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SOME ASPECTS OF THE ECOLOGY OF SEVERAL LARGE,
SYMBIONT-BEARING FORAMINIFERA AND THEIR
CONTRIBUTION TO WARM, SHALLOW-WATER BIOFACIES

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OF THE UNIVERSITY OF HAWAII IN PARTIAL
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DOCTOR OF PHILOSOPHY
IN OCEANOGRAPHY
MAY 1977

By

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ABSTRACT

Fifteen species belonging to four families of large, benthic, symbiont-bearing foraminifera were collected in coral reef-associated environments on Palau, Western Caroline Islands, and Oahu, Hawaii. R-mode cluster analysis revealed four species clusters around Palau. One cluster, dominated by Calcarinidae, was characteristic of seaward reef flats. The second cluster, made up of Marginopora vertebralis, Amphistegina lobifera, and Peneroplis pertusus, was characteristic of more protected shoals having water depths of less than 5 m. The third cluster, typified by A. lessonii, characterized reef slopes at 5-20 m. The fourth cluster consisted of more deeply dwelling species, specifically A. radiata and Nummulites ammonoides. In the samples from Oahu, the calcarinid cluster was absent, M. vertebralis was associated with Spirolina arietina, A. lessonii was associated with A. lobifera and P. pertusus, and A. bicirculata and N. ammonoides typified deeper samples.

A. lessonii, A. lobifera, and Calcarina spengleri reached reproductive sizes in Palau in approximately 3 - 4 months. A. lessonii and A. lobifera in Hawaii matured in about 4 months and one year respectively. A. lessonii and A. lobifera growth rates in the laboratory were light limited. A. lessonii also exhibited photoinhibition of ^{14}C uptake in direct sunlight. A. lobifera, which reproduced at larger sizes and was more fecund than A. lessonii, failed to reproduce at diminished light levels in culture.

Carbonate production rates by selected rotaliine species were up to $1\text{--}6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ on seaward reef flats and $1 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ on lagoonal reef slopes in Palau. Carbonate turnover rates were about 20 times per year. Production rates in Hawaii were up to $0.3 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ on seaward reef slopes, with carbonate turnover rates of about 10 times per year.

Test thickness decreased with habitat depth in the large, symbiont-bearing foraminifera. In rotaliines, change in thickness with diameter ($\Delta t/\Delta d$) was >0.5 in turbulent reef flat species, $0.4\text{--}0.5$ at intermediate depths, and <0.4 in deeper dwelling species. Trends were also evident

in milioline species, although thickness of shallow dwelling miliolines was comparable to deeper dwelling rotaliines. Trochospiral species were thicker than planispiral and discoid forms.

Coiling direction in A. lessonii was predominantly sinistral. A. lobifera was predominantly sinistral in the western Pacific and predominantly dextral in the Hawaiian Islands, with no direction predominant in central Pacific forms. Proportions of minority coiling direction individuals increased in both species in adult size classes. Samples from a 4° C. above ambient thermal effluent were also slightly but significantly enriched in minority coiling individuals of both species. In the laboratory, coiling ratios in clones reflected coiling ratios of the population rather than coiling direction of the individual parent.

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GENERAL INTRODUCTION

THE PROBLEM

Foraminifera have been a common constituent of carbonate biofacies characteristic of warm, shallow seas since the late Paleozoic. Extensive limestone deposits of the early Cenozoic, especially in the Tethyan region, were produced by large, benthic foraminifera. Although more restricted geographically during the late Cenozoic, large, shallow-water, benthic foraminifera still produced substantial amounts of carbonate sediments, particularly on coral reefs and atolls. For example, Chapmann (1900), working with drill cores from Funafuti, noted that the primary constituent of the sand deposits associated with the reef formation were foraminifera. Wells (1957) considered foraminifera third in importance as carbonate producers on modern coral reefs, after corals and calcareous algae.

That foraminifera produce substantial quantities of calcareous sediments in shallow, tropical, nearshore environments is well known, but quantitative rates of production are not. Chave et al (1972) estimated potential carbonate production by a variety of coral reef organisms including benthic foraminifera. Their calculations indicate that foraminifera are potentially as productive as the major reef carbonate producers, coralline algae and coral. Smith (1970) noted similar mean organic carbonate production rates at three temperate localities despite quite different species compositions at the sites. Smith (1973) later found similar seaward coral reef flat carbonate production rates regardless of species composition, and proposed that physical-chemical setting rather than biological composition may be the most important factor controlling calcification rates in marine communities. This hypothesis is consistent with the carbonate production model of Chave et al (1972) that predicts comparable potential carbonate rates for most reef producers. Carbonate production rates by coral and coralline algae are reasonably well known (reviewed by Chave et al 1972, also Littler 1971, others). But estimates of carbonate production rates by foraminifera in tropical environments are limited to the prediction of Chave et al (1972) and a single value from a tidepool population of Amphistegina (Muller 1974).

The purpose of this study is to determine if foraminifera are capable of producing carbonate in the coral reef environment at rates comparable to those of the other major carbonate producers. Carbonate production will be defined as the amount of CaCO_3 produced per unit area of reef. Carbonate will be discussed as CaCO_3 , although up to 16 percent may actually be MgCO_3 (Chave 1954). The term reef will be used as it was used by Chave et al (1972, p. 124), i.e., "includes all of the macro- and microenvironments of the system related to the reef community--lagoon, reef flat, algal ridge, outer slope, and so forth".

Solving the problem of carbonate productivity by foraminifera required information regarding the abundance and population biology of the large species in the reef environment. Therefore, the first section of this paper deals initially with the distribution and abundance of reef foraminifera, then with the population biology of selected species, and finally uses data from both these aspects to estimate foraminiferal production of carbonate material in selected environments.

Observations made while studying the principal problem revealed two aspects of the morphology of large foraminifera related to their distribution and role in the nearshore environment of warm, shallow, tropical seas. These are discussed in the second section of this paper.

SYSTEMATICS

A common characteristic of reef dwelling large foraminifera, including Archaias, Peneroplis, Marginopora, Sorites, Alveolinella, Cycloclypeus, Heterostegina, and Amphistegina, appears to be the maintenance of algal cells (Winter 1907; Cushman 1922, 1930, 1940; Doyle and Doyle 1940; Ross 1972). The relationship may be functionally similar to algal symbiosis in hermatypic corals (Chapronerie 1975). Evidence of algal symbiosis has been reported for several species; Archaias angulatus (Lee and Zucker 1969), Marginopora vertebralis (Smith and Wiebe submitted), Heterostegina depressa (Franzisket and Röttger submitted) and Amphistegina lessonii (Muller submitted).

Fifteen foraminiferal species which are known or suspected to maintain algal symbionts were chosen for this study. These species belong to four families, Asterigerinidae, Calcarinidae, Nummulitidae, and Soritidae, which commonly occur in modern coral reef environments. Specimens were collected in field samples from Palau, Western Caroline Islands, and Oahu, Hawaii.

The term "large foraminifera" is used in this study, mainly for convenience, to refer to the relative size of the individuals. The families chosen for study are included in the "larger foraminiferids" discussed by Murray (1973). However, usage of "large foraminifera" should not be confused with the term "larger foraminifera" used commonly to refer to certain species which are large in size and that are generally identified from thin sections.

The following alphabetic listing includes pertinent remarks on the systematics of the fifteen species discussed in this paper. The holotype reference (asterisk) and brief synonymy are included.

FAMILY: ASTERIGERINIDAE

Amphistegina bicirculata Larsen

Pl. I, fig. 1a, b

1965 Amphistegina radiata (Fichtel and Moll): Todd; p. 34, pl. 14, fig. 3 a-c.

* 1976 Amphistegina bicirculata Larsen: p. 10, pl. 2, fig. 1-5; p. 16, text fig. 9.2, 10.2.

Remarks: This species was found only in samples from Hawaii. However, all samples collected in Palau were from 30 m or less while most occurrences of the species in Hawaii were from greater depths. The absence of the species in Palau samples may reflect failure to sample the habitat of the species rather than the absence of the species from the locality.

Amphistegina lessonii d'Orbigny

Pl. I, fig. 3a, b

* 1826 Amphistegina lessonii d'Orbigny: p. 304, Modeles No. 98, 4 me livraison.

1965 Amphistegina madagascariensis d'Orbigny: Todd; p. 34, pl. 12, fig. 1 a-c, 2 a-c.

1976 Amphistegina lessonii d'Orbigny: Larsen; p.9, pl. 1, fig. 1-5, p. 16, text fig. 9.1, 10.1.

Remarks: This species was included in A. madagascariensis d'Orbigny sensu Muller (1974). Specimens were collected in Hawaii and Palau.

Amphistegina lobifera Larsen

Pl. I, fig. 2a, b

1965 Amphistegina madagascariensis d'Orbigny: Todd; p. 34, pl. 11, fig. 3 a-c.

1975 Amphistegina madagascariensis d'Orbigny: Coulbourn and Resig; p. 112, fig. 8.

* 1976 Amphistegina lobifera Larsen: p. 11, pl. 3, fig. 1-5; p.16, text fig. 9.3, 10.3.

Remarks: This species was included in A. madagascariensis sensu Muller (1974). Specimens were collected in Hawaii and Palau.

Amphistegina radiata (Fichtel and Moll)

Pl. I, fig. 4a, b

*1798 Nautilus radiatus Fichtel and Moll: p. 58, tab. 8, fig. a-d.

1965 Amphistegina lessonii d'Orbigny: Todd; p. 33, pl. 11, fig. 4 a-c.

1976 Amphistegina radiata (Fichtel and Moll) Larsen; p. 13, pl. 5,
fig. 1-4; p. 16, text fig. 9.5, 10.5.

Remarks: This species occurred only in samples collected in Palau.

FAMILY CALCARINIDAE

Baculogypsina sphaerulata (Parker and Jones)

Pl. I, fig. 5

* 1860 Orbitolina concava Lamarck var. sphaerulata Parker and Jones:
p. 33, 38.

1960 Baculogypsina sphaerulata (Parker and Jones): Barker; p. 208,
pl. CI, fig. 4-7.

1965 Baculogypsina sphaerulata (Parker and Jones): Todd; p. 36, pl. 9,
fig. 4 a, b.

Remarks: This species occurred only in samples collected in Palau.

Calcarina calcar d'Orbigny

Pl. II, fig. 3a, b

* 1826 Calcarina calcar d'Orbigny: p. 276, #1.

1960 Calcarina calcar d'Orbigny: Barker; p. 222, pl. CVIII, fig. 3.

Remarks: This species occurred only in samples collected in Palau.

Calcarina hispida Brady

Pl. II, fig. 2a, b

* 1876 Calcarina hispida Brady: p. 590, pl. CVIII, fig. 8, 9.

1959 Calcarina hispida Brady: Graham and Militante; p. 106, pl. 17,
fig. 5-7, a, b.

Remarks: This species occurred only in samples collected in Palau.

Calcarina spengleri (Gmelin)

Pl. II, fig. 1a, b

* 1781 "Ammonshorn" Spengler; p. 373, pl. 2, fig. 9 b-c.

1954 Calcarina spengleri (Gmelin): Cushman et al; p. 363, pl. 82, fig. 10, 11; pl. 92, fig. 1-7.

1959 Calcarina spengleri (Gmelin): Graham and Militante; p. 107, pl. 17, fig. 8-9 a, b; 10-11; 12-13 a, b.

Remarks: This species occurred only in samples collected in Palau.

FAMILY: NUMMULITIDAE

Heterostegina depressa d'Orbigny

Pl. II, fig. 5

* 1826 Heterostegina depressa d'Orbigny: p. 305, n. 2, pl. XVIII, fig. 5-7.

1960 Heterostegina depressa d'Orbigny: Barker; p. 232, pl. CXII, fig. 14-18.

1974 Heterostegina depressa d'Orbigny: Röttger; p. 5-12, fig. 1-6.

Remarks: This species occurred in samples from Hawaii and Palau.

Nummulites ammonoides (Gronovius)

Pl. II, fig. 4a, b

* 1781 Nautilus ammonoides Gronovius: p. 262, pl. 19, fig. 5-6.

1960 Operculina ammonoides (Gronovius): Barker; p. 230, pl. CXII, fig. 3-9.

Remarks: This species occurred in samples from Hawaii and Palau. Adult specimens from Palau tended to be larger and more beaded than specimens from Hawaii.

FAMILY: SORITIDAE

Archaias angulatus (Fichtel and Moll)

Pl. III, fig. 1a, b

* 1798 Nautilus angulatus Fichtel and Moll: p. 113, pl. 22, fig. a-c.1960 Archaias angulatus (Fichtel and Moll): Barker; p.28, pl. XIV,
fig 1, 2, 6.1973 Archaias angulatus (Fichtel and Moll): Brooks; p. 415, pl. 9,
fig. 16-20.

Remarks: This species occurred only in samples collected in Palau.

Marginopora vertebralis Blainville

Pl. III, fig. 2a, b

* 1830 Marginopora vertebralis Blainville: p. 412, pl. 69, fig.6.6 a-c.1960 Marginopora vertebralis Blainville: Barker; p.32, 34, pl. XVI,
fig. 1-6, 8-11; pl. XVII, fig. 1-6.1975 Marginopora vertebralis Blainville: Coulbourn and Resig; p.111, fig.7.

Remarks: This species occurred in samples from Palau and Hawaii.

Specimens which may belong to the species Amphisorus hemprichii Ehrenberg
were included in this species for analysis purposes as in Cole (1954),
Cushman et al (1954), and Graham and Militante (1959).Peneroplis pertusus (Forsk.)

Pl. III, fig. 3a, b

* 1775 Nautilus pertusus Forskal: p. 125, no. 65.1960 Peneroplis pertusus (Forsk.): Barker; p. 26, pl. XIII, fig. 16.

Remarks: This species occurred in samples from Hawaii and Palau.

Sorites marginalis (Lamarck)

Pl. III, fig. 5a, b

* 1816 Orbulites marginalis Lamarck: p. 1961954 Sorites Marginalis (Lamarck): Cushman et al; p. 348, pl. 82, fig. 4.1960 Sorites marginalis (Lamarck): Barker; p. 30, pl. XV, fig. 1-3, 5.

Remarks: This species occurred in samples from Hawaii and Palau.

Spirolina arietina (Batsch)

Pl. III, fig. 4a, b

* 1791 Nautilus (Lituus) arietinus Batsch (part): p. 4, pl. 6, fig. 15 c.

1954 Spirolina arietina (Batsch): Cushman et al; p. 348, pl. 87, fig. 4-5.

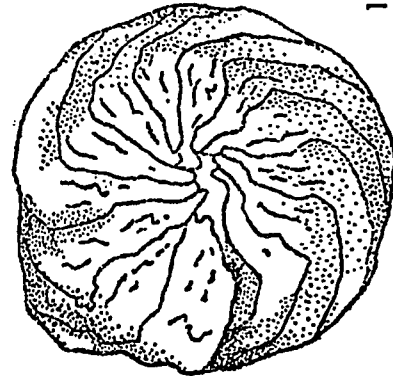
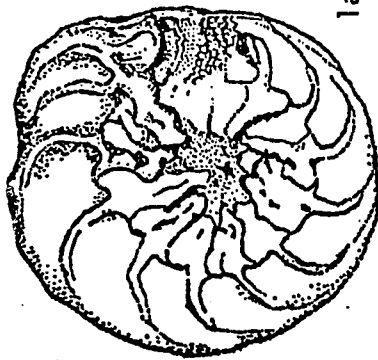
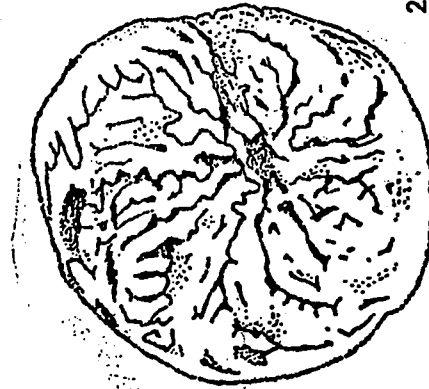
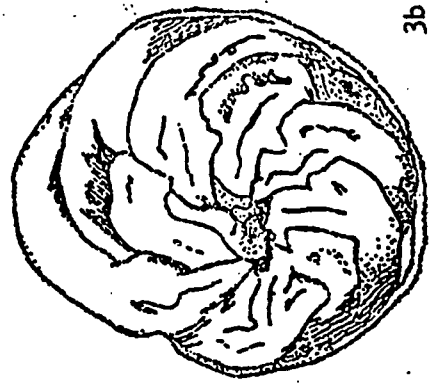
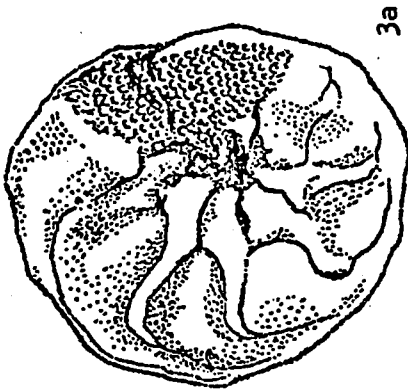
1971 Spirolina arietina (Batsch): Coulbourn; p. 133, pl. III, fig. 2a, b.

Remarks: This species occurred in samples from Hawaii and Palau.

Plate I

Figure

1	<u>Amphistegina</u> <u>bicirculata</u>	(X26)
2	<u>Amphistegina</u> <u>lobifera</u>	(X49.5)
3	<u>Amphistegina</u> <u>lessonii</u>	(X51.5)
4	<u>Amphistegina</u> <u>radiata</u>	(X39)
5	<u>Baculogypsina</u> <u>sphaerulata</u>	(X49)



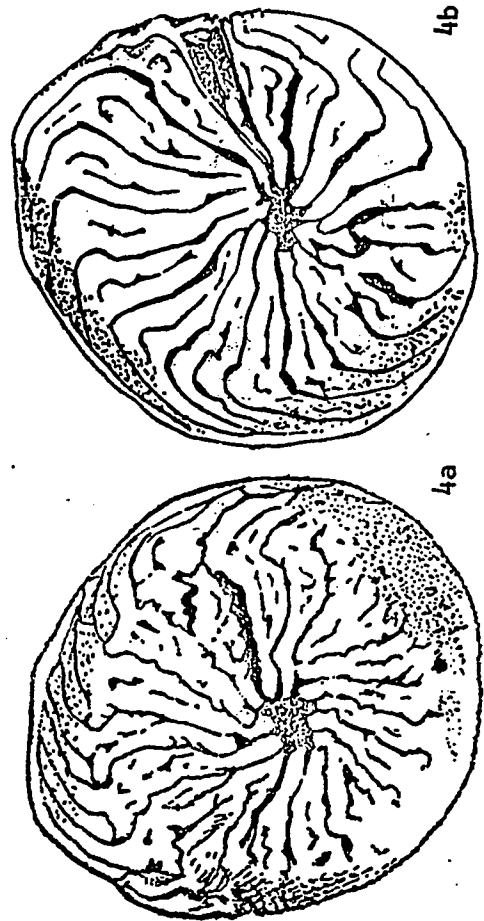
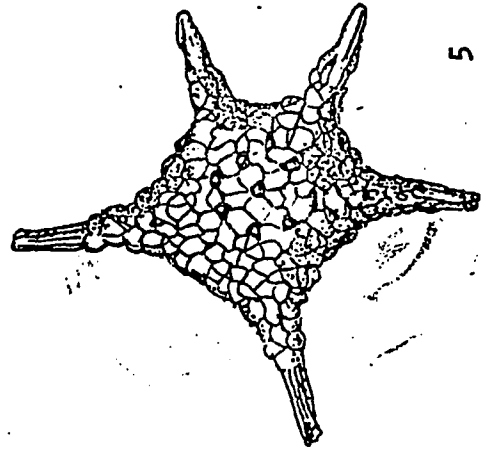
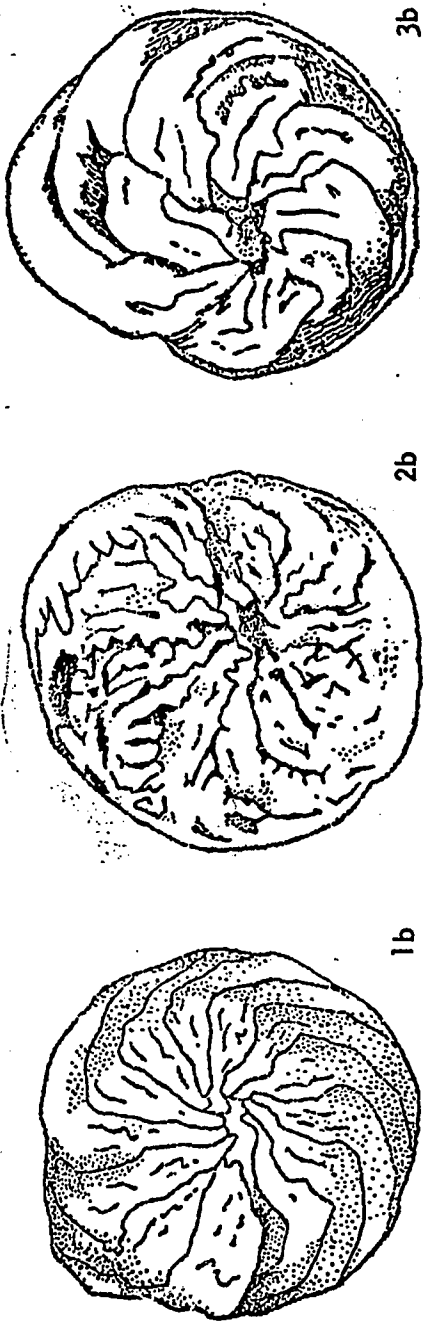
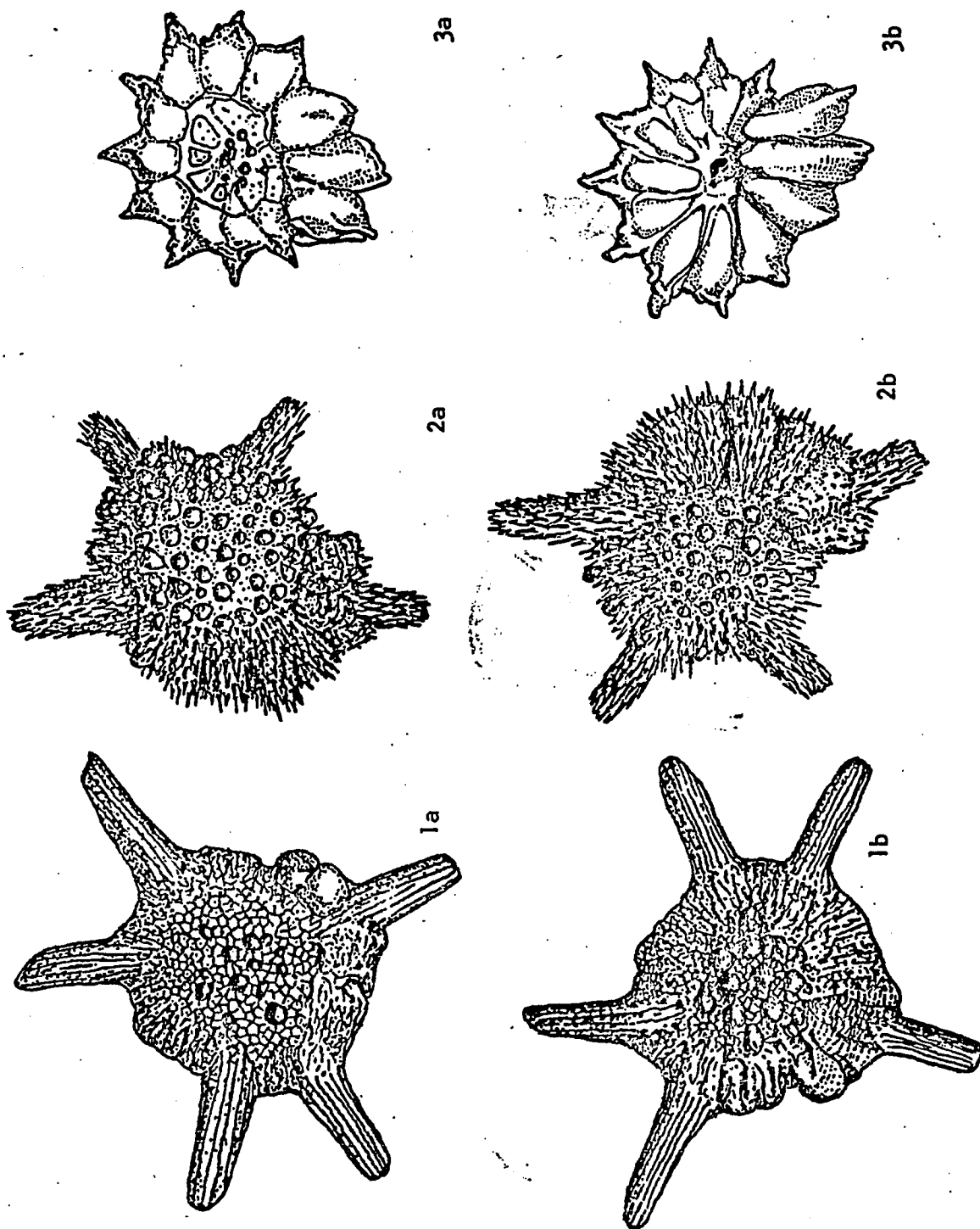


Plate II

Figure

1	<u>Calcarina</u> <u>spengleri</u>	(X46)
2	<u>Calcarina</u> <u>hispida</u>	(X32.5)
3	<u>Calcarina</u> <u>calcar</u>	(X49)
4	<u>Nummulites</u> <u>ammonoides</u> :	
	a. Palau	(X45)
	b. Hawaii	(X90)
5	<u>Heterostegina</u> <u>depressa</u>	(X48)



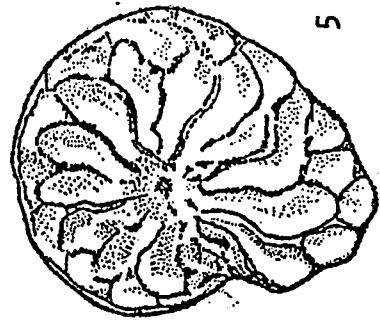
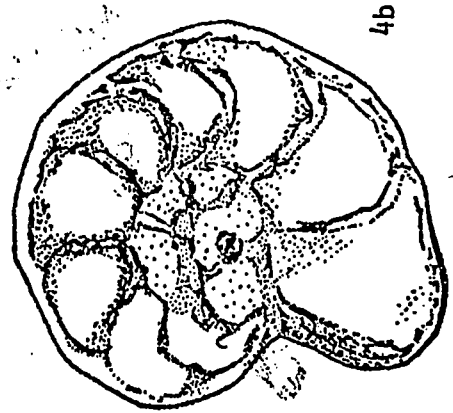
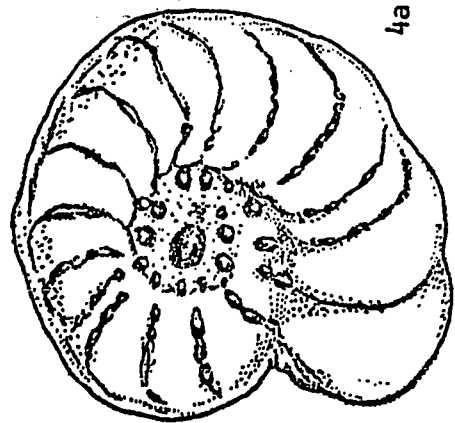
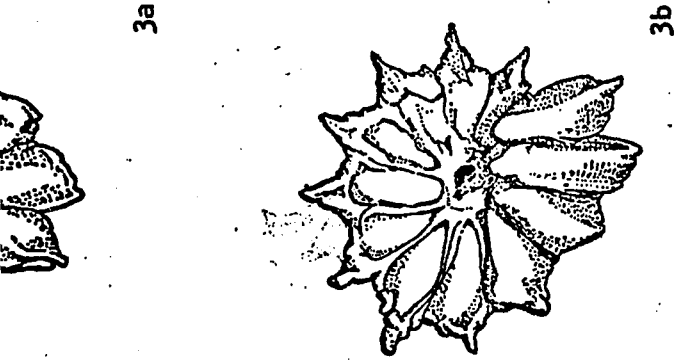
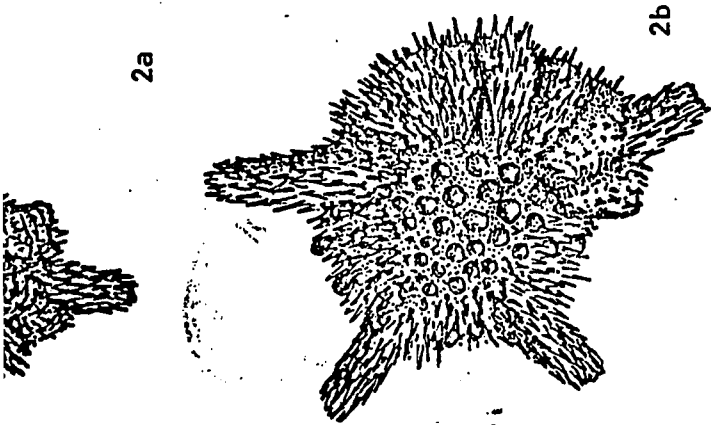
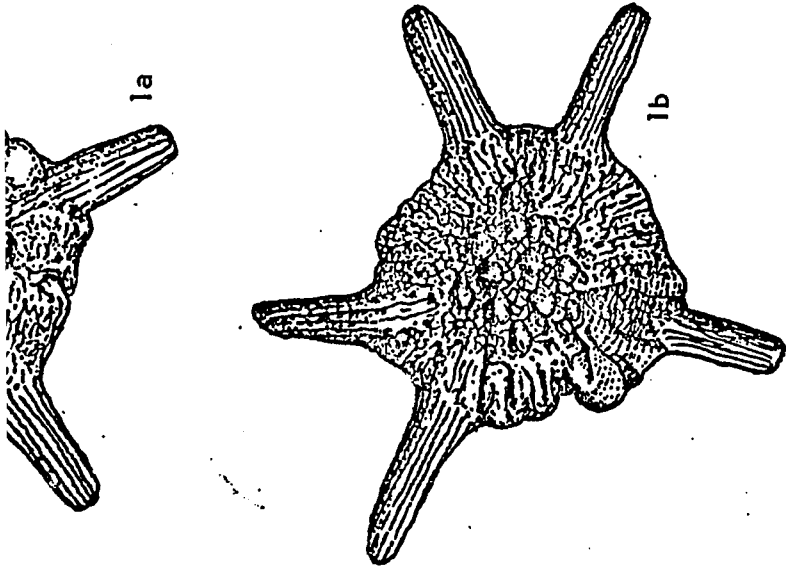
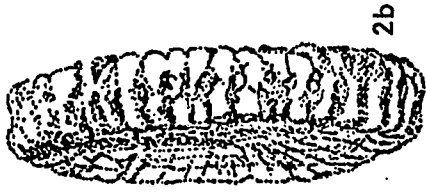


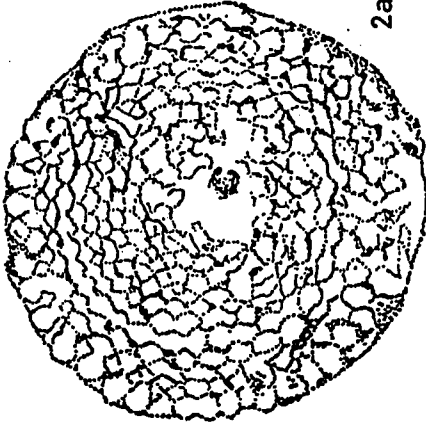
Plate III

Figure

1	<u>Archaias angulatus</u>	(X33.7)
2	<u>Marginopora vertebralis</u>	(X41.5)
3	<u>Peneroplis pertusus</u>	(X50.8)
4	<u>Spirolina arietina</u>	(X26)
5	<u>Sorites marginalis</u>	(X62)



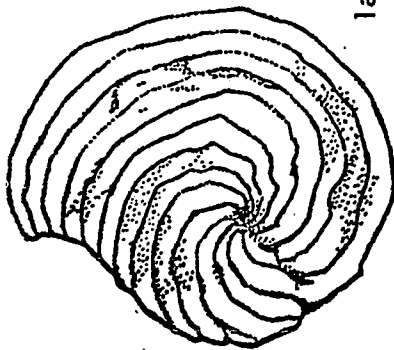
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2a



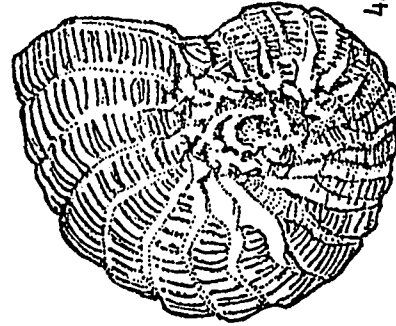
1b



1a



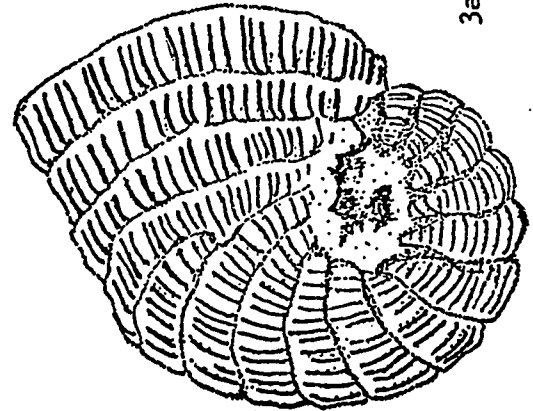
4b



4a



3b



3a



1a



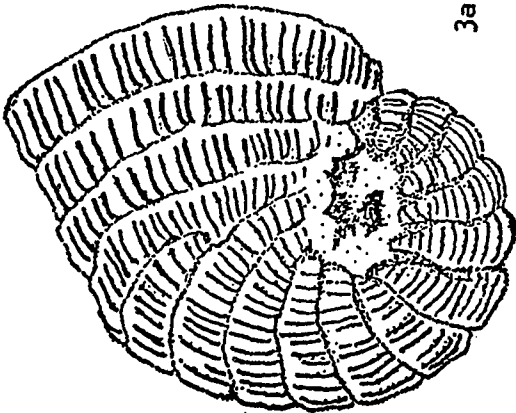
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2a



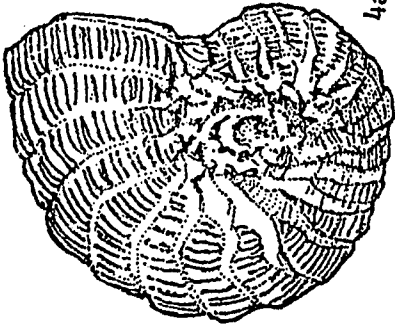
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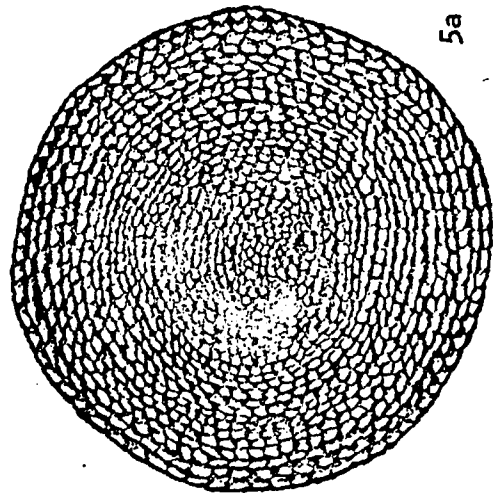
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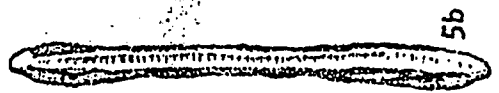
4a



4b



5a



5b

SECTION I. POPULATION BIOLOGY AND CARBONATE PRODUCTIVITY

The parameters necessary to make estimates of carbonate production rates are known for very few populations of foraminifera. Studies of this kind of Holocene species are potentially applicable in a variety of areas of research. Foraminifera as part of the nearshore benthic community are useful environmental indicators as their tests leave a record of past and present conditions. Foraminifera as part of the coral reef community are useful in furthering understanding of both organic and carbonate productivity of this specialized environment. Foraminifera as producers of sand-sized sediments are economically important in beach and nearshore environments both as sediment producers and tracers. Finally, studies of living foraminifera may be paleo-ecologically useful in understanding distributions and productivities of fossil foraminiferal communities.

DISTRIBUTIONAL STUDIES

INTRODUCTION

Distributions of living large benthic foraminifera of the tropical Pacific remain relatively unknown. Most of the early works with assemblages of foraminifera in the Pacific (Brady 1884; Cushman 1921, 1924, 1933; Cushman et al 1954; Graham and Militante 1959; Todd 1961, 1965; others) considered "total fauna", i.e. , all foraminiferal tests found in sediment samples, contributing primarily geographical and general distributional data. Todd (1960, 1965, 1976) synthesized much of this information with respect to distributions of the *Asterigerinidae* and *Calcarinidae*. Hawaiian foraminiferal distributions have been investigated by Coulbourn (1971), Coulbourn and Resig (1975), and Bell (1976) and applied to sedimentological studies. However, few specific ecological data on living assemblage compositions, habitats, depth distributions, and standing crops are available either for species occurring in Hawaii or the Indo-Pacific in general.

The purpose of this study is to determine the assemblages and standing crops of large foraminifera in a variety of reef-associated environments, and to compare these assemblages in Palau and Hawaii. Zoogeographically, Palau lies near the faunistic center of the Indo-West Pacific while Hawaii is considered an outpost of that region (Ekman 1953), so this information may indicate if the coral reef-associated large foraminiferal community in Hawaii is basically a depauperate subset of the comparable Indo-West Pacific community.

STUDY AREAS

The Palau Islands of the Western Caroline Islands are located in the western Pacific at $6^{\circ}53'$ to $8^{\circ}12'$ N. latitude and $134^{\circ}08'$ to $134^{\circ}44'$ E. longitude, on the eastern boundary of the Philippine Sea. Wind systems influencing the chain are the northeast trades from December to March and southwest monsoons from June to October, with variable winds during the other months. Sea surface temperatures range from 26° C. in winter to 29° C. in summer.

The Palau chain, which extends approximately 150 km and consists of more than 200 islands, is partially enclosed by a barrier reef. Environments include barrier reefs, exposed and protected fringing reefs, patch reefs, and open and protected lagoons. Islands range in size from volcanic Babelthup at 285 km^2 to tiny limestone stacks of less than 1 m^2 (Corwin 1951).

