ECOLOGICAL STUDY OF THE DECAPOD CRUSTACEANS COMMENSAL WITH THE BRANCHING CORAL *POCILLOPORA MEANDRINA* VAR. *NOBILIS* VERRILL

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ABSTRACT

A quantitative study of the decapod crustacean community commensal with the coral Pocillopora meandrina var. nobilis Verrill was undertaken and was accomplished through an analysis of communities collected in coral heads in Kaneohe Bay, Oahu. The coral head microhabitat was described and analyzed. The community was described and its relationship to the coral head habitat defined. It was found that community composition was affected by coral head size and that relative composition of the communities changed as the coral heads increased in size. Through stomach contents analysis and trophic behavior experiments the commensals were found to utilize the coral as a source of food, primarily by feeding on material caught on the coral. A correlation between the total biomass of the crustacean community and the surface area of the coral heads in which they were collected was found, suggesting that the community is limited by the amount of surface area of a coral head. This may reflect the amount of food available to the symbionts. There was no good correlation between surface area of the corals and the biomass of the individual components of the community, indicating that other factors, such as the behavioral peculiarity of pairing and interspecific competition probably determine the exact composition of the community that a coral head can support.

It was concluded that the crustaceans studied were true commensals with the coral, and that the commensal association involves the host providing a source of food as well as protection for the symbionts.

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I. Introduction

The intimate association of decapod crustaceans with living coral is conspicuous among the numerous cases of associations between different species of animals of coral reefs. The term commensalism, which refers to a close association between two species of animals where the association is clearly to the advantage of one of the members, the symbiont, without seriously inconveniencing or harming the other, the host (Dales, 1957), is generally applied to this association (Caullery, 1952). This classification is only tentative since the exact nature of the relationship between the crustacean symbionts and the host coral has never been determined.

Most of the literature dealing with marine commensals is descriptive, and has been reviewed by Caullery (1952), Dales (1957), and others. It deals mainly with the identification of symbionts and their hosts. A certain amount of more detailed work has been done on ascertaining the relationships of the symbionts and hosts. A few well known examples are the work of Gohar (1934), Herre (1936), Gudger (1947), Davenport and Norris (1958), and others on the relationship of fishes of the genus *Amphiprion* and large sea anemones. Another example is the extensive research as reviewed by Caullery (1952) and most recently studied by Ross (1960) on the associations of various species of anemones and hermit crabs. Another category of research, which is very limited, concerns fundamental principles in commensal relationships. Most of this work has been carried out by Davenport (1950 et seq.) on physiological and behavioral problems in commensalism.

Very little research, other than taxonomic investigations, has been published on decapod crustaceans commensal with corals. Some descriptive work on one species of commensal crustacean, the gall crab, Haplocarcinus marsupalis, Stimpson, is that of Potts (1915a), Hiro (1937) and MacNamee (1961). The only work on the community of commensal crustaceans in corals is that of Patton (1963), who studied the species of corals that were hosts to commensal crustaceans and the north-south variations in these associations on the Great Barrier Reef in Australia, and more recently a paper by Garth (1964) in which he determined which species of crabs were true commensals in different species of corals on Eniwetok Atoll. To date there has been only one quantitative study of commensal organisms: Gray (1961) worked on the changes in abundance of crabs commensal with sessile polychaetes.

The author could find no published information on factors limiting the commensal organisms on their specific hosts. In this study an attempt was made to determine the factors imposed by the host limiting its decapod crustacean commensal community. The host coral was viewed as a microhabitat, which is both a physical and biotic component of the symbionts' environment, thus both the physical and biotic roles of the coral were considered. Also, because the association involves a community of several species of crustaceans, intra and interspecific interactions of the symbionts were taken into account. An attempt was made to determine whether or not these complicating factors may affect the quantitative relationship of the community to the coral head microhabitat. Two questions arise: are the associated decapod crustaceans true commensals with the coral, and what is the extent of the interaction of the

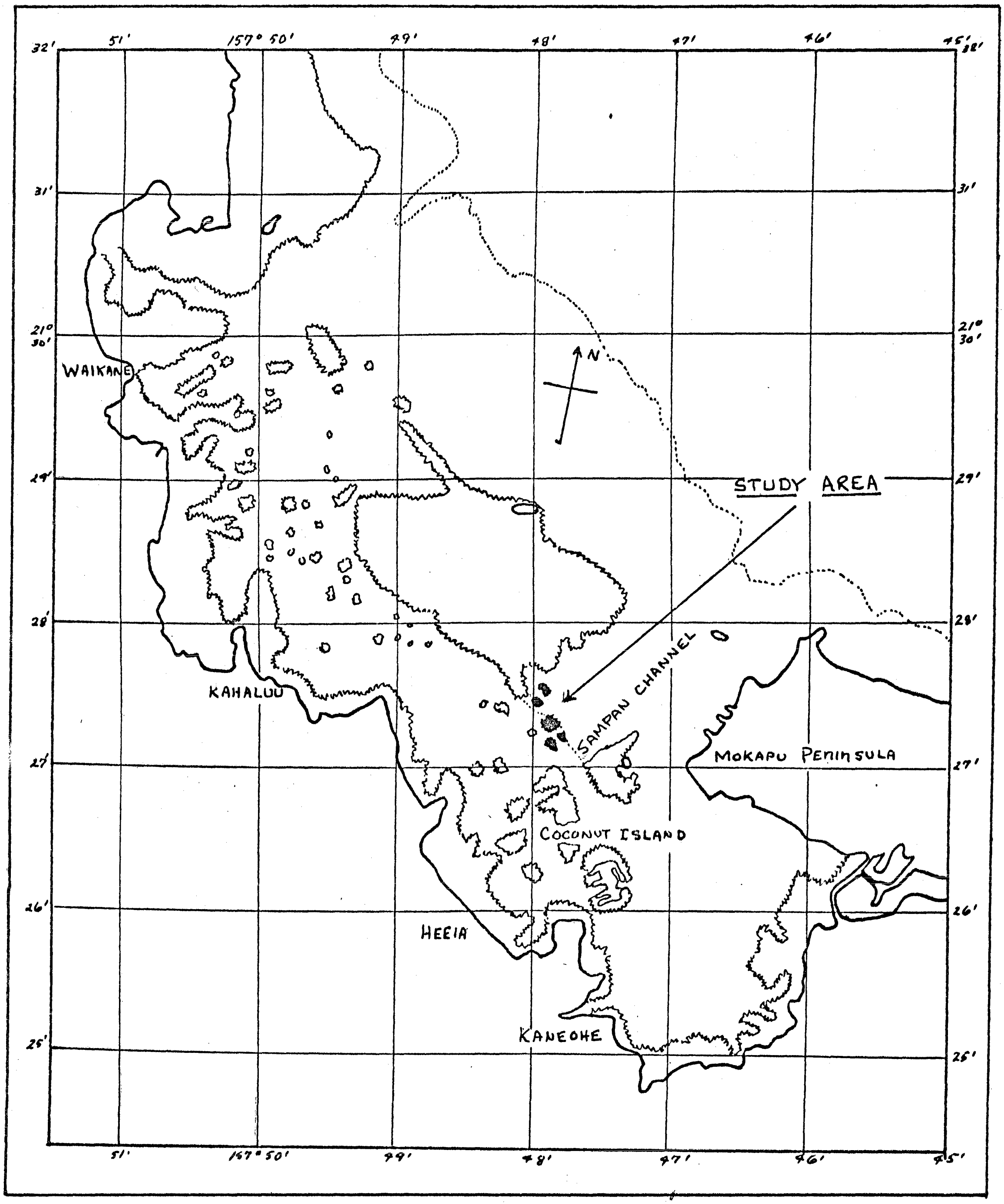

Figure 1. Map of Kaneohe Bay, Oahu, showing the five reefs where the study was made (shaded areas). (from Tester, 1951).

symbionts with the host coral? Answers were sought through an anlysis of the commensal association as it occurs in the field. Experiments supporting these data were also undertaken.

II. Characterization of the Study Area

A. Locations.

Samples of coral heads and associated communities were collected from a group of five adjacent patch reefs on the north side of the Sampan Channel in Kaneohe Bay, Oahu. The collecting site is illustrated in Figure 1.

B. Description of habitat.

The reefs are all small, the largest being approximately 350 meters at its greatest width. Three of the reefs slope from a depth of about one meter on the leeward (southwest) side to a depth of about three meters on the windward (northeast) side at low water. The other two reefs have a more or less uniform depth of about two meters. The substratum is generally sandy with patches of dead and living corals. On the sloping reefs there are large areas on the shallower side which are covered with patches of *Sargassum*, surrounded by sandy areas in which there are no living corals. This grades into an area of dead coral and finally in deeper water is a region of extensive patches of living coral, some dead coral and little *Sargassum*. The dominant coral species on these reefs are *Porites lobata* Dana and *P. compressa* Dana with *Pocillopora meandrina* var. *nobilis* Verrill, *P. ligulata* Dana, and *P. damicornis* (Linnaeus) commonly represented. The two reefs of uniform depth are much like the windward side of the other three reefs, except that the sandy areas on the former are more extensive. *Pocillopora meandrina* is common on these reefs and heads are found unattached on sandy substratum, attached to mounds of dead coral, and occasionally wedged into patches of living *P. compressa*. Smaller heads of this species are not common on these reefs.

Some additional collections of commensals which were used for stomach contents analysis and trophic behavior experiments were made from the reef immediately adjacent to the Waikiki facility, Hawaii Marine Laboratory.

III. The Coral *Pocillopora meandrina* as a Microhabitat

A. Presence of commensals.

A distinct assemblage of crustaceans and other animals representing numerous species and several genera is found only in living colonies of corals of the genus *Pocillopora*. Since these animals are never found in other microhabitats or even in dead colonies of *Pocillopora*, some form of close association between the animals and the living coral is indicated. Contrasted with these animals is another group which is not specific to living coral heads, but is only occasionally found in them, and is found in other habitats. This includes animals which utilize the crevices and holes in the nonliving base of the coral colony. It is conceivable that these animals are utilizing the coral for shelter or possibly are predators on the coral or the symbionts. In the study only the former group of animals, which are commensals on living coral heads, was considered.

In Hawaii three species of *Pocillopora* commonly found on shallow water reefs are *P. meandrina* var. *nobilis*, *P. ligulata*, and *P. damicornis*. All three species have associated with them communities of commensal decapod crustaceans. The communities are almost identical in *P. meandrina* and *P. ligulata*, which are similar in structure and maximum size attained. They consist of the same species of animals and these attain similar maximum sizes. On the other hand, in *P. damicornis*, which differs in structure from the other two, the communities are made up of only a few of the species found in the other two corals and the maximum sizes of individuals are much less.

Aside from the biotic factors imposed by the living coral colony, and by the social interactions of the members of the community, the physical factors imposed by the coral head microhabitat may be important in limiting the commensal community. The interactions of all of these factors probably determines the exact composition of the community in any coral head, but the affect of the coral as a physical entity, with consideration of its biotic role, is probably of primary importance in determining the size or biomass of the whole community found in it. In attempting to define the physical factors which limit the community, it was necessary to first make an analysis of the properties of the coral which relate to these limiting factors. One would expect the coral head microhabitat to be uniform in general configuration since coral colonies are living, and it is generally thought that the form of the colony is genetically fixed for any one species of coral. It is true that this is modified by environmental conditions such as currents, depth, turbitity, et cetera, giving rise to various varieties of a species. It may be assumed that colonies from the same general habitat which are all subjected to the same environmental conditions are similar in form. This assumption will be examined in the analysis of the coral.

