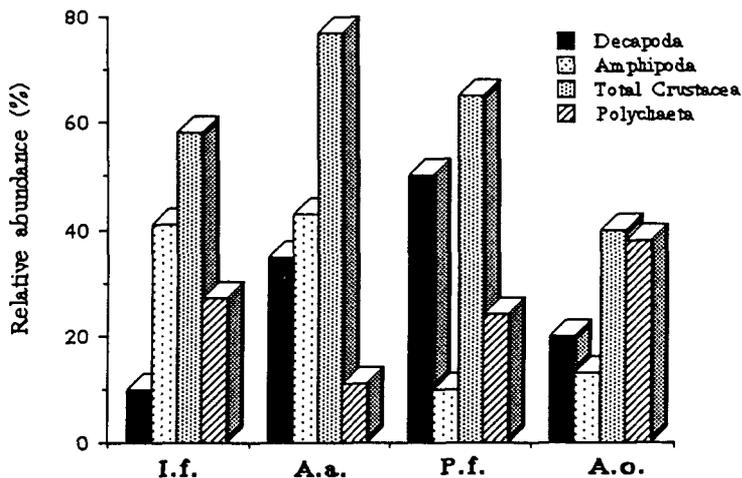


Figure 5. Relative abundance of the most abundant taxa on the four sponge species.

Mean faunal biomass per individual (B/NI) was similar among sponge species *I.v.*, *P.f.* and *A.a.* However, *A.o.* supported significantly heavier animals than the other sponge species ($F=5.5$, $df=51$, $p<.05$). There were no significant regressions of B vs. sponge volume. Fauna biomass was not related to sponge volume for any of the four sponge species. Biomass per individual B/NI were significantly negatively correlated with sponge volume for all sponge species (*A.a.*: $r=-.68$, *I.v.*: $r=-.54$, *P.f.*: $r=-.65$, *A.o.*: $r=-.71$, $p<.05$).

The relative abundances (mean dominances) of associated faunal species were different among sponge species (Figure 5). Polychaetes dominated on *A. oroides* whereas on *I. variabilis*, *A. aerophoba* and *P. ficiformis* crustaceans (especially amphipods) were most abundant. There was a significant negative correlation ($r=-0.624$, $p<0.05$) between amphipod and polychaete abundances when all data for all sponge species were pooled.

Table 1 lists the abundance (per unit sponge volume) for the 25 most abundant species found on their sponge hosts (KOUKOURAS *et al.* 1985). There were significant differences

Table 1. List of selected abundant fauna associated with 4 sponge species; numbers per liter.* (*A.o.* = *Agelas oroides*; *P.f.* = *Petrosia ficiformis*; *I.v.* = *Ircinia variabilis*; *A.a.* = *Aplysina aerophoba*)