Oahu, in the Hawaiian Islands, is located at $21^{\circ}15'$ to $21^{\circ}44'$ N. latitude and $157^{\circ}39'$ to $158^{\circ}17'$ W. longitude. Oahu lies under the influence of the northeast trade winds which are strongest from June to September. During the winter months, December to March, the trades weaken and are replaced by westerly winds of the north temperate zone about 10-15% of the time (Moberly and Chamberlain 1964). Sea surface temperatures range from 23° C. in winter to 26° C. in summer.

Reefs around Oahu can be placed into three major classes: shallow, fringing reefs of east (windward) coasts; shallow, protected reefs of south coasts; and deeper, irregular reefs of the north and west coasts (Moberly and Chamberlain 1964).

METHODS

Spatial distribution of the large species of benthic foraminifera of Palau was studied from bottom samples collected between April 1972 and June 1973. Several types of environments were selected for sampling, including open ocean-exposed barrier and fringing reefs, open lagoon barrier, fringing and patch reefs, and protected lagoon patch and fringing reefs. Seventeen sites were sampled, generally by taking two samples at each of six depths (mean low water, 2, 5, 10, 15, and 20 m), along lines perpendicular to the shore or reef face. Two temporal stations, a lagoon site on the west side of the island chain at 2 m depth (PS-16) and a fringing reef site on the east side at 1 m depth (PS-17), were sampled monthly during the period. At each site each month, three samples were taken along a 20 m transect at locations selected on a random numbers table. All samples were collected by a diver using snorkel or SCUBA, and, depending upon the substrate, consisted of 25 cm² surface area samples of algae or sediment, or cobbles or pieces broken from the bottom whose surface area was measured. Samples were processed as described previously (Muller 1974). Foraminifera determined to be alive at the time of collection were identified and counted.

Spatial distribution of the large species of benthic foraminifera from Oahu was studied from bottom samples collected between May 1974 and May 1976. Diver collected samples were taken at 16 sites around Oahu, with each major reef type sampled at least twice. In most cases, two samples were collected at each of the following depths: mean low water 2, 5, 10, and 15 m, along lines perpendicular to the beach. Samples were collected and processed, as described earlier. Samples from deeper than 30 m were obtained using a small pipe dredge and their depths were determined using a depth recorder. Nine samples were dredged from outside Kaneohe Bay and 23 were dredged offshore from Honolulu Harbor. Dredged samples were analyzed in terms of species composition per cubic centimeter of sediment.

Data analysis

Density of foraminifera in replicate samples tended to be variable, the result of clumping of young as the result of reproduction by multiple

fission. The variance in a set of samples tended to be related to the mean density of the set as higher density populations have increased probability of clusters of young. Logarithmic transformation was applied to the raw density data for two reasons: the transformed data were graphically more manageable and the variances were rendered independent of the means (Sokal and Rohlf 1969) so that parametric analysis of variance could be applied.

Cluster analysis was chosen as a convenient way of graphically illustrating relationships among variables or cases to facilitate data description. Correlation matrices were constructed using the BMDP1M statistical program (Dixon 1975). Cluster analysis of species and samples was performed using an unweighted pair-group method which develops clusters from correlation coefficient matrices. A program developed by McCammon and Wenninger (1970) and adapted by D. Kam (pers. comm.) generated the dendrographs.

RESULTS

Palau

The large foraminiferal species considered in the Palau samples were the miliolines Archaias angulatus, Marginopora vertebralis, Peneroplis pertusus, Sorites marginalis, and Spirolina arietina, and the rotaliines Amphistegina lessonii, A. lobifera, A. radiata, Baculogypsina sphaerulata, Calcarina calcar, C. hispida, C. spengleri, Heterostegina depressa, and Nummulites ammonoides. Sampling stations are shown in figure 1a and described in Appendix A. Data from individual samples are listed in Appendix B.

A general overview of the distributions of large foraminifera by depth was provided by averaging their abundance in samples from each depth (figure 2). Archaias angulatus, B. sphaerulata, C. calcar, and C. spengleri were virtually restricted to depths of less than 5 m. At 1-5 m, P. pertusus and Amphistegina lobifera were relatively abundant. A. lessonii dominated the community between 5 and 20 m. At 20-30 m, A. radiata and N. ammonoides appeared. The remaining species were never abundant, although M. vertebralis, Spirolina arietina, and H. depressa were common throughout the range of depths sampled.

Cluster analysis of species data illustrated the relationships among the species (figure 3), revealing four major clusters (table 1). One species, C. hispida, was not linked to any group, although it was weakly correlated to A. lessonii and H. depressa as individual species (table 2). Clusters I and II were further connected into a large grouping, which, as seen in figure 2 occupied the infralittoral fringe (< 2 m). Over the depth range sampled, the group containing A. lessonii occupied intermediate depths (> 2 m), and A. radiata-N. ammonoides were from the greatest depths sampled (≥ 15 m).

The sample clustering revealed six assemblages whose distributions are shown in figure 1b-d.

Assemblage A, characteristic of exposed reef flats, contained predominantly Cluster I, and secondarily Cluster II, with Clusters III and IV usually absent. The highest densities were recorded in this

Figure 1. Palau: a. Station Locations
b. Assemblages <5 m.
c. Assemblages 5-15 m.
d. Assemblages 20-30 m.
(Assemblages described in Table 1)

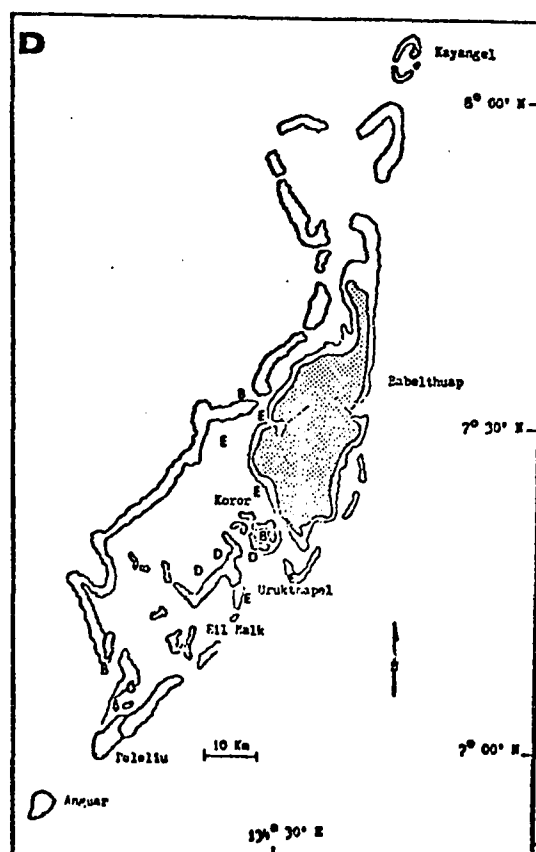
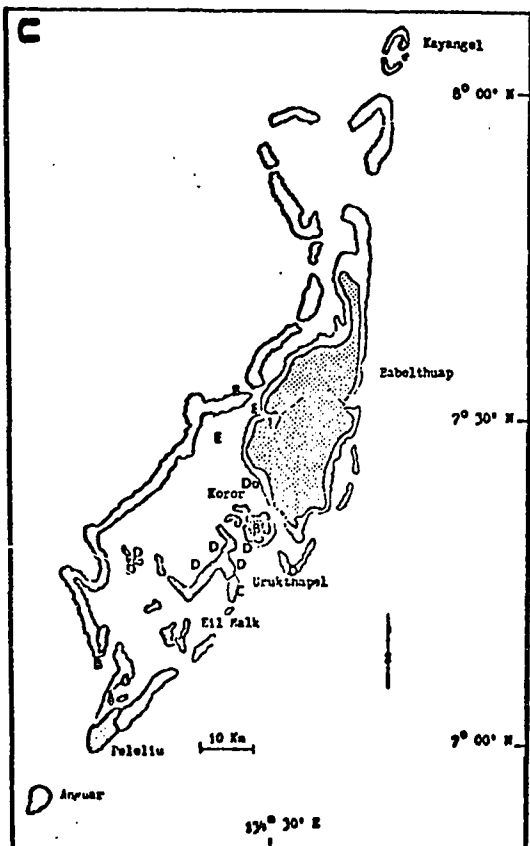
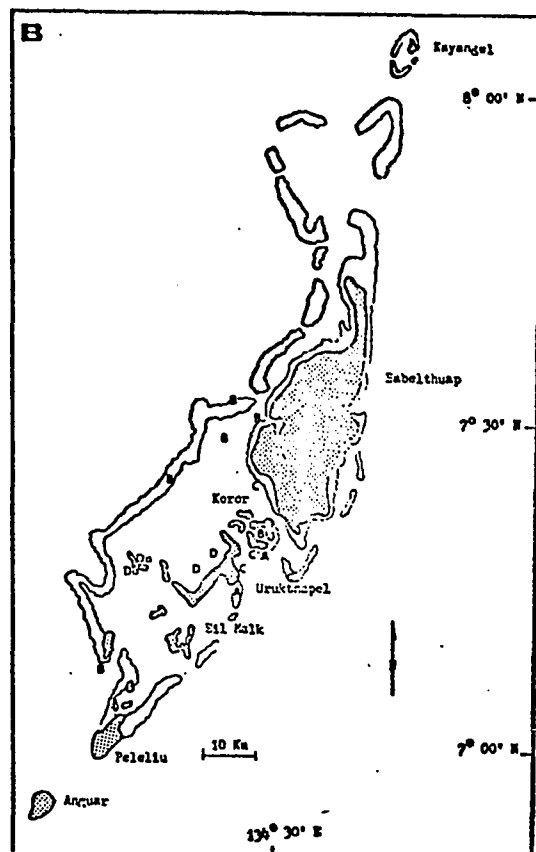
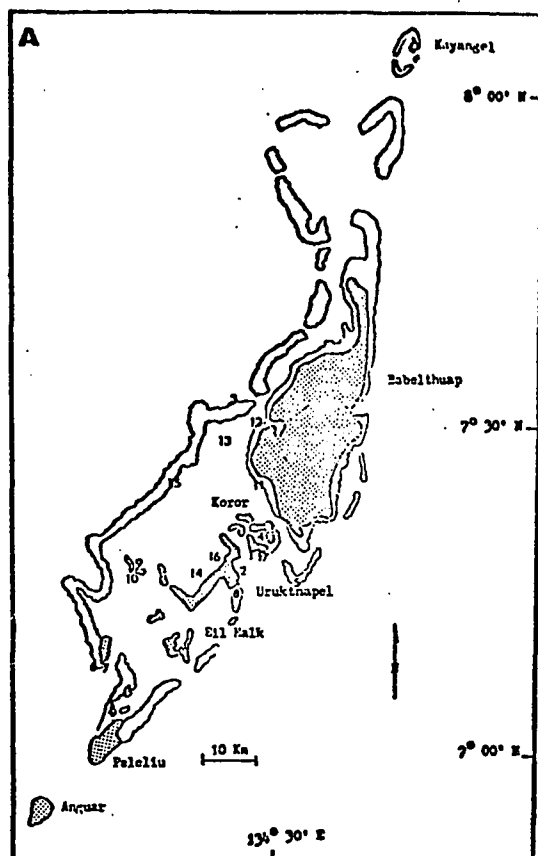


Figure 2. Depth distributions of 14 species of large foraminifera in Palau samples.

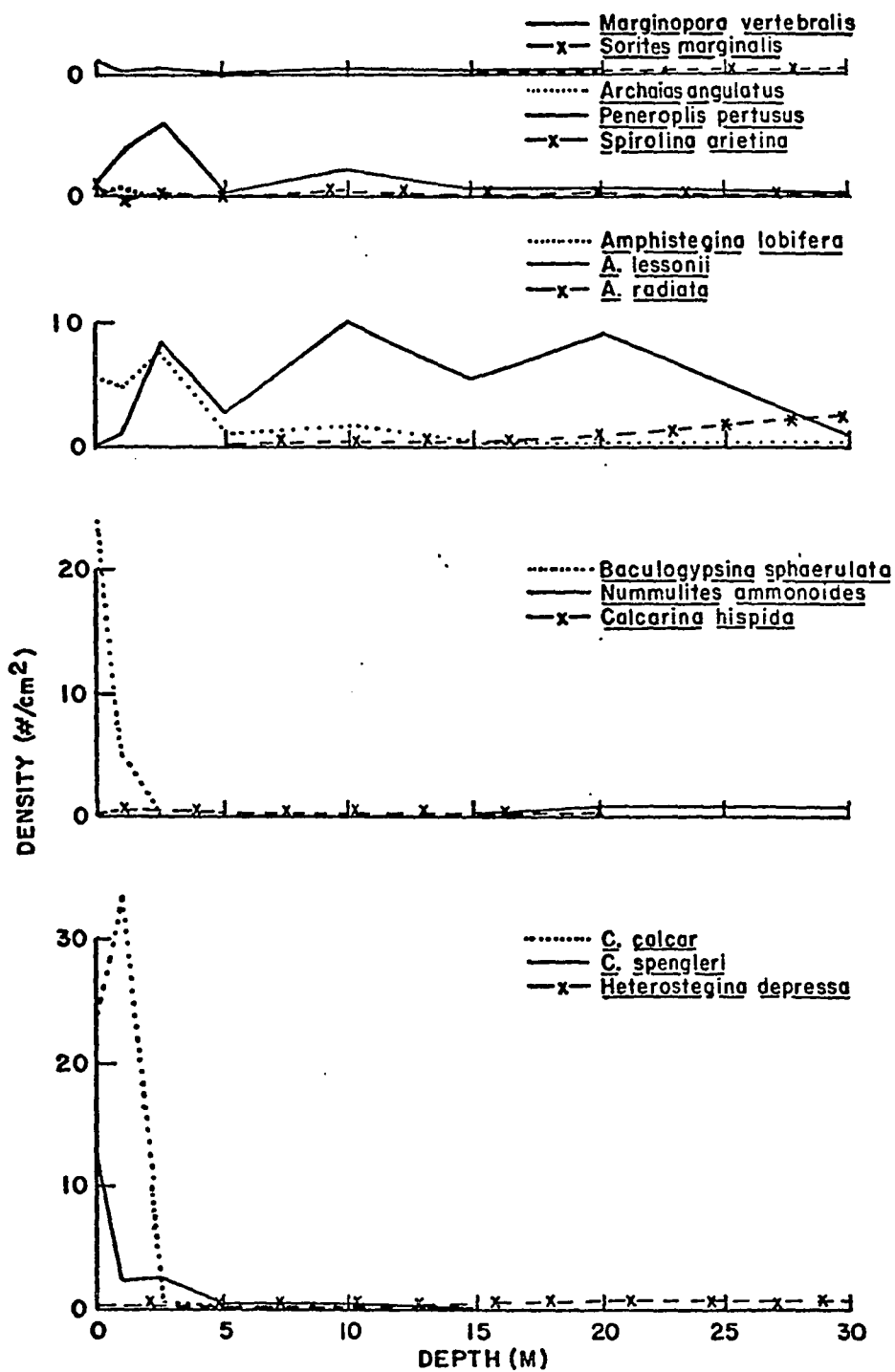


Figure 3. Dendrograph showing species clusters identified in field samples from Palau,

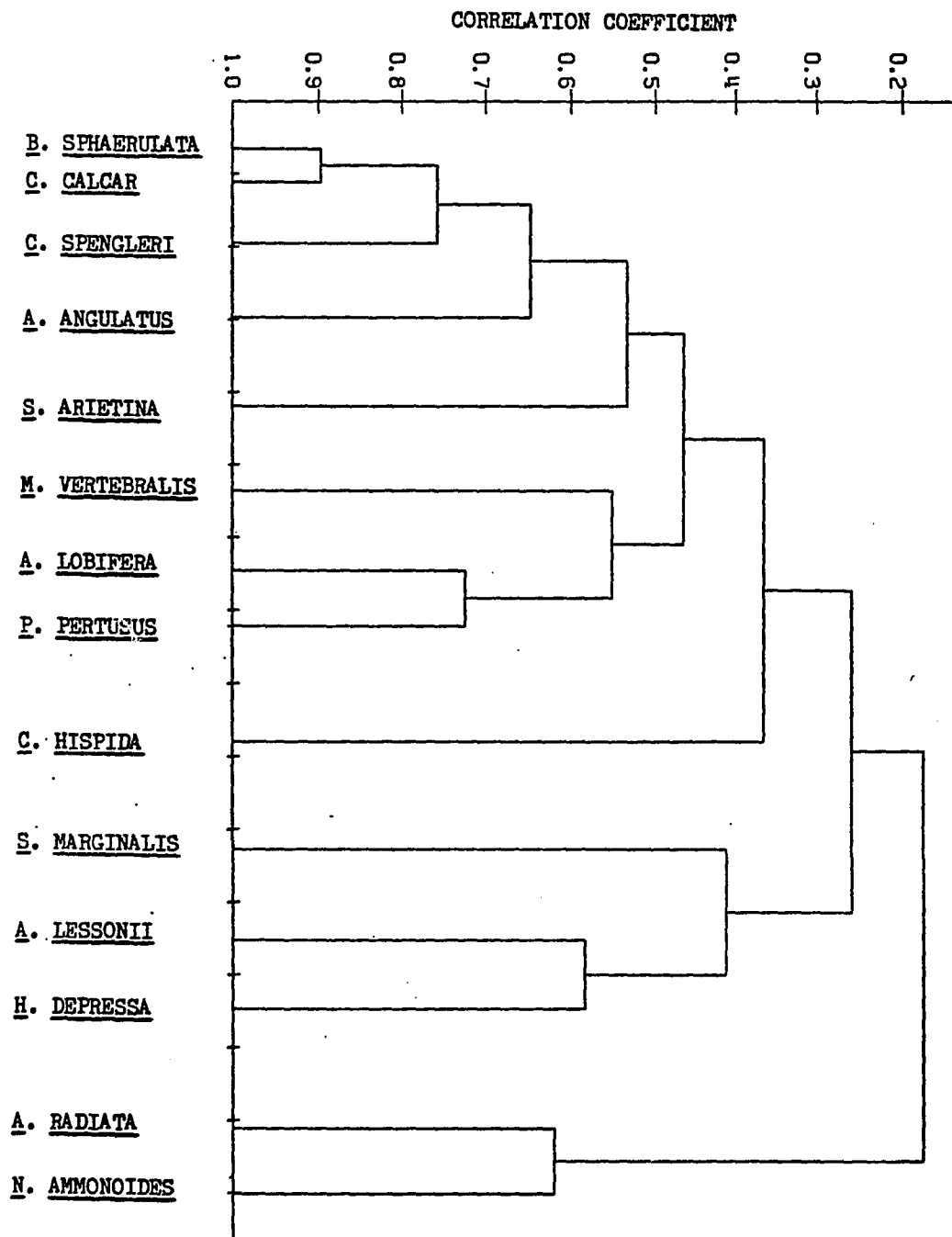


Table 1

Comparison of Compositions of Species Clusters
and Assemblages in Samples from
Palau and Hawaii

Group	Composition	
	Palau	Hawaii
Cluster I	<u>Calcarina calcar</u> <u>Baculogypsina sphaerulata</u> <u>C. spengleri</u> <u>Archaias angulatus</u> <u>Spirolina arietina</u>	None
Cluster II	<u>Amphistegina lobifera</u> <u>Peneroplis pertusus</u> <u>Marginopora vertebralis</u>	<u>Spirolina arietina</u> <u>Marginopora vertebralis</u>
Cluster III	<u>Amphistegina lessonii</u> <u>Heterostegina depressa</u> <u>Sorites marginalis</u>	<u>Amphistegina lessonii</u> <u>Amphistegina lobifera</u> <u>Peneroplis pertusus</u> <u>Heterostegina depressa</u>
Cluster IV	<u>Nummulites ammonoides</u> <u>Amphistegina radiata</u>	<u>Nummulites ammonoides</u> <u>Amphistegina bicirculata</u>
Unassociated	<u>C. hispida</u>	<u>Sorites marginalis</u>
Assemblage A	Cluster I Cluster II	Cluster II
Assemblage B	Very low density	Devoid of large forams
Assemblage C	Cluster II	<u>Amphistegina lobifera</u> Clusters II and III
Assemblage D	<u>A. lessonii</u> Clusters III and II	<u>Amphistegina lessonii</u> Clusters III and II
Assemblage D-a	<u>Calcarina hispida</u> and Cluster III	None
Assemblage E	Clusters III and IV	Clusters III and IV
Assemblage F	Not sampled	Cluster IV

Table 2.

Correlation Matrix of Large Foraminifera from 256 Samples from Palau.

	<u>Archaias</u> <u>angulatus</u>	<u>Marginopora</u> <u>vertebralis</u>	<u>Peneroplis</u> <u>pertusus</u>	<u>Sorites</u> <u>marginalis</u>	<u>Spirolina</u> <u>arietina</u>	<u>Amphistegina</u> <u>lessonii</u>	<u>Amphistegina</u> <u>lobifera</u>
<u>A.angulatus</u>	1.000						
<u>M.vertebralis</u>	0.185**	1.000					
<u>P.pertusus</u>	0.445**	0.358**	1.000				
<u>S.marginalis</u>	-0.050	0.027	0.207**	1.000			
<u>S.arietina</u>	0.256**	0.420**	0.412**	0.375**	1.000		
<u>A.lessonii</u>	-0.192**	0.215**	0.442**	0.352**	0.270**	1.000	
<u>A.lobifera</u>	0.370**	0.544**	0.724**	0.011	0.396**	0.441**	1.000
<u>A.radiata</u>	-0.086	-0.071	-0.242**	0.028	-0.057	-0.017	-0.219**
<u>B.sphaerulata</u>	0.562**	0.317**	0.286**	-0.079	0.408**	-0.314**	0.305**
<u>C.calcar</u>	0.631**	0.314**	0.469**	-0.092	0.356**	-0.236**	0.441**
<u>C.hispida</u>	-0.056	0.013	-0.013	-0.061	-0.013	0.139*	0.015
<u>C.spengleri</u>	0.362**	0.468**	0.499**	-0.112	0.358**	-0.028	0.624**
<u>H.depressa</u>	-0.106	0.213**	0.331**	0.280**	0.381**	0.584**	0.422**
<u>N.ammonoides</u>	-0.067	-0.089	-0.177**	-0.001	0.053	0.068	-0.211**

** Significant correlation ($P < 0.01$)* Significant correlation ($P < 0.05$)

(cont.)

Table 2. (cont.)

	<u>Amphistegina</u> <u>radiata</u>	<u>Baculogypsina</u> <u>sphaerulata</u>	<u>Calcarina</u> <u>calcar</u>	<u>Calcarina</u> <u>hispida</u>	<u>Calcarina</u> <u>spengleri</u>	<u>Heterostegina</u> <u>depressa</u>	<u>Nummulites</u> <u>ammonoides</u>
<u>A. radiata</u>	1.000						
<u>B. sphaerulata</u>	-0.135*	1.000					
<u>C. calcar</u>	-0.174**	0.897	1.000				
<u>C. hispida</u>	-0.029	-0.027	-0.002	1.000			
<u>C. spengleri</u>	-0.213**	0.657**	0.677**	-0.037	1.000		
<u>H. depressa</u>	0.194**	-0.026	0.018	0.151*	0.169**	1.000	
<u>N. ammonoides</u>	0.620**	-0.105	-0.138*	-0.022	-0.182**	0.162**	1.000

** Significant correlation (P. < 0.01)

* Significant correlation (P < 0.05)

assemblage, up to $600/\text{cm}^2$.

Assemblage B, characterized by very low species densities ($<1/\text{cm}^2$) of usually A. lobifera, A. lessonii, and a few other species, were found at sites of high current scour or in sediments.

Assemblage C was dominated by Cluster II, primarily A. lobifera and occasionally Peneroplis or Marginopora, with Clusters III and I usually represented. This was a low density assemblage found at <15 m, usually between Assemblages A and D or on protected reef flats where Cluster I was not abundant.

Assemblage D, dominated by A. lessonii, with the rest of Cluster III, Cluster II, and sometimes Cluster I represented, reached its peak densities ($>100/\text{cm}^2$) within Palau lagoon, away from the volcanic islands, at depths from 2 - 20 m. At more exposed sites, this assemblage dominated at 5 - 20 m.

Assemblage D-a is a subgroup of Assemblage D, differing by its abundance of Calcarina hispida, and occurring in Palau lagoon at depths of 2 - 10 m.

Assemblage E was characteristic of samples deeper than 10 m and was typified by Clusters III and IV. Within Palau lagoon, Cluster IV became prominent at about 10 - 15 m in the vicinity of volcanic islands. On oceanic reefs, Cluster IV appeared deeper, at about 20 - 30 m. Specimen densities associated with this assemblage were usually less than $10/\text{cm}^2$.

Monthly individual species and total densities for temporal sampling site PS-16 from May 1972 to June 1973 are presented in figure 4 and sea surface temperatures and salinities at that site are shown in figure 5. Analysis of variance of the samples for each sampling date illustrated that for the total fauna and for the more abundant species -- P. pertusus, A. lessonii, A. lobifera, C. calcar, and C. spengleri -- variability between dates was significantly greater (0.05 level) than within dates (table 3).

Monthly individual species and total densities for site PS-17 from April 1972 to June 1973 are presented in figure 6 and corresponding sea surface temperatures and salinities are shown in figure 7. Analysis of variance of the samples for each sampling date illustrated that for the total fauna and for most of the abundant species -- Archaias angulatus,

Figure 4. Monthly mean abundances ($\log_e(\#/cm^2)$) of foraminifera at PS-16.

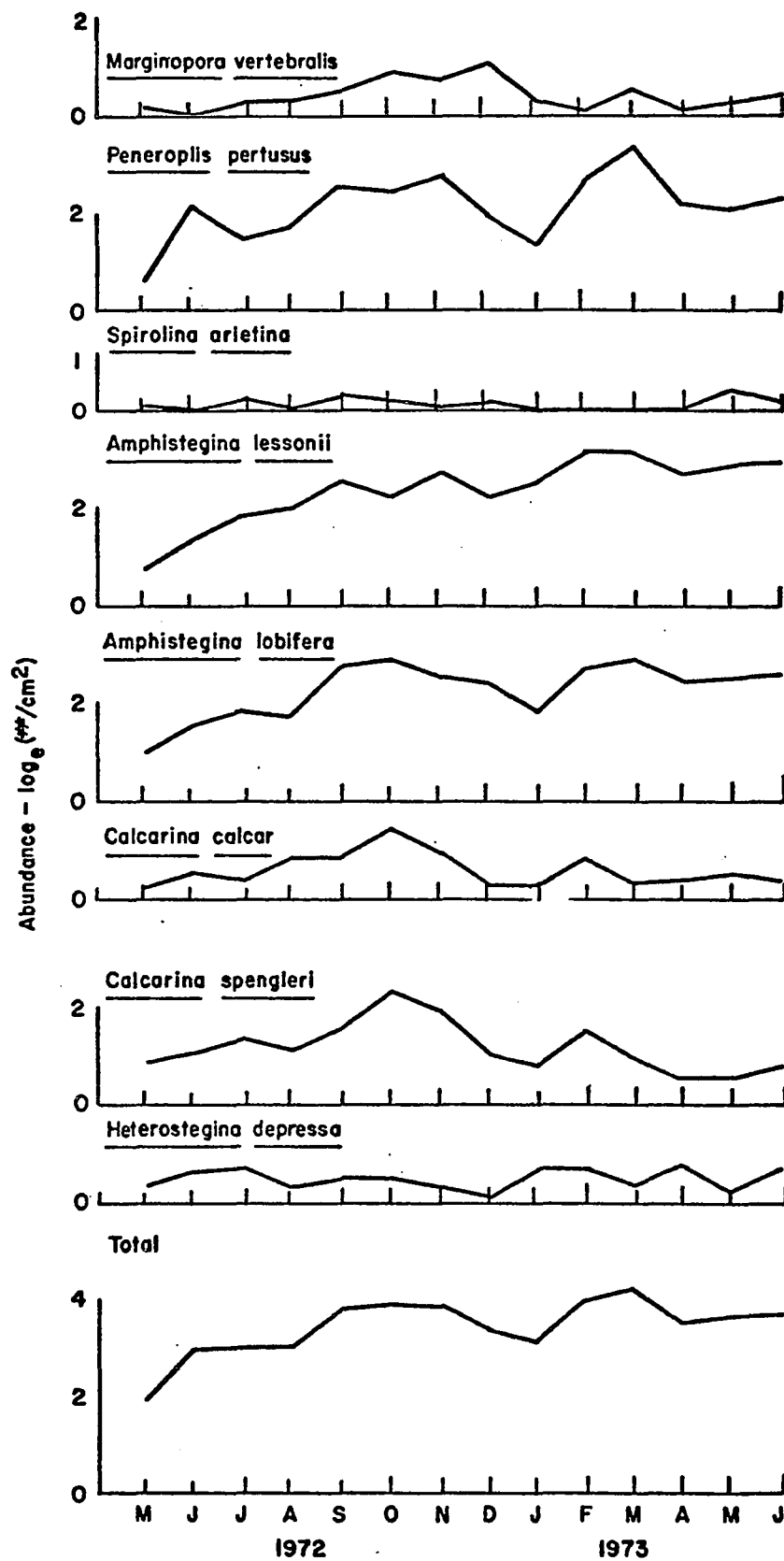


Figure 5. Sea surface temperature and salinity at station PS-16.

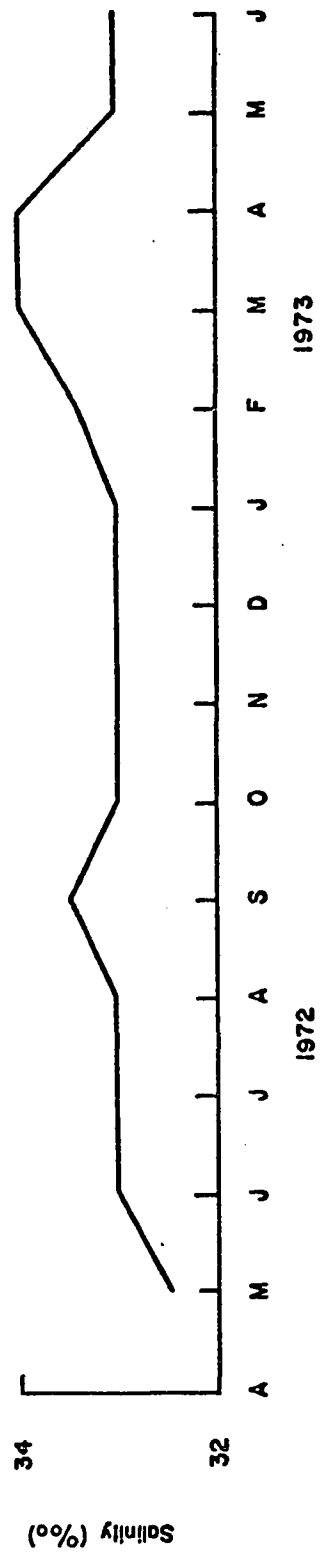
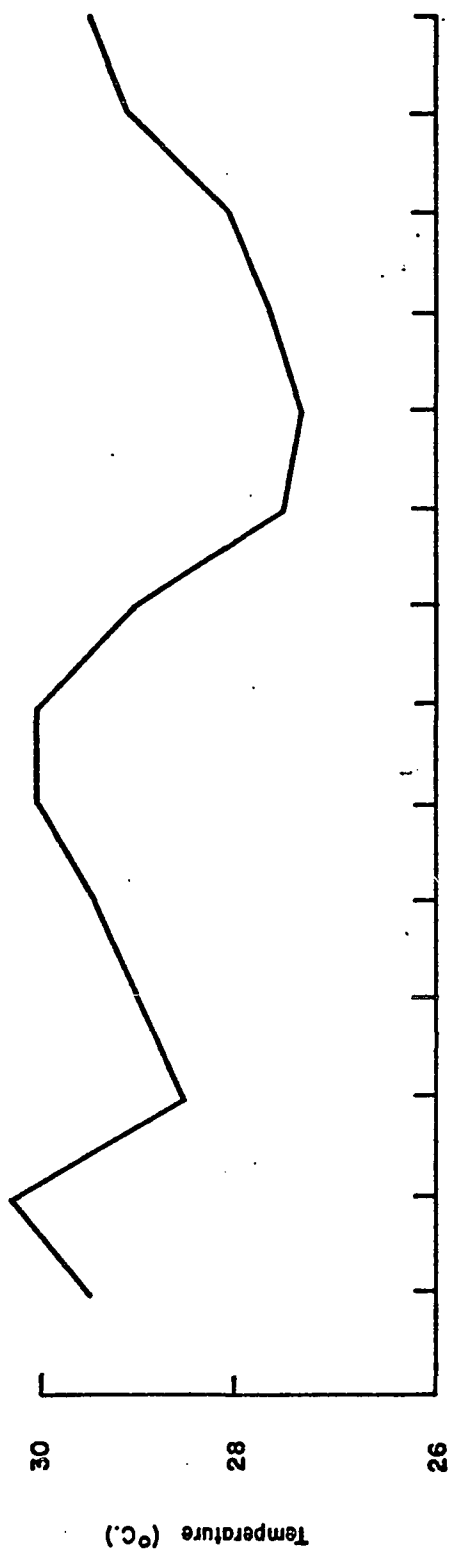


Table 3

F-ratios for One-way Analysis of Variance with Replication
of Sample Date Densities for Most Abundant Species
from Temporal Sampling Site PS-16

Species	F-ratio	Degrees of Freedom	Probability
<u>Marginopora</u> <u>vertebralis</u>	1.38	13,28	0.230
<u>Peneroplis</u> <u>pertusus</u>	2.65	13,28	0.015
<u>Amphistegina</u> <u>lessonii</u>	3.24	13,28	0.004
<u>A. lobifera</u>	2.92	13,28	0.008
<u>Calcarina calcar</u>	2.28	13,28	0.033
<u>C. spengleri</u>	3.31	13,28	0.003
<u>Heterostegina</u> <u>depressa</u>	0.87	13,28	0.589
Total fauna	3.11	13,28	0.005

Figure 6. Monthly mean abundances ($\log_e(\#/cm^2)$) of foraminifera at PS-17.

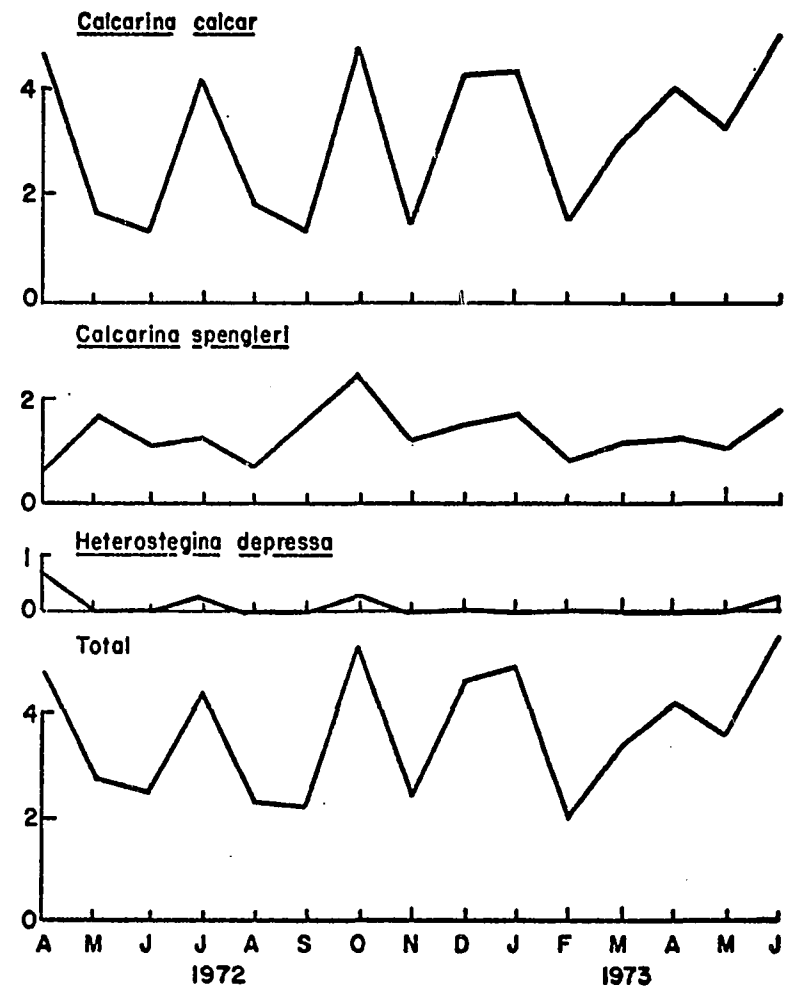
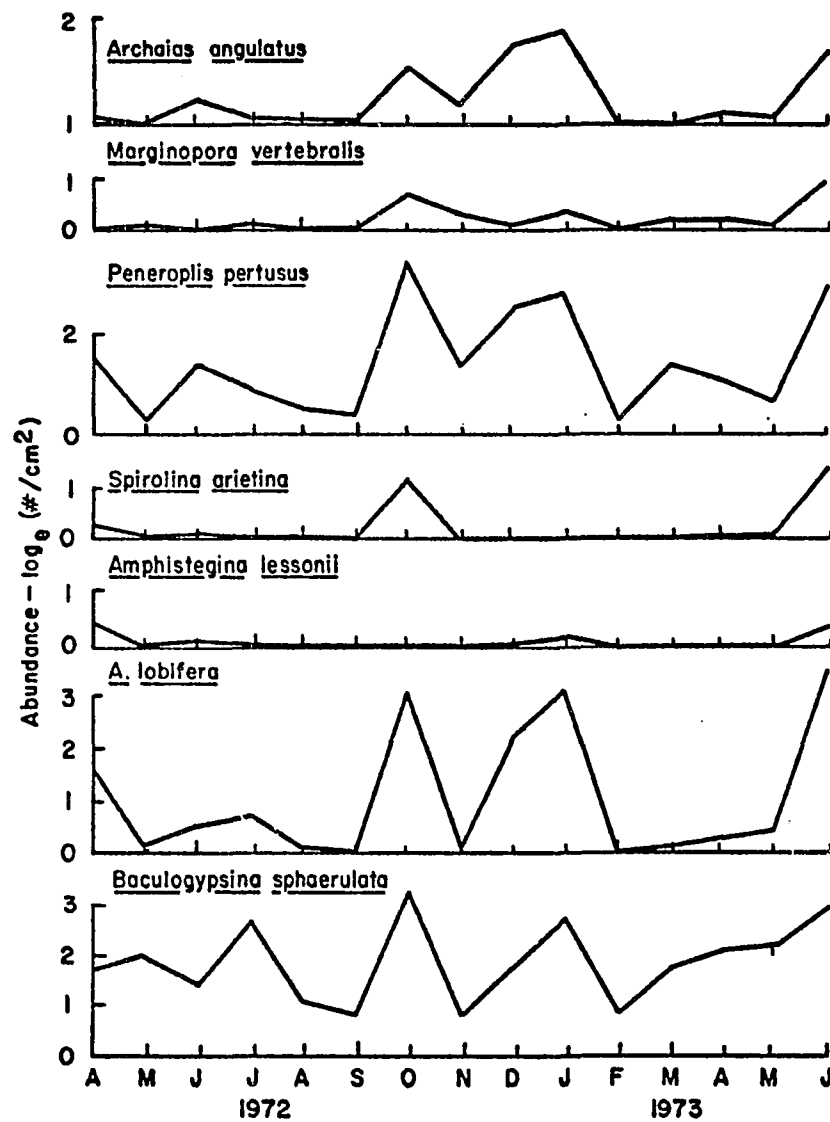
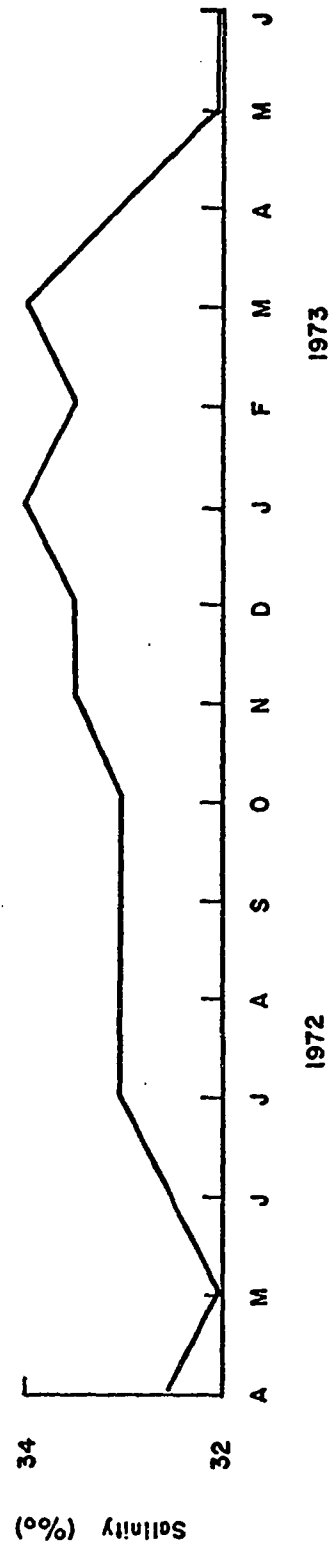


Figure 7. Sea surface temperature and salinity at station PS-17.