B. Description of coral.

In order to give some insight into the nature of the coral as a habitat, a brief description of the coral head configuration is necessary. Colonies of *Pocillopora meandrina* var. *nobilis* Verrill form large, round-topped or hemispherical clumps. It is a ramose coral with typically few branches that are nearly equal in length. The branches are massive and have the appearance of being broadly flattened at the base. Some characteristics of the coral and the branches are illustrated in Figure 2. Terms used in the description are also elucidated. A branch typically has two or three primary bifurcations which occur near to the base and up to ten or more secondary bifurcations on the distal portion of the branch. The different portions of the branches will be referred to as primary, secondary or tertiary branches of the coral head. At each division of the branch, the plane of the bifurcation is positioned at approximately right angles to the plane of the parent branch. The more distal portions of the branches, whether secondary or tertiary, are smaller in width but are similar in thickness. Thus the tips of the branches have an elliptical shape, rather than being broadly flattened as is the case of the primary branches. It can be seen that the alternate orientation of the secondary and tertiary branches at right angles to the parent branch, from the standpoint of the commensals, affords a maximum protection for the area at the base of the coral

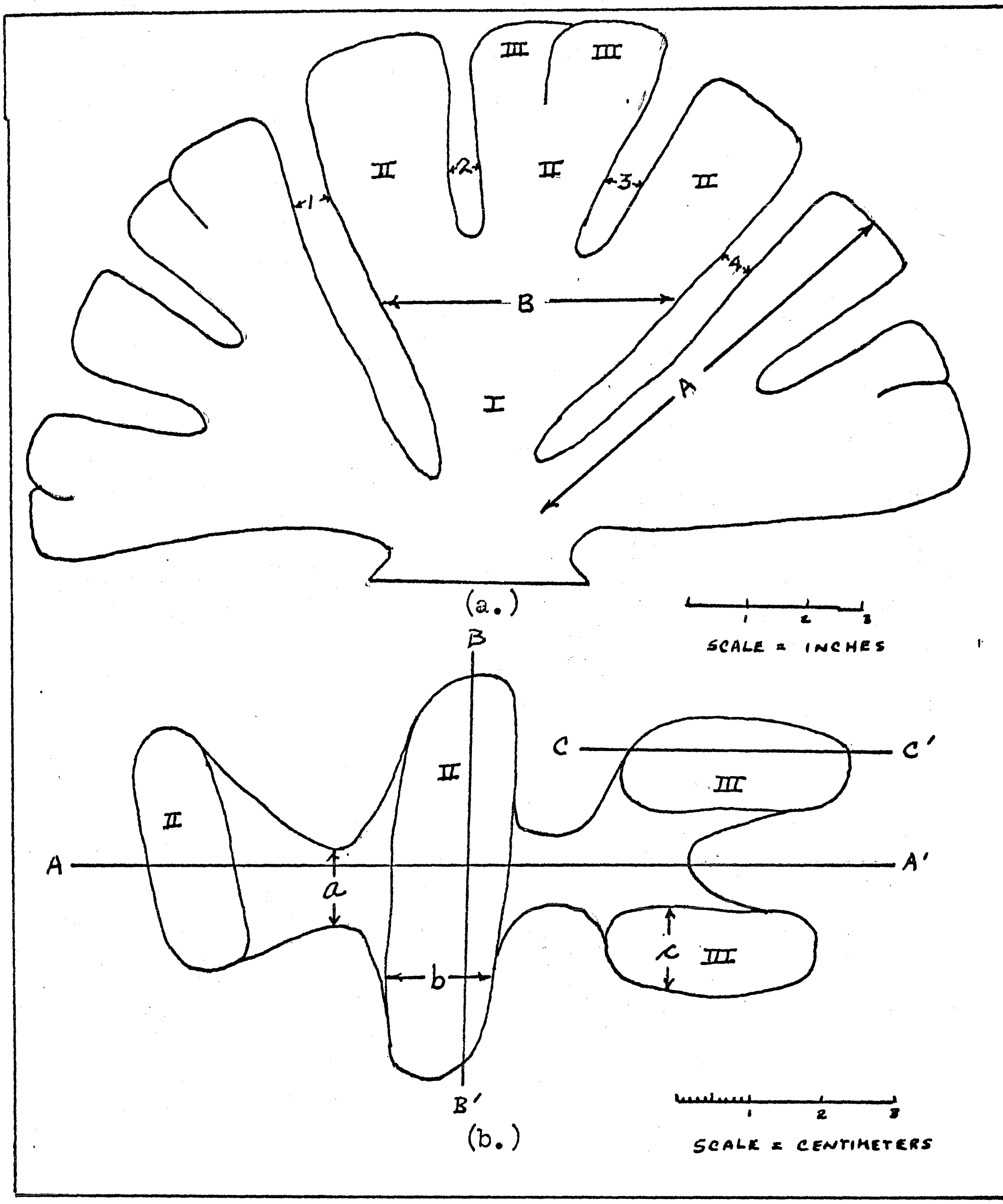

Figure 2. Schematic drawing of coral illustrating some facets of colony and branch formation. a).Cross ection of a coral head, showing primary (I), secondary (II), and tertiary (III) branches. Distances between branches (1,2,3,4) are approximately equal. b) View of single branch from tip looking toward base. Widths of branches (a,b,c) approximately equal. Planes of branches A-A' (I), B-B' (II) and C-C' (III) oriented at alternating right angles. The distance "A" referred to as length, "B" as width, and "a,b,c," as thickness of the branch.

head. It appears that there are two parameters affecting the growth of the branches which are relatively fixed: (1) the thickness of the branches (the narrowest diameter in cross section) and (2) the minimum distance between adjacent branches. As a branch grows in length its thickness remains constant but its width increases, giving it a flattened appearance. This widening continues as the branch grows outward until at the lateral margins it reaches some critical distance from the adjacent branches; at this point the branch ceases to expand in length and width and it begins to bifurcate along its tip. In small heads a relatively similar number of primary branches are present as in larger heads, but they are not bifurcated into secondary and tertiary branches, are less flattened in appearance, and are much shorter. It appears that the total number of primary branches in any coral colony is fixed at an early stage in colony formation and is probably influenced by environmental as well as genetic factors. The number of branches at the periphery of any coral head depends on the size of the colony, which would reflect whether any, one or two stages of bifurcation had occurred. Thus though a very large head of _P. meandrina_ looks on the outside like it has many more branches than a small head, on final analysis it has about the same number of primary branches which in the course of growth have undergone numerous divisions. The conclusion made upon examining a number of coral heads of different sizes was that small heads are not miniatures of larger heads, but that coral heads of different sizes are different in a quantitative rather than a qualitative manner.

The surface of the branches are smooth at the base but distally are covered with numerous knobs or verrucae, which greatly increases the surface area, thus the number of polyps.

The base of the coral, which is smooth in texture, is compact and tends toward being spherical. It usually contains numerous crevices and tunnels lined with living coral, formed by the fusion of smaller branches around the periphery of the base.

It can be seen that further divisions of types of habitats can be made within the general distinction of the coral head microhabitat. The surface of the branches, both distal and basal, afford one type of habitat, the channels and interstices between the branches on the base of the coral another, and the small tunnels and crevices in the base of the coral a third. Thus a variety of habitats are present within the coral head itself.

The color of the live coral, which may be important in regard to the coloration of the commensals, is a yellowish brown, with some heads tending toward a reddish-rose color.

C. Coral analysis.

The coral studied has a wide range in size distribution. Coral colonies range from those consisting of a few polyps measuring less than a millimeter in diameter to colonies with many thousands of polyps which may be half a meter in diameter. Because the heads are three dimensional and of irregular shape, linear measurement is not an accurate method of determining the relative size of colonies. In the study, the volume of corals as measured by displacement of water was used as a parameter of size. The range of sizes of coral heads used (which were sampled from the study area) was from the smallest with a volume of 40 cc to the largest with a volume of 3,880 cc. Eight-eight heads of variable intermediate volumes were also sampled.

Three measurable parameters of the microhabitat which may act as limiting factors on the commensal community were examined in the study. The first of these was the volume of the coral. From an ecological viewpoint, there is no indication how this parameter, which gives only an estimate of the coral head size, may act to limit the community, but the size alone of the habitat may in some way limit the commensals.

The second parameter employed was a measure of what was called the "habitat space" of the coral head. The "habitat space" is that space among the branches within the confines of the coral head. This was also measured by displacement of water. After measuring the volume of the colonies, the heads were placed in polyethylene bags which were stretched tightly over the entire head, and the volumes of the corals in the bags were measured. By doing this the total internal volume of the coral heads was measured. By subtracting the volume of the coral from the total volume of the coral head in the sack, the space amidst the branches of the coral head was calculated. This space was designated the "habitat space".

In order to see if this habitat space increases at a constant rate as coral head size increases, a graph was made (Figure 3) plotting the volume against the "habitat space" of a sample of coral heads. This graph indicates a straight line correlation between the two measurements, suggesting that there is a relatively fixed ratio

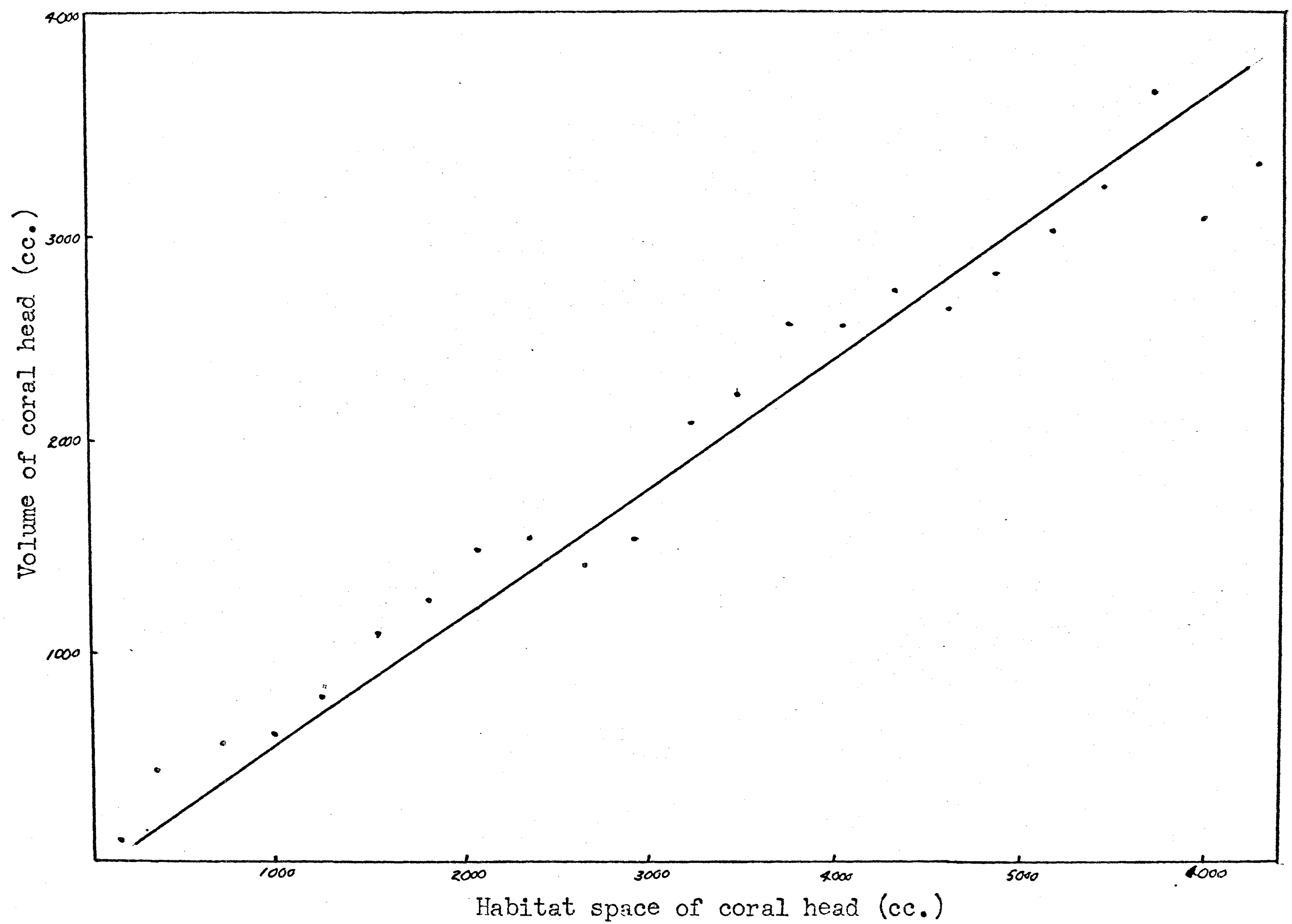

Figure 3. Relationship of volume to "habitat space" of coral heads. Each point is a mean of from one to six samples. Sample size 92. Line fitted by method of least squares (Snedecor, 1956).

between the volume and the "habitat space" and that both increase at a relatively constant rate with increasing coral head size.

Before employing the parameter of "habitat space" in a quantitative manner, it was first necessary to determine if it were qualitatively constant in different sized coral heads. The question was posed whether coral heads of different sizes are compartmentalized similarly. If coral heads of one size range are compartmentalized differently than others, the spaces among the branches would be variable, thus this parameter could not be validly employed. Indeed, then the spaces among the branches themselves could limit the maximum size of the animals. This appears to be what limits the size of animals in the coral _P. damicornis_. The same species attain a much larger size in the other two less compartmentalized species of _Pocillopora_. From an examination of a series of coral heads of varying sizes the spaces appear to be constant and an analysis of the size of the spaces among the branches on a series of different sized coral heads was made to check this point.

Seven coral heads of carying sizes were sampled randomly. On each of these coral heads ten measurements of the distances between a branch and the adjacent branches were made on each of ten of the branches on the coral head. Because smaller coral heads have fewer branches at the periphery, two heads of approximately the same size were used for the two smallest samples. The coral heads were placed under a sheet of plexiglass mounted on a stand. On the plexiglass ten angles, each 36 degrees apart, were drawn through a point. On each coral head ten branches were selected using a table of random numbers (Snedecor, 1955, p. 10) and after placing the approximate center of the tip of the branch under the intersection of the ten lines on the plexiglass, measurements were made of distances from the point each of the ten lines left the branch being considered to where it impinged upon the adjacent branch. The results of the analysis are presented in Table 1.

TABLE 1

Mean distances between adjacent branches of coral heads of different sizes.

Sample Number	Volume cc.	Mean distance Between Branches mm.	Standard Deviation	Range of Means mm.
1 (2 heads)	mean 88	18.96	1.58	16.2 - 21
2 (2 heads)	mean 163	20.73	0.53	19.8 - 21.5
3	550	21.18	1.92	17.4 - 24.6
4	840	20.23	1.01	18.5 - 21.4
5	1200	20.48	1.97	17.2 - 21.7
6	2000	20.89	1.03	19.7 - 22.9
7	2780	19.17	2.27	15.3 - 23.4

All the points fall within a narrow range; the overlap of one standard deviation from the means indicates that the distances among branches in coral heads of different sizes are not statistically different; thus are relatively constant. It was concluded that this measure of "habitat space" changes only in a quantitative and not a qualitative manner in different sized coral heads and thus could be used as a parameter in the study. This parameter appears to be meaningful from an ecological point of view. The "habitat space" is the actual space in which the commensals live, and may be the most important factor in determining the characteristics of the community.