Sponge species	<i>A.o.</i>	<i>P.f.</i>	<i>I.v.</i>	<i>A.a.</i>
Polychaeta				
<i>Ceratonereis costae</i> GRUBE	1.23	0.33	4.35	1.63
<i>Dasychone bombyx</i> (DALYELL)	0.21	0.45	2.31	0.54
<i>Harmothoe spinifera</i> (EHLERS)	0.21	0.02	1.31	0.74
<i>Lysidice ninetta</i> AUDOUIN & MILNE EDWARDS	0.00	0.11	1.06	0.59
<i>Nereis zonata</i> MALMGREN	0.00	0.00	2.99	1.43
<i>Potamilla neglecta</i> (SARS) (= <i>P. torelli</i>)	1.55	0.20	3.17	0.54
<i>Potamilla remiformis</i> (MÜLLER)	0.27	0.27	0.78	0.00
<i>Serpulla vermicularis</i> LINNAEUS	0.48	0.36	0.25	0.39
<i>Trypanosyllis zebra</i> (GRUBE)	0.21	0.42	0.53	0.74
Sipuncula				
<i>Aspidosiphon mülleri</i> DIESING	0.16	0.02	1.40	0.34
<i>Phascolosoma granulatum</i> (LEUCART)	1.07	0.29	1.71	0.25
Amphipoda				
<i>Amphithoe ramondi</i> AUDOUIN	0.00	0.11	5.05	0.30
<i>Colomastix pusilla</i> GRUBE	1.60	0.58	0.23	27.93
<i>Elasmopus posillimanus</i> (BATE)	0.00	0.00	1.58	0.30
<i>Elasmopus rapax</i> COSTA	0.00	0.07	1.11	0.39
<i>Gammaropsis maculata</i> (JOHNSTON)	0.05	0.07	1.18	0.34
<i>Leucothoe spinicarpa</i> (ABILDGAARD)	0.48	0.47	25.73	5.22
<i>Maera inaequipes</i> (COSTA)	0.00	0.25	0.88	0.30
<i>Microdeutopus stationis</i> DELLA VALLE	0.00	0.00	0.90	0.44
Decapoda				
<i>Alpheus dentipes</i> GUERIN	0.96	1.58	3.37	7.04
<i>Athanas nitescens</i> (LEACH)	1.02	0.67	0.68	2.66
<i>Cestopagurus timidus</i> (ROUX)	0.64	2.32	1.63	6.85
<i>Thorulus cranchii</i> (LEACH)	0.05	1.12	0.99	9.61
Mollusca				
<i>Hiatella arctica</i> (LINNAEUS)	1.50	0.22	4.52	0.74
Echinodermata				
<i>Ophiothrix fragilis</i>	0.96	0.51	2.46	4.14
Total volume sampled (<i>I</i>):	18.7	44.8	39.8	20.3
<i>NI</i> per unit volume:	16.7	16.9	96.4	91.5
Total number of species:	61.0	91.0	151.0	104.0
evenness of species (<i>J</i>):	0.78	0.81	0.99	0.64

*) Based on the entire inventory of species and abundance from KOUKOURAS *et al.* 1985.

in the mean abundance N/V of the most abundant associated species among host sponges (ANOVA, $p < .05$). The sponge species pair *I.v.*-*A.a.* supported, in some cases, more abundant faunal species than the sponge pair *P.f.*-*A.o.* However, in general, there was no predictable pattern of faunal abundance among sponge species. Some taxa were found associated only with the sponge species pair *I.v.*-*A.a.*, e.g. the polychaete *Nereis zonata*, the amphipods *Elasmopus pocillimanus* and *Microdeutopus stationis* and the mollusk *Musculus costulatus*. The amphipod *Leucothoe spinicarpa* was significantly more abundant on sponge *I.v.* than on the other 3 sponge species. The amphipod *Colomastix pusilla* had significantly highest abundance on sponge *A.a.*

Based on the entire list of species from all samples (KOUKOURAS *et al.* 1985), total abundances of fauna per total sponge volume were higher for *I.v.* and *A.a.* than for *P.f.* and *A.o.* The evenness (J) of species abundance distribution was lower on the former pair (Table 1) probably because of the very high abundances of the amphipod species *L. spinicarpa* ($n = 1024$) on sponge *I.v.* and *Colomastix pusilla* ($n = 567$) on sponge *A.a.* The total number of species present, from highest to lowest, was *I.V.* (151), *A.a.* (104), *P.f.* (91) and *A.o.* (61).

According to the species composition of the associated fauna the examined sponge species can be generally separated into two groups (Figure 6). Sponge species pair *I.v.*-*A.a.* is relatively different in associated faunal species composition than species pair *P.f.*-*A.o.* The sponge species within each pair support similar taxa.

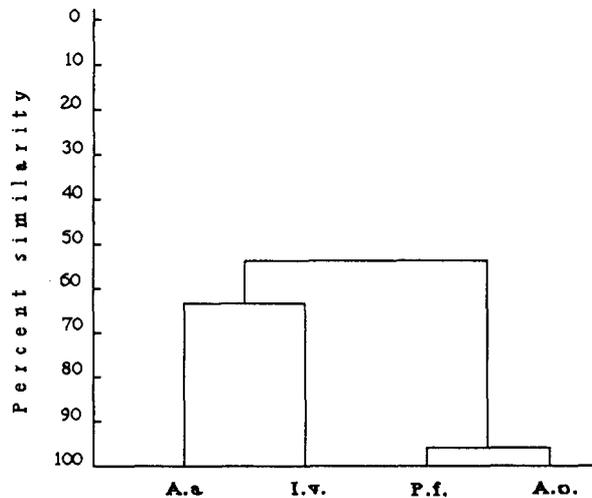


Figure 6. Dendrogram of similarity of species composition of the fauna associated with the four sponge species.