M. vertebralis, P. pertusus, A. lobifera, B. sphaerulata, and C. calcar
-- variability between dates was significantly greater (0.05 level) than within dates (table 4).

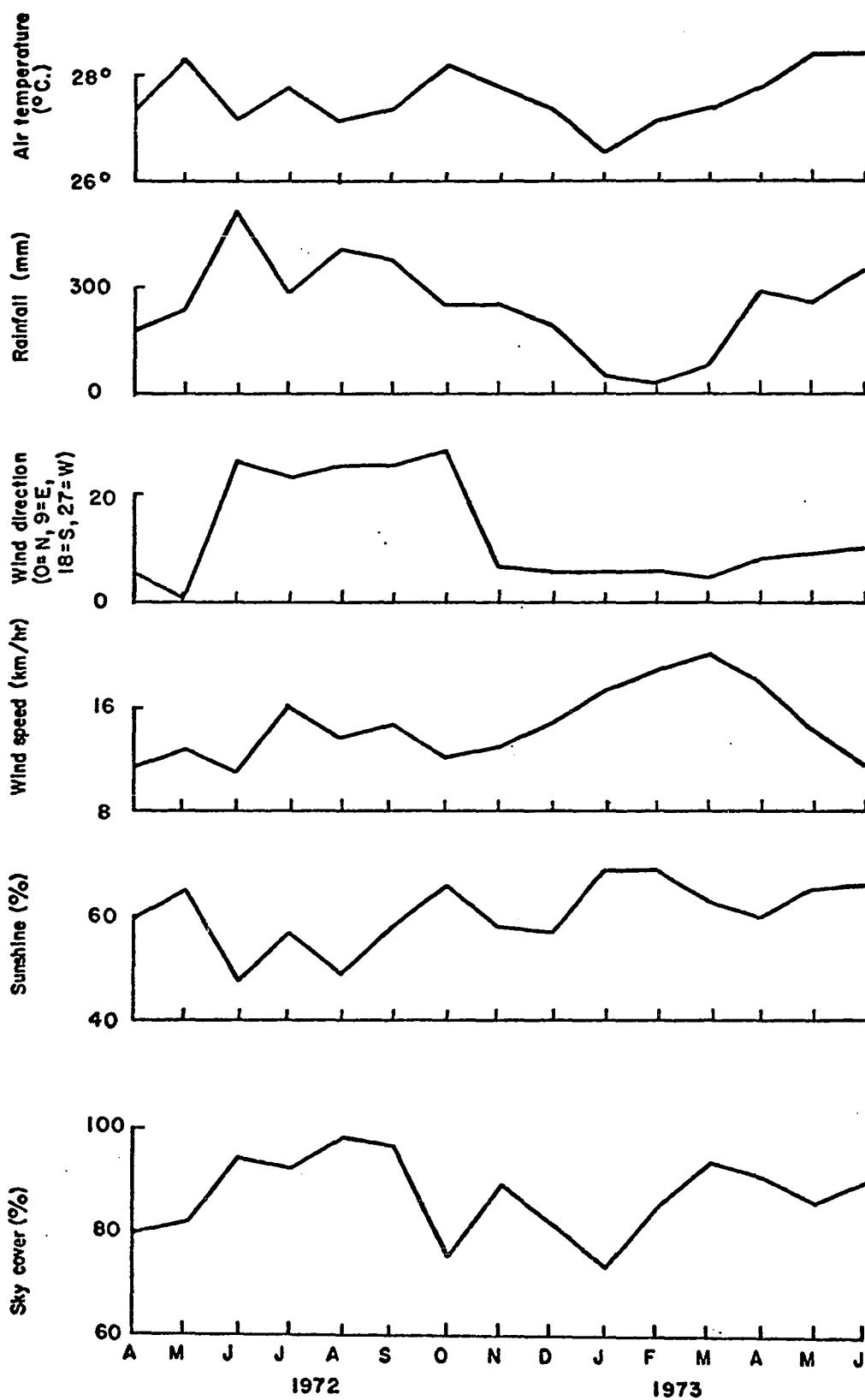
Monthly mean values for air temperature, rainfall, wind speed, wind direction, percent sunshine, and sky cover from U. S. Department of Commerce Local Climatological Data for Koror Island, April 1972 - June 1973 are shown in figure 8.

Table 4

F-ratios for One-way Analysis of Variance with Replication
of Sample Date Densities for Most Abundant Species
from Temporal Sampling Site PS-17

Species	F-ratio	Degrees of Freedom	Probability
<u>Archaias angulatus</u>	8.64	14,30	0
<u>Marginopora vertebralis</u>	5.03	14,30	0
<u>Peneroplis pertusus</u>	9.07	14,30	0
<u>Amphistegina lobifera</u>	27.09	14,30	0
<u>Baculogypsina sphaerulata</u>	2.12	14,30	0.041
<u>Calcarina calcar</u>	7.29	14,30	0
<u>C. spengleri</u>	1.60	14,30	0.137
Total fauna	5.16	14,30	0

Figure 8. Climatological data for Koror Island, April 1972-June 1973.



Oahu

The large foraminiferal species studied in the Hawaii samples were the miliolines M. vertebralis, P. pertusus, Sorites marginalis, and Spirolina arietina, and the rotaliines Amphistegina bicirculata, A. lessonii, A. lobifera, H. depressa, and N. ammonoides. Station locations are shown in figure 9a and descriptions of the stations are given in Appendix C. Standing crop data for each site at each station are presented in Appendix D.

Again, an overview of the distribution of the large foraminifera by depth was provided by averaging their abundance in samples from each depth (figure 10). A. lessonii and A. lobifera were the only relatively abundant species. M. vertebralis, P. pertusus, and Spirolina arietina were common in samples from less than 30 m depth, while Sorites marginalis, A. bicirculata, and N. ammonoides were common in samples from greater depths. H. depressa was common in samples down to 110 m. No living specimens of these nine species were found at depths greater than 110 m.

Cluster analysis of species data illustrated the relationships among the species (figure 11), revealing three clusters. A. lessonii and A. lobifera formed the core of a larger group including P. pertusus and H. depressa and this group was significantly correlated to the M. vertebralis-Spirolina arietina cluster. Sorites marginalis was weakly correlated to N. ammonoides (table 5) but was too rare to deal with further. Essentially, there was the < 30 m community which included Clusters II and III and the deeper community, Cluster IV (table 1).

The sample clustering revealed six assemblages whose distributions are shown in figure 9b - d.

Assemblage A was dominated by Spirolina or Marginopora (Cluster II) with or without Cluster III. Specimen densities at sites characterized by this assemblage were typically less than $10/\text{cm}^2$.

Assemblage B consisted of samples devoid of larger foraminifera.

Assemblage C was dominated by A. lobifera with other members of Cluster III and II usually present. Specimen densities at sites characterized by this assemblage were typically less than $10/\text{cm}^2$ except at Makapuu tidepools (HS-13) where densities up to $50/\text{cm}^2$ were found.

Figure 9. Oahu; a. Station locations
b. Dominant assemblages <5 m.
c. Dominant assemblages 5-30 m.
d. Dominant assemblages >30 m.
(Assemblages described in Table 1)

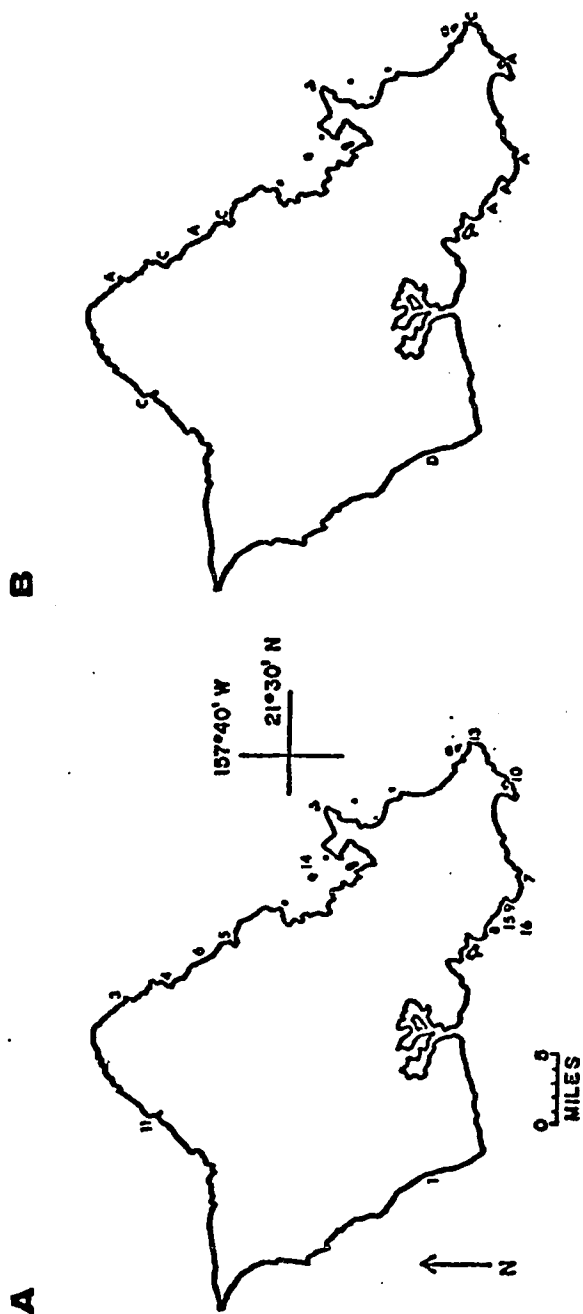


Figure 10. Depth distributions of nine species of large, benthic foraminifera in Hawaii.

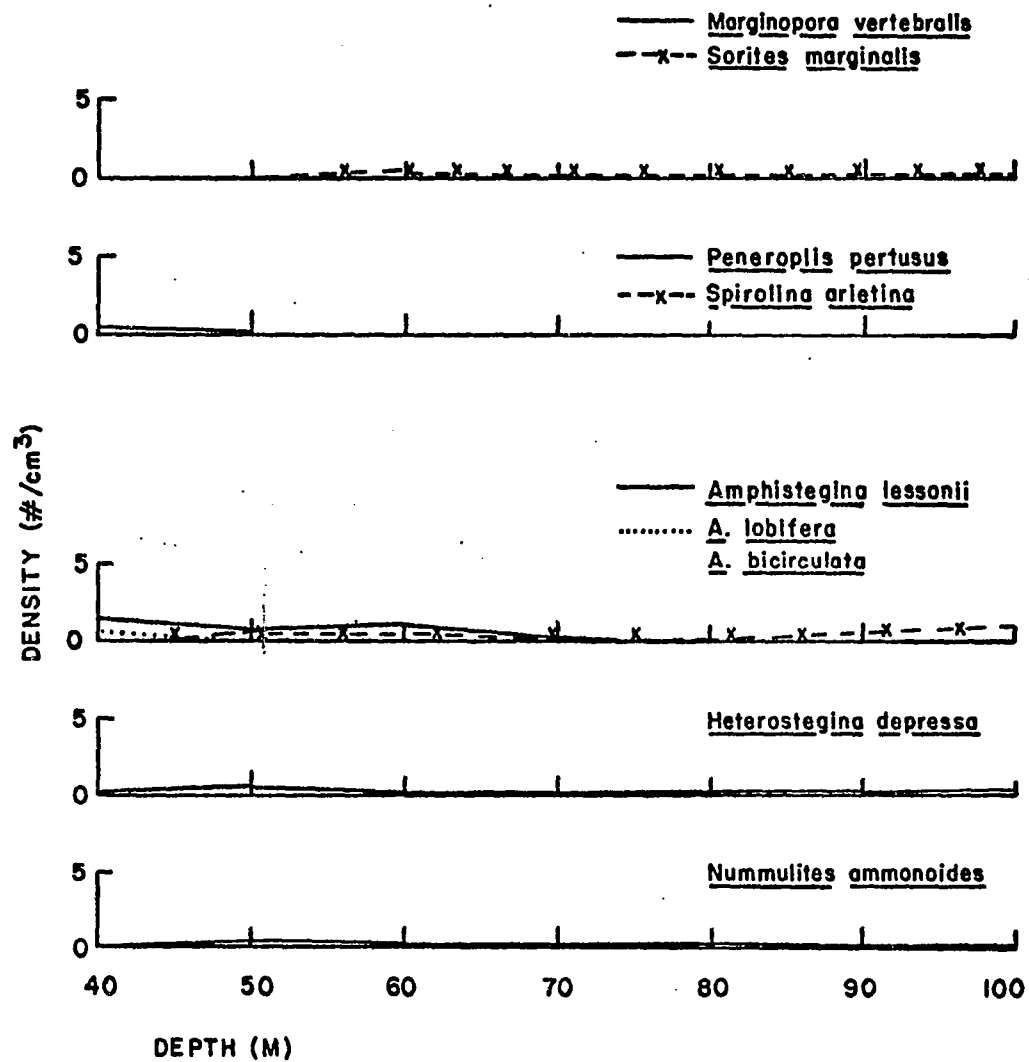
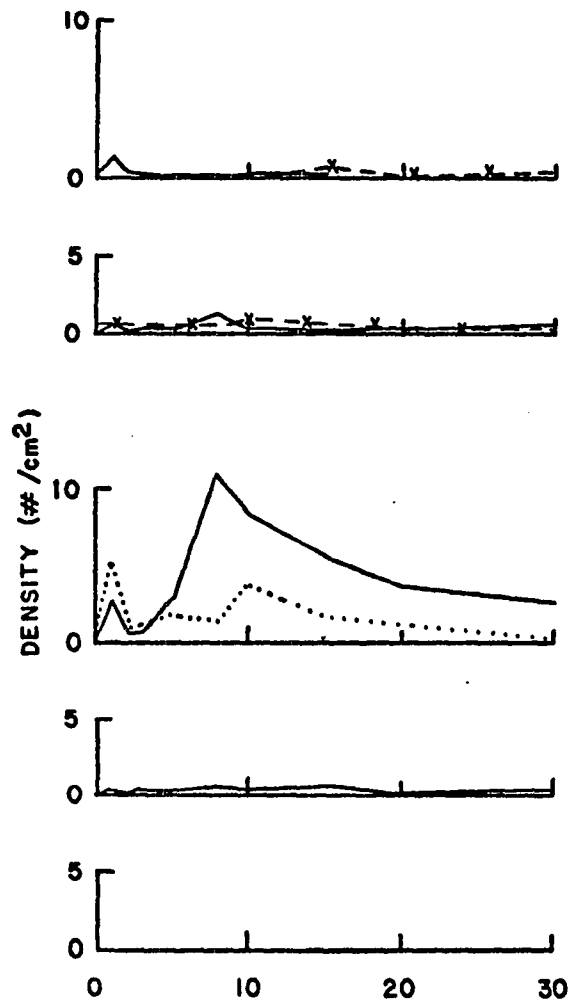


Figure 11. Dendrograph showing species clusters identified in field samples from Oahu.

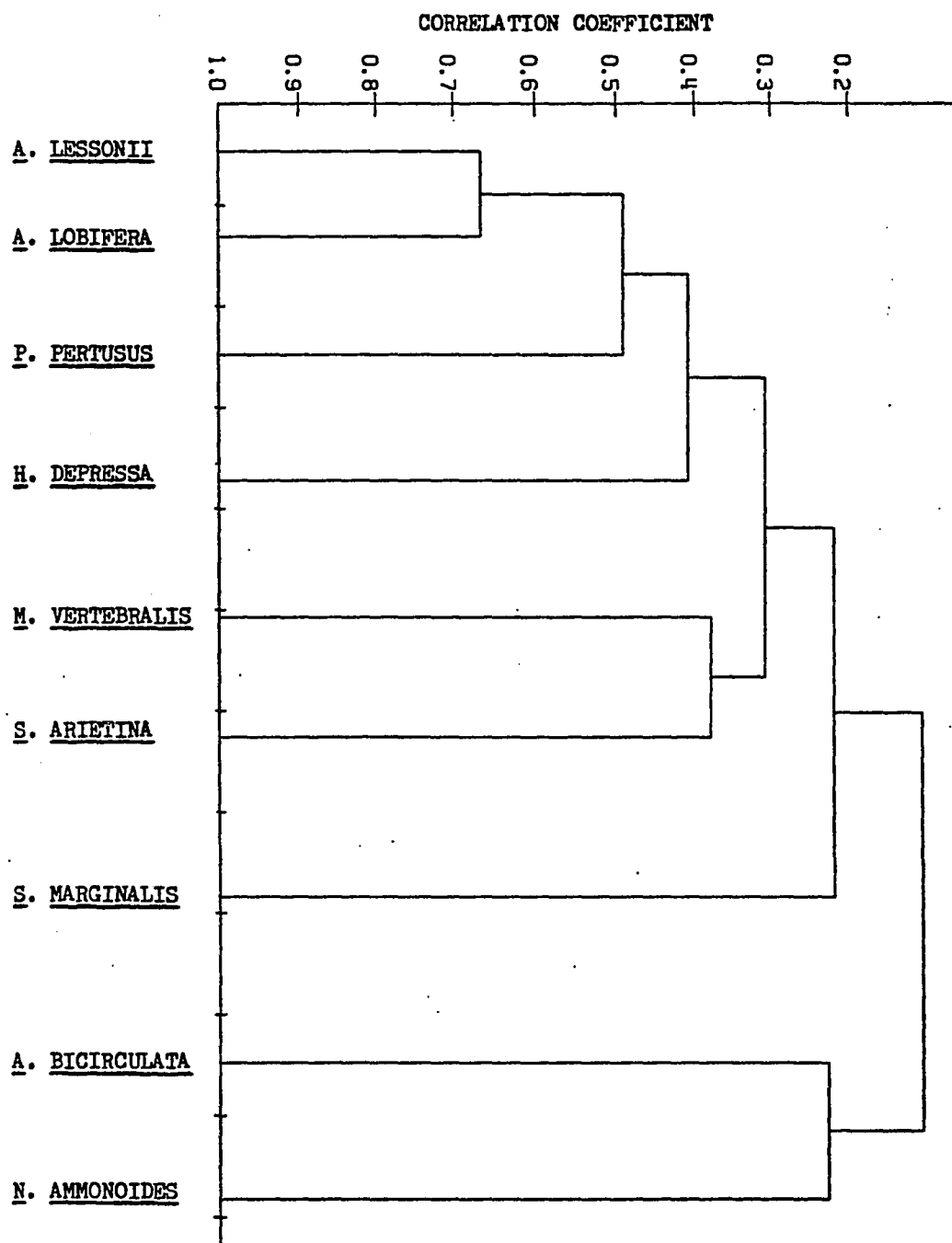


Table 5.

Correlation Marrix of Large Foraminifera from 159 Samples from Hawaii.

	<u>Marginopora</u> <u>vertebralis</u>	<u>Peneroplis</u> <u>pertusus</u>	<u>Sorites</u> <u>Marginalis</u>	<u>Spirolina</u> <u>arietina</u>	<u>Amphistegina</u> <u>bicirculata</u>	<u>Amphistegina</u> <u>lessonii</u>	<u>Amphistegina</u> <u>lobifera</u>	<u>Heterostegina</u> <u>depressa</u>	<u>Nummulites</u> <u>Ammonoides</u>
<u>M.vertebralis</u>	1.000								
<u>P. pertusus</u>	0.281**	1.000							
<u>S.marginalis</u>	-0.048	0.031	1.000						
<u>S.arietina</u>	0.379**	0.078	-0.049	1.000					
<u>A.bicirculata</u>	0.084	-0.089	-0.008	-0.096	1.000				
<u>A.lessonii</u>	0.115	0.508**	0.403	0.267**	-0.084	1.000			
<u>A.lobifera</u>	0.436**	0.277**	-0.052	0.459**	-0.148	0.667**	1.000		
<u>H.depressa</u>	0.004	0.183*	0.020	0.109	0.154	0.478**	0.304**	1.000	
<u>N.ammonoides</u>	-0.037	-0.118	0.205*	-0.233**	0.225**	-0.212**	-0.251**	-0.076	1.000

** Significant at 0.01 level

* Significant at 0.05 level

Assemblage D, dominated by A. lessonii, with other members of Cluster III and Cluster II usually common, characterized the overwhelming majority of the samples from less than 30 m water depth. Densities at sites occupied by this assemblage were typically moderately high, 10-50/cm².

Assemblage E was dominated by Cluster III with members of Cluster IV usually present, i.e. this assemblage represents the transition between the intermediate and deeper assemblages.

Assemblage F was characterized by Cluster IV.

DISCUSSION

The differences between species composition of the communities of large foraminifera in Palau and Hawaii indicate that the Hawaiian community is a subset of the Indo-West Pacific community and may be explained by the relative geographic isolation of Hawaii's reef fauna. Palau, in the Indo-Malay faunistic center of the Indo-Pacific (Ekman 1953), is typified by diverse reef fauna, as shown by the nine species of large rotaliine foraminifera discussed here. Hawaii, an isolated subregion of the Indo-West Pacific, has only four of the same species (A. bicirculata is omitted because its depth range was not sampled in Palau). Certainly, the differences in species content between the rotaliine large foraminiferal assemblages in Palau and Hawaii are not as dramatic as between the reef coral communities. In Iwayama Bay, Palau, Enuchi (1938) recorded 48 genera and 156 species of shallow-water corals, compared to Maragos' (1977) report of only 12 genera and less than 35 species in Hawaii. Nevertheless, the trends are similar.

Comparing the species clusters in the Palau and Hawaii data (table I), the primary difference is the absence in Hawaii of the characteristic species of Cluster I: the calcarinids and Archaias angulatus. The littoral-infralittoral fringe community of exposed fringing reefs is populated by a rather sparse standing crop of Spirolina, Marginopora and A. lobifera, present at about the same densities as in this environment in Palau, which is often occupied by high densities of the calcarinids.

The dendrographs (figures 3 and 11) show that species correlations are higher in the Palau data where 14 species occupy similar habitats that 8 species occupy in Hawaii. This difference may be evidence of a form of "character release" (MacArthur and Wilson 1967) whereby, under decreased competition, affinities between species with similar requirements decrease as the foraminifera display greater variability in habitats.

Actually, a similar trend is evident within the Palau data. Species affinities among the eight shallowest-dwelling species (Clusters I and II) are much closer than among four intermediate depth-dwelling species.

Basically, the high degree of specialization to the seaward reef flat by B. sphaerulata, C. calcar, and C. spengleri is indicated by their high degree of correlation in these samples. No other group exhibited comparable affinities nor such restricted distributions.

The geographical distributions of C. spengleri and B. sphaerulata were considered by Todd (1960), who noted that both species are restricted to the western tropical Pacific. Studies of the life histories and biology of the Calcarinidae may some day indicate why the group has failed to disperse as widely as some other families of large foraminifera. It is interesting to note that the Calcarinidae is primarily a littoral-infralittoral fringe dwelling family. Kay (1972) reported that among Hawaiian marine mollusks, the shallowest dwelling shoreline species have a high degree of endemism. Among the shallowest-dwelling large foraminifera, not only are several species absent in Hawaii, but A. lobifera exhibits a unique morphological feature in the Hawaiian Islands and Johnston Island, a feature that will be discussed in detail in Section II.

Besides the reef flats populated by high densities of calcarinids, the other high density large foraminiferal community and the only consistently relatively high density community on Oahu occurs between 2 and 20 m and is dominated by A. lobifera and A. lessonii. The dominance of lagoon and nearshore sand sediments by Amphistegina, which has been widely reported -- at Funafuti (Chapman 1900), the Marshall Islands (Cushman et al 1954), Kapingamarangi Atoll (McKee et al 1959), Hawaii (Coulbourn and Resig 1965, Muller 1976), and others -- indicates substantial carbonate production by this community.

The relative mutual exclusiveness of the shallow and deep communities of large foraminifera is demonstrated by the number of strong negative correlations that occurred in the data between N. ammonoides and the shallower species, including S. arietina, A. lessonii and A. lobifera in Hawaii (table 5). Likewise, N. ammonoides and A. radiata in Palau were negatively correlated to several of the species from the shallow assemblages (table 2).

The large foraminifera included in this study occurred most abundantly on rubble, dead coral, or coralline algae covered by a veneer of epiphytic

algal growth. The epiphytic algae appears to provide attachment and some degree of protection. In addition, the spines of the calcarinids inhabiting the most exposed habitats probably serve to lodge the individuals into the algae or to each other as is sometimes the case in very dense populations.

Palau is influenced climatologically by winter northeast trades and summer southwest monsoon winds. This seasonality is reflected in the temperature, rainfall, and wind data and in the temporal abundances of some of the large foraminifera.

At site PS-16, total density was variable with peak densities in September-November (fall) 1972 and February-March (spring 1973). The most abundant species also tended to show these two abundance maxima, particularly A. lobifera, in which both maxima were approximately equal. In Calcarina calcar and C. spengleri, the fall maxima was most pronounced. Peneroplis pertusus was most abundant in the spring. A. lessonii increased in density throughout most of the sampling period, possibly due to the corresponding increase in substrate provided by an increase in the algal veneer during the spring. This and the failure of the monsoon winds to develop in June 1973 may also account for the substantially higher total standing crops recorded in June 1973 than in June 1972. Due to the physical setting of the sampling site, the reef was exposed to swell which developed across the lagoon from June to October. The remainder of the year, the reef was sheltered from the trade winds by islands in Palau lagoon. The Calcarina fall maxima developed during the time of maximum exposure to swell, while the spring Amphistegina and Peneroplis maxima occurred during the trade wind season when the site was in the lee of the island.

A correlation matrix was constructed using the monthly climatological and species density data to determine if any corresponding trends were statistically significant (table 6). Sorites was weakly correlated to rainfall and negatively to percent sunshine. Spirolina was weakly correlated to air temperature. C. calcar was correlated with wind direction, as suggested earlier. The abundance of calcarinids at the site appeared to be related to the increased exposure of the site during the summer.

Table 6.

Correlation Matrix for Monthly Climatological Data and Foraminiferal Species Densities at Station PS-16

	<u>Salinity</u>	<u>Sea Surface Temperature</u>	<u>Air Temperature</u>	<u>Rainfall</u>	<u>Wind Direction</u>	<u>Wind Speed</u>	<u>Percent Sunshine</u>	<u>Cloud Cover</u>	<u>Marginopora vertebralis</u>	<u>Peneroplis pertusus</u>
Salinity	1.000									
S.S. Temperature	-0.522	1.000								
Air Temperature	-0.331	0.544	1.000							
Rainfall	-0.519	0.747**	0.349	1.000						
Wind Direction	-0.380	0.465	0.022	0.682**	1.000					
Wind Speed	0.658*	-0.935**	-0.616*	-0.737**	-0.415	1.000				
% Sunshine	0.215	-0.447	0.171	-0.743**	-0.561*	0.336	1.000			
Cloud cover	-0.173	0.125	-0.148	0.572*	0.361	-0.015	-0.687**	1.000		
<u>M. vertebralis</u>	-0.103	0.270	0.036	-0.172	0.015	-0.138	0.052	-0.311	1.000	
<u>P. pertusus</u>	0.366	-0.096	-0.295	-0.136	0.049	0.284	0.030	0.306	0.280	1.000
<u>S. marginalis</u>	0.035	0.414	-0.172	0.561*	0.380	-0.394	-0.549*	0.257	-0.378	0.005
<u>S. arietina</u>	-0.344	0.303	0.595*	0.197	0.169	-0.305	0.161	-0.036	0.220	-0.041
<u>A. lessonii</u>	0.324	-0.503	-0.242	-0.463	-0.268	0.520	0.413	0.015	0.216	0.745**
<u>A. lobifera</u>	0.288	-0.203	-0.080	-0.298	-0.009	0.328	0.323	0.014	0.460	0.865**
<u>B. sphaerulata</u>	-0.414	0.149	-0.083	0.254	0.351	-0.014	-0.117	0.333	0.117	0.184
<u>C. calcar</u>	-0.143	0.372	0.140	0.126	0.551*	-0.268	-0.026	-0.051	0.330	0.410
<u>C. hispida</u>	0.064	0.274	0.297	0.030	0.437	-0.187	-0.008	-0.165	0.326	0.008
<u>C. spengleri</u>	-0.112	0.354	0.038	-0.013	0.462	-0.200	-0.032	-0.093	0.480	0.353
<u>H. depressa</u>	0.198	-0.363	-0.096	-0.018	0.127	0.236	0.237	-0.010	-0.545*	0.003
Total	0.333	-0.245	-0.219	-0.309	-0.011	0.363	0.266	0.076	0.378	0.923**

	<u>Sorites marginalis</u>	<u>Spirolina arietina</u>	<u>Amphistegina lessonii</u>	<u>Amphistegina lobifera</u>	<u>Baculogypsina sphaerulata</u>	<u>Calcarina calcar</u>	<u>Calcarina hispida</u>	<u>Calcarina spengleri</u>	<u>Heterostegina depressa</u>	<u>Total</u>
<u>S. marginalis</u>	1.000									
<u>S. arietina</u>	-0.242	1.000								
<u>A. lessonii</u>	-0.419	0.101	1.000							
<u>A. lobifera</u>	-0.348	0.237	0.865**	1.000						
<u>B. sphaerulata</u>	-0.077	0.347	0.073	0.239	1.000					
<u>C. calcar</u>	-0.053	0.054	0.146	0.425	0.204	1.000				
<u>C. hispida</u>	-0.140	0.199	-0.126	0.098	-0.140	0.492	1.000			
<u>C. spengleri</u>	-0.072	-0.023	0.033	0.335	0.203	0.865**	0.680**	1.000		
<u>H. depressa</u>	0.163	-0.278	0.161	0.033	0.004	-0.069	0.063	-0.101	1.000	
Total	-0.253	0.102	0.907**	0.971**	0.169	0.427	0.078	0.342	0.082	1.000

** Significant at 0.01 level

* Significant at 0.05 level

At PS-17, C. calcar density showed fluctuations with a period of about 3 months with abundance peaks in April, July, October, December-January, March-April, and June. When all species were compared to the climatological data (table 7), the only significant correlations were to cloud cover, which was negatively correlated to eight of the twelve species present at this site. Between species correlations were strongest within four groups: (1) Amphistegina lobifera, Archaias angulatus and P. pertusus, (2) C. calcar, B. sphaerulata, and total density, (3) M. vertebralis, C. spengleri, Spirolina arietina, (4) Amphistegina lessonii, C. hispida, and H. depressa.

Comparing all four sets of correlations data for A. lobifera and P. pertusus indicated some requirements of the two species, which were closely correlated in all situations. Relationships of the two species to other species varied depending on conditions. In the total Palau data, they were linked with M. vertebralis and more distantly, to Cluster I, illustrating the relatively shallow occurrence of all these species. On the exposed reef flat, PS-17, A. lobifera and P. pertusus were linked to Archaias angulatus, possibly indicative of a common requirement in the microenvironment such as slightly less exposure to turbulence. At PS-16 and on Oahu, this pair was linked to A. lessonii. As will be discussed further later, A. lessonii and A. lobifera are two closely related species apparently with similar requirements. A. lobifera is relatively restricted to about the upper 5 m. A. lessonii occurs most abundantly from about 2 - 20 m. The two species overlap most at about 2 - 5 m. At PS-16, with constant depth and restricted exposure to turbulence, A. lessonii, A. lobifera, and P. pertusus tended to respond similarly.

The correlations of A. lobifera and P. pertusus with A. lessonii in the Oahu data may be due to the sampling of essentially one reef type, the seaward fringing reef, where wave turbulence tends to homogenize the foraminiferal community by carrying individuals from the breaker zone into deeper water. Virtually all Oahu samples containing A. lessonii also contained at least a few A. lobifera, unlike the Palau lagoon samples where below 10 m A. lobifera was virtually absent. A. lobifera and

Table 7.

Correlation Matrix for Monthly Climatological Data and Foraminiferal Species Densities at Station PS-17.

	<u>Salinity</u>	<u>Sea Surface Temperature</u>	<u>Air Temperature</u>	<u>Rainfall</u>	<u>Wind Direction</u>	<u>Wind Speed</u>	<u>Percent Sunshine</u>	<u>Cloud cover</u>	<u>Archaias angulatus</u>	<u>Marginopora vertebralis</u>
Salinity	1.000									
S.S. Temperature	-0.386	1.000								
Air Temperature	-0.738**	0.362	1.000							
Rainfall	-0.539*	0.785**	0.308	1.000						
Wind Direction	-0.148	0.435	0.074	0.706**	1.000					
Wind Speed	0.658**	-0.522*	-0.510	-0.635*	-0.378	1.000				
% Sunshine	0.184	-0.715**	0.098	-0.817**	-0.541*	0.432	1.000			
Cloud Cover	-0.060	0.421	-0.166	0.582*	0.401	0.089	-0.697**	1.000		
<u>A. angulatus</u>	0.427	-0.094	-0.196	-0.252	-0.051	-0.027	0.204	-0.673**	1.000	
<u>M. vertebralis</u>	0.342	-0.079	0.146	-0.261	0.135	0.045	0.436	-0.531*	0.541*	1.000
<u>P. pertusus</u>	0.405	0.005	-0.160	-0.234	0.066	-0.116	0.183	-0.656**	0.859**	0.747**
<u>S. arietina</u>	-0.166	0.104	0.380	0.057	0.420	-0.399	0.220	-0.458	0.254	0.737**
<u>A. lessonii</u>	-0.059	-0.129	-0.264	-0.211	-0.219	-0.261	0.040	-0.420	0.199	-0.173
<u>A. lobifera</u>	0.246	-0.144	-0.080	-0.305	0.045	-0.155	0.317	-0.809**	0.868**	0.623*
<u>B. sphaerulata</u>	-0.061	-0.105	0.242	-0.192	0.079	0.010	0.386	-0.592*	0.474	0.646**
<u>C. calcar</u>	0.139	0.008	0.032	-0.359	-0.095	0.102	0.302	-0.591*	0.504	0.496
<u>C. hispida</u>	-0.268	0.027	0.018	-0.133	-0.148	-0.387	0.038	-0.325	-0.101	-0.131
<u>C. spengleri</u>	0.102	-0.004	0.282	-0.060	0.174	-0.106	0.375	-0.516*	0.583*	0.754**
<u>H. depressa</u>	-0.217	0.034	0.133	-0.107	0.089	-0.377	0.049	-0.364	-0.013	0.098
Total	0.104	0.018	0.073	-0.304	-0.066	-0.010	0.301	-0.665**	0.596*	0.563*

	<u>Peneroplis pertusus</u>	<u>Spirolina arietina</u>	<u>Amphistegina lessonii</u>	<u>Amphistegina lobifera</u>	<u>Baculogypsina sphaerulata</u>	<u>Calcarina calcar</u>	<u>Calcarina hispida</u>	<u>Calcarina spengleri</u>	<u>Heterostegina depressa</u>	<u>Total</u>
<u>P. pertusus</u>	1.000									
<u>S. arietina</u>	0.576*	1.000								
<u>A. lessonii</u>	0.288	0.020	1.000							
<u>A. lobifera</u>	0.910**	0.558*	0.452	1.000						
<u>B. sphaerulata</u>	0.602*	0.561*	0.122	0.689**	1.000					
<u>C. calcar</u>	0.678**	0.419	0.452	0.748**	0.794**	1.000				
<u>C. hispida</u>	0.153	0.258	0.867**	0.280	0.058	0.404	1.000			
<u>C. spengleri</u>	0.604*	0.591*	-0.257	0.584*	0.610*	0.312	-0.268	1.000		
<u>H. depressa</u>	0.304	0.480	0.738**	0.430	0.314	0.586*	0.901**	-0.064	1.000	
Total	0.763**	0.485	0.456	0.825**	0.847**	0.979**	0.383	0.449	0.570*	1.000

** Significant at 0.01 level

* Significant at 0.05 level

P. pertusus occurred most abundantly in shallow, hard bottom situations where the substrate, either algal or mineral, was covered by epiphytic algal growth and where exposure to wave turbulence was not extreme.