The third parameter considered was the surface area of the coral. In several of a series of studies on animals epiphytic on seaweeds and aquatic plants (Krecher, 1939; Entz, 1947; Rosine, 1955), surface area was used as a parameter in estimating the abundance of animals. However, surface area to biomass relationships were not analyzed to see if the animals were limited by this parameter. Though these studies were not on commensals, they are analogous to the study undertaken.

Because of the structure of the coral heads no direct method was found of measuring the surface area. However, from the volume of the coral head (V), an estimate of surface area (S), relative to the size of the head, can be calculated: $S = V^{2/3}$. The numerical value of this estimate can be used in a relative way when comparing one coral head to another. It increases with increasing coral size proportionate to the exact measure of surface area. This parameter is thought to be meaningful from an ecological viewpoint. The animals live on the surface of the coral and may have certain space requirements. It may be an important factor in limiting symbionts if they in any way derive nourishment from the coral, either by eating the polyps, mucus or nutrient detrital material caught on the coral.

From the results of the analysis of various factors relative to the configuration of the coral as they relate to the parameters introduced in this section, it was concluded that the parameters may be validly employed in a study of the quantitative relationship of the community to the coral head microhabitat. The results obtained also support the contention that the configuration of coral heads of any one species is uniform and though it is modified by environmental conditions it is probably genetically fixed.

IV. Collecting Methods

All the data on the material used in the study was assembled by collecting heads of the coral Pocillopora meandrina from the reefs in the study area in Kaneohe Bay. Collecting was carried out during the months of November and December 1964 and January 1965. The equipment and facilities of the Hawaii Marine Laboratory at Coconut Island were used in the collection and preliminary analysis of the material.

When the coral heads were collected they were put into polyethylene bags immediately upon detachment from the substratum to prevent the loss of any of the associated animals. The collections were then brought to the Hawaii Marine Laboratory for analysis. All but a few of the heads, which were kept in aquaria in order to observe the commensals, were measured for volume, "habitat space", and weight, and then broken up and all of the animals in them removed.

Data on all of the animals in the coral heads were then collected: the species and numbers of each animal recorded; their live, wet weight (the index of biomass used in the study) measured with a Mettler Analytic Balance; sizes of all of the larger symbionts measured; and sexes and reproductive state of all females (that is whether they were ovigerous or not) ascertained. The animals from each of the collections were then preserved in 70% alcohol.

Observations on the orientation of the symbionts in the coral and behavioral peculiarities were made from coral heads in the field and from ones kept in aquaria at the laboratory. A total of 92 heads of P. meandrina was examined.

V. The Community in Pocillopora meandrina

A variety of animals representing several phyla were collected in the coral head microhabitat. These were divided into three groups: (1) the decapod crustacean commensals, (2) the nondecapod crustacean commensals, and (3) the noncommensal animals. The animals found are listed systematically in Table 2. Data on frequency of occurrence, position in the coral, and relationship to the coral are presented. The list does not include sessile animals such as tunicates, bryozoans, sponges, et cetera which were found on the dead base of the coral.

A. Decapod crustacean commensals.

The first of the three groups of animals, the decapod crustaceans commensal with the coral, was the group which was primarily under study. A total of eleven species, represented by both brachyurans and macrurans, was found in this group. Most of the crabs are members of the family Xanthidae and two out of the three shrimp species are members of the family Alpheidae. Detailed data were recorded on these species and are presented in Tables 3 and 4.

TABLE 2.

Animals collected in heads of *P. meandrina* from study area in Kaneohe Bay.
List arranged systematically, with data on frequency of occurrence,
position on coral head and relationship to coral.
Common refers to occurrence in more than 10% of samples.
Data from a total of 92 samples.

Species and Systematic Position	Frequency of Occurrence: Common	Frequency of Occurrence: Uncommon	Position in the Coral: In Dead Base	Position in the Coral: On Branches	Position in the Coral: In space between Branches	Relationship to Coral: Commensal	Relationship to Coral: Non-commensal
Phylum Chordata							
Class Actinopterygii							
Order Percifomes							
Family Pomacentridae							
Dascyllus albicilla Gill		X			X		X
Family Scorpaenidae							
Scorpaena ballieui Sauvage		X			X		X
Family Blennidae							
Exallias brevis Kner		X			X		X
Family Carachanthidae							
Carachathus maculatus (Gray)		X			X	X	
Phylum Mollusca							
Class Gastropoda							
Order Prosobranchiata							
Family Buccinidae							
Pisania tritonoides (Reeve)		X	X				X
Family Coraliophilidae							
Rhizochilus madreporarum (Sowerby)		X		X		X	
Phylum Echinodermata							
Class Ophioroidea							
Order Ophiurae							

TABLE 2 - continued

Species and Systematic Position	Frequency of Occurrence: Common	Frequency of Occurrence: Uncommon	Position in the Coral: In Dead Base	Position in the Coral: On Branches	Position in the Coral: In Space between Branches	Relationship to Coral: Commensal	Relationship to Coral: Non-commensal
Family Ophiocomidae							
Ophiocoma insularis Lyman		X			X		X
Ophiocoma pica Muller and Troschel		X			X	X	
Phylum Arthropoda							
Class Crustacea							
Class Malacostraca							
Order Decopoda							
Tribe Anomura							
Family Paguridae							
Calcinus latens Randall		X	X				X
Diogenes sp.		X	X				X
Family Porcellanidae							
Pachycheles pisoides (Heller)		X	X				X
Tribe macrura							
Family Caridae							
Hymenocera elegans (Heller)		X	X				X
Family Hippolytidae							
Saron marmoratus (Olivier)		X	X				X
Saron nelgectus DeMann		X	X				X
Family Alpheidae							
Alpheus diadema Dana		X	X				X
Alpheus brevipes Stimpson		X	X				X
Alpheus paragracilis Coutiere		X	X				X
Alpheus collumianus Stimpson		X	X				X
Alpheus paracrinatus Miers		X	X				X
Alpheus clypeatus Coutiere		X	X				X

Species and Systematic Position	Common	Uncommon	Position in the Coral: In Dead Base	Position in the Coral: On Branches	Position in the Coral: In space between Branches	Relationship to Coral: Commensal	Relationship to Coral: Non-commensal
Alpheus gracilis Heller		X	X				X
Alpheus lottini Guerin	X				X	X	
Synalpheus paranaomerus Coutiere		X	X				X
Synalpheus streptodactylus Coutiere		X	X				X
Synalpheus charon (Heller)	X		X*			X	
Family Pontonidae							
Harpiliopsis depressus Stimpson	X			X		X	
Tribe brachyura							
Family Xanthidae							
Etisus laevimanus Randall		X	X				X
Actaea variolosa Borradaile		X	X				X
Actaea speciosa (Dana)	X				X	X	
Carpilodes rugatus (Milne Edwards)		X	X				X
Madaeus simplex A. Milne Edwards		X	X				X
Madaeus elegans A. Milne Edwards		X	X				X
Xanthais canaliculatus Rathbun		X	X				X
Platypodia semigranosa (Heller)		X	X				X
Trapezia intermedia (Miers)	X				X	X	
Trapezia digitalis Latrielle	X				X	X	
Trapezia maculata (Macleay)	X				X	X	
Trapezia cymodoce (Herbst)		X			X	X	
Trapezia flavopunctata Eydoux & Souleyet		X			X	X	
Domecia hispida Eydoux & Souleyet	X				X	X	
Family Haplocarcinidae							
Haplocarcinus marsupalis Stimpson		X		X		X	
Family Portunidae							
Thalamita spiceri Edmondson		X	X				X
Charbdis erythrodactyla (Lamarck)		X			X		X

TABLE 2 - continued

Species and Systematic Position	Frequency of Occurrence		Position in the Coral			Relationship to Coral	
	Common	Uncommon	In Dead Base	On Branches	In Space between Branches	Commensal	Non-commensal
Family Dromecidae							
Cryptodromiopsis tridens Borradaile		X	X				X
Family Maiidae							
Perinia tumida Dana		X	X				X
Family Corysidae							
Gomeza sp.		X	X				X
Order Stomatopoda							
Family Squillidae							
Gonodactylus falcatus (Forskol)		X	X				X

* In base in crevices lined with living coral.

TABLE 3

Data on Decapod crustaceans commensal in the coral, Part A. Information on presence, size, numbers, and reproduction presented. Data from 92 communities sampled.

Species	Presence n = 92 % Frequency	Size: Maximum Size mm.	Size: Maximum Weight gm.	Numbers: Mean Number per Sample	Numbers: % in Pairs	Numbers: % Presence of Juveniles	Reproduction: Min. Size female at maturity mm.	Reproduction: % Females carrying eggs
Trapezia intermedia	96.7	20.5	3.84	2.50 n=89	94.3 n=89	39.7 n=89	8	71.3 n=89
Trapezia digitalis	43.5	16.5	1.86	1.93 n=45	96.8 n=31	14.8 n=31	10.5	86.2 n=29
Trapezia maculata	48.9	20	4.58	1.80 n=44	100 n=12	23.5 n=12	13.5	75.0 n=12
Trapezia cymodoce	4.3	-	-	1.00 n= 3	-	-	-	-
Trapezia flavopunctata	1.1	-	-	1.00 n= 1	-	-	-	-
Actaea speciosa	16.3	20	3.42	1.41 n=12	83.3 n= 6	0 n= 6	15	20.0 n= 5
Domecia hispida	36.0	14	0.46	1.95 n=21	76.9 n=13	83.3 n=13	8	35.7 n=14
Haplocarcinus marsupalis	2.2	-	-	14.00 n= 2	None	-	-	-
Alpheus lottini	92.4	13	2.69	2.44 n=85	96.0 n=76	26.6 n=76	8	75.9 n=85
Synalpheus charon	89.1	6.5	0.28	1.98 n=92	90.6 n=85	0 n=85	5	74.7 n=83
Harpiliopsis depressus	89.1	10	0.32	7.61 n=92	None	-	-	-

TABLE 4

Data on Decapod crustaceans commensal in the coral, Part B.
Information on coral species commensal with, color of animals, and orientation in the coral head.
Data from 92 communities sampled.

Species	Other Coral Species Commensal With	Color	Orientation in Coral
T. intermedia	P. damicornis P. ligulata	Orange brown with darker brown spots.	Deep in coral clinging near the base or frequently further out on branches. Oriented with anterior end pointed outwards. Small juveniles found in tunnels in base of coral.
T. digitalis	P. damicornis P. ligulata	Dark brown	
T. maculata	P. ligulata	White with dark red spots.	
T. cymodoce		Orange	
T. flavopunctata		Orange with white spots.	
A. speciosa	P. ligulata	Mottled black, red, and white	Interstices between branches at base of coral, often wedged in larger crevices and tunnels in coral base, sluggish form.
H. marsupalis	P. damicornis	Translucent	Females enclosed in "galls" on branch, males on branches
A. lottini	P. damicornis	Bright orange with brown spots dorsally	On the base of the coral in channels formed by branches.
S. charon	P. damicornis	Dark orange-red	In crevices and tunnels, lined with living coral, within the base of the coral.
H. depressus	P. ligulata	Transparent	All over branches of coral. Oriented with long axis parallel to that of the branch.

The data on frequency, which is the percentage of samples in which the species was found, show that the four species *Trapezia intermedia*, *Alpheus lottini*, *Synalpheus charon*, and *Harpiliopsis depressus* were the most characteristic components of the community. Crustaceans that were less frequently found, yet were encountered in more than 10% of communities examined were the four crabs *Trapezia digitalis*, *Trapezia maculata*, *Actaea speciosa*, and *Domecia hispida*. The other species were only rarely encountered. The dominant commensals, by size and weight, were the trapezids and *A. lottini*. Of the trapezids, *T. intermedia* and *T. maculata* are of similar size and *T. digitalis* is smaller. *Actaea speciosa* is also a relatively large crab, but was infrequently encountered.

The data on numbers of individuals demonstrate that for all but two species the mean number ranged between one and three individuals per coral head. The more or less uniform number of individuals results because most of the commensals are paired; a condition which probably occurs upon the crustaceans reaching sexual maturity. The mean numbers of individuals was not always just two because in addition to the one pair of adults any number of juveniles may be found in the same coral head. Though adults were usually found in pairs, occasionally in larger coral heads the situation occurred where there were two males and one female or more commonly two females and one male. In one case two pairs of adults were found in one coral head; it may be significant that neither of the pairs were of maximum size, which was the usual case for symbionts in corals of that size. The behavioral peculiarity of pair formation is important in that it limits the number of adults of a species that can live in one coral head. The data on reproduction shows that all species were spawning and a high percentage of some commensals were carrying eggs. Noteworthy is the fact that sympatric species of trapezids have coincident breeding cycles. Though the data were taken from material collected over only a three-month period, commensals collected at every month of the year prior to the study showed a similar picture, suggesting that they spawn the year around.

The commensal crustaceans occupied a variety of different positions within the coral head, which is specific for each species. This is noteworthy since an animal which is found only on the branches of the coral would apparently not come into contact with an animal that was limited to the tunnels in the base of the coral. Thus their specific orientational behavior isolates some species from others and tends to minimize if not exclude interaction of some species. It may be significant that the very small juveniles of trapezid crabs live in a different portion of the coral than the adults.