Sponge surface area (SA) was significantly positively correlated with sponge biomass (B) for all sponge species ($p < .05$). The slopes of the regression lines of SA vs. B were significantly different among sponge species ($F = 47.9$, $df = 4, 30$, $p < .01$) (Figure 7) as well as the means (sqrt transformed) of SA/B ($F = 33.46$, $df = 30$, $p < .001$) (Table 2). Slope comparisons showed the order of sponge complexity to be $I.v. > A.a. = A.o. > P.f.$ Sponge complexities and qualitative characteristics of the four sponge species are presented in Table 2.

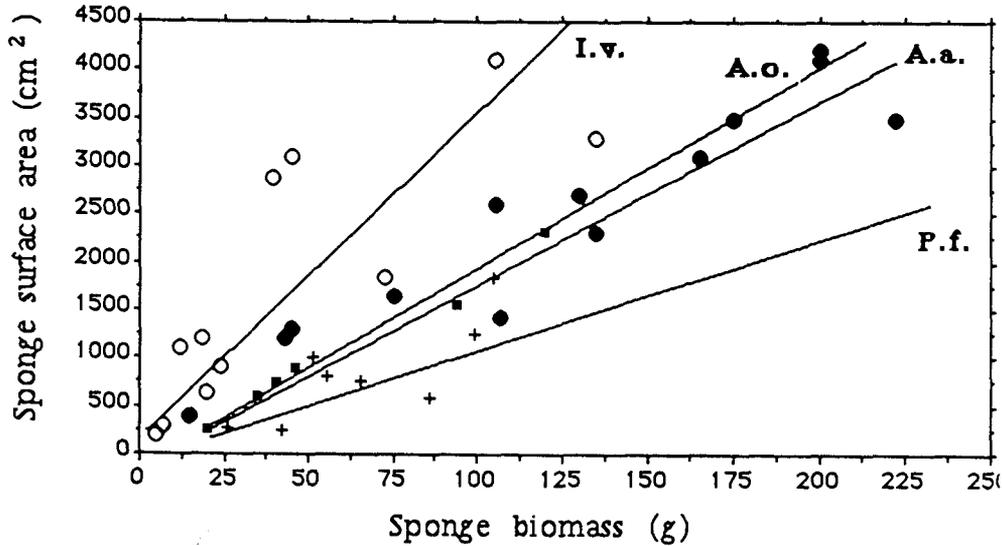


Figure 7 Sponge surface area (*SA*) vs. sponge biomass (*B*) for the four sponge species.

Table 2. Sponge characteristics and complexity.

Species	Form	Consistency	Skeleton	Mean <i>SA/B</i> ($\text{cm}^2 \text{g}^{-1}$) (95 % confidence intervals)	Number of specimens
<i>A. aerophoba</i>	digitations 1–2 mm thick, penetrated by elastic canals (7–10 mm in diam.) terminating with an oscule at top	leathery;	spongine network with fibers equal to one another	21.7 (± 2.7)	13
<i>I. variabilis</i>	massive, lobate with oscules at lobe summits	tough; spongy	reticulate spongine skeleton; primary fibers full of foreign inclusions	58.4 (± 17.6)	10
<i>P. ficiformis</i>	massive, flattened or with long branches, anastomose forming broad cavities on sponge species	very firm; brittle	reticulate skeleton formed of multi-spicular tracts	10.5 (± 2.2)	8
<i>A. oroides</i>	massive, lobate with oscules at lobe summits	toug; elastic	siliceous spicules embeded in spongine fibers	17.1 (± 2.8)	7