GROWTH AND REPRODUCTION

INTRODUCTION

Relatively little is known of the biology and ecology of living species of larger foraminifera. Loeblich and Tappan (1964, p. C70) noted that "probably no other group of organisms can compete with the Foraminiferida in low percentage of living species in which the life history is known". Murray (1973) indicated that the living larger foraminiferids were no exception, for little information is available even on living occurrences of this group. With regard to growth and reproduction in particular, culture studies have been restricted to Heterostegina (Röttger 1972, 1974, 1976; Röttger and Berger 1972), Marginopora (Ross 1972), and Amphistegina (Muller 1974). Growth data from the field are entirely lacking for the group.

A. lessonii, H. depressa, and M. vertebralis are all known to maintain symbiotic algae. Fixation of H^{14}CO_3 as organic carbon by the algal symbionts has been shown for both A. lessonii (Muller submitted) and M. vertebralis (Smith and Wiebe submitted). In short term experiments with A. lessonii, about 90 percent of the H^{14}CO_3 fixed in the light was incorporated into organic material; and this species is at least partially dependent upon its symbionts for growth (Muller submitted).

This study explores field growth rates of three species; A. lessonii, A. lobifera, and Calcarina spengleri. Culture growth data are used for comparison with field data and to determine if growth and reproduction in Amphistegina are light dependent. ^{14}C experiments are used to determine the effect of light on rates of inorganic ^{14}C fixation by symbionts of Amphistegina spp.

METHODS

Field

Sampling sites and collection and processing of field samples were discussed in the previous section (p. 18). Size-frequency data on each species were collected by measuring the greatest spiral diameter (Scott 1974) of specimens to the nearest 50 μm when the individuals were counted.

Temporal size-frequency data for A. lobifera and A. lessonii were available from re-evaluation of the October 1970-September 1971 Makapuu tidepool (HS-13) data (Muller 1974), and from Palau from samples collected at PS-16 between May 1972 and June 1973. Temporal size-frequency data for C. spengleri from Palau were available from samples collected at site PS-17 between April 1972 and June 1973. Growth data were extracted from temporal size-frequency distributions using a progression of modes method. Species data for each sample were converted to percent size-frequency at 100 μm intervals.

The Makapuu data had already been tested for homogeneity of size distribution by the Kolmogorov-Smirnov goodness-of-fit test (Sokal and Rohlf 1969) to determine the probability that the samples collected on a particular date were taken from a single population (Muller 1974). Furthermore, characteristic features (peaks and troughs) in the size frequency plots for both A. lessonii and A. lobifera were fairly evident and were followed directly in successive monthly plots, by assigning a number to the feature the first time it appeared and locating and numbering the feature in successive months.

For each species in the Palau data, relative cumulative percent size-frequency for each sample was tested against the weighted, total cumulative percent size-frequency for that sampling date using the Kolmogorov-Smirnov goodness-of-fit test. Weighted, total percent frequency for a date was calculated by multiplying the percent of the specimens in each size class ($P_{i,j}$) by the density of specimens in the sample ($D_{\Sigma i,j}$)

$$D_{i,j} = P_{i,j} \times D_{\Sigma i,j} \quad (1)$$

to determine density of specimens in each size class (i) in each sample (j)

$(D_{i,j})$, summing each size class over the three samples (S)

$$S = \sum_i \sum_j D_{i,j} \quad (2)$$

then calculating the cumulative percent size-frequency $(P_{i,\Sigma j})$ for the total for the date

$$P_{i,\Sigma j} = \sum_i D_{i,\Sigma j} / S \quad (3)$$

where i denotes size class i , j is sample number.

Then features of the size-frequency plots were amplified by a method developed by T. K. Newbury and used by Szyper (1976). Weighted average densities $(\bar{D}_{i,k})$ for each sample date k

$$\bar{D}_{i,k} = D_{i,\Sigma j} / N_k \quad (4)$$

where N_k is number of samples analyzed for that date, were summed over the entire sampling period (S_T)

$$S_T = \sum_k \sum_i D_{i,k} \quad (5)$$

and weighted, pooled percent size-frequencies for a sampling site through time $(P_{i,\Sigma k})$ were calculated

$$P_{i,\Sigma k} = D_{i,\Sigma k} / S_T \quad (6)$$

Weighted, pooled percent size-frequencies for a site through time were then compared to the weighted, percent size-frequencies for each date by calculating the percent deviation (E_i) of the frequency for a date from the pooled frequency

$$E_i = P_{i,k} - P_{i,\Sigma k} \quad (7)$$

Deviations were plotted and features were identified as previously, by assigning a number to the feature the first time it was seen and following the feature through time.

Composite growth curves were then developed from the procession of features through time. The smallest sizes at which features were observed was 200 or 300 μm which were arbitrarily assigned age 7 or 15 days respectively. Features which first appeared at larger sizes were scaled on the curve according to the progress of features beginning at 200 μm .

Growth curves were then least-squares fitted to a power function of the form

$$d_t = k_1 t^{k_2} \quad (8)$$

where d_t is diameter at time t , k_1 and k_2 are constants, $k_2 < 1$.

Culture methods

Growth

Due to taxonomic confusion within the genus Amphistegina at the time of the previous culture experiments with these protists (Muller 1974), the growth and fecundity experiments were repeated distinguishing between A. lessonii and A. lobifera.

Basic collection and culture methods for Amphistegina were described previously (Muller 1974). Briefly, the foraminifera were maintained in 150x20 mm petri dishes containing an enriched Erdschreiber seawater culture medium. Modifications of earlier methods were that the seawater was filtered and algal food was not provided. Cultures were incubated at 24-26°C and subjected to a 12-hr interval light/dark cycle. Light was provided by three daylight fluorescent bulbs delivering approximately 2600 $\mu\text{w}/\text{cm}^2$ visible light energy to the surface of the cultures placed at the highest levels in the incubator and 300 $\mu\text{w}/\text{cm}^2$ at the lowest levels.

Culture growth rates of A. lessonii and A. lobifera were determined under the conditions just described at light levels of 2400 $\mu\text{w}/\text{cm}^2$. The results of growth in seven culture of A. lobifera and four of A. lessonii, 25 specimens per culture, grown over periods of up to four months were combined by species and fit with a power function growth curve (eq. 8).

Light limitation of growth was examined in two A. lessonii and two A. lobifera clones. Each clone was divided into three groups and grown at three different light levels, 2600 $\mu\text{w}/\text{cm}^2$, 700 $\mu\text{w}/\text{cm}^2$, and 300 $\mu\text{w}/\text{cm}^2$. Clones were approximately one week old at the start of the experiment. Initial and weekly maximum diameter measurements were made on 25 randomly selected specimens of each trial for six weeks.

Light limitation of ^{14}C uptake

Basic techniques for ^{14}C uptake determination in Amphistegina, which were developed and detailed previously (Muller submitted), were used in the following ^{14}C uptake experiments. Greatest spiral diameter of individuals used ranged from 800 to 1000 μm .

To assess light limitation of ^{14}C uptake and to compare inter-specific differences in uptake by Amphistegina spp., three species: A. bicirculata, A. lessonii, and A. lobifera were incubated in ^{14}C at four light levels: sunlight, shade, dim shade, and darkness. Specimens of A. lessonii and A. lobifera were picked from existing stock cultures that were adapted to the same light conditions. A. bicirculata specimens had been collected from the field during the previous week as that species has not been successfully maintained in culture for more than a few days. Twenty specimens of each species were incubated together at each light level at an activity of $0.4 \mu\text{Ci } ^{14}\text{C/ml}$. Each trial was incubated for three hours, then subdivided into four replicates of five specimens each, killed, and prepared for counting in the liquid scintillation counter.

The previous experiment indicated the practicality of the experiment and the necessity of more data points, so a field experiment was designed utilizing "natural" field light conditions. To allow a maximum change in light intensity over a minimal depth range, the experiment was carried out in Kaneohe Bay, Oahu, Hawaii, in eutrophic waters of the southern sector where light limitation of phytoplankton was shown by Lamberson (1974). Light extinction at the site was determined using a Secchi disk. Light extinction coefficient (k) was corrected for eutrophic waters (Lamberson 1974), but spectral shift was disregarded.

Two species, A. lessonii and A. lobifera, were used in the experiment. General procedure was as follows: Foraminifera were placed in 18 cc snap cap vials, 20 specimens per vial, 11 vials per species. The vials were kept overnight in the dark, then inoculated with $0.05 \mu\text{Ci } ^{14}\text{C/ml}$ filtered seawater. Three vials for each species were foil wrapped as dark controls. Three groups of one light and one dark vial per species were placed in small, single-thickness nitex bags, then foil wrapped. The remaining vials were placed in additional bags, one vial of each species per bag, then each bag was foil wrapped. The samples were then transported to the incubation site, the bags were attached to a line, and were lowered into the water. Foil was removed from the bags as they entered the water. Incubation took place at the following depths; 0, 1, 2, 4, 6, 8, 10, and 12 m, with dark controls at 0, 4, and 12 m; and began 0.5 hr after

inoculation. After a 3 hr incubation, bags were brought to the surface and wrapped in foil as they emerged from the water. Within 0.5 hr after incubation ceased, the foraminifera were killed and preparation for counting was begun.

Reproduction

Laboratory observations of asexual reproduction provided fecundity data on A. lessonii and A. lobifera. Number of young produced by each reproducing parent was counted and adult diameter was noted.

RESULTS

Field

Monthly percent size-frequency plots from the Makapuu data from Hawaii are presented for A. lessonii in figure 12 and for A. lobifera in figure 13, with features which were used to interpret growth indicated by numbers. The growth curves fitted to the data are presented in figure 14:

$$\underline{A. lessonii}: \quad d_t = 40 \, t^{0.72} \quad (r=0.983, df=30) \quad (9)$$

$$\underline{A. lobifera}: \quad d_t = 61 \, t^{0.56} \quad (r=0.987, df=31) \quad (10)$$

In the data from Palau, site PS-16, the results of the Kolmogorov-Smirnov goodness-of-fit test showed significant differences (0.01 level) between samples collected on a date and total for the date in only nine of 75 cases for A. lessonii and in two of 75 cases for A. lobifera.

Monthly percent deviation plots for the PS-16 data are presented in figure 15 for A. lessonii and figure 16 for A. lobifera, and the corresponding interpretations of growth are presented in figures 18a and 18b:

$$\underline{A. lessonii}: \quad d_t = 36 \, t^{.79} \quad (r=0.967, df=78) \quad (11)$$

$$\underline{A. lobifera}: \quad d_t = 47 \, t^{.71} \quad (r=0.923, df=71) \quad (12)$$

The results of the Kolmogorov-Smirnov goodness-of-fit test for the C. spengleri data from PS-17 showed significant differences (0.01 level) between samples collected on one date and total for the date in only three

Figure 12. Percent size-frequency distributions for A. lessonii at station HS-13.

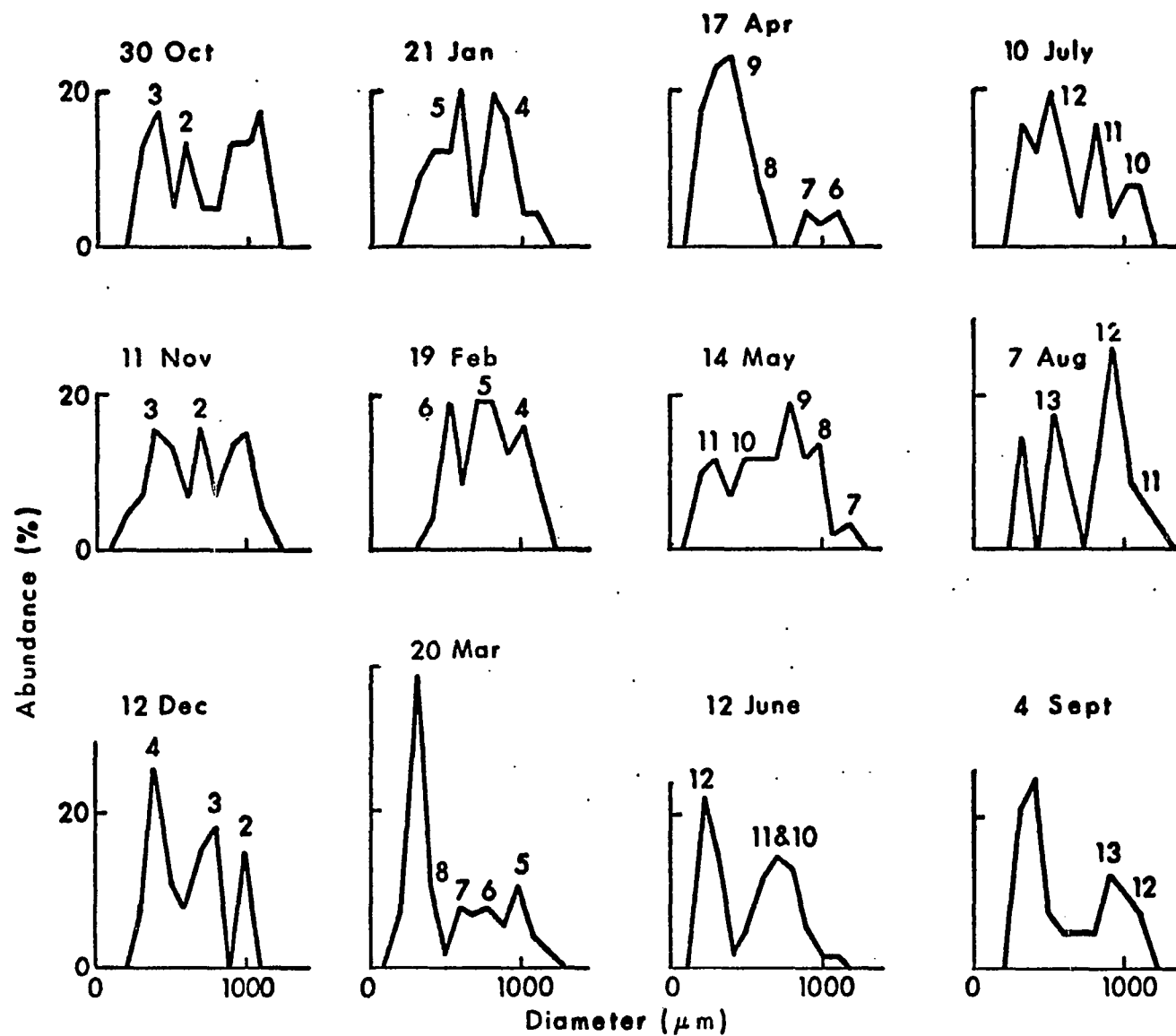


Figure 13. Percent size-frequency distributions for A. lobifera at station HS-13.

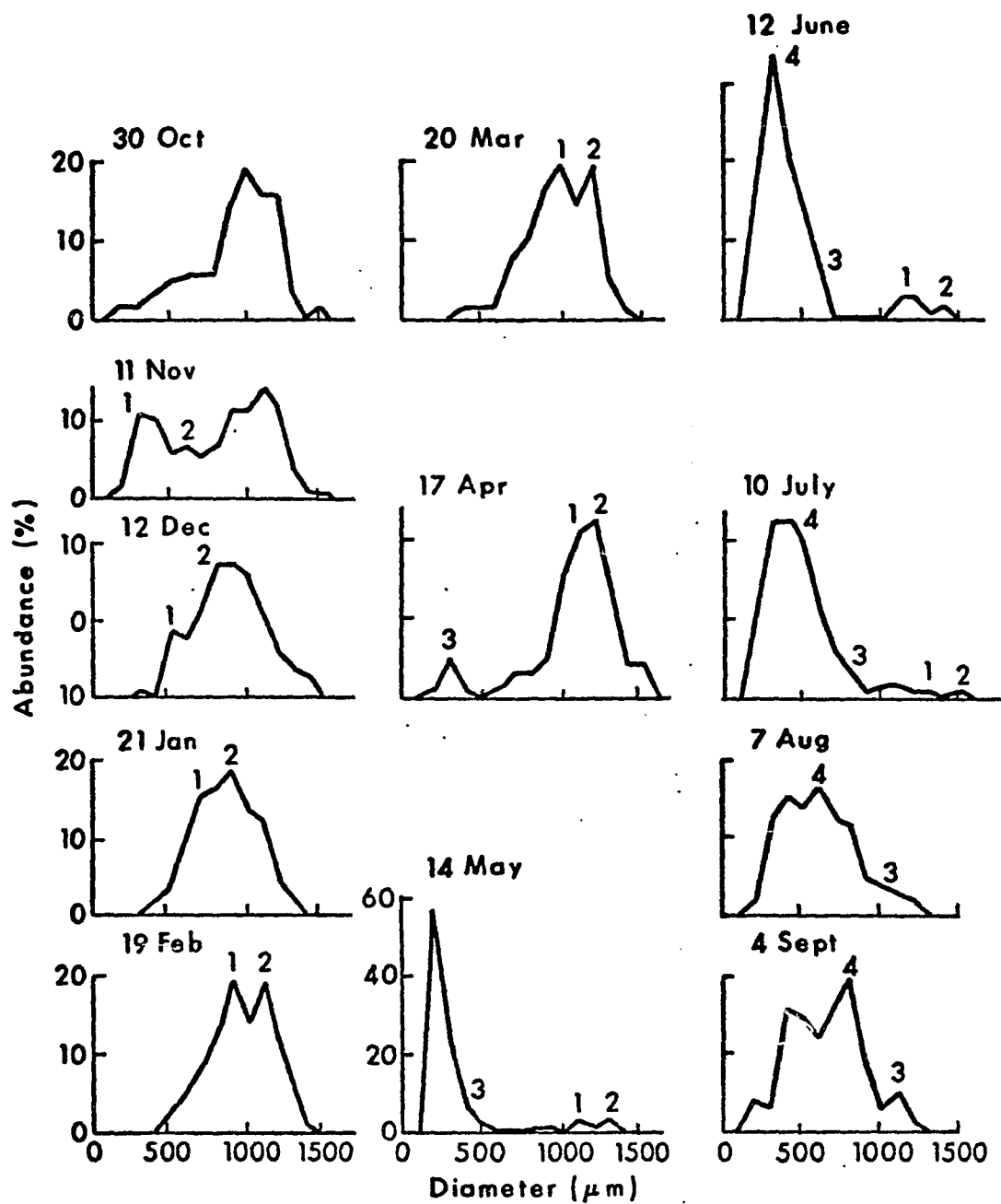


Figure 14. Growth curves interpreted from size-frequency data presented in figures 12 and 13:

- a. A. lessonii (equation 9)
- b. A. lobifera (equation 10)

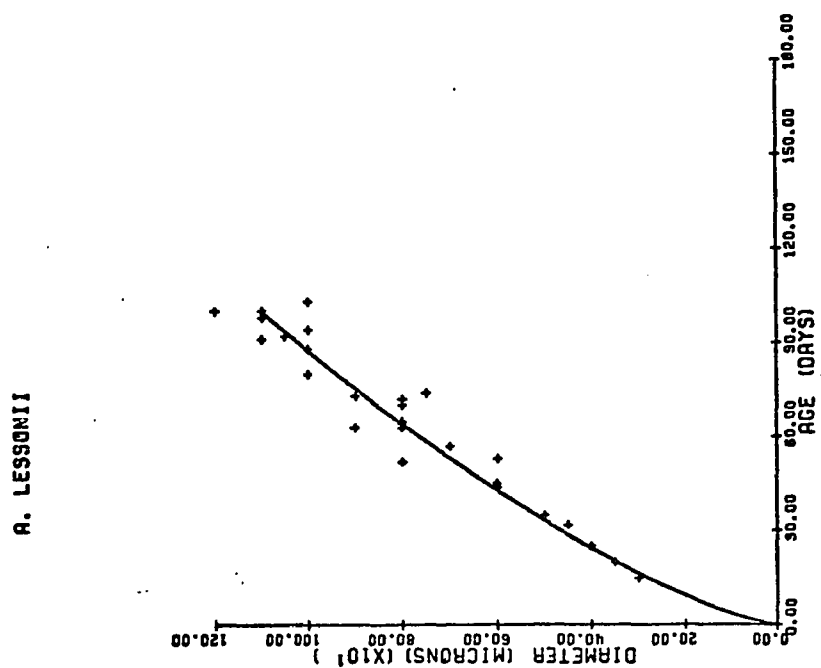
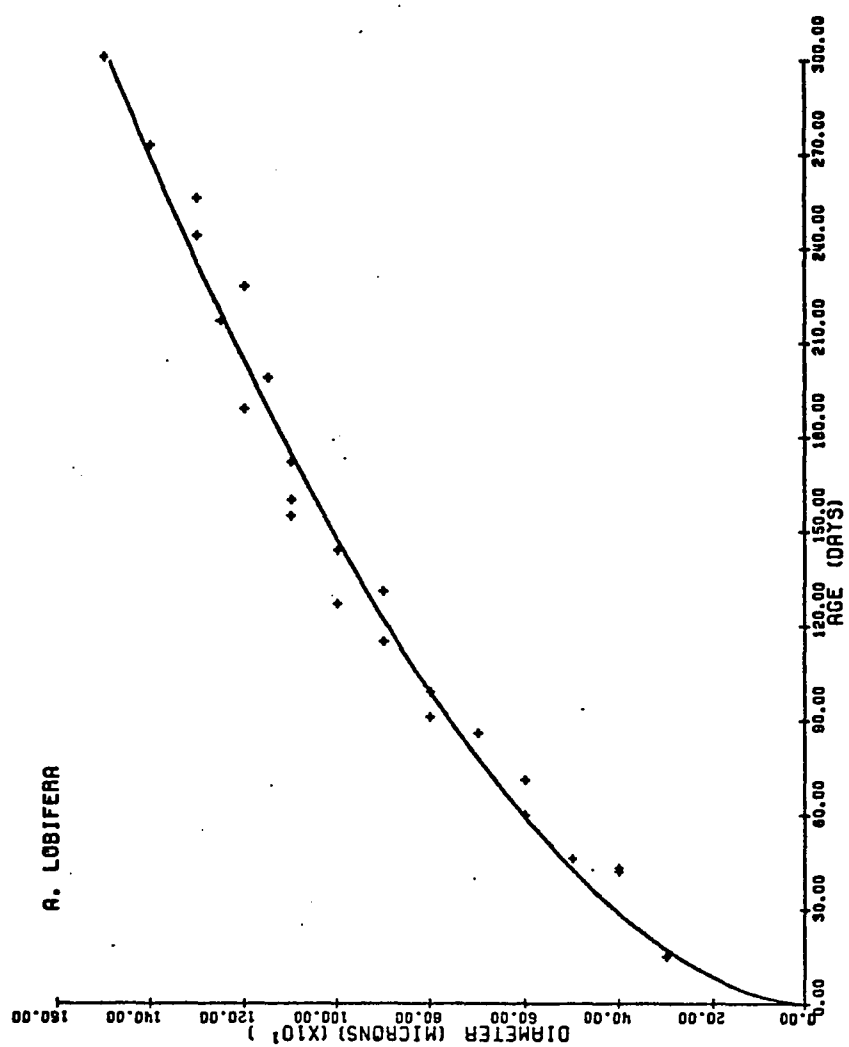


Figure 15. Deviations of percent size-frequency distributions from the reference distribution for A. lessonii at station PS-16.

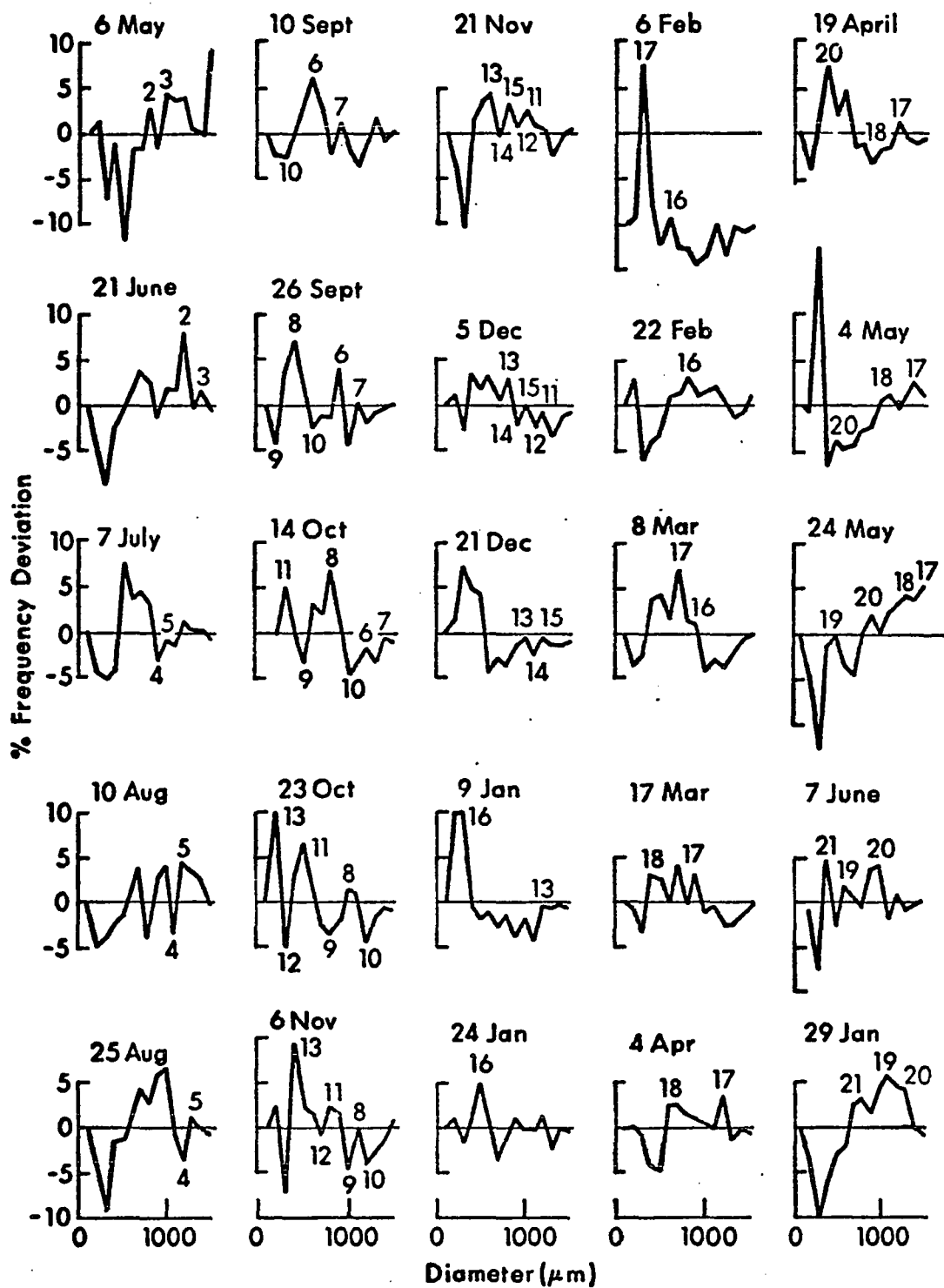
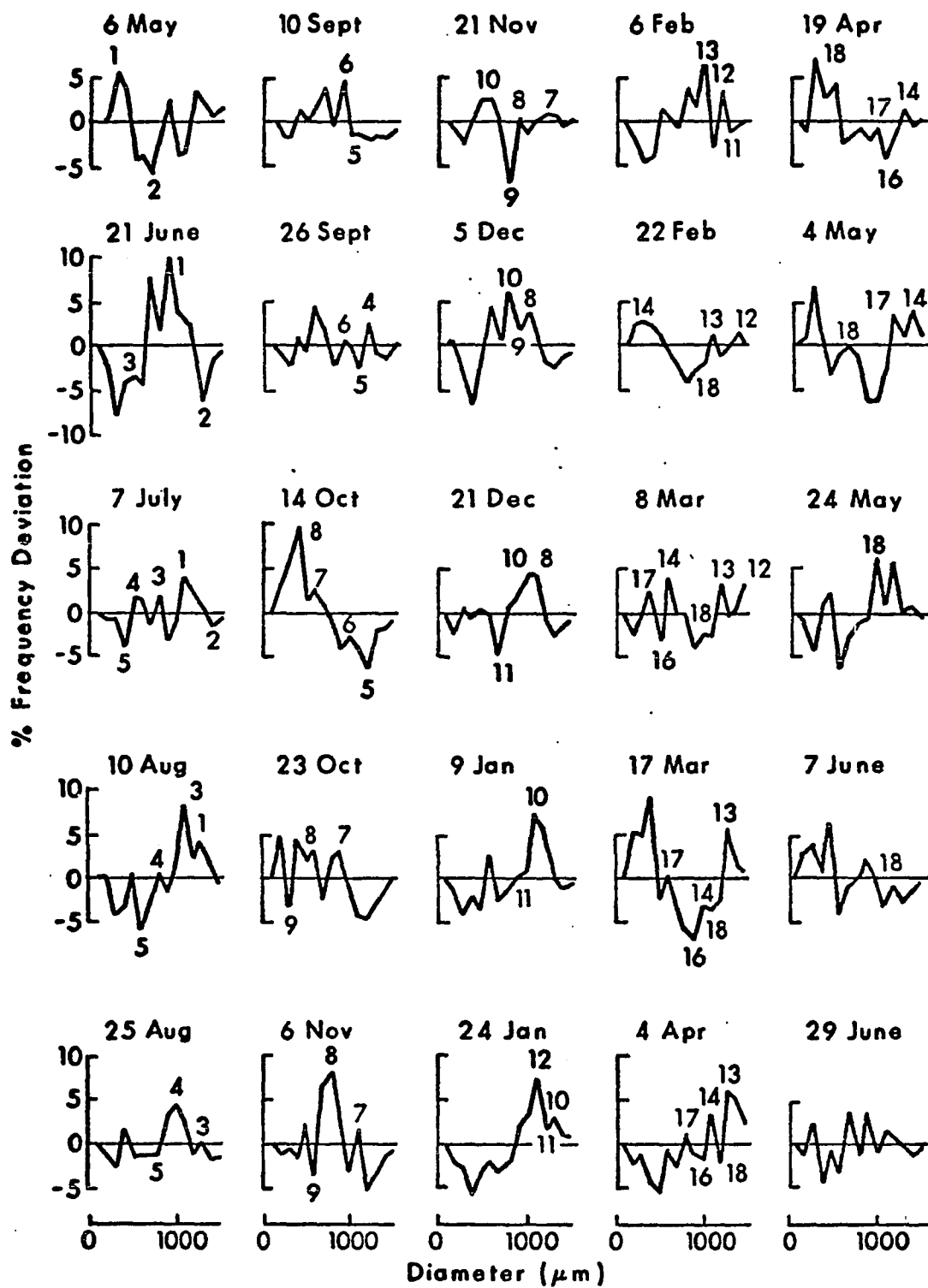


Figure 16. Deviations of percent size-frequency distributions from the reference distribution for A. lobifera at station PS-16.



of 45 cases. Monthly percent deviation plots are presented in figure 17 with corresponding interpretations of growth in figure 18c.

$$d_t = 33 t^{0.85} \quad (r=0.975, df=39) \quad (13)$$

Pooled, wighted, size-frequency plots for A. lessonii and A. lobifera from PS-16, C. spengleri from PS-17, and A. lessonii and A. lobifera from HS-13 are presented in figure 19.

Culture

Growth

Growth in four cultures of A. lessonii and seven of A. lobifera were fitted to power functions (figure 20)

$$\text{A. lessonii:} \quad d_t = 51 t^{0.68} \quad (r=0.990, df=30) \quad (14)$$

$$\text{A. lobifera:} \quad d_t = 54 t^{0.67} \quad (r=0.983, df=73) \quad (15)$$

Analysis of covariance of the growth data for the two species (1 and 105 degrees of freedom) yielded an F-ratio of 0.803, showing no significant difference in variance between the growth rates of the two species under these laboratory conditions.

Growth of A. lessonii and A. lobifera clones at three light levels are shown in figure 21. In all cases growth at the highest light level was substantially more rapid than at the lowest light level. In both A. lessonii clones, differences between growth rates at high and intermediate light levels were substantially less than between intermediate and low levels. In one A. lobifera clone, there was also less difference between high and intermediate levels; in the other A. lobifera clone, differences were less between intermediate and low levels. The regressions for each trial (table 8) were compared against other trials for the clone in table 9.

Light limitation of ^{14}C uptake

The results of the laboratory experiment on light limitation of ^{14}C

Figure 17. Deviations of percent size-frequency distributions from the reference distribution for C. spengleri at station PS-17

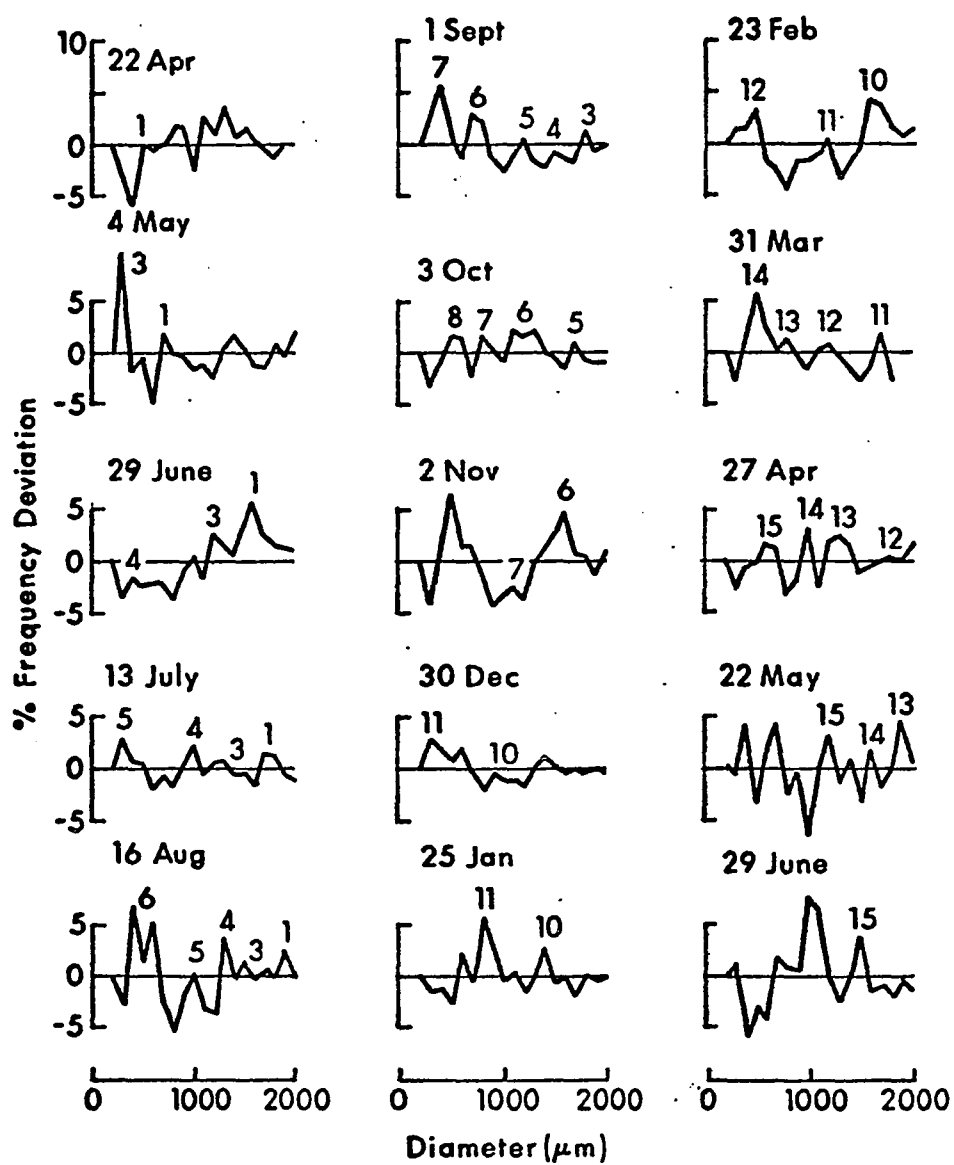


Figure 18. Growth curves interpreted from size-frequency data presented in figures 15-17:

- a. A. lessonii (equation 11)
- b. A. lobifera (equation 12)
- c. C. spengleri (equation 13)

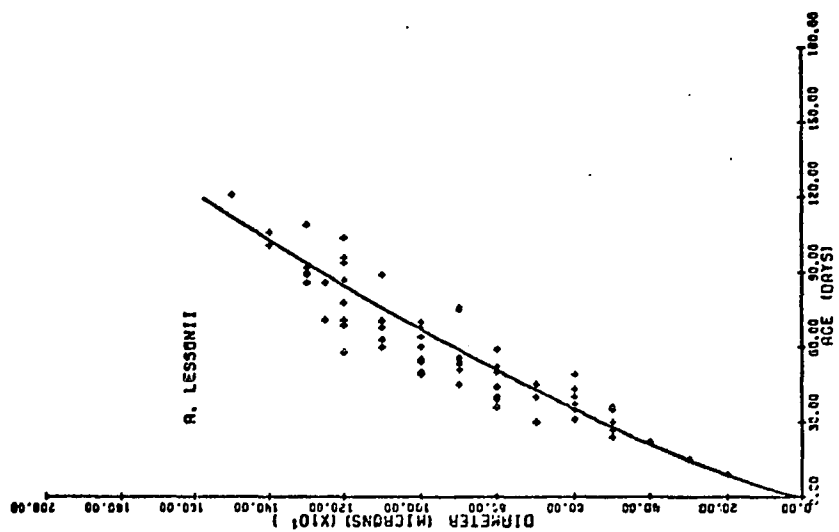
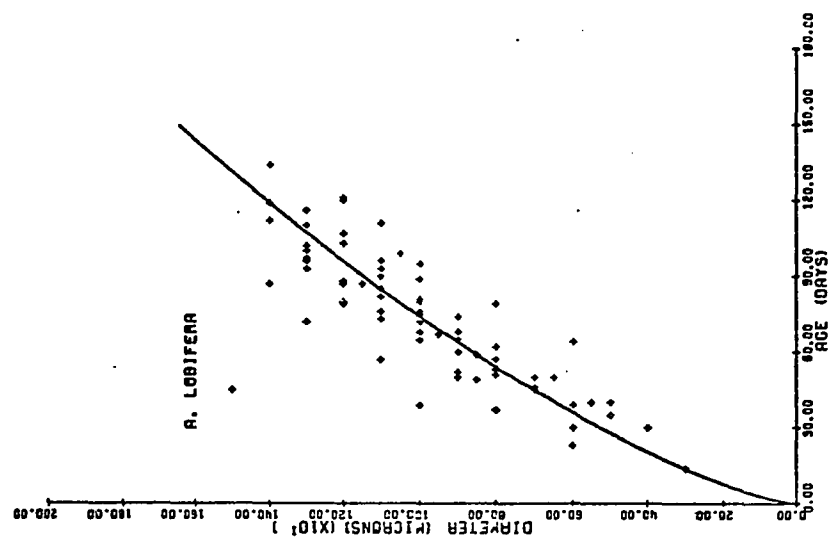
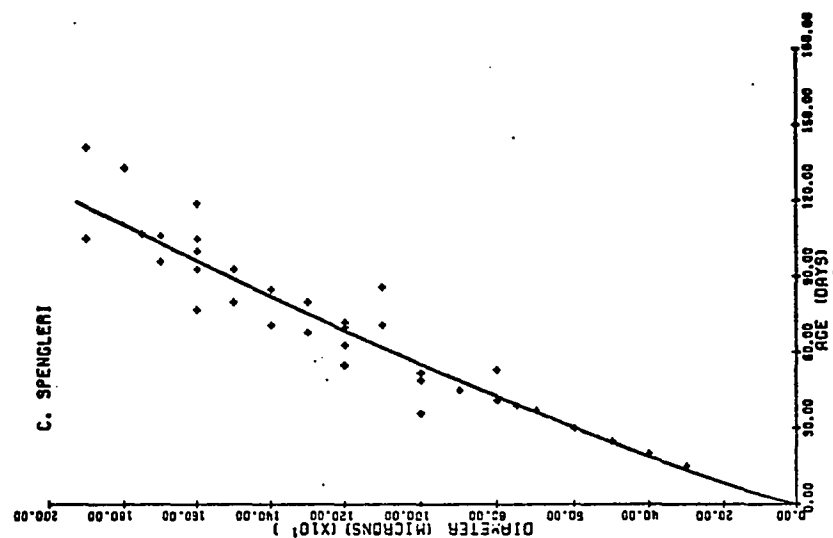


Figure 19. Pooled, weighted percent size-frequency distributions for A. lessonii, A. lobifera, and C. spengleri: from stations PS-16, PS-17, and HS-13.