Most of the symbionts have color patterns which blend in with the coloration of the coral, making them inconspicuous within the coral. In some species such as T. digitalis, D. hispida, or S. charon, the general coloration of the body is indistinguishable from the color of the coral. Another species H. depressus is transparent and thus is undectable against any background. In two of the other symbionts, T. intermedia and A. lottini, the general coloration of the body is conspicuously different from the color of the coral. However, certain areas of the body, in the crab the outer surface of the large chaelae and in the shrimp the dorsal surface of the body, which are the only parts of the animal which are visible when looking into the coral head, are colored differently from the rest of the body. The coloration of these areas is such that it blends in with that of the coral. Cryptic coloration of the commensals is adaptive in that it probably reduces pressure from predators, by making the commensals indistinguishable from the coral. The agreement in color and color pattern between symbionts and hosts is a commonly occurring phenomenon amongst commensals. One of the well known works on this is that of Potts (1915b) on the cryptic coloration of crustaceans commensal with crinoids.

In several of the coral heads sampled, specimens of Alpheus lottini were collected which were marked differently from the usual specimens. They had distinct blue-black borders on the orbits of they eyes and rows of paired spots of the same color along the dorsal part of the carapace and abdomen. This color variety was recognized by Banner (personal communication), who found that it did not differ morphologically from the usual color variety. It was noted though, that whenever specimens of this color variety were encountered, both the male and female of the pair were marked in this manner. One juvenile with this same marking was found in the collections.

Another aspect of coloration, particularly that of sympatric species of Trapezia, is its possible role in species recognition. It has been shown in some animals that coloration has a signal function (Tinbergen, 1951). A number of species of crabs of the genus Trapezia were found in the coral; they are all similar morphologically but each species has a color pattern, often striking, which is distinctly different from that of the other species. It is very likely that these distinct color patterns are important as sign stimuli in species recognition, and subserve barriers to interbreeding.

B. Other commensals.

The second group, the other commensals, included three species, representing three phyla. More specific data on them are presented in Table 5.

TABLE 5

Data on nondecapod crustacean commensals in the coral. Information on frequency, number of individuals, size, and orientation in coral presented. Sample size = 92.

Species	Frequency	Mean number individuals per sample	Maximum size gm.	Orientation in Coral
Rhizochilus madreporarum	16.30	1.76 n=17	3.72	Affixed to branches causing a sear where attached.
Opiocoma pica	13.00	9.48 n=12	1.20	Wrapped around base of branches.
Carachanthus maculatus	3.26	3.16 n= 3	2.5	In interstices at base of branches

Although these animals are large relative to most of the crustacean commensals, few were found and they were not present in many samples. These animals were not included in a consideration of the quantitative aspects of the study.

C. Noncommensals.

The third group of animals, those which are not commensal with the coral, make up the majority of the species of animals in Table 2. The majority of these animals were xanthid crabs and alpheid shrimps, but representatives of three other phyla were found. Of many species only one individual or a pair were collected in the total of 92 coral heads sampled. None of these was found in more than 10% of the samples. Almost all of the animals were found in the dead base of the coral and it appears that they utilize the holes and crevices in the base of the coral as shelter.

Most of these animals probably did not affect the commensals because none occupy exactly the same habitat space, and thus there would be no competition for this or other aspects of their respective niches. Some of the animals, such as stomatopods or fishes, probably are predators on commensals, but these make up only a small fraction of all the animals found, and were not encountered frequently. Since the interactions of these animals and the commensals is probably minimal, their affect in limiting the commensals probably is minimal as compared with other limiting factors.

VI. Relationship between Coral and the Decapod Crustacean Community

A. Affect of the size of the coral head upon the commensal community.

Since the coral head microhabitats are not uniform in size, but range from very small colonies to ones many times as large, the question arises whether the commensal community is different in coral heads of different sizes.

The first thing examined was the relationship between the number of animals and the size of the coral head in which they were found. It is graphically demonstrated in Figure 4 that larger coral heads did support more commensals than smaller ones. In addition to having more symbionts, larger heads had a greater number of species. This data is presented in Table 6.

TABLE 6

Mean numbers of species collected in coral heads of different size classes. Samples size = 92.

Coral head size range (H.S.*cc.)	Mean no. of species	Sample size	Range
0 - 1,000	3.16	18	1-5
1 - 2,000	4.66	12	3-6
2 - 3,000	5.47	17	4-7
3 - 4,000	5.71	14	4-7
4 - 5,000	5.90	10	4-8
5 - 6,000	6.55	9	5-8
6 - 7,000	5.71	7	4-7
7 - Up	7.20	5	6-9

* Habitat space.

There was a difference in community composition found in coral heads of different sizes both from a standpoint of biomass or weight and numerical composition. This is illustrated in Figure 5. In the

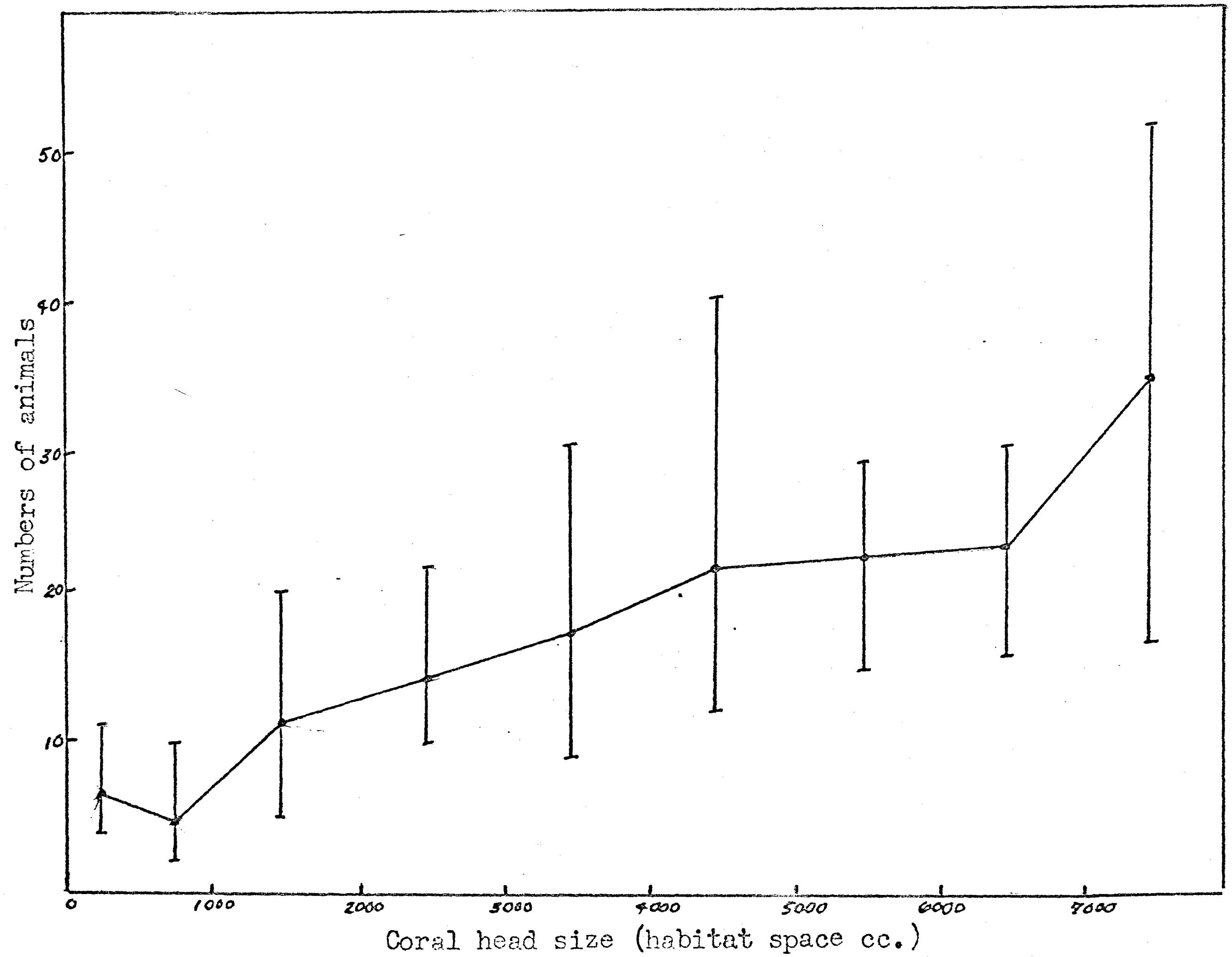

Figure 4. Total numbers of animals in coral heads plotted against coral head size. Means and total ranges for each size class presented. Means represent from one to six samples.

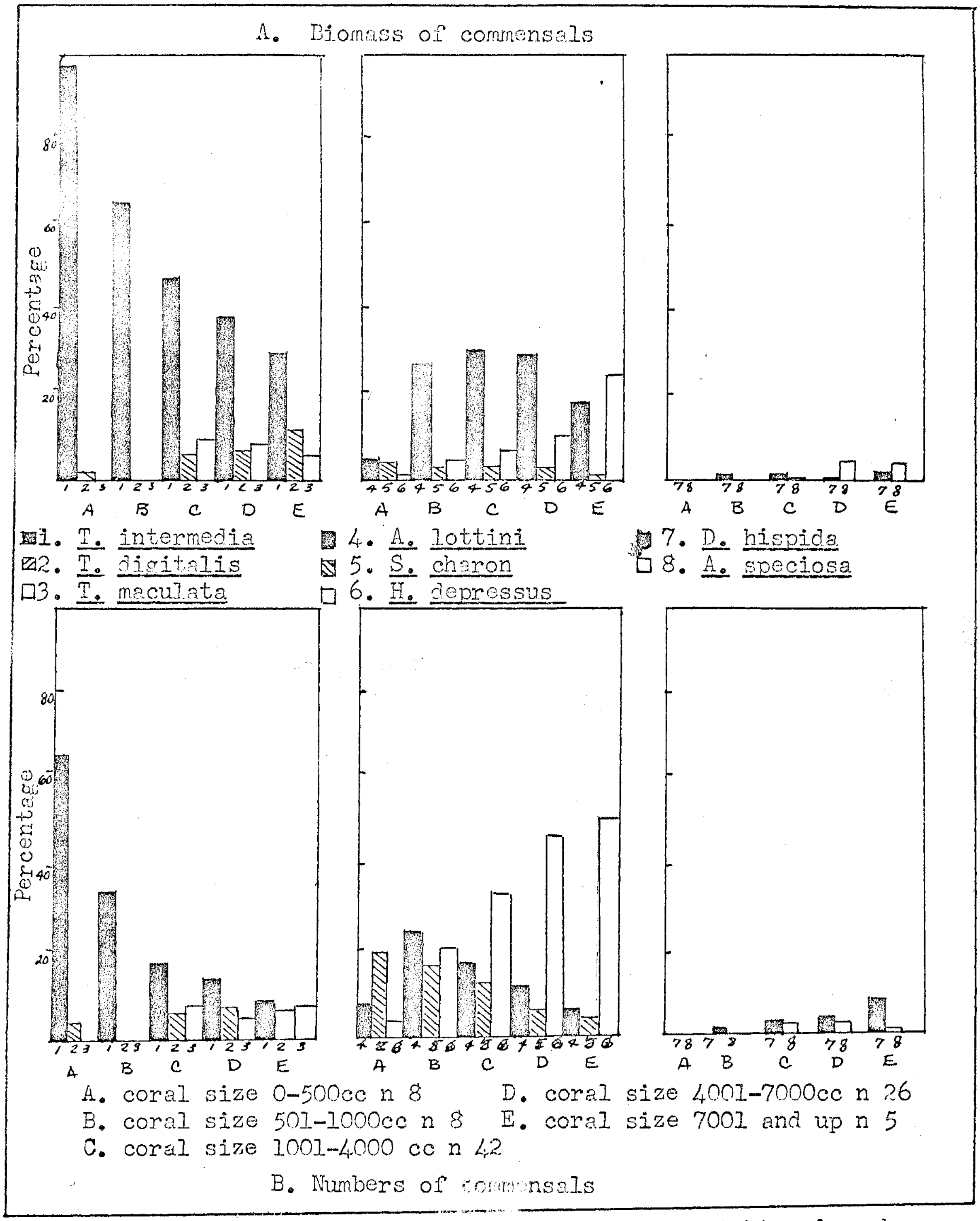

Figure 5. Composition of commensal communities by weight and numbers of symbionts as a function of coral head size. Mean weights and numbers presented as precentages of totals. Sample size indicated. Graphs divided into trapezid crabs, shrimps, and other crabs. Coral head size in terms of volume of "habitat space".

graphs the coral heads were grouped into size classes based on "habitat space", which is indicative of relative size, and the mean weight and number of each commensal species calculated for each of the classes. To facilitate comparison of different size classes the mean weights and numbers were presented as percentages of the total mean weights or numbers. The size classes do not cover the same ranges in coral head size, but were grouped into segments which demonstrated significant differences among one another. For ease in reading, the data on the symbionts were grouped into the trapezid crabs, the shrimps, and the other crabs found in the community.

The composition of the community was different in each of the different size classes (Figure 5). As one would expect, the most striking differences were seen between the communities in very small corals and those of the largest coral heads sampled. Coral heads intermediate in size showed a gradation in composition between the two extremes. The smaller coral heads with a volume less than 500 cc. had a community composition, based on both weight and numbers, markedly different from that of larger heads. In the smaller heads fewer species were represented and the same species were dominant in both biomass and numbers. The predominant component of the community was <u>Trapezia intermedia</u>. It demonstrates marked dominance constituting 88% of the biomass and 64.7% of the number of commensals. In coral heads of this size typically one or a pair of <u>T. intermedia</u> were present and one other species of symbiont, usually the shrimp <u>Synalpheus charon</u>. The situation in coral heads from this size to

1,000 cc. was similar, but in these communities no one species was as predominant and more species were present. The trend toward no one species demonstrating such marked dominance, more species being represented, but the species having relatively similar positions within the community, continued in larger coral heads and was culminated in very large coral heads.