4. Discussion

Faunal abundance and numbers of species were related to sponge volume. The number of associated faunal taxa increased asymptotically with sponge volume as predicted by the island habitat hypothesis of MAC ARTHUR (1972). These relationships were also observed in a study of fauna associated with the sponge *Sphaciospongia vesparia* (WESTINGA & HOETJES 1981). However, WESTINGA and HOETJES found a significantly high correlation ($r = 0.99$) between faunal biomass and sponge volume. We found no relationship between biomass and sponge volume for any of the four sponge species studied. The habitat space may be fully utilized by associated fauna and there may be competition for space and food resources. The weight per individual of associated fauna decreased with increasing sponge volume. Animal size may be density dependent and, if total food resources are constant and animal abundance increases with habitat volume, then the weight per individual may decrease as competition for food or space increases. However, there is not enough evidence from this study to support these hypotheses.

No abundant faunal species was limited in distribution to one sponge species and their relative abundances differed significantly among sponge species. These results agree with studies of associated fauna on other living substrata with varying morphologies (e.g. algae, seagrass) WEISER 1952; IMADA *et al.* 1981; STONER 1983; LEWIS 1984). The sponges *I. variabilis* and *A. aerophoba* supported similar taxa as did *P. ficiformis* and *A. oroides*. When taken as pairs they supported dissimilar taxa. The qualitative and quantitative rationale for this is uncertain except that the sponge surface area to biomass ratios among these sponge pairs were different. None of the associated fauna were host obligatory and most were found on all four sponge hosts. A few taxa were found on some sponge species (e.g. *Nereis zonata* on *I. v.* and *A. a.*) but were absent from the others. The high abundance of the amphipod *Leucothoe spinicarpa* found associated with the sponge *I. variabilis* may be due to parasitism (ARNDT 1933; ORTIZ 1975) or to the fact that this species completes its life cycle within its host (ORTIZ 1975). This amphipod was found on all four sponge species.

Some animals because of their morphology, may conform better to some substrata than others (CAINE 1978). The high abundance of the amphipod *Colomastix pusilla* on the sponge *A. aerophoba* may reflect an interaction with sponge morphology. *A. aerophoba* has small openings and canals which can prevent larger animals from entering but may be suitable for smaller ones such as *C. pusilla*. *A. oroides*, a sponge with large canals and openings, supported an abundant population of large polychaetes and relatively few amphipods. The biomass per animal was highest on this sponge species and polychaete abundance was negatively correlated with amphipod abundance on all four sponge species. This may indicate interference competition and/or predator – prey interaction between the two taxa.

Generally, among sponge species, there was no direct relationship between associated fauna abundance or numbers of species and sponge complexity. Although the most complex sponge *I. variabilis* supported the most individuals (per unit volume) there were no clear relationships of abundance with complexity among the remaining sponge species. For example, the sponge *P. ficiformis*, which had the lowest complexity, supported the same number of animals as *A. oroides*. The sponge species *A. aerophoba*, equal in complexity to *A. oroides* supported 5 to 6 times more individuals. The more complex sponge species pair *I. v.* and *A. a.* supported more total numbers of faunal species than the other sponge species, however *P. ficiformis*, the lowest in complexity, supported more species than *A. oroides*. The results showed that complexity, as measured by surface area to biomass ratio, does not, alone, completely or adequately predict the patterns of distribution of associated fauna on the four sponge species studied.

Differences in associated faunal abundance and number of species among sponge

hosts of differing morphologies, chemical structures and complexities may be, to some extent, a function of biotic interactions among the fauna within each sponge species. Differences in habitat complexity may mediate predation (NELSON 1981; RUSSO 1987). Competition can also affect the associated fauna community dynamics (GUNNILL 1982; EDGAR 1983). Other forces may regulate the distribution and abundance of associated fauna. Among sponge species allelochemical attractants or defenses may interact with associated fauna (HAY *et al.* 1987; STEINBERG 1984). The patchiness in food quality and quantity on living substrata can affect the faunal community (BELL *et al.* 1984). Until more work is done on the importance of these factors and, until complexity is better defined, the role of sponge host habitat complexity in structuring associated faunal communities will remain unclear.

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