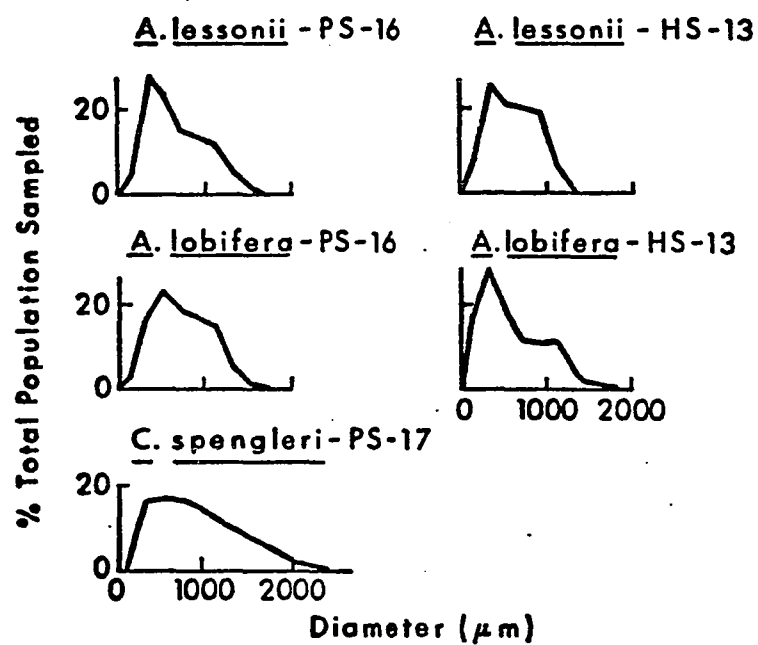


Figure 20. Laboratory growth curves:

A. lessonii (equation 14)
A. lobifera (equation 15)

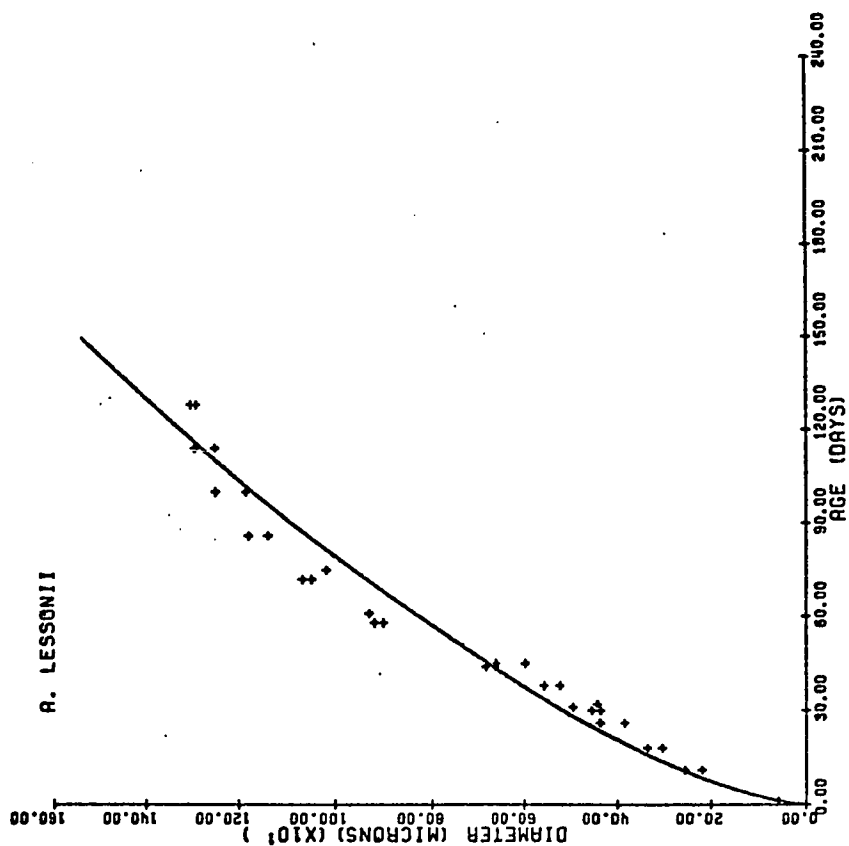
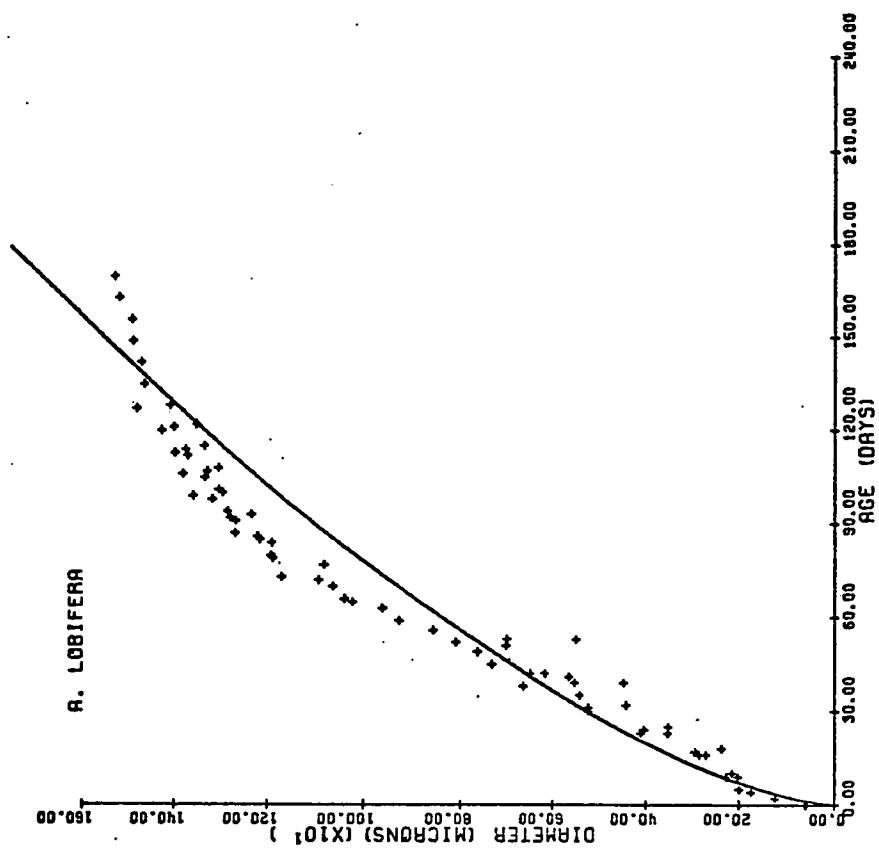
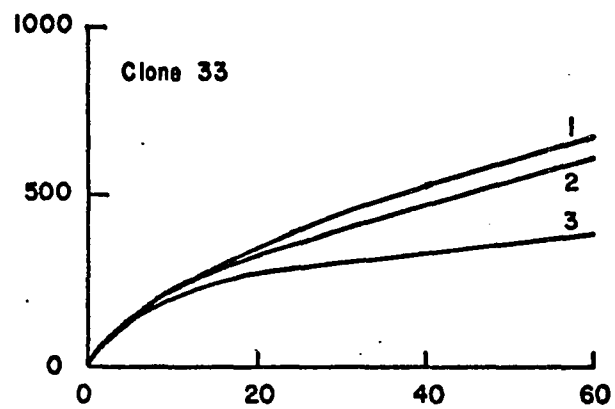
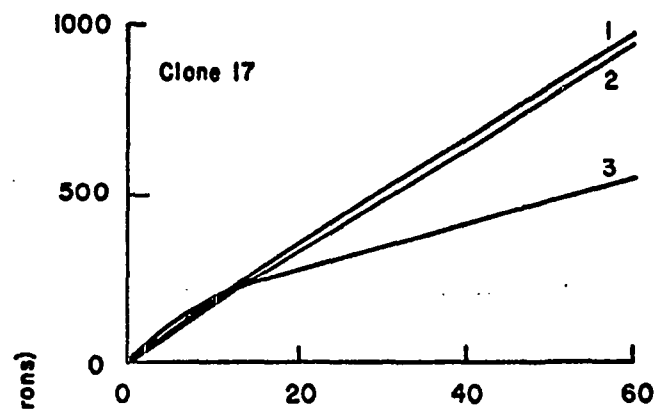
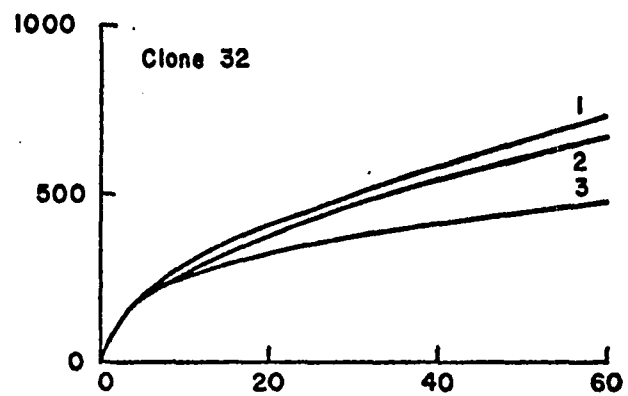
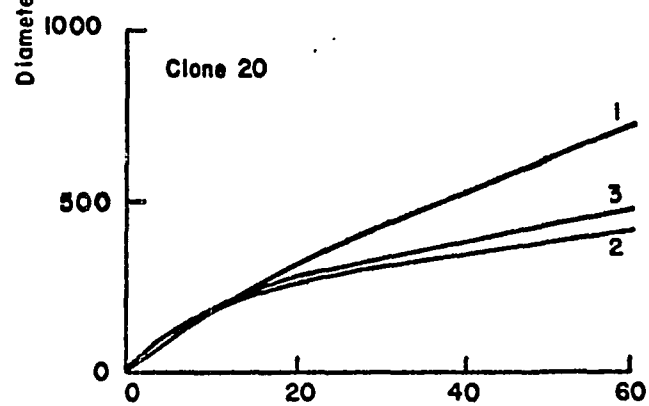


Figure 21. Regressions of diameter to time for two clones each of A. lessonii (17 and 33) and A. lobifera (20 and 32) grown at three light levels. Equations are listed in Table 9.

A. lessonii



A. lobifera



Time (days)

Table 8

Regressions of Diameter (d) to Time (t) for Two Clones of
Amphistegina lessonii and Two Clones of A. lobifera
 Grown at Three Light Levels

Species	Clone	Trial	Light ($\mu\text{W}/\text{cm}^2$)	Equation	r	df
<u>A. lessonii</u>	17	1	2600	$d = 25.8 t^{0.887}$	0.977	150
		2	700	$d = 22.8 t^{0.908}$	0.983	125
		3	300	$d = 42.2 t^{0.627}$	0.897	150
	33	1	2600	$d = 59.1 t^{0.598}$	0.985	126
		2	700	$d = 64.0 t^{0.552}$	0.980	126
		3	300	$d = 96.0 t^{0.346}$	0.938	125
<u>A. lobifera</u>	20	1	2600	$d = 34.3 t^{0.746}$	0.944	150
		2	700	$d = 75.1 t^{0.417}$	0.880	125
		3	300	$d = 61.8 t^{0.502}$	0.880	176
	32	1	2600	$d = 79.9 t^{0.541}$	0.988	124
		2	700	$d = 86.3 t^{0.500}$	0.981	124
		3	300	$d = 107 t^{0.371}$	0.963	124

Table 9
Comparisons of Regressions of Growth with Time Under
Three Light Levels for Amphistegina Clones

<u>Amphistegina lessonii</u>			
Trial 1	Trial 2	t-value	Significant*
C17HI	C17MD	-2.78157	Yes
C17HI	C17LW	9.18233	Yes
C17MD	C17LW	15.3606	Yes
C33HI	C33MD	3.05056	Yes
C33HI	C33LW	18.122	Yes
C33MD	C33LW	14.9495	Yes
<u>Amphistegina lobifera</u>			
C20HI	C20MD	18.9731	Yes
C20HI	C20LW	10.6964	Yes
C20MD	C20LW	-4.66767	Yes
C32HI	C32MD	3.94285	Yes
C32HI	C32LW	14.5115	Yes
C32MD	C32LW	8.78882	Yes

* 0.01 level

uptake are presented in table 10. In bright sunlight, A. lobifera fixed carbon relatively more rapidly than A. lessonii. A. bicirculata died in bright sunlight. At about 1% of bright sunlight, all three species fixed carbon at relatively similar rates. At 0.01% of sunlight, fixation was insignificantly different from dark fixation ($P < 0.01$).

Results of the field experiment (table 11) confirmed the observation made in the laboratory. ^{14}C fixation by A. lobifera under full sunlight was more rapid than by A. lessonii. Just below the surface, fixation by A. lessonii sharply increased. At lower light levels, the fixation rates of the two species converged. Fixation rates for both species remained relatively high to about 30% of surface light, then decreased rapidly at lower light levels.

Reproduction

All reproduction observed in A. lessonii and A. lobifera in the laboratory was by multiple fission external to the test. A. lessonii individuals reproduced throughout the range of available light levels in the incubator ($300\text{--}2600 \mu\text{w}/\text{cm}^2$), whereas A. lobifera individuals only reproduced at the highest level ($2600 \mu\text{w}/\text{cm}^2$). No specimens produced in culture reproduced.

Tables 12 and 13 list the size of the adults that reproduced in culture and the number of young produced by each reproduction. Number of young (F_d) as a power function of greatest spiral diameter of the parent (d) was calculated for both species by a least squares fit of the data:

$$\text{A. lessonii:} \quad F_d = 0.00513 d^{1.60} \quad (r=0.620, df=46) \quad (16)$$

$$\text{A. lobifera:} \quad F_d = 0.00309 d^{1.74} \quad (r=0.583, df=18) \quad (17)$$

Table 10

^{14}C Fixation Rates ($\times 10^{-5}$ mg $^{14}\text{C/hr-foram}$)
of Three Species of *Amphistegina* as a Function
of Light and Comparisons Between All Trials

Conditions	Species	Light ($\mu\text{watt/cm}^2$)	Mean	Standard Deviation	t-value	df	F-ratio	df
Sunlight	<u>A. lobifera</u>	10^4	2.91	0.176	10.2*	6	6.38	3,3
	<u>A. lessonii</u>		1.95	0.070				
Shade	<u>A. lobifera</u>	10^2	0.674	0.016	5.08*	6	6.77	3,3
	<u>A. lessonii</u>		0.835	0.062				
Shade	<u>A. lobifera</u>	10^2	0.674	0.016	1.01	6	0.078	3,3
	<u>A. bicirculata</u>		0.644	0.058				
Shade	<u>A. lessonii</u>	10^2	0.835	0.062	4.55*	6	1.15	3,3
	<u>A. bicirculata</u>		0.644	0.058				
Dim shade	<u>A. lobifera</u>	1	0.025	0.004	7.85*	6	0.26	3,3
	<u>A. lessonii</u>		0.057	0.007				
Dim shade	<u>A. lobifera</u>	1	0.025	0.004	1.39	6	0.10	3,3
	<u>A. bicirculata</u>		0.034	0.012				
Dim shade	<u>A. lessonii</u>	1	0.057	0.007	3.43	6	0.39	3,3
	<u>A. bicirculata</u>		0.034	0.012				
Dim shade Dark	<u>A. lobifera</u>	0-1	0.025	0.004	5.40*	6	1.30	3,3
			0.038	0.003				
Dim shade Dark	<u>A. lessonii</u>	0-1	0.057	0.007	1.46	6	0.14	3,3
			0.072	0.019				
Dim shade Dark	<u>A. bicirculata</u>	0-1	0.034	0.012	0.55	6	5.27	3,3
			0.030	0.005				

*significant at 0.01 level

Table 11

^{14}C Fixation Rates ($\times 10^{-5}$ mg $^{14}\text{C/hr-foram}$)
of Two Species of Amphistegina
as a Function of Light Intensity

Depth (m)	Light (% surface intensity)	<u>A. lobifera</u>		<u>A. lessonii</u>		t-value	df	F-ratio	df
		Mean	Standard Deviation	Mean	Standard Deviation				
0	100	2.92	0.109	2.40	0.114	6.64*	6	0.90	3,3
1	82	2.74	0.176	3.44	0.302	4.04*	6	0.34	3,3
2	67	2.53	0.308	3.04	0.264	2.54	6	1.36	3,3
4	45	2.63	0.094	2.74	0.193	1.04	6	0.24	3,3
6	30	2.02	0.383	2.48	0.129	2.28	6	8.80	3,3
8	20	1.56	0.116	1.34	0.250	1.56	6	0.21	3,3
10	14	0.72	0.148	0.75	0.226	0.27	6	0.43	3,3
12	9	0.42	0.040	0.26	0.027	6.64*	6	2.19	3,3
0	0	0.02	0.014	0.04	0.029	1.56	6	0.21	3,3
4	0	0.01	0.007	0.02	0.005	2.89	6	2.05	3,3
12	0	0.03	0.032	0.02	0.013	0.56	6	6.17	3,3

*significant at 0.01 level

Table 12

Sizes of Amphistegina lessonii That Reproduced in
Culture and the Numbers of Young Produced

Clone #	Parent Diameter (μ m)	# Young	Clone #	Parent Diameter (μ m)	# Young
1	1250	-	2	1500	-
3	1350	859	4	1400	679
5	1360	500	6	1400	464
7	1450	760	8	1450	625
10	1150	383	11	1200	702
12	1700	1542	13	1175	337
14	1150	-	15	1450	837
16	1275	-	17	1450	803
19	1150	241	21	1350	-
23	1325	562	24	1200	-
28	1500	765	33	1700	790
37	1500	819	38	1600	600
39	1500	400	40	1500	608
41	1575	875	42	1200	-
43	1650	574	44	1200	190
45	1250	604	46	1275	583
47	1725	841	48	1475	857
49	1600	773	50	1475	660
51	1500	920	52	1675	694
53	1700	864	54	1700	712
55	1800	961	56	1800	657
57	1700	962	58	1900	907
59	1750	800	60	1800	737
61	1800	625	62	1750	810
63	1500	428	64	1750	849
65	1750	871	66	1750	762
67	1900	865	69	1700	731
70	1850	534			

Table 13

Sizes of Amphistegina lobifera That Reproduced in
Culture and the Numbers of Young Produced

Clone #	Parent Diameter (μm)	# Young	Clone #	Parent Diameter (μm)	# Young
18	1900	2360	20	1650	1576
22	2000	1600	25	1725	1335
26	1800	1650	27	1800	977
29	1750	-	30	2150	-
31	1850	1872	32	2200	2005
34	1900	1745	35	1750	1648
36	1975	1613	68	1700	873

DISCUSSION

Within the limited-sized areas studied, size-frequency distributions of Amphistegina spp. and C. spengleri populations tend to be relatively homogenous, especially when the smallest size classes are omitted from consideration (Muller 1974). These foraminifera reproduce by multiple fission which initially tends to cluster juveniles. But by age 3-4 weeks about (400 μ m), the young foraminifera are dispersed through the population. This behavior may partially account for the apparent truncation of pooled size-frequency plots in the smaller size classes, and indicate that caution must be used in analyzing such data with standard statistical procedures without taking into account the biology of the protists. In the size-frequency data tested here using the Kolmogorov-Smirnov goodness-of-fit test, only a small percentage of the samples were significantly different from the pooled frequencies for the date, so homogeneity of populations with respect to size distribution was assumed without elimination of small size classes from consideration.

Power function growth curves with age raised to a power <1 were used to fit the growth data because the curves consistently fit the data very closely. Within the observed range of data, the growth of the protists in the field appeared to gradually slow throughout life, which is the characteristic of the function employed. The slight tendency towards sigmoidal growth observed in the laboratory (figures 20) may be due to sensitivity of smaller individuals to culture conditions and handling, and to the obvious lack of some factors in the environment which results in the failure of individuals produced in culture to reproduce and to eventually stop growing and die. However, it is important to point out that A. lessonii and A. lobifera in culture do grow at similar rates to those in the field at similar temperatures at intermediate sizes (approximately 500-1000 μ m or more depending on the species), which indicates that laboratory experiments utilizing healthy, intermediate-sized specimens probably yield valuable insights on growth responses in the protists.

Probably the most important point concerning the choice of a growth curve is that within the range of available data, nearly any curve that reasonably represents the trend in the data, even a linear fit, probably

introduces less error than is inherent in the data due to the relatively crude progression of modes method used to determine growth in the field. The purpose in fitting any curve to the data was to summarize the behavior of the data to facilitate further comparison and discussion.

Scaling of the data by assuming that 300 μm individuals were about two weeks old was based upon growth of Amphistegina in culture, and even for Calcarina should introduce only a few days error at most.

As shown by the size-frequency plots, large specimens are extremely rare in the populations. In field populations A. lessonii larger than 1200 μm in size in Hawaii data and 1400 μm in Palau samples and A. lobifera larger than 1400 μm in both cases are seldom encountered. Reproduction by multiple fission is one cause of mortality in adult foraminifera and this biological factor, coupled with the observed scarcity of large specimens may indicate that the foraminifera in the field in actively reproducing populations may be reproducing soon after reaching adult size. This observation facilitates use of the growth curves because, although growth data are not available for the entire range of sizes observed in the field, very large specimens beyond the range of the curves make up only a very small fraction of a percent of the total population.

If indeed the foraminifera commonly reproduce soon after reaching reproductive size, time than an individual takes to grow to reproductive size may be a reasonable indicator of generation time. While growth is somewhat slower in the Hawaiian A. lessonii population, the apparently smaller reproductive size, about 1200 μm as compared to 1400 μm in Palau, resulted in similar 3-4 month generation times. A. lobifera growth was also markedly slower and generation time longer in Hawaii, about one year, than in Palau, about 4 months. Temperature may be a factor in the growth rate differences in both species, as ambient temperature in Hawaii is about 4° lower than in Palau. All temporal sampling sites were at depths of 2 m or less so light limitation of growth should not have been a factor between localities. Generation time in C. spengleri in Palau also appears to be about 3-4 months.

Culture growth and generation time are available for two other large species of foraminifera, H. depressa (Röttger 1972, 1974, 1976; Röttger and Berger 1972; Röttger and Spindler 1976) and Marginopora vertebralis (Ross 1972). H. depressa grows to reproductive size and individuals begin to reproduce under favorable conditions in the laboratory, 24.5°C., 450-600 lux illumination in approximately 3-4 months (Röttger 1976) although most reproductions occur at age six months (Röttger and Spindler 1976). This is similar to the rates of growth and generation times found in this study for Amphistegina and Calcarina. M. vertebralis which belongs to a different suborder of foraminifera than the other three genera, is a much slower growing protist, probably requiring at least a year and commonly longer to reach reproductive maturity (at 26-29°C.) according to Ross (1972).

Light limitation of both ^{14}C fixation and growth rate of Amphistegina was demonstrated in the laboratory. ^{14}C fixation rates remained relatively high, about 70 percent of the maximum measured, in both A. lessonii and A. lobifera down to about 30% of surface light intensity, then dropped off rapidly below that level. Both A. lessonii clones also showed that growth rate can remain similar over a fairly wide range of light levels, as the trials grown at the highest and intermediate light levels grew at very similar rates, while growth in the trials at the lowest light level was substantially depressed. A. lobifera showed this trend in only one of two clones. H. depressa showed a similar trend when grown under several light intensities (Röttger 1976, fig. 2), growth at 450 lux was only slightly slower than at 600 lux and first reproduction occurred only days apart in the two trials; growth at 150 and 300 lux was substantially depressed. That microalgae have a range of optimum light intensities over which growth rate and photosynthesis change very little has been widely reported (see Caperon 1967).

Both A. lessonii and A. lobifera are apparently more light-tolerant than H. depressa. Maximum light in the Amphistegina cultures was about 2600 μw per cm^2 or about 26% of zenith sea surface light intensity on a clear day. Using 600 lux as optimum light intensity for H. depressa (Röttger 1976) and 120,000 lux as sea surface light intensity on a clear

day with the sun at zenith (Sverdrup et al 1942), optimum light intensity for H. depressa is about 0.5 percent of surface light intensity under those conditions.

Assuming an extinction coefficient $k=0.08$, a fairly typical value for nearshore Oahu (Appendix E) and for the open lagoon in Palau (R. Muller 1976), 30 percent of surface light intensity reaches about 15 m depth, which is about the depth at which A. radiata begins to replace A. lessonii in Palau lagoon. Assuming that natural populations respond to light similarly to the experimental specimens in the ^{14}C uptake experiments, and that carbon fixation by the symbionts is proportional to growth, growth rates of A. lessonii and A. lobifera may remain relatively similar with respect to light intensity over depths of 0-15 m.

Light inhibition of photosynthesis is well known in phytoplankton (Ryther 1956), so the significant light inhibition of ^{14}C fixation in A. lessonii was not surprising, nor were the deaths of A. bicirculata individuals when exposed to full sunlight, as the latter species occurs at the lower limits of the euphotic zone. Röttger (1976) also reported inhibition of growth in H. depressa by light intensities of 1200 lux or higher,

Trends exhibited by Amphistegina spp. in the light experiments are probably more important qualitatively than quantitatively. However, light inhibition is probably an important aspect in niche separation of A. lessonii and A. lobifera. A. lessonii, inhibited by high light intensities, is not competitive in the "infralittoral fringe" (of Stephenson and Stephenson 1949) occupied by A. lobifera. A. lobifera appears to require higher light intensities for reproduction than does A. lessonii. The two species may be compared in the data presented in Table 14. The location of the sampling sites at Makapuu and PS-16 are both very shallow, 1 and 2 m depth respectively, which may be within the depths of photoinhibition for A. lessonii. Optimum growth rates for the species at the temperatures characteristic of the geographic locations may actually be up to 30% higher than the growth data shows (values in parentheses, Table 14). Given comparable mortality rates for A. lessonii

Table 14.
Age of Maturation, Fecundity, and Birth Rate
of Four Species of Large Foraminifera.

Species	Location	Maturation size (μm)	Age ¹ (days)	Fecundity # young/adult	Birth Rate # young/adult/day ¹
<u>A. lobifera</u>	Hawaii	1400	280	900 ²	3
<u>A. lobifera</u>	Palau	1400	125	900 ²	7
<u>A. lessonii</u>	Hawaii	1200	100(75)	400 ³	4(6)
<u>A. lessonii</u>	Palau	1400	100(75)	400 ⁴	7(9)
<u>H. depressa</u>	Culture ⁵	1800	100	80	1
<u>M. vertebralis</u>	Culture ⁶	15000	730	100	.1

¹ Values in parentheses are estimates accounting for photoinhibition.

² Extrapolated from equation 17, outside range of laboratory data.

³ Mean for laboratory A. lessonii, 1150-1275 μm .

⁴ Mean for laboratory A. lessonii, 1300-1500 μm .

⁵ From Röttger (1972, 1976).

⁶ From Ross (1972).

and A. lobifera in the infralittoral from about 5-15 m, A. lessonii should be and is clearly dominant. In the infralittoral fringe, differential mortality as well as photoinhibition of A. lessonii may provide A. lobifera with the competitive advantage not clearly evident in Table 14.

Comparison of fecundity with longevity and habitat of these species reveals a pattern. A. lobifera, which occurs in the turbulent infralittoral fringe where the probability of reproductive success by multiple fission external to the test may be quite low, is relatively long-lived, grows to relatively large sizes, and produces up to about 2000 young per parent. A. lessonii, which occurs lower in the infralittoral where chances of reproductive success may be somewhat better, is relatively shorter-lived, may mature at somewhat smaller sizes, and produces up to about 1000 young per parent. H. depressa, which is also an infralittoral species that requires very calm conditions for growth (Röttger 1976) where chances for reproductive success are probably quite good, is also relatively rapidly maturing and produces only up to about 200 young per parent (Röttger 1972). M. vertebralis, whose distribution is similar to A. lobifera, and in which reproduction occurs internally within reproductive chambers, is very slow to mature, grows to a very large size, and produces only 60-150 or more young per parent (Ross 1972).

A. lobifera and M. vertebralis, which both dwell in a relatively rigorous environment, appear to sacrifice time (maturation rate) to insure reproductive success, and by two different and very basic methods. A. lobifera grows to a relatively large volume thereby increasing fecundity (to be discussed further in Section II. Shape Trends...). M. vertebralis attains a very large diameter and produces massive reproductive chambers within which the young develop. A. lessonii and H. depressa, which are restricted by light inhibition and possibly other factors, to physically less rigorous environments, are less fecund than A. lobifera. The low fecundity of H. depressa is indicative of the physically benign environment in which the species occurs.

CARBONATE PRODUCTION

INTRODUCTION

Carbonate sediments of foraminiferal origin make up a substantial portion of the beach and nearshore sand in subtropical and tropical Pacific islands and atolls (Cushman et al 1954, Emery et al 1954, McKee et al 1959, Moberly and Chamberlain 1964, others). The large species whose distributions and abundances were discussed previously, particularly Amphistegina and Calcarina, contribute the bulk of the foraminiferal fraction of sand-sized sediments. However, the predominance of foraminiferal tests in nearshore sands is not totally indicative of the carbonate production potential of the protists, as hydrodynamic sorting (Hedgepeth 1957) and differential abrasion (Moberly 1968, Muller 1976) tend to concentrate the tests in beach sands.

The purpose of this paper is to test the hypothesis that foraminifera are capable of producing carbonate in the coral reef environment at rates comparable to those of other major carbonate producers. Growth and abundance data presented earlier are used to calculate carbonate production over a year by Amphistegina lessonii, A. lobifera, and Calcarina spengleri at three temporal sampling sites. Then, carbonate production by selected foraminifera in the reef environment is discussed by extrapolating from the carbonate production rates exhibited by these three species.

The three species studied in detail are rotaliine species which occur primarily on reef flats or shallow reef faces and lagoon slopes (0-15 m). Although 12 other species were sampled and their distributions discussed earlier, carbonate production by only four of these species, Baculogypsina sphaerulata, Calcarina calcar, C. hispida, and Heterostegina depressa is considered in addition to the three species studied directly. Carbonate production by the milioline species is not

considered, as they are phylogenetically quite distant from the rotaliine species. Furthermore, the population biology of Marginopora vertebralis, a milioline, is very different from that of the rotaliine species studied (see table 14). Thus, extrapolating from the population biology of the rotaliines to the miliolines may not be valid. In addition, since growth and ^{14}C uptake by Amphistegina and Heterostegina are depressed at reduced light levels (see p. 90 and Röttger 1976), foraminiferal carbonate production at depths greater than 15 m is not estimated; production by deeper dwelling species is not considered.

Carbonate production is taken to be the mass of carbonate per unit area lost to the population by loss of living individuals from the population by any means, i.e., apparent mortality. Loss of carbonate by dissolution is neglected. Carbonate productivity or carbonate production is discussed in terms of the mass of carbonate produced on a yearly basis ($\text{g CaCO}_3 \text{m}^{-2} \text{yr}^{-1}$).

PROCEDURE

Diameter-mass relationships

Diameter-mass relationships in the seven species of foraminifera whose carbonate productivity was considered were determined by weighing dry test mass in grams and measuring the greatest spiral diameter in microns of at least 25 individuals of each species. Data for each species were fit to power functions of diameter to mass by a least squares fit, and the resulting equations are presented in table 15.

Observed carbonate production in A. lessonii, A. lobifera, and C. spengleri

Annual production (P) was calculated by a method similar to that derived and used previously (Muller 1974):

$$P = \left(\sum_i \sum_j (N_{i,j} - N_{i+g,j+1}) (w_{i+g} - w_i) / 2 \right) C \quad (18)$$

Table 15

Diameter-mass Relationships
for Seven Species of Large Foraminifera,
Where Diameter (d) is in Microns and Mass (w) is in Grams

Species	Equation	r^2	df	Size range
<u>Amphistegina lessonii</u>	$w = 1.27 \times 10^{-12} d^{2.74}$	.9802	48	220 - 1840
<u>A. lobifera</u>	$w = 1.07 \times 10^{-11} d^{2.50}$	.9636	48	245 - 1925
<u>Baculogypsina sphaerulata</u>	$w = 6.79 \times 10^{-14} d^{3.34}$	.9513	23	280 - 1120
<u>Calcarina calcar</u>	$w = 3.44 \times 10^{-12} d^{2.63}$	.9521	23	228 - 665
<u>C. hispida</u>	$w = 2.43 \times 10^{-12} d^{2.73}$	.9714	23	375 - 1200
<u>C. spengleri</u>	$w = 1.46 \times 10^{-12} d^{2.82}$	.9919	23	475 - 1800
<u>Heterostegina depressa</u>	$w = 2.00 \times 10^{-12} d^{2.62}$	.9728	23	280 - 3500

where $N_{i,j}$ is number of individuals per m^2 in size class i in microns on sampling date j , $N_{i+g,j+1}$ is number of individuals per m^2 in the size class to which individuals of size i have grown between dates j and $j+1$, w_i is the mass in grams of an individual of size i , w_{i+g} is mass of an individual of size $i+g$. C is a correction factor standardizing estimates to yearly rates, necessitated because total sampling periods were not exactly one year.

Mortality and annual carbonate production by size class are listed for A. lessonii and A. lobifera at PS-16, C. spengleri at PS-17 (table 16), and A. lessonii and A. lobifera at HS-13 (table 17).

Juvenile production

Due to incomplete sampling in size classes under 500 μm , the figures presented in tables 16 and 17 do not include production by juveniles which died or were washed away before attaining a size at which they were consistently observed in the sampled population. As indicated previously (Muller 1974), juvenile production may be a substantial portion of the total production by a species. Therefore, juvenile mortality and production were calculated using fecundity data for A. lessonii and A. lobifera from equations 16 and 17 and by estimating the proportion of reproducing adults.

From the size-specific mortality data, a recurring trend is evident. Mortality in subadults (500-800 μm for A. lessonii from Hawaii, 700-1000 μm for all A. lobifera and A. lessonii from Palau) is comparatively low. Mortality in adult size classes is comparatively high. Reproduction is one cause of mortality in adults, and from these trends, it appears to be a major cause.