In the largest coral heads sampled, those with a volume over 7,000 cc., numerically all of the species of commensals present, with the exceptions of *Harpiliopsis depressus* and *Haplocarcinus marsupalis*, made up approximately equal percentages of the total community. Of the two exceptions *H. depressus* was the predominant symbiont, constituting over half of the number of animals found and *H. marsupalis* made up an insignificant percentage of the number of animals found. From the standpoint of total biomass of the community, three species *T. intermedia*, *A. lottini*, and *H. depressus* were the dominant forms. None of these was markedly predominant, but they all made up relatively similar percentages of the biomass. The other commensals present made up small percentages of the total biomass, with the two other species of *Trapezia* predominating in this group. The percentage of the biomass represented by *H. marsupalis* was so small (less than one percent) that it was not entered on the graph.

As pointed out in the foregoing section, the relative position of each of the symbionts in the community changed with increasing coral size. The trapezid crabs were predominant in biomass in all sizes of coral heads; they were also a dominant group numerically in smaller colonies, but their percentage composition shows an initial drop, followed by a leveling out in coral heads larger than 500 cc. Trapezia intermedia was the predominant species of trapezid in all size classes of coral heads. It made up a considerable portion of the biomass and number of individuals in very small coral heads. Its dominance relative to the other species of trapezids decreased in larger coral heads and though it always made up a greater percentage of the biomass of this group, the other two species were approximately equal in numbers to T. intermedia in the largest coral heads. The other two species of Trapezia commonly found in the community, T. maculata and T. digitalis, became more important constituents of the community as coral head size increased. It is noteworthy that they were not present except for one T. digitalis in coral heads smaller than 1,000 cc. Their position relative to one another, both in numbers and biomass, was about equal and a variable pattern of dominance existed between the two.

The shrimp Alpheus lottini was the second most important commensal from a standpoint of biomass in all sizes of coral heads except very large ones. Though insignificant in very small corals it made up a sizeable portion of the biomass in other larger heads and this portion remained constant, showing a slight decrease in only very large coral heads. Numerically, it was also dominant in all sizes heads, but its percentage of the total number of symbionts declined as heads became larger.

Synalpheus charon, which was present in all sizes of coral heads, made up about the same percentage of the total biomass in coral heads of all sizes. It was numerically the second most important component of the community in very small heads, but decreased steadily in larger heads until in the largest sized heads it was insignificant amongst the other commensals.

The shrimp Harpiliopsis depressus was not an important component of the community of smaller heads, but as coral heads increased in size it became more important numerically and as a portion of the biomass. In very large heads, over 7,000 cc. volume, it was the second largest component of the total biomass. Numerically it was the predominant symbiont in coral heads larger than 1,000 cc.

In all sizes of coral heads the crabs Domecia hispida and Actaea speciosa made up a very small percentage of the total number, and the total biomass of animals. They were not found in coral heads smaller than 1,000 cc. volume, but occurred occasionally in larger heads. Though there were usually more individuals of D. hispida than A. speciosa present than in the samples, because A. speciosa is a much larger crab it made up a greater percentage of the total biomass.

The crab Haplocarcinus marsupalis rarely occurred in the communities, and it was found only on larger coral heads. These were very tiny crabs which, though they may occur in great numbers on one coral head, made up only a very small percentage of the total biomass.

The data indicate that there were four general groups of commensals present in the coral heads. Three of these include animals which formed pairs, and the fourth did not. The first group was paired and found in small coral heads as well as larger ones. Animals in this group reached a maximum size in medium-sized coral heads; thus they dominated in smaller colonies but as more species and numbers of commensals appeared in larger colonies they became a less important component of the community. Trapezia intermedia, A. lottini, and S. charon represent this group. The second paired group of commensals which were a less important component of the community, were found only in larger coral heads. They maintained about the same percentage of the biomass and numbers of individuals in the sizes of coral heads in which they were found. Trapezia digitalis and T. maculata fall into this category. The third group of symbionts were similar to the ones just described except that they constituted a larger percentage of the community as the coral heads in which they are found increased in size. This was so because they increase in size as the corals increase in size. The crabs Domecia hispida and Actaea speciosa represent this group. The last group of animals, as represented by Harpiliopsis depressus, were animals which did not pair and increased in number and total biomass as coral head size increased. They were insignificant in smaller heads, but became an important component of the community in larger heads.

The general effects observed concurrent with increasing size of the coral head microhabitat were as follows:

1. The number of individuals and of species increased with increasing coral head size.

2. The species which were dominant and the pattern of dominance was different in coral heads of different size.

3. The relative percentage each commensal made up of the total biomass or numbers of individuals in the community varied with differences in sizes of coral heads.

B. Coral as source of food.

An obvious question raised when considering the relationship of the crustacean community to the host coral is whether they derive any nourishment from the coral. They they do not normally leave the coral habitat, they might feed directly upon the polyps or mucus secreted by the coral, or utilize the coral indirectly by feeding on material caught in the mucus or by the polyps. Alternate hypotheses are that they prey upon animals which seek shelter in the coral or that they filter planktonic organisms from the currents passing through the colony. This last hypothesis seems doubtful as the mouth parts of all of the commensals, except _Haplocarcinus marsupalis_, are of a generalized type and not modified for filter feeding.

1. Restriction of symbionts to coral head.

In considering the role the coral plays in the trophic behavior of the symbionts it was important to determine whether they normally leave the coral head. It appears from collections and observations made both at night and during the day that the crustacean commensals do not leave the corals. In all cases when coral heads were examined there were a pair of each of the more conspicuous commensals present and no commensal was ever seen, night or day and even in areas with a substratum of uniform, bare, smooth rock where they would be very conspicuous, outside of their coral heads. It was concluded that they normally remain inside the coral head microhabitat and thus must obtain their food in the coral head.

2. Stomach contents analysis.

The most direct method of ascertaining the diet of the commensals is to identify stomach contents. This was attempted for all commensals, but the difficulty of locating and removing the stomachs because of their small size, and the pulverized condition of the stomach contents made the analysis difficult, so that the results in most cases were not conclusive. The results of the examinations of stomach contents are presented in Table 7.

TABLE 7

Results of Stomach Contents Analysis

Species	No. of Individuals Examined	Coral				Other Material						
		Coral Fragments	Mucus	Zooxanthellae	Nematocysts	Benthic Algae	Diatom	Algal Spore	Sponge Spicule	Mollusk Radula	Small Crustacea	Empty
T. intermedia	30	9	0	5	5	6	4	2	3	2	12	9
T. digitalis	7	0	0	3	0	0	0	1	0	0	0	3
T. maculata	1	0	0	1	1	0	0	0	0	0	0	0
T. flavopunctata	3	0	0	0	0	0	0	0	0	0	0	3
A. lottini	13	0	1	0	0	5	2	0	2	1	8	5
S. charon	3	0	0	0	0	1	1	0	0	0	1	1
D. hispida	3	0	0	0	0	0	1	0	0	0	1	1
A. speciosa	5	1	1	0	2	1	1	0	1	0	1	3
H. depressus	4	0	1	2	0	0	0	1	0	0	0	0

It can be seen from the examination of stomach contents that a variety of plant and animal material was utilized as food. In most of the symbionts, including the dominant forms, both mucus and tissue of the coral were found in the stomachs. More frequently material other than coral was found; particularly common were small crustaceans. In two of the commensals, S. charon and D. hispida, no material from the coral was detected. The stomach contents of H. marsupalis were not examined, but Potts (1915a) reports that they are filter feeders, with mouth parts similar to those in porcellanid crabs, and that he found nannoplankton in their stomachs.

3. Trophic behavior experiments.

In order to substantiate the role of the coral as a source of food for the commensals, trophic behavior experiments were devised. Two points were examined: (1) whether the commensals eat the coral polyps or mucus, or (2) whether they feed on material caught on the coral. The experiments were carried out at the Waikiki Marine Laboratory. Initially all of the commensals present in the coral were to be used, but because of difficulties arising from the small size ot some and scarcity of others, only two large symbionts were used. Trapezia intermedia and A. lottini, both of which are common, large and represent both the shrimps and crabs found in the community, were used in the experiments. All of the coral heads and animals used were either collected from the study area in Kaneohe Bay or from the reef in front of the Waikiki Laboratory.

In the first of the experiments, which were the controls, the animals were placed in a bare aquarium with only sand and a rock in it. They were starved for twenty-four hours, then a piece of tuna stained with neutral red was placed in each aquarium. A total of ten animals of each species was used. After another twenty-four hour period the animals were taken out and the stomach contents examined for traces of the stained meat. In the second experiment the same procedure was used as in the first except that coral stained with neutral red was added instead of tuna. The procedure was the same in the third experiment except that after the initial twenty-four hour period of starvation, an unstained coral head and stained brine shrimp were put into the aquaria. Again the stomachs were examined after twenty-four hours. The results of these three experiments are presented in Table 8.

TABLE 8

Results of trophic behavior experiments.

Experiment #1 - control experiment.

Species	Meat Present	Meat Absent	Stomach Empty	Total # Animals Tested
Trapezia intermedia	8	1	1	10
Alpheus lottini	7	3	0	10

Experiment #2 - stained coral.

Species	Coral Present	Coral Absent	Stomach Empty	Total # Animals Tested
Trapezia intermedia	6	1	3	10
Alpheus lottini	3	1	2	6

Experiment #3 - Stained brine shrimp given to symbionts in coral.

Species	Shrimp Present	Shrimp Absent	Stomach Empty	Total # Animals Tested
Trapezia intermedia	7	2	1	10
Alpheus lottini	2	1	2	5

What little is known about the diets of the two major groups of symbionts, the xanthid crabs and alpheid shrimps, indicates that they have generalized diets, probably primarily as predators on small animals and omniverous scavengers. It appears that there has been some trophic specialization in the symbionts as a consequence of their commensal habits, which is probably developed to a greater extent in some of the symbionts than in others. It was concluded from this part of the study that the symbionts do feed on the coral. Most of the symbionts, the known exceptions being *H. marsupalis*, probably derive some nourishment from the coral either directly by eating material from the polyps or indirectly by eatning material caught on the coral. There is some evidence, such as the presence of the radula of molluscs, that some of the commensals feed on larger animals which occasionally enter the coral head. It appears from the data on stomach contents that, though most of the symbionts had utilized the polyps for food, it is a less important component of their diet than materials which collect on the coral polyps. The commensals appear to have no adverse affect upon the coral colonies, indicating that their predation on the coral polyps is minimal.

C. Quantitative relationship of the symbionts to the coral habitat.

In attempting to define the factors limiting the community of commensal crustaceans in the coral P. meandrina several hypotheses were set up. The hypotheses all dealt with parameters imposed by the coral head as primarily a physical entity. It was thought that physical factors imposed by the coral head may be the most important factors in limiting the biomass of the community. It was realized that biotic factors imposed by the community could not be disregarded, but these factors, which are difficult to ascertain, may be of secondary importance. The limiting factors imposed by the behavioral peculiarities and interactions of the symbionts may not be important in determining the size of the community, but working within the framework of the physical or biotic limits imposed by the coral head, may determine the exact composition of the total community which the coral head can support.

1. Relationship of community to coral head.

The first hypothesis was that the size of the coral, as measured by volume, was important in limiting the community. The second was that the space within the coral head, or "habitat space" was the limiting factor, indicating that the commensals have minimum space requirements and thus the total amount of space available determined the size of the community. The last hypothesis was that the surface area, as estimated from the volume measurement, was the factor limiting the community. This would mean that the commensals, all of which live on the living surface of the coral, have minimum surface area requirements. This is particularly meaningful since the commensals are dependent upon the coral for food.

In order to see if there was any positive correlation between the biomass of the communities found and any of the three parameters, the data collected on the biomass of the community sampled were plotted graphically against the three parameters of the coral in which it was found. The graphs are shown in Figures 6, 7, and 8; data on the 92 communities which were sampled are represented in the graphs. In the first of the graphs the total biomass of the community is plotted against the volume of the coral head. In the second the total biomass is plotted against the "habitat space" of the coral, and in the third the total biomass is plotted against the estimate of surface area of the coral.

The best linear correlation was seen in the last of the three graphs, suggesting some causal relationship between the surface area and the biomass of the commensal community. It is plausible that the surface area may be the most important factor limiting the commensal community in view of the fact that the commensals were found to utilize the coral as a source of food. This is though to be by feeding on the material caught on or by the polyps or in the mucus; thus the symbionts may in a sense be said to "graze" on the surface of the coral. If this were the case, the total amount of surface area available would directly influence the amount of food available to the commensals. Thus in the last analysis, food, which in the classical

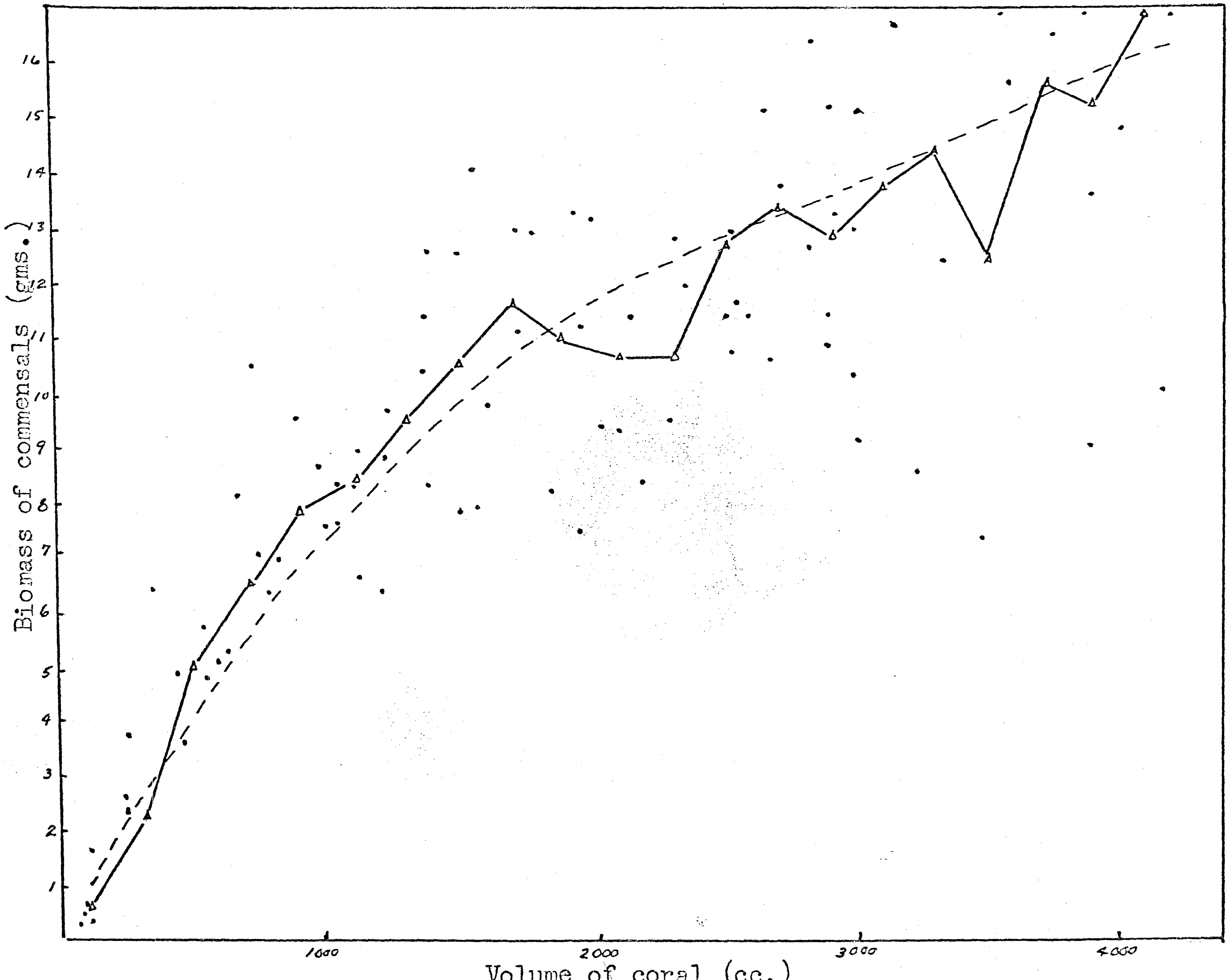

Figure 6. Biomass of commensal community plotted against volume of coral heads. Δ means. Dotted line is approximate line of best fit. Sample size 92.

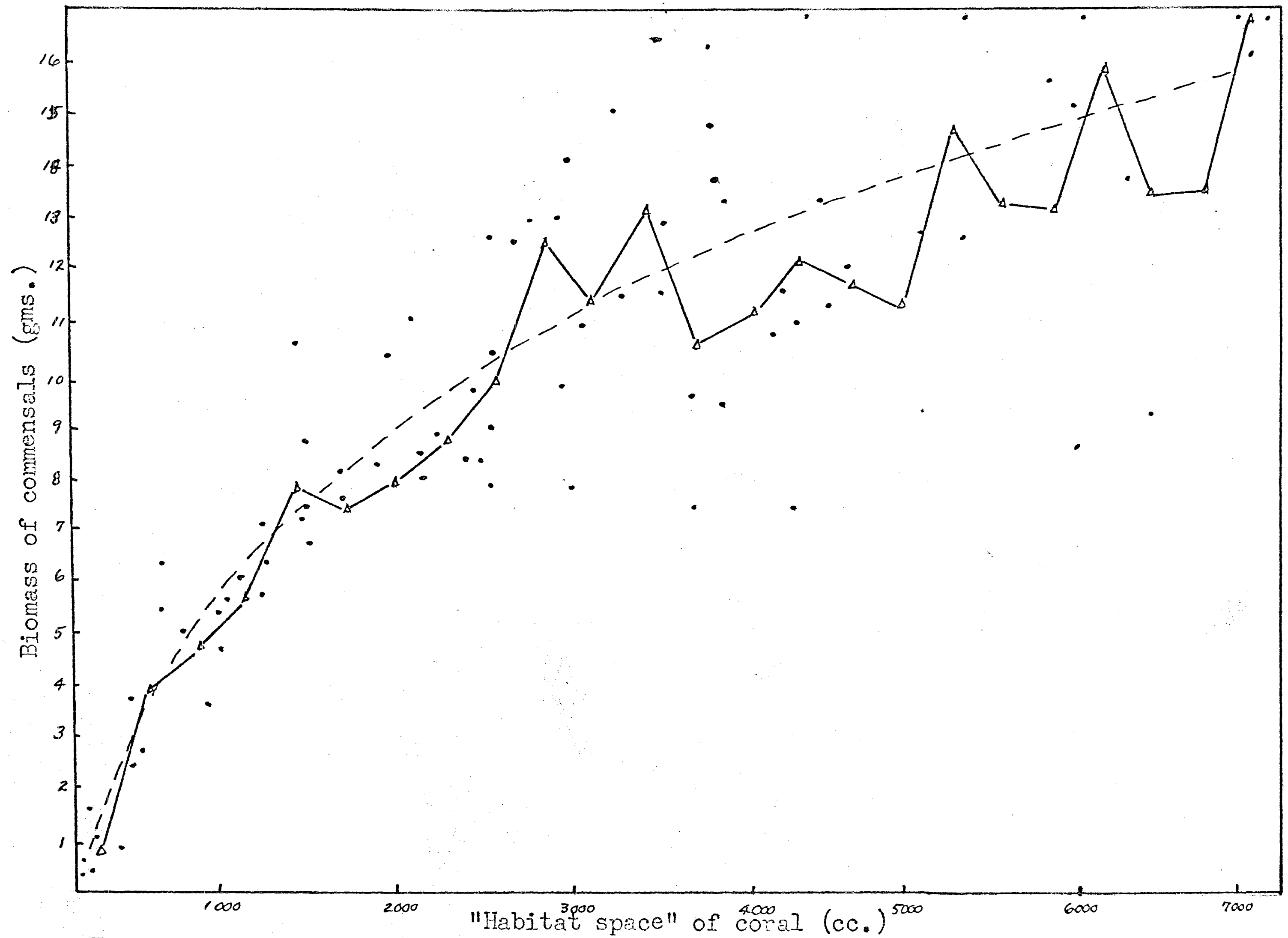

Figure 7. Biomass of commensal community plotted against "habitat space" of coral head. Δ means. Dotted line is approximate line of best fit. Sample size 92.

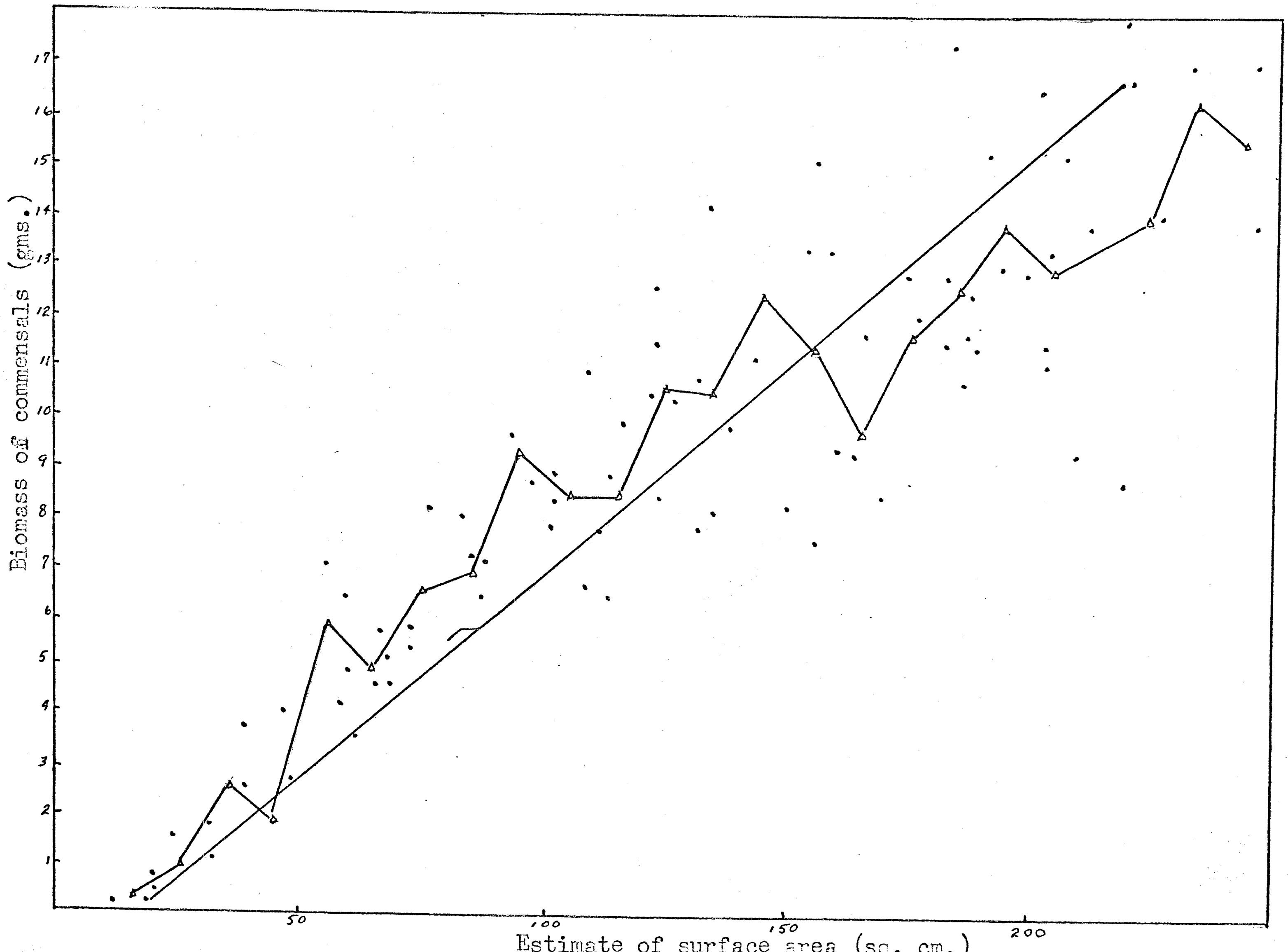

Figure 8. Biomass of commensal community plotted against estimate of surface area of coral head. Δ means. Line fitted by method of least squares (Snedecor, 1956). Sample size 92.

ecological sense has been shown to be a limiting factor in animal populations (Lack, 1954), may be the factor limiting the commensal community in the coral head habitat.

2. Relationship of components of community to surface area of coral head.

The next point examined was whether the individually important components of the community were limited by the same factors which limit the community as a whole. The data on the biomass of each of the commensals within the community sampled were plotted against the estimate of surface area for the coral head in which it was collected. Graphs for the trapezid crabs, A. lottini, H. depressus, and one for the minor commensals are illustrated in Figures 9, 10, 11 and 12.

Only the species H. depressus, which does not occur in pairs, showed a linear correlation with the parameter similar to that of the whole community. None of the other members of the community, all of which typically pair, showed a similar correlation. This suggested that the exact composition of the total community that any coral head can support is probably determined by social factors arising from interactions of the symbionts. Biotic limiting factors such as these are always complex and difficult to ascertain.