As a rough estimate of the magnitude of the carbonate contribution by juveniles, production was calculated making the following assumptions:

1. One half of adult mortality is due to reproduction by multiple fission.

Table 16

Mortality, Carbonate Production, and Turnover Rates
for Three Species of Benthic Foraminifera from Palau

Line #	Size	<u>A. lessonii</u> PS-16		<u>A. lobifera</u> PS-16		<u>C. spengleri</u> PS-17	
		# dying	g CaCO ₃	# dying	g CaCO ₃	# dying	g CaCO ₃
		$\frac{\text{m}^2}{\text{yr}} \times 10^4$	$\frac{\text{m}^2}{\text{yr}} \times 10^3$	$\frac{\text{m}^2}{\text{yr}} \times 10^4$	$\frac{\text{m}^2}{\text{yr}} \times 10^3$	$\frac{\text{m}^2}{\text{yr}} \times 10^4$	$\frac{\text{m}^2}{\text{yr}} \times 10^3$
1	200	-	-	-	-	-	-
2	300	17.6	3.0	-	-	-	-
3	400	8.5	2.7	-	-	0.71	0.7
4	500	17.6	9.1	3.9	3.6	0	0
5	600	11.5	9.1	9.7	13.5	.92	2.1
6	700	5.2	5.9	1.2	2.3	.65	2.0
7	800	0	0	5.0	13.1	1.02	4.3
8	900	3.3	7.5	4.2	14.3	.95	5.2
9	1000	4.3	11.8	4.0	17.2	.93	6.5
10	1100	8.5	29.4	8.9	47.5	.97	8.5
11	1200	8.4	36.3	10.9	70.9	.82	8.9
12	1300	5.9	31.4	5.0	39.4	1.19	15.8
13	1400	4.4	28.2	2.2	20.5	.94	14.9
14	1500	3.4	26.1	2.4	26.4	.59	11.0
15	1600	-	-	-	-	.87	19.3
16	1700	-	-	-	-	.93	23.8
17	1800	-	-	-	-	.90	26.8
18	1900	-	-	-	-	.60	20.4
19	2000	-	-	-	-	.60	23.5
20	Observed Total	98.6	201	57.4	269	13.6	194
21	Juvenile	8.2×10^3	96	1.1×10^4	317	_____	_____
22	Total	8.2×10^3	297	1.1×10^4	586	_____	_____
23	Observed $\Sigma \bar{N}_{i,w}$	12.5		20.8		17.1	
24	Turnovers (yr ⁻¹)	16		13		11	
25	Total $\Sigma \bar{N}_{i,w}$	16		33		_____	
26	Turnovers (yr ⁻¹)	18		18		_____	

Mortality, Production, and Turnover Rates
for Two Species of Benthic Foraminefera in Hawaii (HS-13)

line #	size	<u>A. lessonii</u>		<u>A. lobifera</u>	
		$\frac{\# \text{ dying}}{\text{m}^2 \text{ yr}} \times 10^4$	$\frac{\text{g CaCO}_3}{\text{m}^2 \text{ yr}}$	$\frac{\# \text{ dying}}{\text{m}^2 \text{ yr}} \times 10^4$	$\frac{\text{g CaCO}_3}{\text{m}^2 \text{ yr}}$
1	200	-	-	6.2	1.1
2	300	3.3	.78	9.4	3.2
3	400	0.9	.41	7.7	4.6
4	500	0	0	9.1	6.9
5	600	0.1	.09	5.8	6.7
6	700	0	0	1.4	2.4
7	800	4.0	6.3	1.9	4.4
8	900	3.6	7.6	1.7	5.0
9	1000	4.6	12.5	0.5	1.9
10	1100	2.6	8.9	3.4	16.1
11	1200	0.8	3.5	3.4	20.0
12	1300	-	-	2.8	20.3
13	1400	-	-	0.3	2.4
14	1500	-	-	0.8	7.7
15	1600	-	-	0.01	0.1
16	Observed Total	19.9	40	54.9	103
17	Juvenile	1.3×10^3	16	3.9×10^3	114
18	Total	1.3×10^3	56	3.9×10^3	217
19	Observed $\sum \bar{N}_i w_i$	3.5		16.4	
20	Turnovers (yr^{-1})	11		6	
21	Total $\sum \bar{N}_i w_i$	4.8		25.9	
22	Turnovers (yr^{-1})	12		8	

2. Juveniles not appearing in the sampled population are dying at an average size of 150 μm .

3. Fecundity in the field is similar to that observed in the laboratory.

4. A. lessonii from Palau and all A. lobifera reproduce at $\geq 1100 \mu\text{m}$. A. lessonii from Hawaii reproduce at $\geq 1000 \mu\text{m}$.

Comparison of the estimates of juvenile production with adult production in tables 16 and 17 indicates that disregarding juvenile production may result in underestimates of production of one third to one half. The error is greater in the more fecund species.

Turnover rates

Average standing crop in terms of $\text{g CaCO}_3 \text{ m}^{-2} (\sum \bar{N}_i w_i)$ was calculated using the average densities of the populations (Appendices B and D) and the weighted, pooled percent frequencies of the populations (figure 19). Annual sediment production (P) for the population was then divided by the average standing crop to yield turnover rate (τ):

$$\tau = P / \sum_i \bar{N}_i w_i \quad (19)$$

where $\bar{N}_i$ is average number at size i , w_i is mass in grams at size i .

Population turnover rates for each species were calculated from observed adult production figures (table 16, line 20, and table 17, line 16) and were reasonably similar in all three species (table 16, line 24, and table 17, line 20). Turnover rate in A. lessonii, the smallest of the three species was highest in both Palau and Hawaii. However, when juvenile abundance and production were considered (table 16, line 22, and table 17, line 18), turnover rates of A. lessonii and A. lobifera were more similar, almost 20 times per year in Palau (table 16, line 26) and about 10 times per year on Oahu (table 17, line 22).

Carbonate production by other species

Carbonate production rates (P) of B. sphaerulata, C. calcar, C. hispida, and H. depressa were estimated using the simple method

$$P = N \tau w \quad (20)$$

where N is abundance per unit area, τ is turnover rate (per year), and w is mass in grams of a "typical" individual (Chave et al 1972, Muller 1976).

To determine the mass of a "typical" individual of the three species for which carbonate production rates were available (tables 16 and 17), equation 20 was solved for w

$$w = P / n \tau \quad (20')$$

The results shown in table 18_a indicate that a "typical" individual is about half the size of a large adult specimen, i.e., "typical"

A. lessonii and A. lobifera are about 700-800 μm in diameter and individuals of either species larger than 1500 μm are rarely encountered. Likewise, a "typical" C. spengleri is about 1100 μm and large specimens over about 2200 μm are seldom seen in the population. Assuming that a "typical" individual is about half the size of a large adult, the masses in table 18_b were used for the other four species.

Turnover rates for the four species were also estimated using those for the observed adult populations. Turnover rates for the calcarinid species were assumed to be similar to C. spengleri (table 16). Turnover rates for H. depressa were assumed to be similar to that of A. lessonii (tables 16 and 17).

Carbonate production by foraminifera in selected environments

Based on the assumptions just presented concerning turnover rates and sizes, carbonate production by the seven species of foraminifera was calculated for several sites on Palau (table 19) and Oahu (table 20).

Table 18.

Diameter and Mass of "Typical" Individuals
of Seven Species of Foraminifera.

a.

Location	Species	Diameter (μm)	Mass ($\text{g} \times 10^{-14}$)
Palau	<u>Amphistegina lessonii</u>	799	1.14
Palau	<u>A. lobifera</u>	834	2.15
Palau	<u>Calcarina spengleri</u>	1122	5.82
Hawaii	<u>A. lessonii</u>	723	0.866
Hawaii	<u>A. lobifera</u>	744	1.62

b.

Location	Species	Diameter (μm)	Mass ($\text{g} \times 10^{-14}$)
	<u>Baculogypsina sphaerulata</u>	500	.702
	<u>C. calcar</u>	350	.169
	<u>C. hispida</u>	650	1.16
	<u>Heterostegina depressa</u>	1000	1.45

Table 19.

Predicted Annual Carbonate Production
by Selected Benthic Foraminifera in Palau
(Estimated Production by Juveniles is not Included).

Species	Annual Carbonate Production ($\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)						
	Seaward Reef Flat	Seaward Reef Slope	Seaward Reef Flat	Lagoonal		Reef Slopes	
	PS-8	PS-8	PS-17	PS-9 & 10		PS-16	
	<5m	5-15m	1m	2m	5-15m	2m	5-15m
<u>A. lessonii</u>	-	58	1	208	268	201	967
<u>A. lobifera</u>	363	106	173	299	50	269	134
<u>B. sphaerulata</u>	456	-	610	-	-	-	-
<u>C. calcar</u>	86	-	91	2	-	2	-
<u>C. hispida</u>	-	3	2	3	3	1	-
<u>C. spengleri</u>	2369	115	194	192	1	44	-
<u>H. depressa</u>	11	11	2	5	3	11	14
Total	3285	293	1073	709	325	528	1115

Table 20.

Predicted Annual Carbonate Production
by Selected Benthic Foraminifera at Sites
on Oahu.
(Estimated Production by Juveniles is not Included).

Species	Annual Carbonate Production ($\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)							
	West Coast		S.E. Coast		North Coast		South Coast	East Coast
	HS-1		HS-10		HS-11		HS-15	HS-13
	<5m	5-10m	<5m	5-15m	<5m	5-15m	5-15m	1m
<u>A. lessonii</u>	29	10	1	36	13	79	40	40
<u>A. lobifera</u>	19	16	2	17	22	49	11	103
<u>H. depressa</u>	9	9	-	16	0	3	14	2
Total	57	35	3	69	35	131	65	145

Juvenile production was not considered in these estimates, so actual carbonate production rates may be as much as twice what is indicated in tables 19 and 20. Production figures for sites PS-16 (2 m), PS-17, and HS-13 were based on samples collected monthly over a year, while values for other sites were calculated from average standing crops on a single sampling date.

DISCUSSION

The purpose of this paper was to determine if foraminifera are capable of producing carbonate at rates comparable to other major reef carbonate producers. The lower limit of foraminiferal carbonate production rates is known: where foraminifera do not occur, foraminiferal production is zero. To determine the range of carbonate production rates by foraminifera in the reef environment, upper limits of production are of primary interest. Thus, sites with relatively high standing crops of foraminifera were chosen for the productivity estimates presented in tables 19 and 20.

The seaward reef flats PS-8 and PS-17 were both sites where foraminifera were among the most evident carbonate producers, i.e., there was little coral and the foraminifera were densely intermeshed in the algal veneer over coralline algal pavement. Foraminifera, especially the calcarinids, in this type of habitat appear to produce up to several $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$. Reef slopes are somewhat less productive, with A. lessonii contributing the major fraction. Reef flat and slope productivity on Palau appeared to be far higher than on Oahu, both because many of the species do not occur and because growth and turnover rates of A. lessonii and A. lobifera are lower on Oahu.

These foraminiferal production rates are compared with production rates from the literature for other carbonate producers and for the reef environment as a whole (table 21). Foraminiferal production on seaward reef flats compares favorably with nearly all the literature values, whether for coral, coralline algae, macrobenthos, or seaward reef flats

Table 21.

Carbonate Production Rates for Reef Carbonate Producers and Environments

<u>Location</u>	<u>Environment or Major Producer</u>	<u>Production Rate¹ kg CaCO₃ m⁻² yr⁻¹</u>	<u>Method</u>	<u>References</u>
Indo-Pacific 2 sites 6 sites	Coral	24-31 1.4-7	Coral growth X standing crop	see Chave et al 1972
Hawaii	Coralline algae	0.5-2.5	⁴⁵ Ca uptake	Littler 1971
St. Croix	Coralline algae	0-7	accretion rates	Adey and Vassar 1975
Florida Bay	<u>Penicillus</u>	0.003-0.025	standing crop X turnovers	Stockman et al 1966
Bahamas	Calcareous green algae	0.09	standing crop X turnovers	Neumann and Land 1975
Hawaii	<u>Amphistegina</u> (Tidepool)	0.5	growth X standing crop	Muller 1974
Hawaii	Benthic foraminifera	0.26	growth X standing crop	Muller 1976
Hawaii	Benthic foraminifera (3 spp.) Reef flat (<5m) Reef slope (5-15m)	0.1 0.1-0.3	growth X standing crop	Muller (this study)
Palau	Benthic foraminifera (7 spp.) Seaward reef flat Seaward reef slope Lagoon reef slope	1-6 0.6 0.6-1	growth X standing crop	Muller (this study)
Florida	Macrobenthos Littoral Sublittoral	1 0.4	Calculated from organic productiv- ity	Moore 1972
	(more)			

Table 21. (cont.)

<u>Location</u>	<u>Environment or Major Producer</u>	<u>Production Rate kg CaCO₃ m⁻²yr⁻¹</u>	<u>Method</u>	<u>References</u>
Indo-Pacific Reefs				
6 sites	Shallow seaward reef flats	3.4-4.5	Alkalinity depression	See Smith and Kinsey 1976
4 sites	Lagoon	0.3-1.5		
1 site	Top of coral pinnacle	3.7		
Enewetak Atoll	Reef slope	1-2	Alkalinity depression	Smith pers. comm.
Bahama Banks	Bank	0.5	Alkalinity depression	Broeker and Takahashi 1966
Tropical	Shallow, non-reef	0.1-0.5	Lit. summary	Smith 1970

in general. One of the shallow, windward reef flat alkalinity depression values (Smith and Kinsey 1976, originally reported by Smith 1973) is from an algal turf-covered pavement environment with abundant Calcarina and other foraminifera, a site that may be similar to PS-8 of this study. The Palau lagoon and reef slope values for the rotaliine foraminifera are also similar to the alkalinity depression values from comparable environments (Smith and Kinsey 1976 and Smith pers. comm.).

Basically, these figures indicate that foraminifera can be major carbonate producers in the reef environment, i.e., at sites dominated by foraminifera, carbonate production rates may be comparable to rates at sites dominated by other carbonate producers. This production potential in foraminifera further supports the hypothesis proposed by Smith (1973) that calcification rates in marine communities are controlled by the physical-chemical setting rather than the biological composition.

Foraminifera play an important role in the total carbonate budget of tropical reef environments. To name a few examples, Maxwell (1973) stated that foraminiferal detritus is possibly the most abundant and widespread organic component of the Great Barrier Reef Province. Chapman (1900) noted that foraminifera, principally Amphistegina, constitute the greater proportion of sand deposits associated with the Funafuti reef formation. Emery et al (1954) noted that foraminifera, principally C. spengleri, comprise at least 10 percent (locally over 60 percent) of consolidated beachrock, beach sand, and much of the lagoon sediments of several Marshall Islands atolls. Whether on Caribbean coral reefs (Milliman 1973) or Pacific coral reefs (McKee et al 1959, Moberly and Chamberlain 1965, Wiens 1965, Maxwell 1968, Muller 1976, others), foraminifera consistently account for at least 5-10 percent of the carbonate sediments. While in most cases foraminifera are indeed secondary to coralline algae and corals in total reef carbonate production, foraminifera are capable of carbonate production at rates comparable to those of coral and coralline algae and locally produce substantial quantities of carbonate sediments.

SECTION II. MORPHOLOGICAL CONSIDERATIONS

Tests are the raw materials used in foraminiferal research, especially in paleontological and sedimentological studies. Morphological aspects of the tests are usually the prime clues to taxonomy and paleoecology of a species. The significance of morphological studies of living populations is that they provide direct observations which can be applied to interpretations of fossil populations. Two morphological features are considered here. The first, test shape in large, symbiont-bearing species, may have paleoecological significance in interpreting depth ranges of fossil species and assemblages. The other feature, coiling direction in Amphistegina spp., not only provides some insights into control of coiling direction in trochospiral foraminifera, but may also have zoogeographical significance in relation to dispersal patterns of Indo-Pacific species.

TRENDS IN TEST SHAPE WITH DEPTH

INTRODUCTION

Test shape trends among large foraminifera have been reported and associated with a variety of environmental and metabolic factors, principally depth distribution and algal symbiosis. Smout (1954) suggested that shapes tend toward those giving maximum surface to volume ratios. Haynes (1965) proposed that shape in larger foraminifera is a compromise between hydrodynamic factors and the metabolic requirements of algal symbiosis and that internal structure and test shape evolved in response to those requirements, with maximum sphericity seen in current-swept reefal conditions. Chaproniere (1975, p. 38) stated that "the test of larger foraminiferids is ideally suited to house symbiotic algae". Hottinger and Dreher (1974) noted thickness variations with depth in Operculina (=Nummulites) ammonoides and Heterostegina depressa and suggested that variations are due to changes in light intensity that affect the "greenhouse effect" of the test. Larsen (1976) reported both intra- and interspecific tendencies toward increasing surface to volume ratios with increasing habitat depth in Amphistegina spp., and suggested that the protists have balanced their surface area to the amount of incoming light.

The purpose of this paper is to show that test shape in large, symbiont-bearing foraminifera is related to their depth distributions. The problem will be approached in terms of interspecies, intraspecies, and intraclonal variation in test shape in relation to environmental factors.

METHODS

To compare relative thicknesses of the 15 species of large foraminifera encountered in this study, 50 specimens of each species were selected from available material. For species occurring in both Hawaii and Palau, 25 specimens from each geographical location were used. For

each specimen, maximum and minimum diameter as seen from the spiral or umbilical side and maximum thickness were measured. These dimensions are equivalent to Scott's (1974) greatest spiral diameter (gsd), spiral diameter at 90° to greatest spiral diameter (sd90), and length respectively. Average spiral diameter, which will be referred to simply as diameter (d), was calculated by

$$d = (gsd + sd90) / 2 \quad (21)$$

In spine-bearing species, spines were not included in diameter measurements.

Shape variation within Amphistegina lessonii and A. lobifera populations was compared at three sites: an exposed fringing reef site in Palau (PS-8), a lagoon site in Palau (PS-16), and an exposed fringing reef site on Oahu (PS-1). Comparisons were made by randomly picking 20 specimens of each species from the shallowest and deepest samples in which the species occurred, measuring thickness (t) and diameter (d) and calculating the proportion t/d for each specimen, calculating the mean and standard deviation of that proportion at each depth and site, and calculating students t and F values of those statistics (Sokal and Rohlf 1969).

Intraclonal shape variation was examined in two A. lessonii and two A. lobifera clones discussed earlier (p. 62). Each clone was divided into three groups and grown at three different light levels. Clones were one week old at the start of the experiment. After approximately four months in culture, ten individuals from each trial from each clone were harvested and diameter, thickness, and t/d were determined for each individual.

RESULTS

Thickness (t) was plotted against diameter (d) for the 15 species of large foraminifera (figures 22 and 23).

Figure 22. Regressions of test thickness on diameter for five milioline species:

- | | | |
|---|--------------------------|--------------------|
| a. <u>Archaias angulatus</u> | $t=d/(0.793+0.00131\ d)$ | $(r=0.774, df=48)$ |
| b. <u>Spirulina arietina</u> | $t=d/(1.34 +0.00176\ d)$ | $(r=0.943, df=48)$ |
| c. <u>Peneroplis pertusus</u> | $t=d/(0.371+0.00395\ d)$ | $(r=0.406, df=48)$ |
| d. <u>Marginopora</u>
<u>vertebralis</u> | $t=d/(3.32 +0.00321\ d)$ | $(r=0.680, df=48)$ |
| e. <u>Sorites marginalis</u> | $t=d/(3.42 +0.00519\ d)$ | $(r=0.750, df=48)$ |

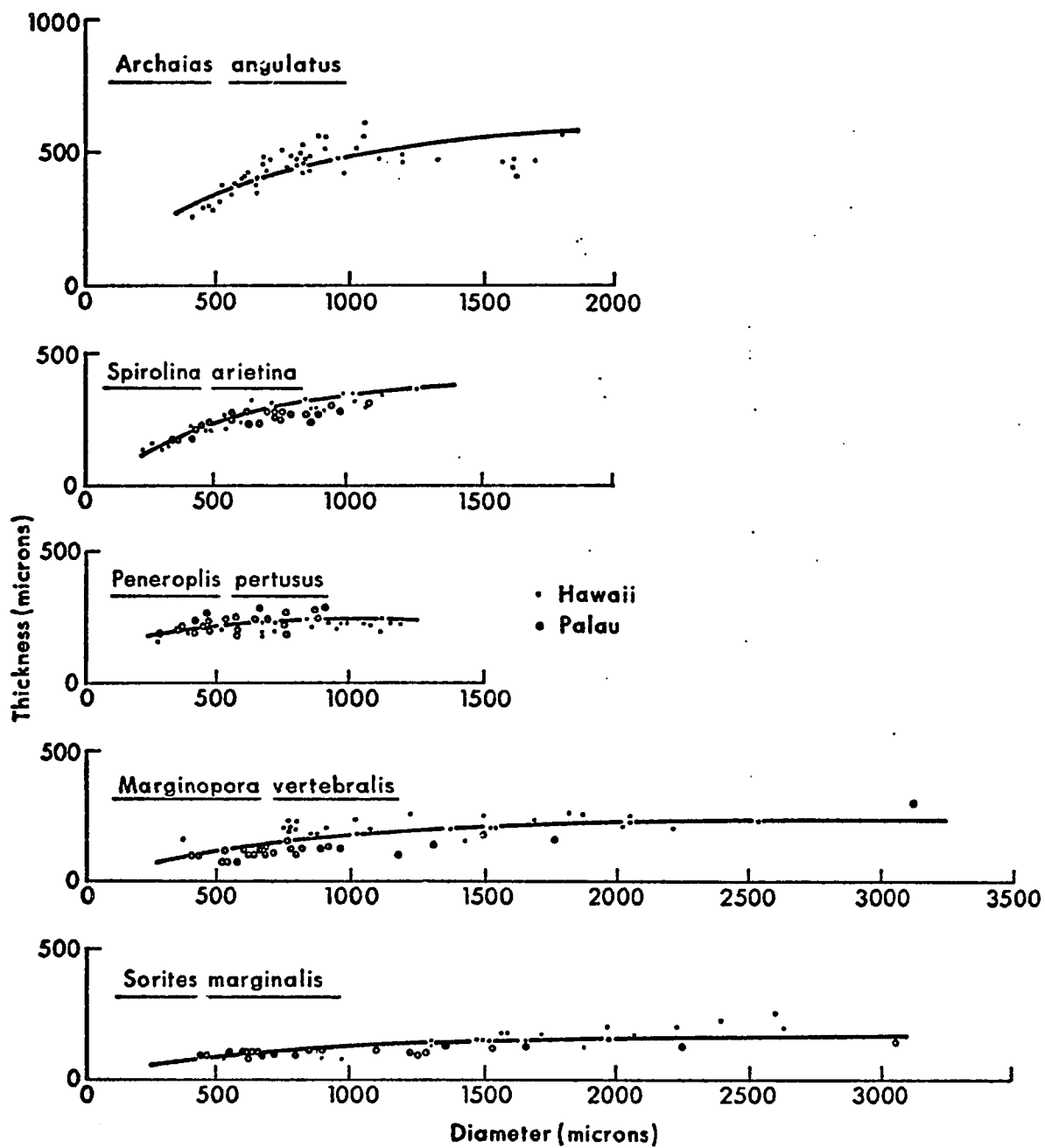
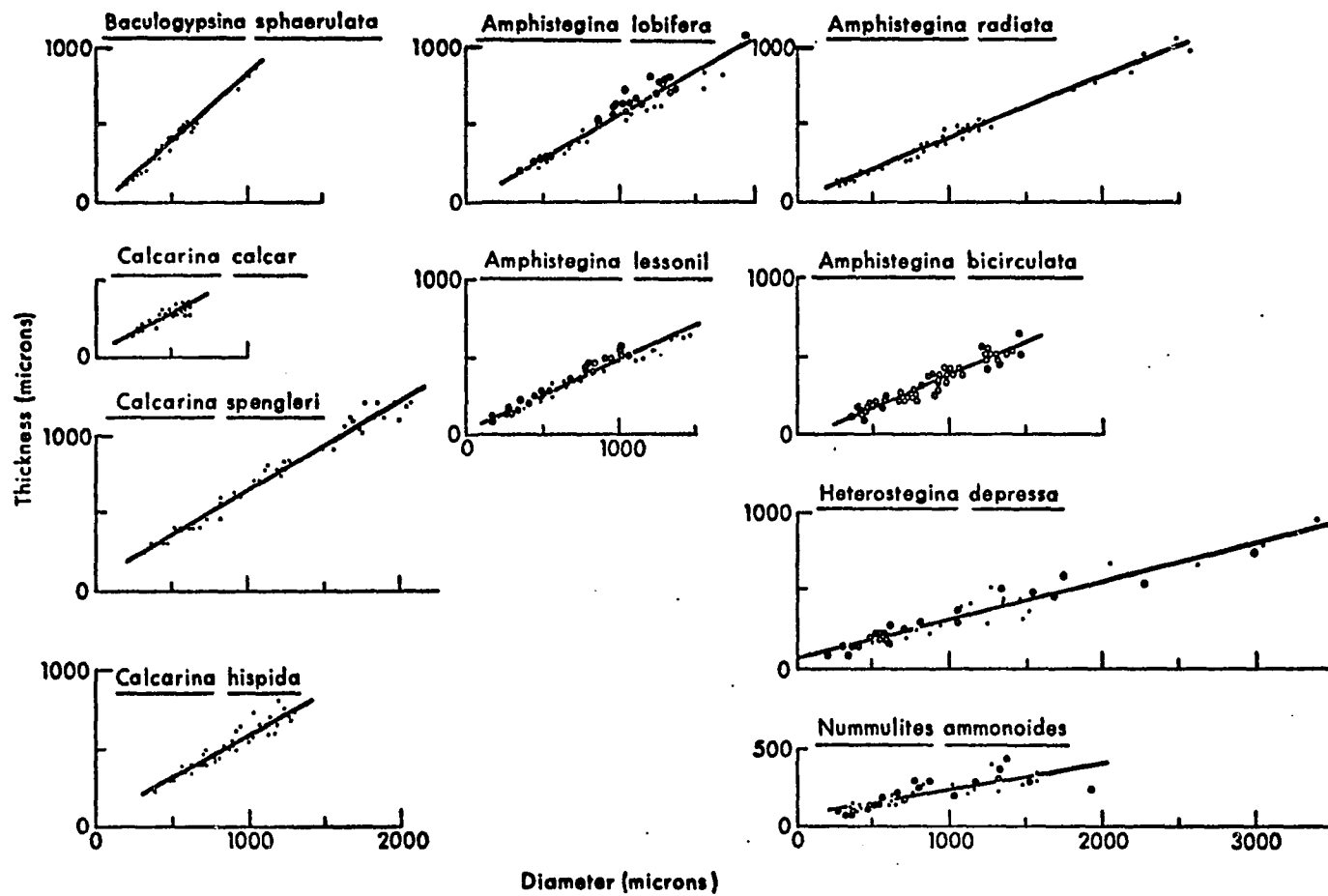


Figure 23. Regressions of thickness on diameter for ten rotaliine species:

a.	<u>Baculogypsina</u>			
	<u>sphaerulata</u>	t=0.876	d-46.9	(r=0.989, df=48)
b.	<u>Calcarina calcar</u>	t=0.511	d+34.6	(r=0.927, df=48)
c.	<u>C. spengleri</u>	t=0.574	d+63.3	(r=0.986, df=48)
d.	<u>C. hispida</u>	t=0.524	d+58.8	(r=0.947, df=48)
e.	<u>Amphistegina lobifera</u>	t=0.561	d- 0.25	(r=0.961, df=48)
f.	<u>A. lessonii</u>	t=0.449	d+32.3	(r=0.981, df=48)
g.	<u>A. radiata</u>	t=0.397	d+12.7	(r=0.993, df=48)
h.	<u>A. bicirculata</u>	t=0.415	d-30.4	(r=0.950, df=48)
i.	<u>Heterostegina depressa</u>	t=0.248	d+72.3	(r=0.963, df=48)
j.	<u>Nummulites ammonoides</u>	t=0.171	d+69.5	(r=0.812, df=48)



As a general pattern, the milioline species were highly compressed, attaining a fairly characteristic thickness early in life and increasing primarily in diameter thereafter. To reflect this pattern, the data for each species were fitted to a hyperbolic function of the form

$$t = d / (k_1 + k_2 d) \quad (22)$$

where k_1 and k_2 are constants: $1/k_2$ represents calculated asymptotic thickness and k_1/k_2 represents calculated diameter at which half asymptotic thickness is attained.

The rotaliine species tended to increase in thickness throughout life. To reflect this pattern, the data for each species were fitted to a linear function

$$t = b + md \quad (23)$$

where b is the y-intercept of the line and m represents change in thickness with diameter ($\Delta t/\Delta d$).

Shape variation in A. lessonii and A. lobifera within and between sample sites are compared in table 22. Significant differences in shape between depths occurred only once each for A. lessonii and A. lobifera. In Palau significant differences between sites at similar depths were evident at the maximum depths sampled. In all cases, there was a tendency for thicker tests at more exposed sites.

Intraclonal shape variation data (table 23) were subjected to two-way analysis of variance to determine if differences in shape (thickness/diameter) between trials was significantly greater ($P < 0.05$) than differences within trials; and in one clone of A. lessonii (C-17) and one of A. lobifera (C-32) that was the case. In the other two clones individuals from the high light trials were also thicker than those from the low light trials, but intratrial variability rendered the differences insignificant.

Table 22

Comparison of Mean Thickness of Amphistegina spp.
Between Depths Within Sites and Within Depths
Between Seaward (S) and Lagoonal (L) Sites

Species	Location	Depth (m)	Mean	S.D.	t-value	df	F-ratio	df
<u>A. lobifera</u>	PS-8 (S)	1 15	0.571 0.574	0.0325 0.0467	-0.236	38	0.484	19,19
<u>A. lobifera</u>	PS-16 (L)	2 10	0.552 0.533	0.0435 0.0369	1.49	38	1.39	19,19
<u>A. lobifera</u>	HS-1 (S)	1 8	0.571 0.606	0.0349 0.0454	-2.73	38	0.59	19,19
<u>A. lobifera</u>	PS-8 (S) PS-16 (L)	1 2	0.571 0.552	0.0325 0.0435	1.56	38	1.79	19,19
<u>A. lobifera</u>	PS-8 (S) PS-16 (L)	15 10	0.574 0.533	0.0467 0.0369	3.08*	38	1.60	19,19
<u>A. lessonii</u>	PS-8 (S)	10 20	0.503 0.492	0.0483 0.0406	0.78	38	1.42	19,19
<u>A. lessonii</u>	PS-16 (L)	2 20	0.481 0.467	0.0331 0.0302	1.40	38	1.20	19,19
<u>A. lessonii</u>	HS-1 (S)	1 30	0.526 0.490	0.0381 0.0443	2.76*	38	0.74	19,19
<u>A. lessonii</u>	PS-8 (S) PS-16 (L)	20 20	0.492 0.467	0.0406 0.0302	2.21*	38	1.81	19,19

* significant at 0.05 level

Table 23

Results and Anova Table for Thickness of the Test
as a Function of Growth Under Different
Light Conditions in Four Clones

		Thickness/diameter					
<u>A. lessonii</u>	Parent	2600	$\mu\text{w}/\text{cm}^2$	700	$\mu\text{w}/\text{cm}^2$	300	$\mu\text{w}/\text{cm}^2$
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Clone 17	0.375	0.474	0.146	0.427	0.185	0.386	0.150
Clone 33	0.358	0.490	0.127	0.461	0.100	0.469	0.094
<u>A. lobifera</u>							
Clone 20	0.649	0.555	0.118	0.526	0.128	0.541	0.083
Clone 32	0.529	0.526	0.0689	0.495	0.090	0.472	0.116

Anova table

A. lessonii

Clone 17	F-ratio	Prob.	Clone 33	F-ratio	Prob.
Within treatments	0.632	0.756		0.567	0.807
Between treatments	18.9	0		3.299	0.060

A. lobifera

Clone 20			Clone 32		
Within treatments	1.96	0.108		1.07	0.429
Between treatments	2.48	0.112		15.4	0

DISCUSSION

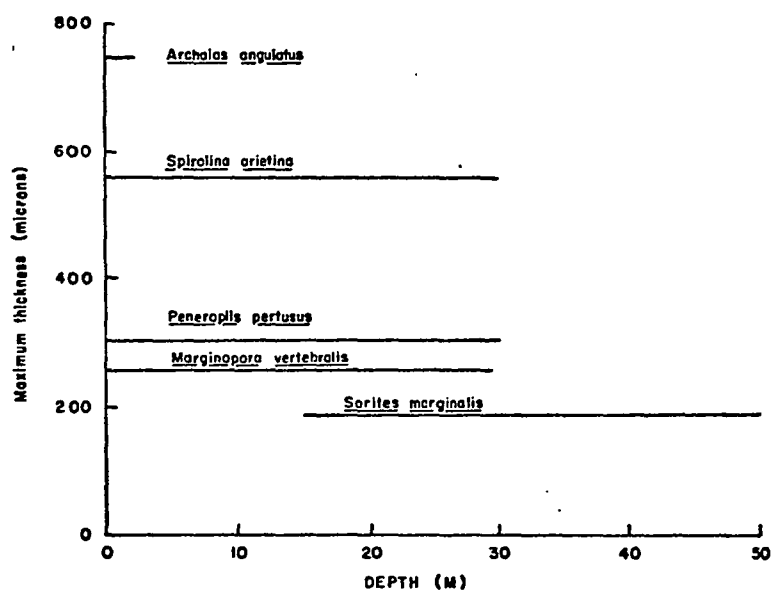
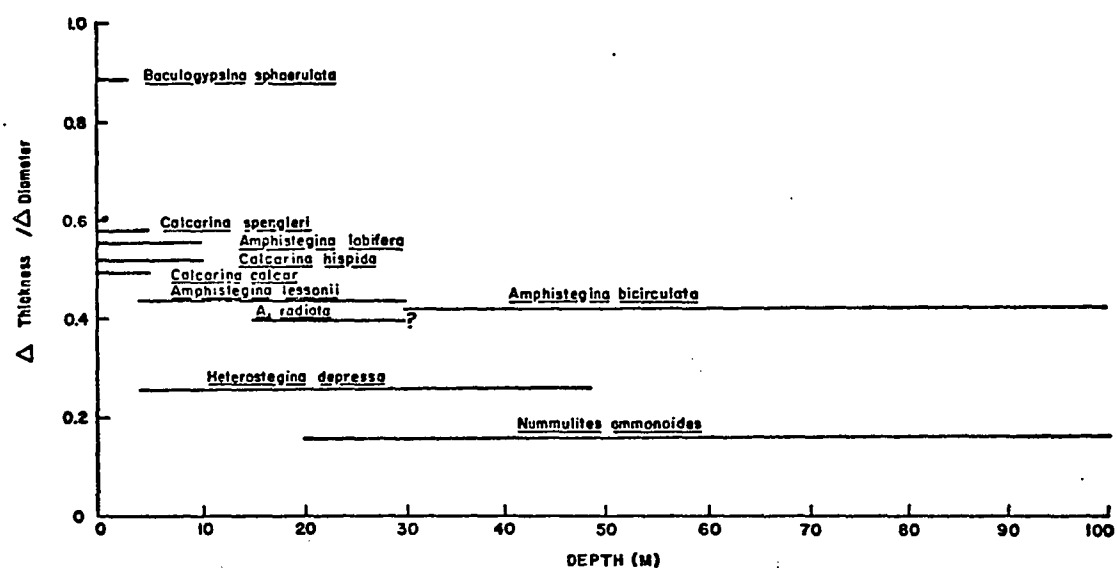
As noted earlier, test shape has been associated with depth distribution in large, symbiont-bearing foraminifera, with maximum sphericity in reef conditions (Haynes 1965) and increasing surface to volume ratios with increasing habitat depth (Larsen 1976). To determine if this trend is evident among these 15 species of large foraminifera, the miliolines and rotaliines were first compared separately due to the general differences in growth patterns observed.

The rotaliine species tend to increase in thickness throughout life, as shown in figure 23 and by the highly significant fits of the linear functions to the species data. Substantial differences in the rates of increase in thickness with increasing diameter are noticeable between species as shown by the differences in the slopes of the lines fit to the species data. The value of the slope for a species is generally indicative of the shape of a species. In a perfectly round species, rate of change in thickness would be equal to change in diameter and the slope ($\Delta t / \Delta d$) would be 1. In a completely flat species, i.e., thickness remained the same throughout life, $\Delta t / \Delta d = 0$. Therefore, the slope of the regression of thickness on diameter for each rotaliine species was used as an indicator of the shape of the species: B. sphaerulata was the most spheroid with a slope of about 0.9, N. ammonoides was the thinnest with a slope of about 0.2.

To determine if the shape of a species is indeed related to depth, the slope for each species was plotted against the depth over which that species occurred relatively frequently (figure 24a). Indeed, the general trend is towards decreasing test thickness with increasing habitat depth. More specifically, there is a rapid initial decrease in test thickness with increasing depth followed by steadily decreasing change with increasing depth. The one species that disrupts this general pattern, A. bicirculata, appears to be aberrantly rotund in Hawaii (Larsen pers. comm.). Specimens from similar depths in the Gulf of Elat, from which the species was described, exhibited a slope of

Figure 24. Comparison of relative thickness to depth distribution:

- a. Rotaliine species: $(\Delta t/\Delta d)$ to depth
- b. Milioline species: maximum thickness to depth



0.26 (Larsen 1976) rather than 0.4 seen in the specimens from Hawaii.

When the trochospiral Asterigerinidae (Amphistegina spp.) and Calcarinidae (Baculogypsina and Calcarina spp.) are compared to the planispiral Nummulitidae (Heterostegina and Nummulites), the trochospiral forms are characterized by thicker tests and greater variability while the planispiral species are more highly compressed. The morphological restrictions of the taxa may have partially dictated the paths along which these groups evolved and the niches they now fill.

The milioline species were more difficult to compare, as the data are more variable and the curve-fits were poorer, though significant. Nevertheless, the same general trend of decreasing thickness with increasing depth is evident within the group and is shown in figure 24b by plotting calculated maximum thickness to depth of occurrence. Again the tendency is for a rapid initial decrease in thickness with depth followed by a leveling off at increasing depths. There are also morphological differences in this group: Archaias, Peneroplis, and Spirolina are planispiral compressed, while the Marginopora and Sorites are discoid.

Some indication of intraspecific variability in test thickness is available from several sources. In the individual species plots of thickness on diameter, data points from Hawaii and Palau were plotted separately. Using data from more than one sample probably increased evident variability and reduced the significance of the curve-fits. However, this method also showed that changes in thickness with diameter were characteristic within a species.

Environmental factors also may induce intraspecies variability as indicated by the increase in test thickness with increasing light intensity in some A. lessonii and A. lobifera in the laboratory. Evident trends in test thickness with depth within a species were not

seen in the field in this study, unlike previous reports for Amphistegina spp. (Larsen 1976) and for Heterostegina and Operculina (Hottinger and Dreher 1974). However, substantial differences in test thickness within species were seen between exposed and lagoon reef environments, with thicker tests characteristic of greater exposure to turbulence. However, intraspecies variation is not sufficient to disrupt the general interspecies thickness to depth patterns shown in figure 24.

Test thickness in the shallowest dwelling miliolines, Archaias and Spirulina, is comparable to test thickness in the deeper dwelling rotaliines, Heterostegina and Nummulites. Haynes (1965) suggested that the crystal structure of the milioline test provides more protection from ultraviolet radiation in very shallow water than the rotaliine crystal structure. Towe and Cifelli (1967) illustrated that the calcium carbonate crystals in the hyaline rotaliine test show a preferred orientation, while the crystals of the milioline test wall are arranged in a three-dimensional random array of crystals covered by a thin veneer of crystals showing, in part, preferred orientation. They suggest that the random arrangement of crystals scatters incoming light which is why the milioline test appears opaque or porcelaneous. The milioline crystal structure may restrict the penetration of light into the test so that surface to volume ratios must be higher in shallow-water symbiont-bearing species than in comparable rotaliine species. Test thickness in Sorites, the deepest dwelling of the miliolines studied, appears to be a compromise between maximum surface to volume ratio and thickness necessary to maintain structural integrity of the test.

In the large foraminiferal species examined, the trend toward decreasing test thickness with increasing habitat depth was obvious. Several workers previously suggested that the trend is related to the light and metabolic requirements of the algal symbionts in the foraminifera (Haynes 1965, Hottinger and Dreher 1974, Chaproniere 1975,

Larsen 1976). The intraclonal trends in test thickness in the two species in the laboratory demonstrated that light intensity is a key factor in shape regulation.

In the ocean, both light intensity with depth and water particle motion with depth are negative exponential functions of depth (Sverdrup et al 1942) and trends in test shape are qualitatively similar. Thus, differentiating between the effects of light and water motion on test thickness is very difficult, as the cumulative effect of the two processes is also exponential. Besides the intraclonal laboratory data, probably the best evidence presented favoring light as the principal factor in determining test shape is the presence of compressed, planispiral miliolines in very shallow environments. However, these species seldom reach the densities that the spheroidal rotaliine species attain in highly exposed environments. And, except for Archaias, which is relatively round as a juvenile, these species are relatively general in their depth distribution.

The very restricted depth distributions of the more spheroidal species and the more general depth distributions of the compressed species is an interesting aspect of the relationship between test thickness and depth distribution in the large foraminifera. The planispiral compressed species H. depressa, Spirulina arietina and P. pertusus occur over a wide range of depths from tidepools to more than 30 m. Their low density occurrence at very shallow depths may indicate their selection for (or differential survival in) suitable micro-environments. Röttger (1976) noted that H. depressa distribution in a tidepool was restricted to comparatively shaded, calm locations. The spheroidal species are restricted to the infralittoral fringe probably because they are highly specialized for the turbulent, brightly illuminated environment by their shape, spines, and possibly light and metabolic requirements. If the ^{14}C uptake and laboratory growth experiments with A. lessonii, A. lobifera, and H. depressa (Röttger 1976) are an indication, the more compressed species are restricted by

the physical rigors of light and motion while the spheroidal species are not competitive with the faster-growing, more generalized species at intermediate depths.

Haynes (1965) suggested that hydrodynamic factors would select for maximum sphericity in high energy environments. One of these factors tending to favor spheroidal individuals may be related to fecundity. In high energy environments, multiple fission external to the test is probably a rather high risk reproductive process. Spheroidal individuals have low surface to volume ratios and may, for relatively comparable amounts of carbonate, contain larger quantities of protoplasm. For example, A. lobifera, A. lessonii, and H. depressa produce similar-sized megalospheric young (approximately 60-80 μm). Using the diameter-mass and diameter-fecundity relationships presented earlier (p.103 and 90) and information from Röttger (1972), fecundity/mg was calculated (table 24). A. lobifera produced more young per unit weight than the A. lessonii and about 10 times as many as H. depressa. Marginopora vertebralis, whose habitat is similar to A. lobifera and whose thickness is similar to H. depressa, produces its young internally in reproductive chambers and its fecundity is low, similar to H. depressa (Ross 1972).

Undoubtedly, both light and water motion interact to influence test shape in symbiont-bearing foraminifera. Paleoecologically, the trends noted here may be applicable to defining relative depths of fossil assemblages of large foraminifera. Assemblages of highly spheroidal rotaliine forms ($\Delta t / \Delta d > 0.5$) characterize highly restricted depths of turbulent reef flats. Assemblages of predominantly intermediate forms ($0.4 < \Delta t / \Delta d < 0.5$) characterize depths of about 5-20 m. Assemblages dominated by compressed rotaliines ($\Delta t / \Delta d < 0.4$) are from the maximum depths of the euphotic benthos.

Table 24
Comparison of Fecundity Per Milligram of Three Species

Species	Diameter (μm)	Fecundity/mg
<u>Amphistegina lessonii</u>	1765	803
<u>A. lobifera</u>	1543	1091
<u>Heterostegina depressa</u>	2090	105

NOTES ON COILING DIRECTION IN AMPHISTEGINA

INTRODUCTION

Coiling direction is a simple morphological aspect in trochoidal animals. Two of the earliest reports of coiling ratios in foraminiferal populations were by Cosijn (1938), and Gandolfi (1942). Bolli (1950) first applied coiling direction to studies of the evolution of foraminifera. Subsequently, coiling direction has been widely used in planktonic foraminiferal research in local stratigraphic correlation and paleoclimatic interpretation (reviewed by Kennett 1976).

Scott (1974) noted that while coiling direction has been extensively used in studies of planktonic species, little attention has been given the trait in benthic foraminifera. Longinelli and Tongiorgi (1960) reported temperature and depth related variation in coiling in Ammonia beccari. O'Herne (1974) mentioned coiling direction in Amphistegina, noting that A. lessonii was predominantly sinistral in lower Miocene samples from Java-Madura and in Holocene samples from the Admiralty Islands, but was dextral in middle Miocene samples from Java-Madura. A. quoyi d'Orbigny (= A. radiata (Fichtel and Moll) by Larsen's 1976 revision) in the same sequence was predominantly dextral throughout.

Investigation of coiling direction of Amphistegina spp. was prompted by the observation that coiling direction in all A. lessonii populations encountered were predominantly sinistral, while Hawaiian A. lobifera were mostly dextral and Palauan A. lobifera were mostly sinistral.

METHODS

Size and coiling direction were noted for Amphistegina spp. determined to be alive when collected from field samples (Muller 1974). Greatest spiral diameter of each individual was measured to the nearest 50 μm . Coiling direction was determined with specimens oriented spiral side up. Due to the small percentages of minority coiling direction individuals, all counts were pooled by species.

Coiling direction of Amphistegina spp. from sediment samples from a variety of locations throughout the Pacific and a few other areas were also determined by counting and noting coiling direction in all specimens, whether living or dead at the time of collection.

When living specimens were collected and brought to the laboratory, the largest individuals were isolated and observed for signs of reproduction. Size and coiling direction of the clone parent and coiling direction and number of young were recorded for each reproduction. All laboratory work involved specimens collected in Hawaii.

Statistical analysis utilized the 95 percent confidence limits for proportions from twofold binomial distributions (Tate and Clelland 1957), by testing the hypothesis that the proportion of minority coiling specimens in a sample was the same as the proportion in the total population.

RESULTS

Palau

Both A. lessonii and A. lobifera were predominantly sinistral in the Palau samples. Of 7458 A. lessonii individuals, 289 or 3.88 percent were dextral; and of 6315 A. lobifera, 211 or 3.34 percent were dextral. The proportion of dextrals of each species in each of the 256 samples that comprised these totals were individually tested against the total population proportions to determine if the coiling proportions of the two species in the individuals samples differed significantly ($P < 0.05$) from those of the totals. No differences occurred in the samples for A. lobifera. Four A. lessonii samples differed significantly from the total

population, each with a surplus of dextrals occurring in the large size classes ($>1000\text{ }\mu\text{m}$).

The observed predominance of large dextrals indicated that coiling ratios may change with size in Amphistegina. In figure 25, maximum diameter is plotted against percentage of dextral individuals for the pooled data. In both species, individuals $>1200\text{ }\mu\text{m}$ showed significantly higher percentages of dextrals than the averages for the populations -- 6.98 percent in A. lessonii and 7.14 percent in A. lobifera -- indicating that indeed the coiling ratios are size dependent in the two species (table 25).

The proportions of dextral individuals in the two species were similar, with 3.88 percent in the A. lessonii population and 3.34 percent in the A. lobifera population. Likewise, the coiling proportions of the $>1200\text{ }\mu\text{m}$ size were similar in the two species, 6.98 and 7.14 percent respectively.

Amphistegina radiata were predominantly dextral in the Palau samples (table 26).

Oahu

In samples from Oahu, A. lessonii was predominantly sinistral and A. lobifera was predominantly dextral, and the proportions of minority coiling individuals were similar in both species. Of 6226 A. lessonii individuals, 317 or 5.09 percent were dextral; and of 2177 A. lobifera, 124 or 5.70 percent were sinistral. The 142 samples that comprised these totals were individually tested against the total population proportions as before. In 142 samples, significant differences occurred only twice for A. lobifera and in four samples for A. lessonii. Five of these cases, all representing a surplus of minority coiling individuals, occurred at the same station at the same depth: HS-1, 1 m, in the Kahe Point power plant thermal effluent plume.

Coiling ratio changes with size were again examined (figure 26). Both species increased in proportion of minority coiling direction individuals in the adult sizes; however, the sizes at which the increases began were quite different for the two species, unlike the situation in

Figure 25. Coiling direction changes with diameter in Palau samples

- 1 - AMPHISTEGINA LESSONII
2 - AMPHISTEGINA LOBIFERA

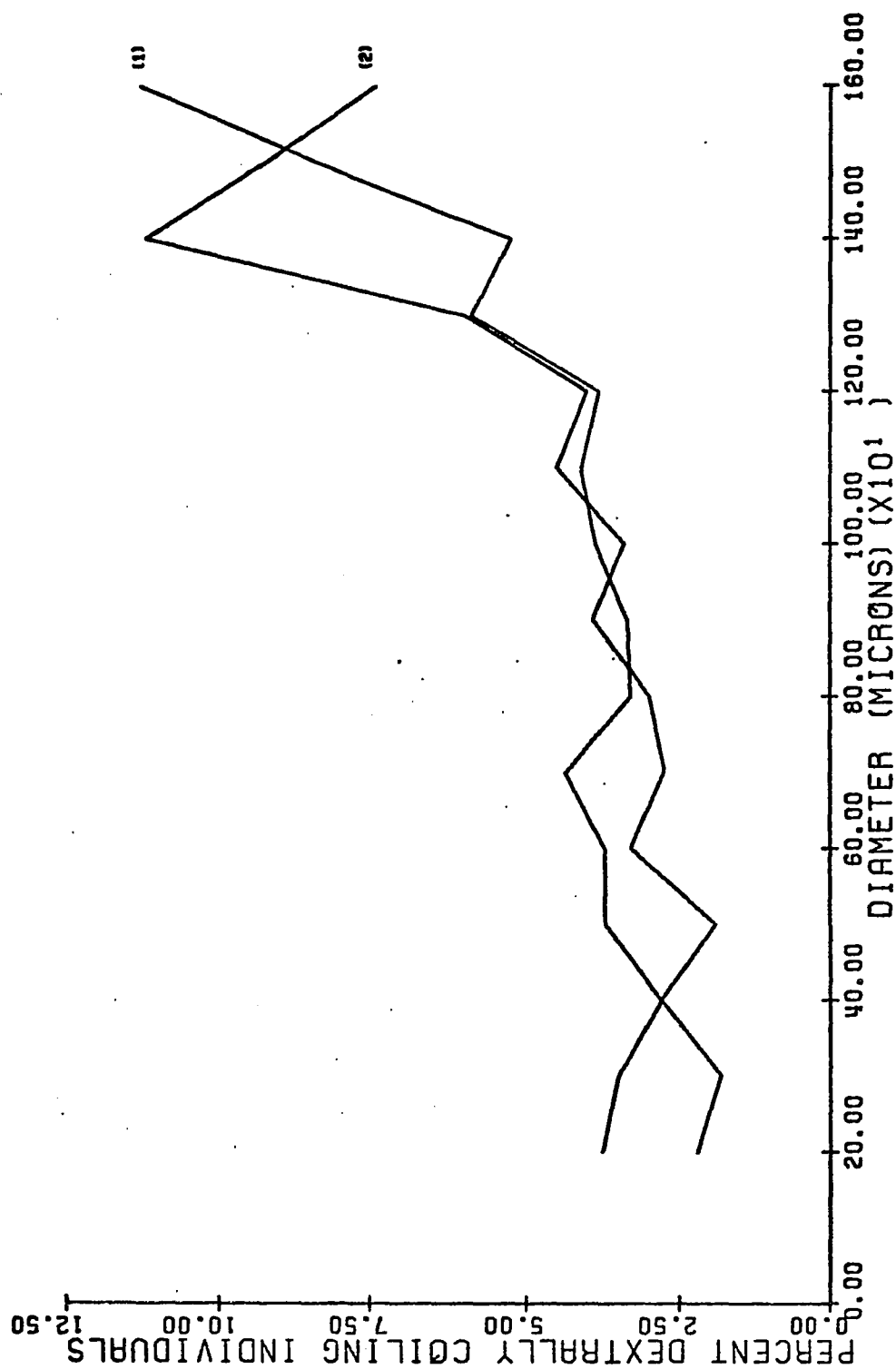


Table 25

Results for a Variety of Coiling Proportion Comparisons,
Testing the Hypothesis (at the 0.05 Level) that the Tested
Proportion is the Same as the Total (Expected) Population Proportion

Species	Location	Expected Proportion	Coiling Direction	Test Conditions	Test Proportion	Coiling Direction	Number	Significant
<u>Amphistegina lessonii</u>	Palau	0.0388	dex	d>1200 μ m	0.0680	dex	588	yes
<u>A. lobifera</u>	Palau	0.0334	dex	d>1200 μ m	0.0764	dex	432	yes
<u>A. lessonii</u>	Hawaii	0.0509	dex	d>1000 μ m	0.19	dex	216	yes
<u>A. lobifera</u>	Hawaii	0.0570	sin	d>1400 μ m	0.25	sin	28	yes
<u>A. lessonii</u>	Hawaii HS-1, 1m	0.0509	dex	+ 4°C.	0.0978	dex	368	yes
<u>A. lobifera</u>	Hawaii HS-1, 1m	0.0570	sin	+ 4°C.	0.113	sin	221	yes

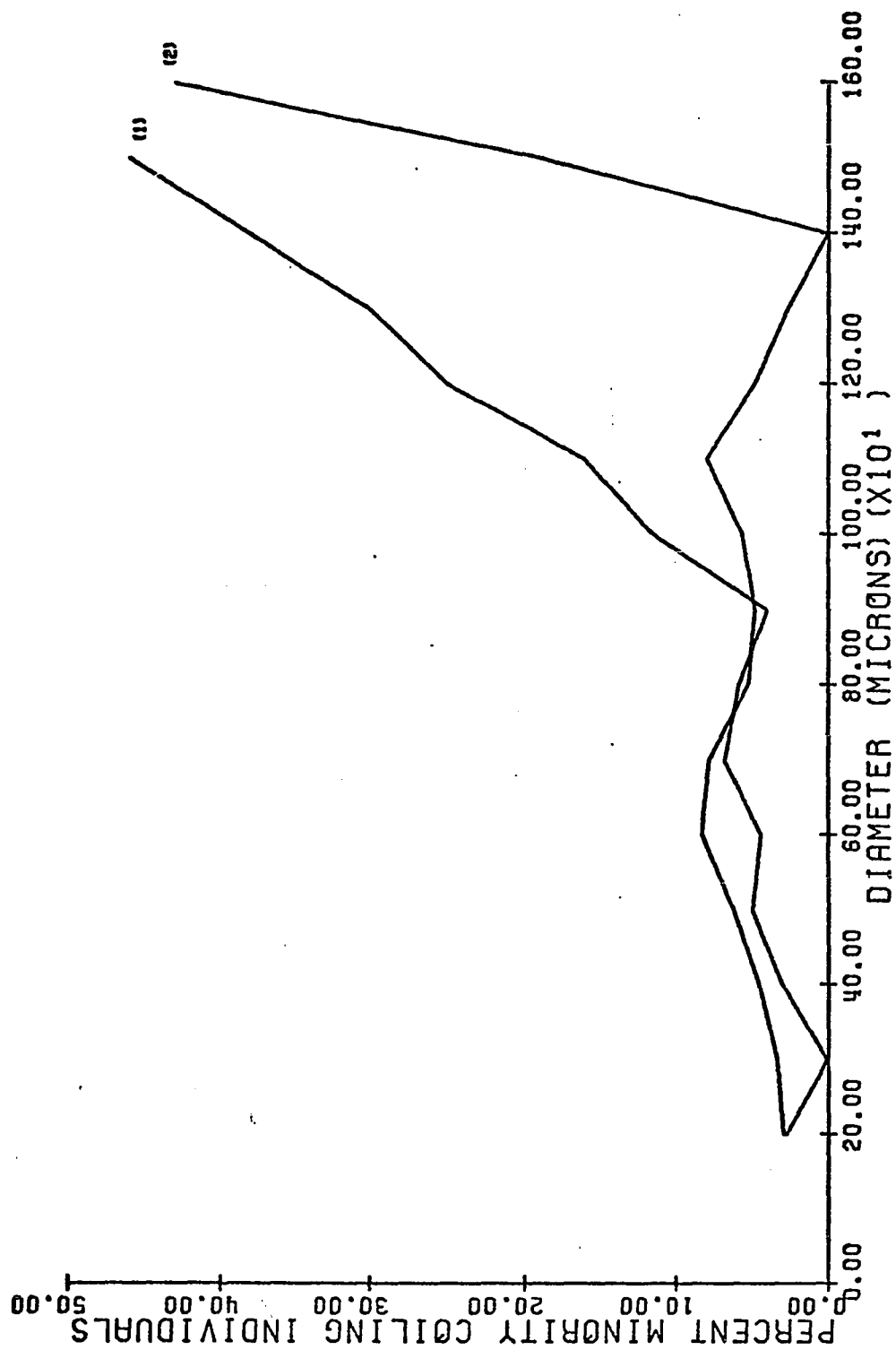
Table 26

Proportion of Sinistral Coiling Individuals of Amphistegina spp.
from a Variety of Locations Throughout the World

Location	<u>A. lobifera</u>		<u>A. lessonii</u>		<u>A. bicirculata</u>		<u>A. radiata</u>		<u>A. gibbosa</u>	
	percent sinistral	number counted	percent sinistral	number counted	percent sinistral	number counted	percent sinistral	number counted	percent sinistral	number counted
Oahu	6	2177	95	6169	98	199	-	-	-	-
Nehoa	8	25	100	23	100	25	-	-	-	-
Pearl & Hermes	12	25	96	25	-	-	-	-	-	-
Midway	0	25	88	25	-	-	-	-	-	-
Johnston Island	14	50	100	10	-	-	-	-	-	-
Fanning Island	48	50	-	-	-	-	-	-	-	-
Christmas Island	32	50	-	-	-	-	-	-	-	-
Canton Island	20	50	-	-	-	-	-	-	-	-
Sydney Island	34	100	-	-	-	-	-	-	-	-
Vaitupu Island	44	50	100	5	-	-	-	-	-	-
Samoa	50	50	-	-	-	-	-	-	-	-
Funafuti	47	100	100	32	-	-	-	-	-	-
Pagan Island	45	20	92	25	-	-	-	-	-	-
Gorco Island	-	-	80	50	-	-	-	-	-	-
Rota	46	50	-	-	-	-	-	-	-	-
Enewetak	68	50	90	10	-	-	-	-	-	-
Kwajalein	38	50	-	-	-	-	-	-	-	-
Majuro	51	100	-	-	-	-	-	-	-	-
Ponape	74	50	-	-	-	-	-	-	-	-
Nukuoro Atoll	92	100	-	-	-	-	-	-	-	-
Kapingamarangi	48	100	-	-	-	-	-	-	-	-
Truk	96	50	100	25	-	-	-	-	-	-
Palau	97	6315	96	7458	-	-	6	339	-	-
Okinawa	86	50	-	-	-	-	-	-	-	-
Gaudalcanal	96	25	100	10	-	-	12	25	-	-
Arlington Reef	-	-	-	-	-	-	-	-	-	-
(Great Barrier Reef)	-	-	92	25	-	-	-	-	-	-
Western Australia	-	-	92	50	-	-	-	-	-	-
Mombasa, Kenya	92	50	80	25	-	-	-	-	-	-
Yucatan	-	-	-	-	-	-	-	-	6	50

Figure 26. Coiling direction changes with size in Oahu samples

- 1 - AMPHISTEGINA LESSONII
2 - AMPHISTEGINA LOBIFERA



the Palauan populations. The proportion of dextral A. lessonii began to increase at 1000 μm and at 1200 μm , 25 percent of the population was dextral. The corresponding increase in sinistral A. lobifera did not occur until size >1400 μm , and, although the number of individuals was small, the difference was significant (table 25).

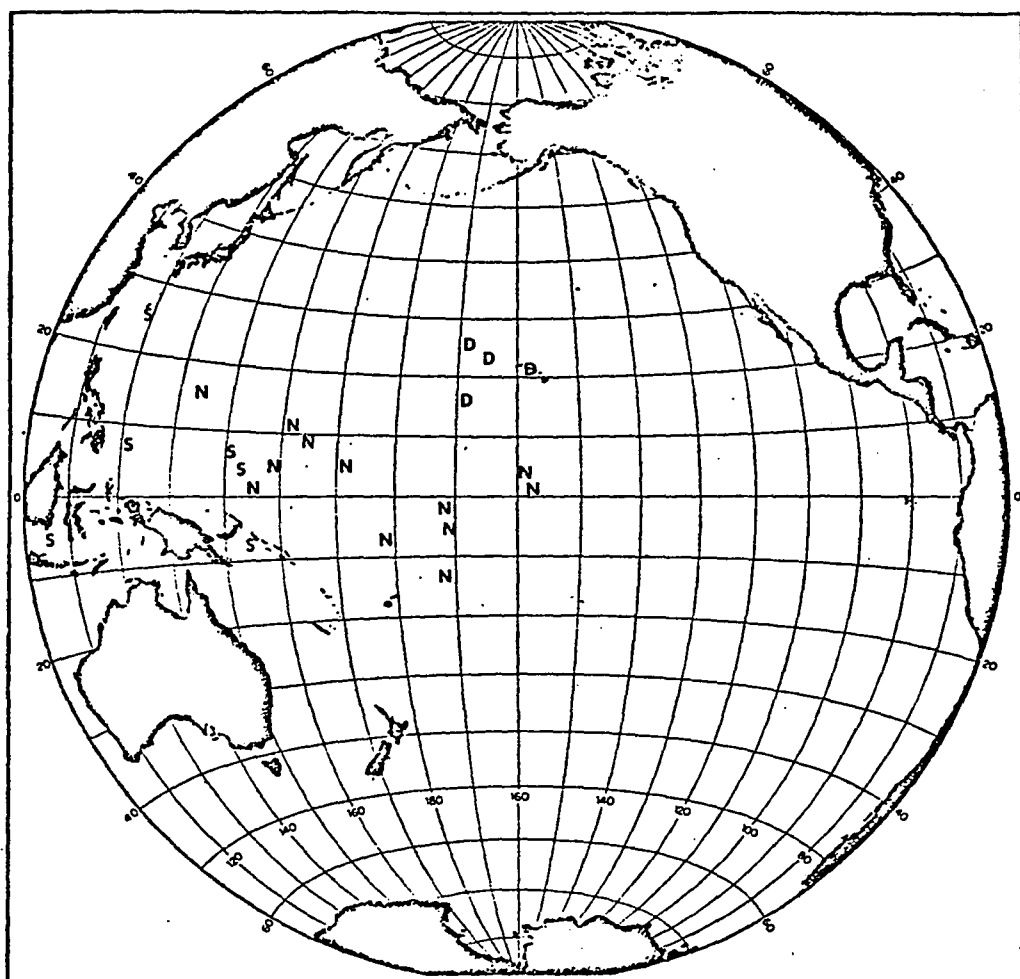
The four samples from 1 m at station HS-1 were individually tested against the total proportions for the station and depth and were found to be homogenous for both species. The total proportions for the stations were compared to the total for Hawaii and were significantly different (table 25). In fact, almost twice as many dextral A. lessonii and sinistral A. lobifera were found in the four samples collected in the Kahe Point power plant thermal effluent plume than predicted by the average proportions for all Hawaiian samples.

In Amphistegina bicirculata, over 90 percent of the population sampled was sinistral (table 26).

Other locations

The coiling ratios of Amphistegina spp. were noted from 26 Pacific and 2 Indian Ocean locations, and 1 Atlantic location (table 26). A. lessonii was present in samples from 16 of those sites and in all cases, sinistral individuals predominated. A. bicirculata and A. radiata each were present in samples at only 2 locations and were predominantly sinistral and dextral respectively at both locations. Most of the samples were beach sand which is probably why the deeper-dwelling species were found so infrequently. A. lobifera was present in samples from 25 locations and showed that coiling direction was not constant in the species throughout its range (figure 27). In the western Pacific at Guadalcanal, Okinawa, Palau, Truk, and Nukuoro, and in the single western Indian sample, A. lobifera was predominantly sinistral. The central Pacific A. lobifera showed little or no coiling direction preference. And in Johnston Island and the Hawaiian Island samples, A. lobifera was predominantly dextral.

Figure 27. Change in coiling direction in A. lobifera from predominantly sinistral (S) in the western Pacific to no predominance (N) in the central Pacific to dextral (D) in the Hawaiian Islands.



Laboratory

Fifty-five A. lessonii and fourteen A. lobifera reproduced in culture (table 27 and 28). Only schizogony (asexual multiple fission) was observed. Nearly half the A. lessonii and half the A. lobifera that reproduced were of the minority coiling direction for the species. Nevertheless, all the clones reflected the coiling direction of the local population rather than that of the parent, i.e., the A. lessonii clones were predominantly sinistral and the A. lobifera clones were predominantly dextral. Although there was some variation in coiling ratios between clones, the variation did not appear to be related to the coiling direction of the clone parent, as both parent types of both species produced about 8 percent minority coiling offspring.

DISCUSSION

The tendency for a predominant coiling direction in Amphistegina spp. appears to be a common characteristic of the genus. All A. lessonii and A. bicirculata populations observed in this study are predominantly sinistral, which is consistent with Larsen's (pers. comm.) observations. The small number of samples of A. radiata and A. gibbosa are predominantly dextrally coiling, again in accord with Larsen's observations and with O'Herne (1974). Larsen also noted that A. lobifera in samples from the Mediterranean, Elat, East Africa, Indonesia, and Thailand were predominantly sinistral, again supporting my observations of sinistral A. lobifera in the western Pacific and Indian Oceans (figure 27). However, A. lobifera changes coiling direction eastward across the Pacific, and A. lobifera in Hawaii are dextral.

The predominance of dextral A. lobifera at Johnston Island and the Hawaiian Islands supports Gosline's (1972) contention, based on similarities in reef fish faunas, that Johnston Island is faunistically a Hawaiian outlier. Kay (pers. comm.) also noted affinities between the molluscan faunas of the Hawaiian Islands and Johnston Island.

Changes in coiling direction in planktonic foraminifera have been related to two factors -- historical development of the taxa (Bolli 1950, 1951), and changes in temperature or salinity of the environment

Table 27

Coiling Directions of Amphistegina lessonii
That Reproduced in Culture and the
Coiling Proportions of the Young Produced

Sinistral parent		Dextral parent	
Clone #	% dextrals	Clone #	% dextrals
1	7.3	4	1.3
2	0.3	7	7.73
3	11.0	8	7.3
5	3.0	11	24.5
6	5.5	14	29.3
10	4.0	15	12.0
12	11.0	16	2.0
13	7.7	19	10.8
17	1.0	24	23.0
21	23.3	28	2.3
23	2.0	38	2.5
33	5.0	42	-
37	10.0	43	1.7
39	10.5	47	1.5
40	30.0	50	2.3
41	3.5	52	13.3
44	6.8	53	4.8
45	34.2	56	8.2
46	4.0	57	4.0
48	1.9	58	9.2
49	7.7	59	2.4
51	5.5	64	5.3
54	8.3	65	1.7
55	8.9	70	9.0
60	15.0		
61	13.2		
62	2.0		
63	5.4		
66	7.1		
67	5.5		
69	-		

Table 28

Coiling Directions of Amphistegina lobifera
That Reproduced in Culture and the
Coiling Proportions of the Young Produced

Sinistral parent		Dextral parent	
Clone #	% sinistral	Clone #	% sinistral
22	5.0	18	3.0
26	1.0	20	6.3
27	0.3	25	2.0
29	10.0	30	8.0
32	26.3	31	8.0
34	7.0	35	15.0
68	10.5	36	4.7

(Ericson 1959, Bandy 1960, Ericson et al 1963, Jenkins 1967, Thiede 1971, others). The coiling direction changes in A. lobifera may be related to temperature. The small but significant shifts in coiling ratios of both A. lessonii and A. lobifera in the warm (4° above ambient) effluent of a power plant indicate that coiling ratios of these species can be influenced by temperature. However, another possible explanation for the changes observed in A. lobifera may simply be genetic drift or change as the species moved across the Pacific. Migration of A. lobifera from west to east across the Pacific, the usual route assumed for Indo-Pacific species, provides no evident temperature stimulus for coiling ratio changes, as the change from sinistral to no preference occurs in the center of the equatorial Pacific.

Scott (1974) suggested that age-specific differences in coiling proportions should be considered to avoid interpretation problems when coiling ratios are used in stratigraphic correlations. Age-specific changes in Amphistegina populations were found in this study. The increase in the proportion of individuals of the minority coiling direction in the adult size classes may indicate that differential mortality is occurring between majority and minority coiling individuals. Data from a previous study (Muller 1974) and Section I of this study indicate that this differential mortality is occurring in reproductive-age individuals. Furthermore, the earlier report proposed that reproduction is a major cause of mortality in the adult size classes. Thus, in nature, the minority coiling direction individuals may not be reproducing as early as the majority coiling individuals.

Thiede (1971) and Vella (1974) also found size-specific differences in coiling ratios of planktonic foraminifera. Globorotalia truncatulinoides off Morocco tended to be dextral, but the proportion of sinistrals increased abruptly in the size fraction >355 µm. Thiede (1971) suggested the differences in coiling proportions in the size fractions may be due to differences in coiling direction and reproductive sizes in asexual and sexual generations. Vella (1974) observed that Neogloboquadrina pachyderma changed from over 90 percent dextral at about 30° S. latitude to over 90 percent sinistral at 50° S., and suggested that

two populations, a dextral temperate race and a sinistral Antarctic race were mixing at their boundary. Between 40° and 50° S., Vella's data showed changes in coiling proportions between size fractions. At $<40^{\circ}$ S. dextrals overwhelmingly dominate all size classes. At 40° S., there was a sharp increase in the proportion of sinistrals in the finest size fraction, while medium and coarse size fractions remained predominantly dextral. At 45° S., the increase in sinistrals was seen in the medium size fraction. At $47-50^{\circ}$ S., the coarse size fraction also became predominantly sinistral.

Size-specific differences in coiling proportions indicates size-specific mortality differences between sinistral and dextral members of a population. If, as Ericson (1959) proposed, there is a genetic linkage between coiling direction and some other characteristic, perhaps related to temperature tolerance in N. pachyderma, the differences in coiling proportion between size fractions may indicate how the species is affected. For example, the high proportion of sinistral N. pachyderma in the fine size fraction at $40-45^{\circ}$ S. may indicate that sinistral juveniles produced slightly farther south are carried northward where they fail to survive to grow larger. The strong West Wind Drift (Sverdrup et al 1942) would serve as the transport mechanism. Meanwhile, the dextrals produced at $40-45^{\circ}$ S. or carried down from the north survive to reproduce. The increase in sinistrals in the medium size fraction at $45-47^{\circ}$ S. may indicate that the sinistrals at this latitude are surviving to reproduce and are reproducing at smaller sizes than the dextrals, which still dominate the coarse fraction. At $>50^{\circ}$, few dextrals are produced or survive, so sinistrals dominate the population.

In summary, where tests of a particular coiling direction are enriched only in the fine size fraction, unfavorable conditions and high juvenile mortality of those individuals may be indicated; where tests of a particular coiling direction are enriched in the coarse size fraction, marginal conditions and reduced reproduction by those individuals may be indicated.

The high proportion of minority coiling direction individuals that reproduced in culture may be a sampling artifact. When field specimens were brought into the laboratory for culture work, the largest individ-

uals were isolated and observed for signs of reproduction. This isolation process selected for minority coiling individuals in reproductive cultures because, as seen in figure 25, a relatively high percentage of very large individuals in field populations in Hawaii are minority coiling. There is evidence that foraminifera respond to some environmental changes by reproducing (Ross 1972, Arnold 1974). Perhaps minority coiling individuals require a stronger stimulus to induce reproduction than majority coiling individuals, and that strong stimulus is provided by the change from natural to culture environment.

The stability of coiling direction in a population as evidenced by the consistency of coiling ratios in the Palau samples as a group and in the Hawaii samples as a group may indicate that coiling direction is genetically controlled. The coiling ratio shifts with age, temperature, and depth exhibited by A. lessonii and A. lobifera only represent changes of a few percent in the total population. The possibility that minority coiling direction individuals do not reproduce in nature at the same rate as the majority coiling individuals provides a mechanism for control and persistence of the coiling ratios even though a small percentage of minority coiling young are continuously produced.

The obvious problem with this interpretation lies in the consistent coiling ratios of young produced by Hawaiian clone parents regardless of their coiling direction. The coiling ratios of the young reflect the coiling ratios of the local population rather than that of the parent, indicating either environmental inducement of coiling direction, or possibly a more complicated extrachromosomal or multi-nuclear controlled inheritance factor. Since nothing is specifically known about inheritance nor the nuclear and chromosomal status of Amphistegina spp., and since foraminifera in particular and protozoa in general tend to be quite heterogenous in those respects (Grell 1973), the resolution of this dilemma is beyond the scope of this study.

CONCLUSIONS

Light and water motion are two factors influencing distribution, productivity, fecundity, and test shape in large, benthic, symbiont-bearing foraminifera. Specifically:

1. Four species groups characterize the reef-associated, large foraminifera: the seaward reef flat group of predominantly Calcarinidae, the general infralittoral fringe-shallow infralittoral group including Amphistegina lobifera and several miliolines, the intermediate infralittoral (5-20 m) group usually dominated by A. lessonii, and a deeper dwelling group which extends to the lower limits of the euphotic benthos and includes Nummulites and several Amphistegina spp.

2. Algal symbionts in Amphistegina spp. actively photosynthesize.

3. ^{14}C fixation by A. lessonii symbionts is inhibited in full sunlight.

4. ^{14}C fixation by A. lessonii and A. lobifera remains relatively high from surface down to about 30% of surface light intensities.

5. Growth in A. lessonii and A. lobifera is light limited.

6. Carbonate production rates of large, symbiont-bearing rotaliine foraminifera are comparable to those of coral and coralline algae.

7. Carbonate turnover rates by large rotaliines are on the order of 10-20 times per year in infralittoral fringe-shallow infralittoral reef environments.

8. Test thickness in large, symbiont-bearing species decreases with increasing habitat depth.

9. Compressed species generally occur over a wider depth range than spheroidal species which are limited to infralittoral fringe conditions.

10. Test shape in shallow-dwelling milioline species is similar to that of deeper-dwelling rotaliine species.

Zoogeographically:

1. The Hawaiian large foraminiferal community is basically a subset of the Indo-West Pacific community, missing several components, including the Calcarinidae, Amphistegina radiata, and Archaias angulatus.

2. A. lessonii and A. lobifera grow more rapidly and are more productive in Palau than in Hawaii.

3. A. lobifera is predominantly sinistral in the western Pacific, predominantly dextral in the Hawaiian Islands and Johnston Island, and shows no predominant coiling direction in the central Pacific.

In regard to coiling ratios in Amphistegina:

1. Coiling ratios are size dependent in A. lessonii and A. lobifera, with highest proportions of minority coiling individuals in the very large size classes.

2. Small changes in coiling ratios may be induced by changes in temperature.

3. Coiling ratios in clones resulting from multiple fission are independent of the coiling direction of the parent and reflect the coiling ratios of the local population.

APPENDIX A. PALAU SAMPLE SITES

Site #	Location	Bottom type	Setting
1	North side of Malakal Channel	Predominantly rubble	Fringing reef sloping off into Malakal Channel
2	Reef by Malakal Channel Light-house	Predominantly coralline algal pavement with thin algal veneer	Southeast facing barrier reef
3	West Passage	Coralline algal pavement to 7 m, coral 7-20 m	Northwest facing barrier reef
4	Iwayama Bay	Coral and sand	Fringing reef of limestone stack in enclosed bay
5	East side barrier reef	Predominantly coral	Southeast facing barrier reef
6	Ngemelis I	Predominantly coral and <u>Halimeda</u>	Southwest facing barrier reef
7	Ngemelis II	Predominantly coral	Passage of southwest facing barrier reef
8	Ngeremdiu	Reef flat - coralline algal pavement with algal veneer, 5-20 m - coral and rubble	Southeast facing fringing reef
9	Aulong I	Coralline algal pavement sloping into coral and rubble	North facing fringing reef
10	Aulong II	Coralline algal pavement sloping into rubble (5-10 m) then coral and sand	South facing fringing reef in enclosed bay
11	Aimelik	Reef flat - rubble and coral, 5-15 m - rubble	South facing fringing reef of large, volcanic island
12	Ngetpang Bay Channel Marker 23	Predominantly coral	West facing fringing reef of large volcanic island
13	Channel Marker 28	Reef flat - coral, 5-15 m - rubble and coral	Patch reef in Palau lagoon west of Babeldoap Island
14	Baiting Area	Passage 0-2 m coral and rubble, 5-15 m - predom. sand	Small passage into small protected bay in Rock Islands of Palau lagoon

Site #	Location	Bottom type	Setting
15	West side barrier reef	Predominantly sand	Lagoon side of west side barrier reef
16	Adorius	Rubble and sand	West facing fringing reef of limestone island in Palau lagoon
17	Red Cave	Rubble	Southwest facing fringing reef of limestone island

Remarks: Rubble was generally covered by a thin algal veneer.
Lagoon bottom type at all lagoon sites graded into
fine sand at 15-20 m.