Social interactions may be divided into two components. The first is intraspecific interaction and the other is interspecific interaction. The type of interaction which is probably

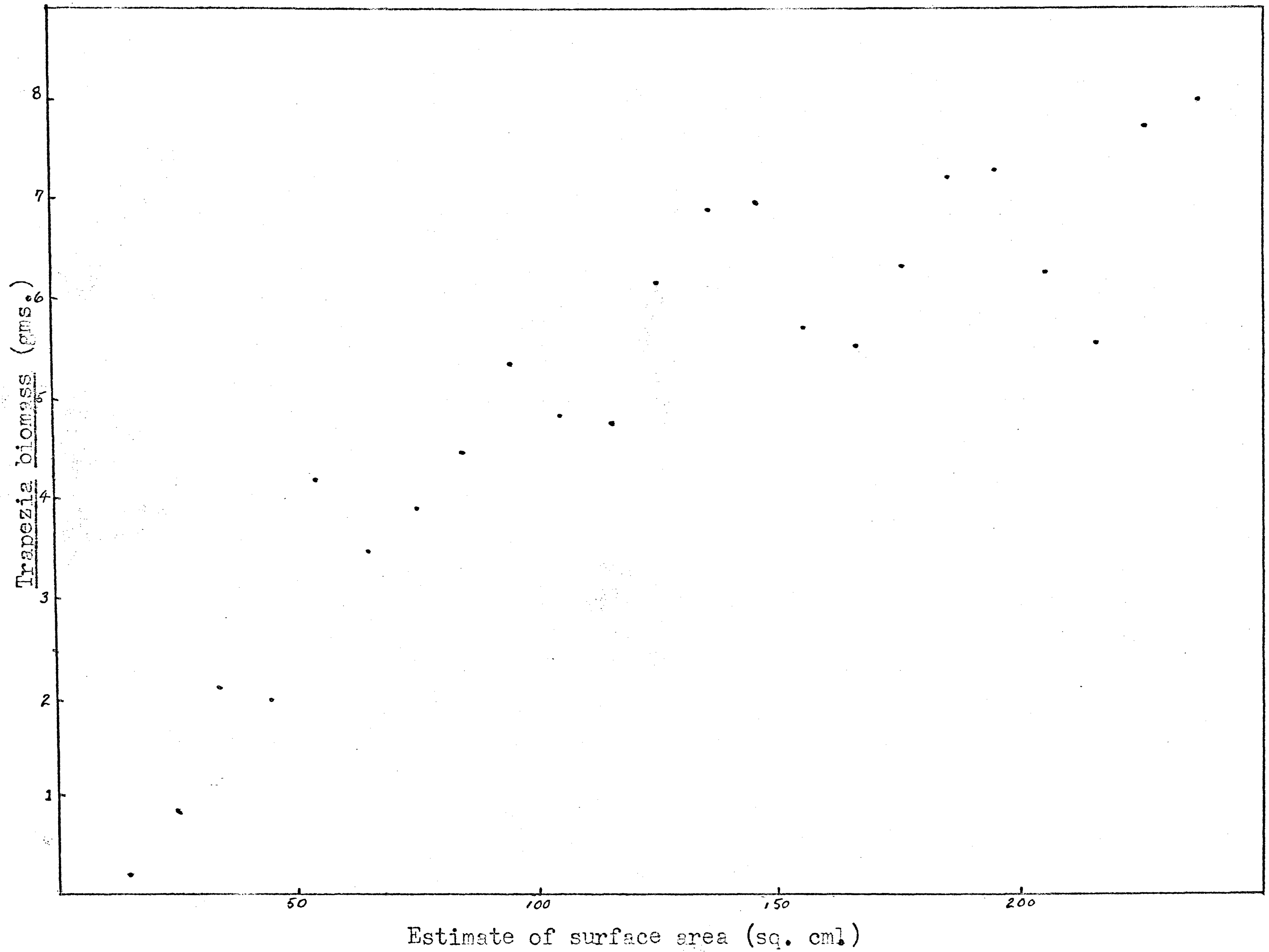

Figure 9. Relationship of biomass of trapezid crabs to surface area estimate of coral heads. Each point represents a mean of from one to six samples. Sample size 92.

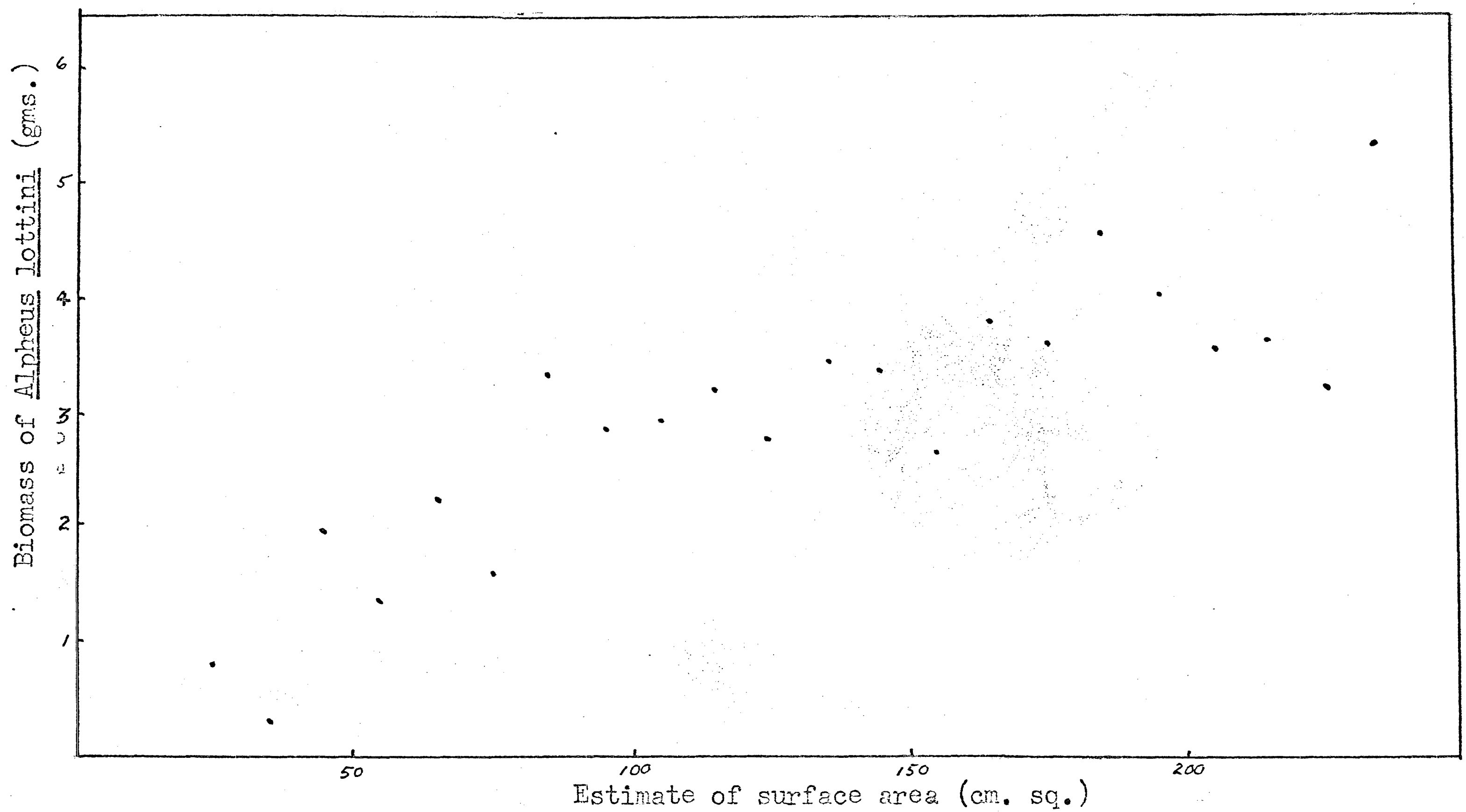

Figure 10. Relationship of biomass of Alpheus lottini to surface area estimate of coral heads. Each point represents a mean of from one to six samples. Sample size 92.

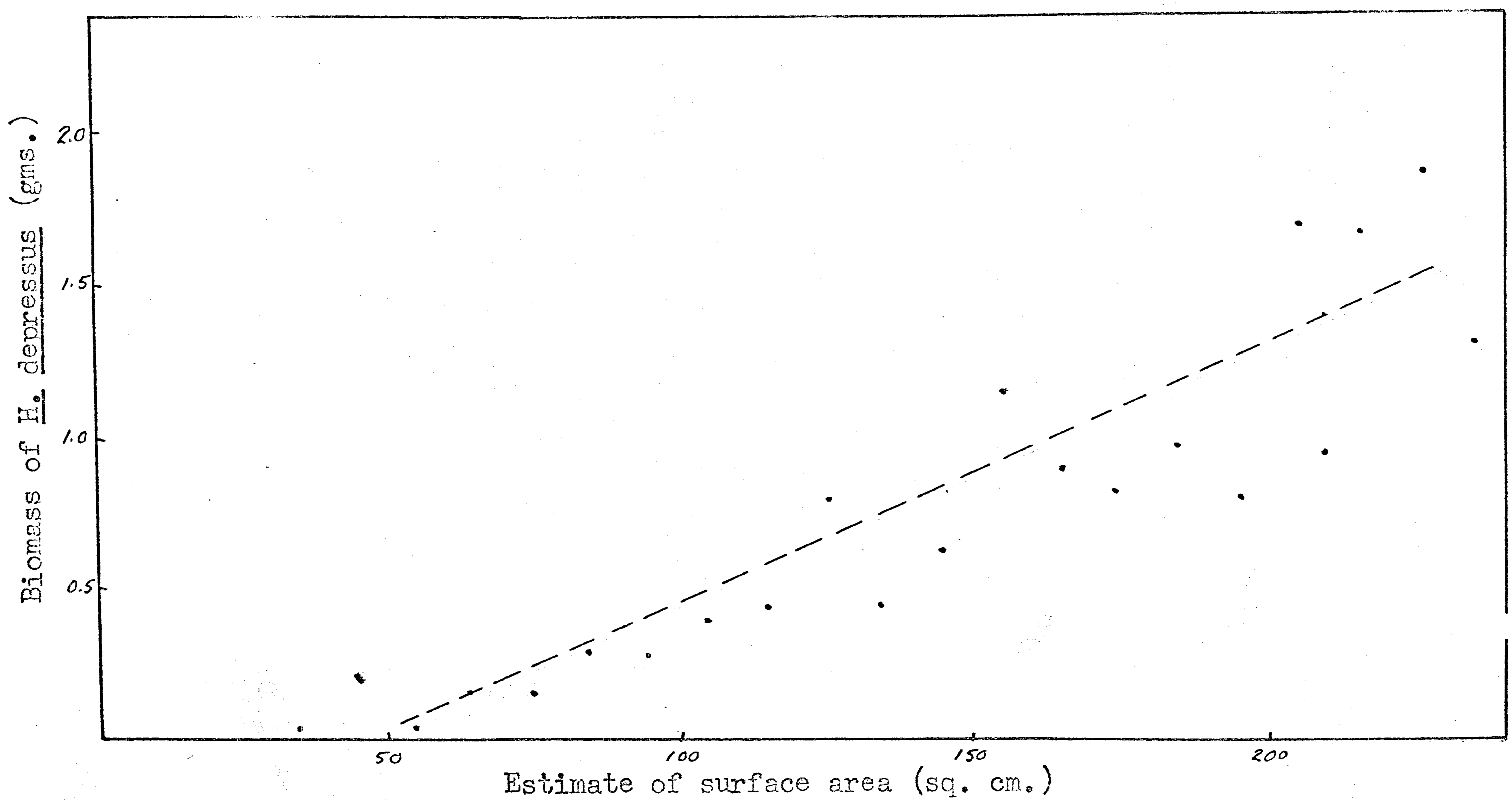

Figure 11. Relationship of biomass of Harpiliopsis depressus to surface area estimate of coral heads. Each point represents a mean of from one to six samples. Sample size 92. Dotted line is approximate line of best fit.

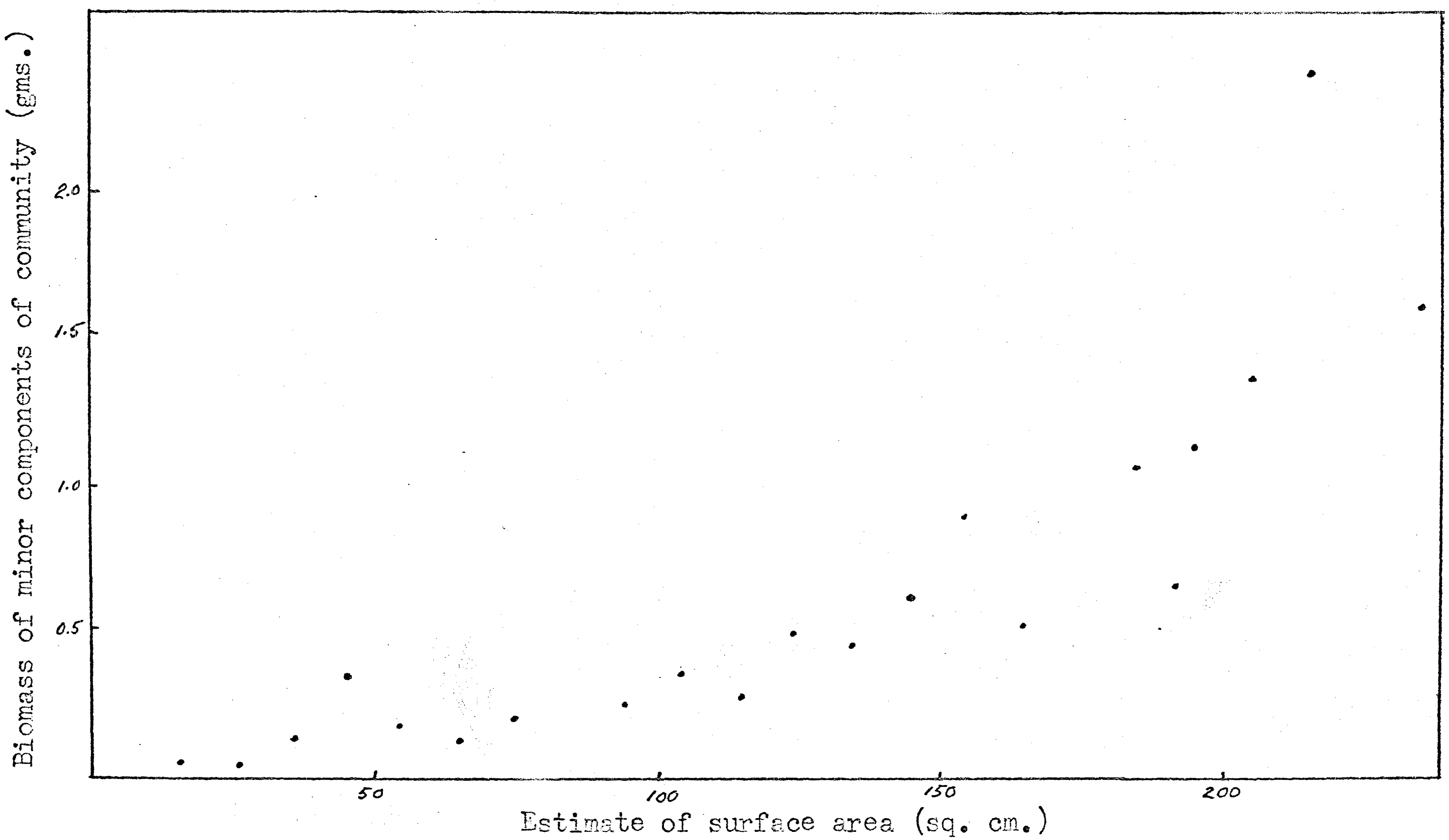

Figure 12. Relationship of biomass of minor components of the commensal community to estimate of surface area of coral head. Minor components include: H. marsupalis, D. hispida, A. speciosa, and S. charon. Each point represents a mean of from one to six samples. Sample size 92.

most important is competition. Competition has more of a direct effect on limiting the commensals than other factors. More definitive conclusions about these can be made only after extensive laboratory experiments on the animals' social behavior, coupled with more knowledge of the ecological niche of each species within the community. However, some speculation can be made, based upon the conditions observed in the communities as they existed in the field.

a. Intraspecific interaction.

There is evidence for intraspecific competition in many groups of animals, including crabs (Reese, 1962), and it is apparent from the study that it is an important factor limiting the numbers of individuals in the commensal community. Social interaction of all of the species but <u>H. depressus</u> probably primarily centers around the behavioral peculiarity of pairing. There was, with but a few exceptions, only one pair of adult animals of a species inhabiting any one coral head. Though numerous juveniles of the same species may be present, any sexually mature adult of the same species is excluded from the community. This behavioral peculiarity of the crustacean symbionts has also been noted by Garth (1964). Though a coral head may theoretically be able to support more than one pair of adults of that species in it, the crabs themselves limit their numbers. Though no extensive observations were made, cases have been observed under laboratory conditions where an adult T. intermedia was put into a coral head which already had a pair of adult T. intermedia living in it. The introduced crab was driven from the coral head by one of the incumbent animals.

Competition arising from factors such as food, space, et cetera, probably also occurs among the pairs of animals that are present, but probably affects the animals by limiting their maximum sizes rather than having the severe effect of totally excluding other animals from living in the community. Thus it appears that pair formation is the most important single factor limiting the numbers of animals of most of the species found in the commensal community.

b. Interspecific interaction.

Though interspecific competition is not as widely substantiated as intraspecific competition, there is some evidence (Brower, 1962, and Reese, 1962) that it does exist. There is circumstantial evidence that there is interspecific competition among the sympatric species of Trapezia in the community. This is feasible because the data show that there is probably considerable overlap in the ecological niches of the different species of Trapezia. Coincidences were seen in the habitat space utilized, diet, and reproductive cycles. Some speculation based upon the reoccurring situation observed in communities in the field was made as to what the interactions of the trapezids may be. It was pointed out in a previous section that the community changes as the size of the coral increases. The changes in the composition of trapezid crabs in the community relative to the changes in the community as coral size increases (Figure 13) gave some insight into how the species of *Trapezia* may affect one another.

The species *Trapezia intermedia* was present in all of the communities from the very smallest to the largest ones examined. On the other hand, the species *T. maculata* and *T. digitalis* were present in significantly fewer samples and were absent, except for one small *T. digitalis*, in coral heads with a volume less than 1300 cc. In 80 of the 92 communities *T. intermedia* was the predominant trapezid based on size. In the twelve exceptions *T. maculata* was predominant; in all other cases where *T. maculata* was present (32) it was the most insignificant species of trapezid found. *T. digitalis* was not predominant in any of the communities but occupied a position which is typically intermediate between the two other species; this is expected since it is a smaller species than the other two. A notable point in the data illustrated in Figure 13 is the absence of species other than *T. intermedia* in coral heads smaller than 1300 cc. It was further noted that it was in coral heads of about this size that pairs of *T. intermedia* reached their maximum size, generally decreasing in size with smaller heads and being of relatively the same size in larger heads.

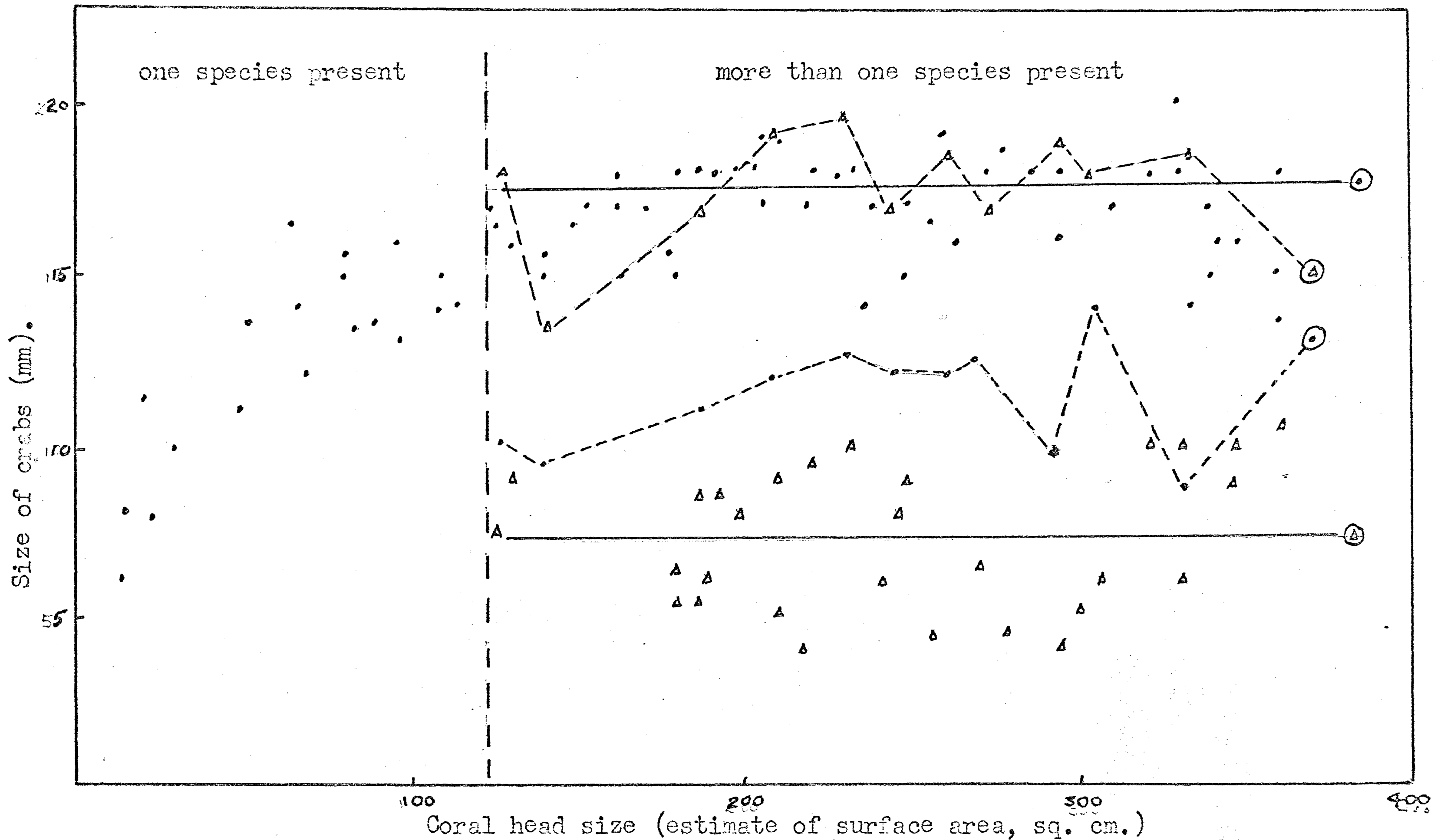

Figure 13. Relationship of maximum size of crabs (measurement across carapace) to size of coral head. Each point represents the size of the largest individual of trapezid crab in each sample. • are T. intermedia, Δ are T. maculata. Solid line indicates usual pattern of dominance between two species, dashed line indicates unusual pattern of dominance. Sample size 92.

The data suggest that in heads smaller than 1300 cc. the coral head itself may limit the maximum size of trapezids. In coral heads larger than this there are no restrictions imposed by the coral head on the size of the crabs, but the latter have reached their maximum size and because they pair they exclude all but one pair of that species from inhabiting the head.

The occurrence of the other two species in the community at this point where the species *T. intermedia* attains maximum size and its numbers are regulated, may indicate that interactions of the different species regulates their presence. A hypothesis which would explain, at least in part, the situation observed in the communities is postulated. Each species of *Trapezia* has a minimum space requirement, or in this case surface area requirement, within the microhabitat. The total surface area present in small coral heads, which may be less than the required amount, would limit the size or total biomass of the symbiont pair. Thus in smaller heads where surface area is at a premium, all species of *Trapezia*, except for the most aggressive would be excluded. In the community studied *T. intermedia* appears to be the most aggressive animal. In larger coral heads this surface area would increase and likewise the crabs would increase in size up to the point where they attain their maximum size. It was observed that the most dominant species, *T. intermedia*, reached its maximum size and biomass in coral heads which fall short of the greatest size the coral heads attain. The surface area of the coral head increases in heads larger than this, and the total amount of surface area present could exceed the amount required by the pair of T. intermedia. Thus there is additional surface area, or habitat space, available in the larger coral heads to the other less aggressive species of Trapezia, and pairs of the other two species begin to appear in the communities of the larger coral. It is inherent in this theory that as long as the amount of available habitat space is equal to or less than the minimum requirement of a pair of trapezids, the animals will compete and exclude any other species from inhabiting the coral head, but this competition breaks down when the amount of available surface area exceeds the minimum requirements of the dominant species. How the other species affect one another is not evident from the data. However, it is evident from the data on the relationship of the total biomass of the trapezids to the increasing surface area (Figure 10) that this theory does not completely account for the regulation of trapezid crabs, since the total biomass of the trapezids does not show a linear correlation with increasing surface area, but it is probable that these are some of the factors entering into the regulation. Furthermore, it is probable that the extent of interaction is much more complex and involves other symbiont species than the trapezids, particularly other crab species which are also found only in larger coral heads.

Another point is brought out in the data concerning the two species T. intermedia and T. maculata (Fig. 13). Although T. intermedia is usually predominant in the community, occasionally the other large species, T. maculata, is predominant. In these latter cases T. intermedia is relegated to a subordinate position in the community. A similar situation was reported by Park (1962) in his study of competition between two species of flour beatles. In the usual situation one species was dominant over the other, which was relegated to a subordinate position, but it was not dominant in all cases; there was always a certain percentage of cases where the other species was able to dominate.

Both of these two hypotheses are speculative and have been suggested as such; only with extensive laboratory experiments, which were beyond the scope of the study, could one substantiate them.

Aside from the points examined, there are probably other interactions among the other symbionts of the community, but no direct evidence of such interaction was found in the study.

An additional point concerning an aspect of interspecific interaction of the symbionts is that because of the consistency in community composition of most of the symbionts, it is improbable that the symbionts are predators on the adults of the other species, but they may prey upon the immature forms which settle out on the coral. This was suggested by stomach contents, where though exact identification of animals was impossible, it was found that all of the animals, particularly crustaceans eaten, were of small size. (Table 7.)

It may be pointed out in conclusion that though there is circumstantial evidence for interspecific competition, no definitive statements can be made about its nature.

VII. Summary and Conclusions

A. The coral head microhabitat is qualitatively uniform in the same habitat and differences among coral heads are mainly quantitative. This suggests that though there is a phenotypic response to the particular environmental conditions where the coral is found, the conformation of the colony is genetically fixed.

B. The species composition of the community in *P. meandrina* is relatively constant. A total of eleven obligate decapod crustacean commensals are found in the coral with four ubiquitous species: *T. intermedia*, *A. lottini*, *S. charon*, and *H. depressus*. Adults of all of the symbionts, with the exception of *H. depressus* and *H. marsupalis*, are found in sexual pairs.

C. The biomass, numerical composition, and species diversity of the community varies with coral head size. There is a marked difference between the communities in very small and the largest sized coral heads.

D. The obligate crustacean commensals do not normally leave the coral head microhabitat.

E. The coral head is a source of food for the commensals. Though it appears that the symbionts feed directly upon the coral polyps and mucus, a more important source of food is the material which is caught on the surface of the coral.

F. The decapod crustacean community as a whole is probably limited by the amount of surface area of the living coral head, which is related to the amount of food available to the commensals.

G. The exact composition of the community is not determined by physical or physical-biotic limitations imposed by the coral head, but probably is influenced by biotic factors arising from intra and interspecific interactions of the symbionts. Circumstantial evidence for both intra and interspecific competition among the symbionts was obtained from the study.

H. The study has given some insight into the nature of the commensal relationship. It has substantiated the opinion that the species of decapod crustaceans are true commensals with the coral. The eleven species of symbionts found in this study are found only in living pocilloporid corals, and do not normally leave the confines of the coral head. It has also been shown that the symbionts derive more from the association than shelter provided by the coral. They depend upon the coral for food, primarily by feeding off of material caught on the coral.

VIII. Acknowledgments

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