APPENDIX B. STANDING CROP DATA (#/CM²) FOR 14 SPECIES OF FORAMINIFERA FROM 256 SAMPLES FROM PALAU

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	ARCHAIS ANGULATUS	MARGINIFERA VERTEERLIS	PENEROPLIS PERTUSUS	SORITES MARGINALIS	SPIROLINA ARIETINA
1	123072	1.	2.	0.0	0.06	0.71	0.0	0.0
1	123072	2.	5.	0.0	0.07	0.48	0.0	0.0
1	123072	3.	5.	0.0	0.07	1.45	0.0	0.0
1	123072	12.	10.	0.0	0.04	0.0	0.0	0.0
1	123072	13.	10.	0.0	0.16	0.54	0.0	0.0
1	123072	8.	13.	0.0	0.07	0.27	0.0	0.0
1	123072	14.	13.	0.0	0.0	0.12	0.0	0.0
1	123072	4.	15.	0.0	0.45	0.27	0.0	0.0
1	123072	15.	15.	0.0	0.08	0.19	0.04	0.0
2	012573	7.	1.	0.0	0.27	0.82	0.0	0.0
2	012573	8.	1.	0.0	0.09	0.28	0.0	0.0
2	012573	10.	1.	0.0	0.10	0.05	0.0	0.0
2	012573	1.	5.	0.0	0.12	0.48	0.0	0.06
2	012573	5.	5.	0.0	0.0	0.0	0.0	0.0
2	012573	6.	5.	0.0	0.04	0.29	0.0	0.04
2	012573	2.	10.	0.0	0.07	0.29	0.0	0.0
2	012573	3.	10.	0.0	0.03	0.69	0.0	0.0
2	012573	4.	10.	0.0	0.0	1.41	0.0	0.0
3	012673	1.	5.	0.0	0.05	0.10	0.0	0.0
3	012673	5.	5.	0.0	0.09	0.0	0.0	0.0
3	012673	2.	10.	0.0	0.0	0.0	0.0	0.0
3	012673	4.	10.	0.0	0.0	0.0	0.0	0.0
3	012673	3.	15.	0.0	0.0	0.0	0.0	0.0
3	012673	11.	20.	0.0	0.0	0.0	0.0	0.0
4	031773	9.	2.	0.0	0.17	0.0	0.0	0.0
4	031773	10.	2.	0.0	0.0	0.0	0.0	0.0
4	031773	6.	5.	0.0	0.0	0.0	0.0	0.0
4	031773	7.	5.	0.0	0.12	0.0	0.0	0.0
4	031773	4.	10.	0.0	0.0	0.0	0.0	0.0
4	031773	5.	10.	0.0	0.0	0.0	0.0	0.0
4	031773	2.	15.	0.0	0.0	0.09	0.0	0.0
4	031773	3.	15.	0.0	0.0	0.0	0.0	0.0
5	031873	33.	0.	0.0	0.10	3.68	0.0	0.05
5	031873	34.	0.	0.0	0.05	1.78	0.0	0.0
5	031873	35.	1.	0.0	0.0	0.04	0.0	0.0
5	031873	36.	1.	0.0	0.0	0.0	0.0	0.0
5	031873	25.	3.	0.0	0.19	0.05	0.0	0.0
5	031873	26.	3.	0.0	0.06	0.30	0.06	0.06
5	031873	23.	5.	0.0	0.22	0.03	0.03	0.03
5	031873	24.	5.	0.0	0.30	0.0	0.0	0.0
5	031873	27.	10.	0.0	1.83	0.0	0.0	0.0
5	031873	28.	10.	0.0	1.84	0.0	0.0	0.0
5	031873	13.	15.	0.0	0.20	0.0	0.0	0.0
5	031873	14.	15.	0.0	0.19	0.0	0.10	0.0
5	031873	15.	20.	0.0	0.74	0.11	0.11	0.05
5	031873	16.	20.	0.0	0.53	0.0	1.10	0.03
5	031873	21.	30.	0.0	0.50	0.08	0.21	0.04
5	031873	22.	30.	0.0	0.26	0.0	0.05	0.0
6	040873	1.	0.	0.10	0.44	0.27	0.0	0.0
6	040873	2.	0.	0.06	0.23	0.17	0.0	0.0
7	040873	19.	0.	0.0	0.17	0.05	0.0	0.0
7	040873	20.	0.	0.0	0.25	0.0	0.0	0.0
6	040873	9.	5.	0.0	0.17	0.0	0.0	0.0
6	040873	10.	5.	0.0	0.0	0.43	0.0	0.0
7	040873	17.	5.	0.0	0.10	0.14	0.0	0.0
7	040873	18.	5.	0.06	0.0	0.62	0.0	0.06
6	040873	7.	10.	0.0	0.33	0.05	0.0	0.0
6	040873	8.	10.	0.0	0.17	0.11	0.0	0.0
7	040873	12.	10.	0.0	0.20	0.0	0.0	0.0
7	040873	14.	10.	0.0	0.0	0.0	0.0	0.0
6	040873	5.	15.	0.0	0.27	0.0	0.0	0.0
7	040873	6.	15.	0.0	0.0	0.0	0.0	0.0
7	040873	15.	15.	0.0	0.06	0.0	0.0	0.0
6	040873	16.	15.	0.0	0.25	0.0	0.0	0.0
6	040873	3.	20.	0.0	0.27	0.0	0.0	0.0
8	051173	4.	20.	0.0	0.0	0.0	0.0	0.0
8	051173	1.	22.	0.0	0.0	0.12	0.0	0.62
8	051173	2.	22.	0.0	0.28	0.19	0.0	1.20
8	051173	3.	5.	0.0	0.0	0.0	0.0	0.08
8	051173	4.	5.	0.0	0.15	0.0	0.0	0.05
8	051173	5.	10.	0.0	0.25	0.0	0.0	0.13
8	051173	6.	10.	0.0	0.18	0.0	0.0	0.72
8	051173	7.	15.	0.0	0.50	0.40	0.0	0.0
8	051173	8.	15.	0.0	0.23	0.34	0.0	0.0
8	051173	11.	20.	0.0	0.11	0.0	0.0	0.0
8	051173	12.	20.	0.0	0.04	0.0	0.0	0.0
9	051573	9.	2.	0.0	1.85	2.77	0.0	0.31
9	051573	10.	2.	0.0	0.0	0.0	0.0	0.0
9	051573	3.	5.	0.0	0.15	0.05	0.0	0.0
9	051573	4.	5.	0.0	0.0	0.32	0.0	0.0
9	051573	1.	10.	0.0	0.84	3.14	0.0	0.54

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	ARCHAIS ANGULATUS	MARGINCPCRA VERTEERALS	PENEROPLIS PERTUSUS	SORITES MARGINALIS	SPIROLINA ARIETINA
9	051573	2.	10.	0.0	0.0	1.47	0.0	0.0
9	051573	5.	15.	0.0	0.0	0.54	0.0	0.23
9	051573	6.	15.	0.0	0.0	2.04	0.0	1.02
9	051573	7.	20.	0.0	0.12	0.61	0.0	0.24
9	051573	8.	20.	0.0	0.33	0.82	0.0	0.66
10	051573	10.	1.	0.0	0.53	1.07	0.0	0.0
10	051573	20.	1.	0.0	0.67	0.86	0.0	0.10
10	051573	11.	5.	0.0	0.17	0.0	0.0	0.0
10	051573	12.	5.	0.0	0.0	0.23	0.0	0.0
10	051573	13.	10.	0.0	0.38	1.02	0.0	0.0
10	051573	14.	10.	0.0	0.67	1.12	0.0	0.22
10	051573	15.	15.	0.0	0.10	0.10	0.0	0.0
10	051573	16.	15.	0.0	0.08	0.08	0.0	0.0
10	051573	17.	20.	0.0	0.07	0.0	0.0	0.39
10	051573	18.	20.	0.0	0.0	0.16	0.0	0.78
11	060573	21.	0.	0.0	0.56	12.39	0.0	0.0
11	060573	22.	1.	0.0	0.0	3.73	0.0	0.0
11	060573	21.	1.	0.0	0.08	1.19	0.0	0.0
11	060573	22.	1.	0.0	0.32	7.04	0.0	0.0
11	060573	1.	2.	0.0	0.0	0.06	0.0	0.0
11	060573	2.	2.	0.0	0.12	0.12	0.0	0.0
11	060573	3.	5.	0.0	0.0	0.09	0.0	0.0
11	060573	4.	5.	0.0	0.06	0.0	0.0	0.0
11	060573	5.	10.	0.0	0.0	0.42	0.0	0.24
11	060573	6.	10.	0.0	0.0	0.0	0.0	0.06
11	060573	7.	15.	0.0	0.21	0.14	0.0	0.07
11	060573	8.	15.	0.0	0.04	0.04	0.0	0.23
11	060573	9.	20.	0.0	0.0	0.0	0.0	0.25
11	060573	10.	20.	0.0	0.0	0.0	0.0	0.0
12	060573	11.	1.	0.0	0.0	0.0	0.0	0.0
12	060573	12.	1.	0.0	0.0	0.0	0.0	0.0
12	060573	13.	5.	0.0	0.0	0.0	0.0	0.0
12	060573	14.	5.	0.0	0.0	0.0	0.0	0.0
12	060573	15.	10.	0.0	0.05	0.0	0.0	0.0
12	060573	16.	10.	0.0	0.0	0.0	0.0	0.0
12	060573	17.	15.	0.0	0.05	0.0	0.0	0.0
12	060573	18.	15.	0.0	0.0	0.0	0.0	0.0
12	060573	19.	20.	0.0	0.0	0.0	0.0	0.0
12	060573	20.	20.	0.0	0.07	0.0	0.0	0.0
13	060573	33.	1.	0.0	0.0	0.0	0.0	0.0
13	060573	34.	1.	0.0	0.0	0.0	0.0	0.0
13	060573	35.	5.	0.0	0.0	0.0	0.0	0.0
13	060573	36.	5.	0.0	0.0	0.0	0.0	0.0
13	060573	37.	10.	0.0	0.06	0.0	0.0	0.0
13	060573	38.	10.	0.0	0.10	0.0	0.0	0.0
13	060573	39.	15.	0.0	0.0	0.0	0.0	0.06
13	060573	40.	15.	0.0	0.05	0.0	0.0	0.14
13	060573	41.	20.	0.0	0.0	0.0	0.0	0.04
13	060573	42.	20.	0.0	0.0	0.0	0.0	0.07
14	060673	43.	1.	0.0	0.0	0.25	0.0	0.0
14	060673	44.	1.	0.0	0.0	0.0	0.0	0.0
14	060673	45.	1.	0.0	0.0	0.57	0.0	0.0
14	060673	46.	1.	0.0	0.0	0.0	0.0	0.0
14	060673	47.	20.	0.0	1.18	0.0	0.0	0.18
14	060673	48.	20.	0.0	1.41	0.07	0.0	0.07
14	060673	49.	20.	0.0	0.06	0.18	0.0	0.06
14	060673	50.	20.	0.0	0.14	0.20	0.0	0.0
14	060673	41.	5.	0.0	0.12	0.0	0.0	0.0
14	060673	42.	5.	0.0	0.0	0.0	0.0	0.0
14	060673	51.	5.	0.0	0.33	0.17	0.0	0.0
14	060673	52.	5.	0.0	0.0	0.06	0.0	0.0
14	060673	43.	10.	0.0	0.0	0.06	0.0	0.0
14	060673	44.	10.	0.0	0.0	0.0	0.0	0.0
14	060673	53.	10.	0.0	0.04	0.0	0.0	0.0
14	060673	54.	10.	0.0	0.06	0.0	0.0	0.0
14	060673	45.	15.	0.0	0.0	0.0	0.0	0.0
14	060673	46.	4.	0.0	0.0	0.0	0.0	0.0
14	060673	55.	15.	0.0	0.0	0.44	0.07	0.0
14	060673	56.	15.	0.0	0.11	0.53	0.0	0.21
16	031773	1.	5.	0.0	0.27	3.51	0.0	0.68
16	031773	2.	5.	0.0	0.0	3.18	0.0	0.0
16	031773	3.	10.	0.0	0.43	22.75	0.86	1.72
16	031773	4.	10.	0.0	0.68	40.54	0.68	3.38
16	031773	5.	15.	0.0	0.37	5.24	0.37	1.50
16	031773	6.	15.	0.0	0.0	10.04	0.84	0.84
16	031773	7.	20.	0.0	0.28	9.75	0.28	2.79
16	031773	8.	20.	0.0	0.0	4.31	1.18	2.35
17	062972	16.	3.	0.04	0.0	1.79	0.0	0.11
17	062972	17.	3.	0.97	0.0	7.74	0.0	0.0
17	100372	9.	3.	0.0	0.38	0.38	0.0	0.0
17	100372	10.	3.	0.0	0.04	0.11	0.0	0.0
8	050573	17.	0.	0.0	2.01	0.50	0.0	1.01
8	050573	18.	0.	0.0	0.58	0.0	0.0	0.0
8	050573	19.	0.	0.0	7.56	0.0	0.0	4.78
8	050573	20.	0.	0.0	0.0	0.0	0.0	0.0
15	032473	1.	1.	0.0	0.04	0.08	0.0	0.0
15	032473	2.	1.	0.0	0.07	0.07	0.0	0.0
15	032473	3.	1.	0.0	0.0	0.0	0.0	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (#)	ARCHAIS ANGULATUS	MARGINIFERA VERTEBRALIS	PENEROPLIS PERTUSUS	SORITES MARGINALIS	SPIROLINA ARIETINA
16	C50672	2.	2.	0.0	0.24	C.72	0.0	0.0
16	050672	4.	2.	0.0	0.24	1.20	0.0	0.24
16	050672	6.	2.	0.0	0.0	C.55	0.0	0.0
16	062172	1.	2.	0.0	0.0	3.41	0.0	0.0
16	062172	5.	2.	0.0	0.0	7.10	0.0	0.0
16	062172	6.	2.	0.0	0.0	E.39	0.0	0.0
16	062172	7.	2.	0.0	0.0	11.06	0.48	0.0
16	070772	1.	2.	0.0	0.09	3.19	0.0	0.0
16	070772	6.	2.	0.0	0.0	2.04	0.0	0.0
16	070772	7.	2.	0.0	0.0	E.13	0.0	0.67
16	081072	2.	2.	0.0	0.23	E.53	0.0	0.0
16	081072	3.	2.	0.0	0.02	1.76	0.0	0.0
16	081072	5.	2.	0.0	0.0	E.80	0.0	0.0
16	091072	1.	2.	0.0	0.12	E.52	0.0	0.0
16	091072	4.	2.	0.0	0.09	16.96	0.0	0.45
16	091072	6.	2.	0.0	0.01	13.22	0.0	0.41
16	101472	1.	2.	0.0	1.04	4.11	0.0	0.26
16	101472	4.	2.	0.0	0.03	10.16	0.0	0.0
16	101472	5.	2.	0.0	2.07	16.82	0.0	0.23
16	110672	1.	2.	0.0	0.0	15.68	0.0	0.0
16	110672	4.	2.	0.0	0.05	E.35	0.0	0.18
16	110672	5.	2.	0.0	2.44	24.15	0.0	0.0
16	120572	1.	2.	0.0	0.20	10.34	0.0	0.20
16	120572	3.	2.	0.0	4.00	6.20	0.0	0.10
16	120572	5.	2.	0.0	0.44	1.55	0.0	0.11
16	010973	1.	2.	0.0	0.09	3.78	0.0	0.0
16	010973	3.	2.	0.0	0.08	3.26	0.0	0.0
16	010973	5.	2.	0.0	0.12	1.62	0.0	0.0
16	020673	2.	2.	0.0	0.10	18.02	0.0	0.0
16	020673	4.	2.	0.0	0.0	6.45	0.0	0.0
16	020673	6.	2.	0.0	0.0	17.59	0.0	0.0
16	031773	9.	2.	0.0	0.22	15.38	0.0	0.0
16	031773	18.	2.	0.0	1.04	38.86	0.0	0.0
16	041973	3.	2.	0.0	0.0	1.64	0.0	0.0
16	041973	4.	2.	0.0	0.0	1.82	0.0	0.0
16	041973	5.	2.	0.0	0.33	21.00	0.0	0.0
16	052473	11.	2.	0.0	0.15	1.97	0.0	0.15
16	052473	12.	2.	0.0	0.08	16.86	0.0	1.16
16	052473	13.	2.	0.0	0.18	3.09	0.0	0.18
16	062573	22.	2.	0.0	0.74	5.56	0.0	0.0
16	062573	24.	2.	0.0	0.08	15.03	0.0	0.58
16	062573	16.	2.	0.0	0.30	2.30	0.0	0.0
17	040872	1.	1.	0.40	0.0	7.60	0.0	0.0
17	040872	3.	1.	0.0	0.0	2.80	0.0	0.80
17	040872	9.	1.	0.0	0.0	C.80	0.0	0.0
17	050472	2.	1.	0.0	0.18	C.92	0.0	0.18
17	050472	3.	1.	0.0	0.0	C.0	0.0	0.0
17	050472	8.	1.	0.03	0.0	C.07	0.0	0.03
17	062572	11.	1.	0.42	0.0	3.05	0.0	0.11
17	062572	12.	1.	0.58	0.0	2.09	0.0	0.23
17	062572	18.	1.	0.62	0.0	3.67	0.0	0.0
17	071372	4.	1.	0.18	0.05	0.64	0.0	0.0
17	071372	6.	1.	0.10	0.10	2.01	0.0	0.10
17	071372	7.	1.	0.0	0.24	1.71	0.0	0.0
17	081672	1.	1.	0.0	0.05	0.21	0.0	0.0
17	081672	2.	1.	0.0	0.06	0.58	0.0	0.06
17	081672	5.	1.	0.20	0.0	1.42	0.0	0.07
17	090172	1.	1.	0.04	0.0	C.28	0.0	0.0
17	090172	2.	1.	0.0	0.08	C.28	0.0	0.0
17	090172	3.	1.	0.06	0.0	C.90	0.0	0.0
17	100372	1.	1.	0.78	C.20	15.22	0.0	2.16
17	100372	3.	1.	3.41	0.31	16.58	0.0	0.93
17	100372	4.	1.	1.67	1.07	42.78	0.0	3.33
17	110272	1.	1.	1.24	0.00	6.81	0.0	0.0
17	110272	2.	1.	0.14	0.09	2.17	0.0	0.0
17	110272	5.	1.	0.0	0.0	C.09	0.0	0.0
17	12307	2.	1.	0.30	0.15	7.41	0.0	0.0
17	12307	3.	1.	9.03	0.23	11.96	0.0	0.0
17	12307	4.	1.	1.22	0.0	14.63	0.0	0.0
17	012573	11.	1.	4.29	0.48	13.33	0.0	0.0
17	012573	13.	1.	4.55	0.12	23.38	0.0	0.0
17	012573	10.	1.	5.95	0.10	7.12	0.0	0.0
17	022373	1.	1.	0.0	0.05	C.10	0.0	0.0
17	022373	2.	1.	0.05	0.05	1.02	0.0	0.05
17	022373	3.	1.	0.0	0.0	C.0	0.0	0.0
17	033173	1.	1.	0.0	0.02	7.19	0.0	0.0
17	033173	2.	1.	0.0	0.0	C.81	0.0	0.0
17	033173	3.	1.	0.0	0.06	1.08	0.0	0.0
17	042773	1.	1.	0.0	0.0	0.15	0.0	0.15
17	042773	3.	1.	0.51	0.01	5.05	0.0	0.0
17	042773	4.	1.	0.21	0.01	1.06	0.0	0.0
17	052273	1.	1.	0.35	0.05	2.48	0.0	0.35
17	052273	2.	1.	0.0	0.0	C.23	0.0	0.0
17	052273	3.	1.	0.10	0.0	C.10	0.0	0.0
17	062573	12.	1.	3.45	0.05	20.00	0.0	2.76
17	062573	13.	1.	2.01	1.68	7.38	0.0	1.68
17	062573	14.	1.	2.69	1.92	20.00	0.0	3.85

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	AMPHISTEGINA LESSONII	AMPHISTEGINA LCBIFERA	AMPHISTEGINA RADIATA	BACULOGYPSINA SPHAERULATA
1	123072	1.	2.	0.48	1.13	0.0	0.0
1	123072	2.	5.	1.58	0.21	0.0	0.0
1	123072	12.	5.	1.10	0.14	0.0	0.0
1	123072	3.	10.	0.45	0.09	0.0	0.0
1	123072	13.	10.	2.30	0.89	0.0	0.0
1	123072	6.	13.	2.75	0.74	0.0	0.0
1	123072	14.	13.	6.12	0.0	0.0	0.0
1	123072	4.	15.	1.61	0.09	0.09	0.0
1	123072	15.	15.	0.92	0.23	0.04	0.0
2	012573	7.	1.	0.61	7.41	0.0	0.0
2	012573	8.	1.	0.14	1.79	0.0	0.0
2	012573	10.	1.	0.15	2.89	0.0	0.05
2	012573	1.	5.	1.63	5.18	0.0	0.0
2	012573	5.	5.	0.19	0.63	0.0	0.06
2	012573	6.	5.	0.34	2.39	0.0	0.0
2	012573	2.	10.	0.73	1.02	0.15	0.0
2	012573	3.	10.	2.18	1.42	0.03	0.0
2	012573	4.	10.	1.67	1.47	0.0	0.0
3	012673	1.	5.	0.33	0.86	0.0	0.0
3	012673	5.	5.	0.09	1.03	0.0	0.04
3	012673	2.	10.	0.20	0.31	0.0	0.0
3	012673	4.	10.	0.09	0.22	0.0	0.0
3	012673	3.	15.	0.18	0.15	0.0	0.0
3	012673	11.	20.	0.05	0.05	0.10	0.0
4	031773	9.	2.	0.09	0.0	0.0	0.0
4	031773	10.	2.	0.0	0.0	0.0	0.0
4	031773	6.	5.	0.71	0.0	0.06	0.0
4	031773	7.	5.	0.0	0.0	0.0	0.0
4	031773	4.	10.	0.0	0.0	0.0	0.0
4	031773	5.	10.	0.23	0.05	0.0	0.0
4	031773	2.	15.	0.0	0.0	0.0	0.0
4	031773	3.	15.	0.0	0.0	0.0	0.0
5	031873	33.	0.	0.0	1.00	0.0	0.0
5	031873	34.	0.	0.0	0.23	0.0	0.0
5	031873	35.	1.	0.0	0.26	0.0	0.04
5	031873	36.	1.	0.0	0.54	0.0	0.0
5	031873	25.	3.	0.09	1.04	0.0	0.0
5	031873	26.	3.	0.24	1.07	0.0	0.0
5	031873	23.	5.	2.05	2.56	0.06	0.0
5	031873	24.	5.	3.67	2.31	0.06	0.0
5	031873	27.	10.	2.65	1.55	0.09	0.0
5	031873	28.	10.	0.25	0.25	0.04	0.0
5	031873	13.	15.	0.91	0.26	0.23	0.0
5	031873	14.	15.	2.04	0.64	0.73	0.0
5	031873	15.	20.	2.01	0.26	0.85	0.0
5	031873	16.	20.	1.23	0.73	0.27	0.0
5	031873	21.	30.	0.23	0.12	2.11	0.0
5	031873	22.	30.	1.77	0.36	4.53	0.0
6	040873	1.	0.	0.0	1.16	0.0	0.0
6	040873	2.	0.	0.0	1.79	0.0	0.0
7	040873	19.	0.	0.05	0.84	0.0	0.0
7	040873	20.	0.	0.0	0.50	0.0	0.0
6	040873	9.	5.	0.0	0.0	0.0	0.0
6	040873	10.	5.	0.0	2.38	0.0	0.0
7	040873	17.	5.	0.34	1.92	0.05	0.0
6	040873	18.	5.	0.06	0.90	0.06	0.0
6	040873	7.	10.	0.14	0.95	0.0	0.0
6	040873	8.	10.	0.17	1.36	0.0	0.0
7	040873	13.	10.	0.0	0.10	0.0	0.0
7	040873	14.	10.	0.0	0.15	0.0	0.0
6	040873	5.	15.	0.04	0.08	0.04	0.0
6	040873	6.	15.	0.0	0.36	0.0	0.0
7	040873	15.	15.	0.0	0.18	0.06	0.0
7	040873	16.	15.	0.25	1.16	0.0	0.0
6	040873	3.	20.	0.04	0.08	0.04	0.0
6	040873	4.	20.	0.0	0.36	0.0	0.0
8	051173	1.	2.	0.0	2.86	0.0	0.25
8	051173	2.	2.	0.0	5.28	0.0	0.28
8	051173	3.	5.	0.17	1.01	0.0	0.0
8	051173	4.	5.	0.31	1.18	0.0	0.0
8	051173	5.	10.	2.53	5.06	0.13	0.0
8	051173	6.	10.	5.21	5.92	0.54	0.0
8	051173	7.	15.	8.60	6.30	1.40	0.0
8	051173	8.	15.	2.64	3.22	0.11	0.0
8	051173	11.	20.	1.97	0.0	0.25	0.0
8	051173	12.	20.	0.66	0.04	0.22	0.0
9	051573	9.	2.	19.38	15.08	0.0	0.0
9	051573	10.	2.	9.60	4.80	0.0	0.0
9	051573	3.	5.	3.35	0.66	0.0	0.0
9	051573	4.	5.	13.33	2.70	0.0	0.0
9	051573	1.	10.	8.56	1.95	0.0	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	AMPHISTEGINA LESSONII	AMPHISTEGINA LCBIFERA	AMPHISTEGINA RADIATA	BACULOGYPSINA SPHAERULATA
9	051573	2.	10.	56.86	9.80	0.0	0.0
9	051573	5.	15.	10.85	0.23	0.08	0.0
9	051573	6.	15.	12.81	0.29	0.0	0.0
9	051573	7.	20.	5.39	0.12	0.12	0.0
9	051573	8.	20.	17.93	0.33	0.16	0.0
10	051573	19.	1.	9.47	11.87	0.0	0.0
10	051573	20.	1.	7.14	7.24	0.0	0.0
10	051573	11.	5.	4.57	0.83	0.0	0.0
10	051573	12.	5.	21.81	1.86	0.0	0.0
10	051573	13.	10.	3.74	0.94	0.04	0.0
10	051573	14.	10.	24.16	1.57	0.0	0.0
10	051573	15.	15.	7.71	0.16	0.0	0.0
10	051573	16.	15.	8.48	0.56	0.08	0.0
10	051573	17.	20.	3.40	0.03	0.29	0.0
10	051573	18.	20.	7.27	0.08	0.31	0.0
11	060573	22.	0.	0.0	0.0	0.0	0.0
11	060573	24.	0.	0.0	0.0	0.0	0.0
11	060573	21.	1.	0.08	0.63	0.0	0.08
11	060573	22.	1.	0.75	1.28	0.0	0.11
11	060573	1.	2.	0.47	0.24	0.0	0.0
11	060573	2.	2.	13.05	0.60	0.0	0.0
11	060573	3.	5.	1.50	0.18	0.09	0.0
11	060573	4.	5.	0.51	0.0	0.0	0.0
11	060573	5.	10.	2.42	0.12	0.06	0.0
11	060573	6.	10.	0.56	0.06	0.39	0.0
11	060573	7.	15.	1.67	0.0	0.35	0.0
11	060573	8.	15.	4.06	0.0	0.68	0.0
11	060573	9.	20.	3.98	0.0	1.86	0.0
11	060573	10.	20.	1.21	0.0	1.31	0.0
12	060573	11.	1.	0.24	0.33	0.04	0.0
12	060573	12.	1.	0.05	0.0	0.0	0.0
12	060573	13.	5.	0.0	0.0	0.0	0.0
12	060573	14.	5.	0.03	0.0	0.14	0.0
12	060573	15.	10.	0.14	0.05	0.33	0.0
12	060573	16.	10.	0.17	0.0	0.84	0.0
12	060573	17.	15.	0.32	0.05	2.45	0.0
12	060573	18.	15.	0.31	0.03	1.02	0.0
12	060573	19.	20.	0.62	0.0	5.16	0.0
12	060573	20.	20.	0.29	0.0	2.19	0.0
13	060573	32.	1.	0.04	0.04	0.0	0.0
13	060573	34.	1.	0.0	0.0	0.0	0.0
13	060573	25.	5.	0.13	0.0	0.0	0.0
13	060573	26.	5.	0.24	0.0	0.16	0.0
13	060573	27.	10.	1.56	0.0	0.89	0.0
13	060573	28.	10.	1.01	0.03	0.40	0.0
13	060573	29.	15.	2.19	0.13	1.00	0.0
13	060573	30.	15.	1.34	0.0	0.97	0.0
13	060573	31.	20.	2.57	0.0	1.09	0.0
13	060573	32.	20.	0.57	0.04	1.56	0.0
14	060673	57.	1.	1.27	0.06	0.0	0.0
14	060673	58.	1.	0.44	0.0	0.0	0.0
14	060673	59.	1.	23.50	2.61	0.0	0.0
14	060673	60.	1.	24.80	2.17	0.0	0.0
14	060673	47.	2N.	0.45	0.18	0.0	0.0
14	060673	48.	2N.	0.74	0.30	0.0	0.0
14	060673	49.	2N.	0.55	0.12	0.0	0.0
14	060673	50.	2N.	1.62	0.47	0.0	0.0
14	060673	41.	55.	0.18	0.0	0.0	0.0
14	060673	42.	55.	0.0	0.0	0.0	0.0
14	060673	51.	55.	4.53	0.06	0.0	0.0
14	060673	52.	55.	0.29	0.0	0.0	0.0
14	060673	43.	10.	0.38	0.0	0.0	0.0
14	060673	44.	10.	0.40	0.0	0.0	0.0
14	060673	53.	10.	0.67	0.0	0.0	0.0
14	060673	54.	10.	1.42	0.0	0.0	0.0
14	060673	45.	15.	0.16	0.0	0.0	0.0
14	060673	46.	4.	0.0	0.0	0.0	0.0
14	060673	55.	15.	0.44	0.0	0.0	0.0
14	060673	56.	15.	7.23	0.0	0.0	0.0
16	031773	1.	5.	12.03	1.76	0.0	0.0
16	031773	2.	5.	10.55	1.14	0.0	0.0
16	031773	3.	10.	104.72	5.15	0.0	0.0
16	031773	4.	10.	106.76	20.27	0.0	0.0
16	031773	5.	15.	27.71	0.0	0.0	0.0
16	031773	6.	15.	53.55	0.42	0.0	0.0
16	031773	7.	20.	46.52	0.56	0.0	0.0
16	031773	8.	20.	73.34	0.78	0.0	0.0
17	062972	16.	3.	0.19	2.05	0.0	0.14
17	062972	17.	3.	0.32	7.74	0.0	2.90
17	100372	9.	3.	0.77	3.33	0.0	0.16
17	100372	10.	3.	0.62	1.14	0.0	0.0
8	050573	17.	0.	0.0	7.03	0.0	44.22
8	050573	18.	0.	0.0	11.03	0.0	13.54
8	050573	19.	0.	0.0	39.81	0.0	234.47
8	050573	20.	0.	0.0	0.0	0.0	0.58
15	032473	1.	1.	0.0	0.65	0.0	0.04
15	032473	2.	1.	0.0	1.15	0.0	0.0
15	032473	3.	1.	0.0	0.08	0.0	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	AMPHISTEGINA LESSONII	AMPHISTEGINA LCBIFERA	AMPHISTEGINA RADIATA	BACULOGYPSINA SPHAERULATA
16	050672	2.	2.	2.16	2.40	0.0	0.0
16	050672	4.	2.	0.0	0.96	0.0	0.0
16	050672	6.	2.	1.00	1.71	0.0	0.0
16	062172	1.	2.	2.50	2.27	0.0	0.0
16	062172	5.	2.	5.48	8.39	0.0	0.0
16	062172	6.	2.	0.56	1.44	0.0	0.0
16	062172	7.	2.	2.40	3.37	0.0	0.0
16	070772	1.	2.	9.40	7.45	0.0	0.0
16	070772	6.	2.	2.04	3.40	0.0	0.0
16	070772	7.	2.	4.69	5.36	0.0	0.0
16	081072	2.	2.	8.99	5.53	0.0	0.0
16	081072	3.	2.	3.06	2.71	0.0	0.0
16	081072	5.	2.	7.20	6.40	0.0	0.0
16	081072	1.	2.	8.20	6.31	0.0	0.0
16	081072	4.	2.	17.86	24.11	0.0	0.0
16	091072	6.	2.	8.26	12.81	0.0	0.41
16	101472	1.	2.	4.88	7.46	0.0	0.0
16	101472	4.	2.	4.59	16.72	0.0	0.0
16	101472	5.	2.	14.75	23.96	0.0	0.0
16	110672	1.	2.	14.77	13.33	0.0	0.0
16	110672	4.	2.	4.06	5.90	0.0	0.0
16	110672	5.	2.	23.77	14.34	0.0	0.0
16	120572	1.	2.	6.56	8.95	0.0	0.0
16	120572	3.	2.	8.50	11.80	0.0	0.0
16	120572	5.	2.	9.54	8.99	0.0	0.0
16	010973	1.	2.	13.49	5.13	0.0	0.0
16	010973	3.	2.	4.56	4.56	0.0	0.0
16	010973	5.	2.	17.09	6.12	0.0	0.0
16	020673	2.	2.	48.05	25.53	0.0	0.0
16	020673	4.	2.	12.67	6.45	0.0	0.0
16	020673	6.	2.	5.53	12.06	0.0	0.0
16	031773	9.	2.	12.75	7.91	0.0	0.0
16	031773	18.	2.	30.57	26.43	0.0	0.0
16	041973	3.	2.	10.77	7.48	0.0	0.0
16	041973	4.	2.	10.39	4.55	0.0	0.0
16	041973	5.	2.	20.00	20.00	0.0	0.0
16	052473	11.	2.	5.30	3.48	0.0	0.0
16	052473	12.	2.	31.39	20.35	0.0	0.0
16	052473	13.	2.	12.73	10.55	0.0	0.0
16	062573	22.	2.	5.15	5.15	0.0	0.0
16	062973	24.	2.	34.10	24.85	0.0	0.0
16	062573	16.	2.	12.55	7.25	0.0	0.0
17	040872	1.	1.	0.40	2.40	0.0	6.40
17	040872	3.	1.	0.40	3.20	0.0	6.80
17	040872	9.	1.	0.80	8.00	0.0	0.80
17	050472	2.	1.	0.0	0.37	0.0	14.92
17	050472	3.	1.	0.0	0.07	0.0	3.94
17	050472	8.	1.	0.0	0.14	0.0	0.0
17	062972	11.	1.	0.11	0.74	0.0	1.58
17	062972	12.	1.	0.0	0.70	0.0	7.91
17	062972	18.	1.	0.13	0.87	0.0	0.38
17	071372	4.	1.	0.0	0.16	0.0	3.53
17	071372	6.	1.	0.10	1.11	0.0	24.75
17	071372	7.	1.	0.0	2.20	0.0	12.84
17	081672	1.	1.	0.0	0.11	0.0	0.43
17	081672	2.	1.	0.0	0.19	0.0	2.86
17	081672	5.	1.	0.0	0.07	0.0	3.11
17	090172	1.	1.	0.0	0.0	0.0	2.66
17	090172	3.	1.	0.0	0.0	0.0	0.71
17	130372	1.	1.	0.0	0.13	0.0	1.23
17	100372	3.	1.	0.0	7.06	0.0	10.20
17	130372	4.	1.	0.0	12.69	0.0	7.43
17	110272	1.	1.	0.0	45.00	0.0	60.00
17	110272	2.	1.	0.0	0.27	0.0	2.74
17	110272	5.	1.	0.0	0.19	0.0	0.71
17	12307	2.	1.	0.15	0.0	0.0	0.17
17	12307	3.	1.	0.0	6.66	0.0	0.15
17	12307	4.	1.	0.0	4.97	0.0	6.77
17	012573	11.	1.	0.0	14.41	0.0	8.54
17	012573	13.	1.	0.65	42.86	0.0	21.90
17	012573	15.	1.	0.0	8.61	0.0	20.13
17	022373	1.	1.	0.0	0.0	0.0	2.62
17	022373	2.	1.	0.0	0.15	0.0	0.81
17	022373	3.	1.	0.0	0.12	0.0	2.63
17	033173	1.	1.	0.0	0.41	0.0	0.81
17	033173	2.	1.	0.0	0.07	0.0	12.32
17	033173	3.	1.	0.0	0.11	0.0	2.36
17	042773	1.	1.	0.0	0.30	0.0	0.57
17	042773	3.	1.	0.0	0.51	0.0	13.84
17	042773	4.	1.	0.0	0.21	0.0	7.58
17	052273	1.	1.	0.0	1.24	0.0	1.27
17	052273	2.	1.	0.0	0.46	0.0	4.07
17	052273	3.	1.	0.0	0.10	0.0	9.80
17	062973	12.	1.	0.69	25.52	0.0	10.46
17	062973	13.	1.	0.0	25.50	0.0	30.34
17	062973	14.	1.	0.38	48.46	0.0	9.40
17	062973	14.	1.			0.0	12.31

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	CALCARINA CALCAR	CALCARINA HISPICA	CALCARINA SPLENGERI	HETEROSTEGINA DEPRESSA	NUMMULITES AMMONOIDES
1	123072	1.	2.	0.0	0.0	0.0	0.0	0.0
1	123072	2.	5.	0.14	0.07	0.0	0.0	0.0
1	123072	12.	5.	0.0	0.14	0.0	0.0	0.0
1	123072	3.	10.	0.04	0.09	0.0	0.0	0.0
1	123072	13.	10.	0.04	0.04	0.0	0.27	0.0
1	123072	8.	13.	0.07	0.07	0.0	0.81	0.0
1	123072	14.	13.	0.06	0.0	0.0	0.18	0.0
1	123072	4.	15.	0.0	0.0	0.0	0.36	0.0
1	123072	15.	15.	0.0	0.0	0.0	0.46	0.08
2	012573	7.	1.	0.07	0.0	0.48	0.16	0.0
2	012573	8.	1.	0.05	0.0	0.24	0.05	0.0
2	012573	10.	1.	0.0	0.0	0.05	0.10	0.0
2	012573	1.	5.	0.0	0.0	0.12	0.0	0.0
2	012573	5.	5.	0.06	0.0	0.0	0.06	0.0
2	012573	6.	5.	0.0	0.0	0.04	0.04	0.0
2	012573	2.	10.	0.0	0.0	0.0	0.07	0.0
2	012573	3.	10.	0.03	0.03	0.0	0.0	0.0
2	012573	4.	10.	0.0	0.06	0.0	0.06	0.0
3	012673	1.	5.	0.0	0.0	0.10	0.0	0.0
3	012673	5.	5.	0.04	0.0	0.13	0.0	0.0
3	012673	2.	10.	0.0	0.0	0.10	0.0	0.0
3	012673	4.	10.	0.0	0.0	0.0	0.0	0.0
3	012673	3.	15.	0.0	0.0	0.0	0.0	0.0
3	012673	11.	20.	0.0	0.0	0.0	0.0	0.0
4	031773	9.	20.	0.0	0.0	0.0	0.0	0.0
4	031773	10.	20.	0.0	0.0	0.0	0.0	0.0
4	031773	6.	5.	0.0	0.0	0.0	0.0	0.0
4	031773	7.	5.	0.0	0.0	0.0	0.0	0.0
4	031773	4.	10.	0.0	0.0	0.0	0.0	0.0
4	031773	5.	10.	0.0	0.0	0.0	0.0	0.0
4	031773	3.	15.	0.0	0.0	0.0	0.0	0.0
4	031773	1.	15.	0.0	0.0	0.0	0.0	0.0
4	031773	33.	0.	0.24	0.0	0.10	0.0	0.0
4	031773	34.	0.	0.33	0.0	0.09	0.0	0.0
4	031873	35.	1.	0.09	0.0	0.09	0.0	0.0
4	031873	36.	1.	0.07	0.0	0.40	0.0	0.0
4	031873	37.	3.	0.0	0.0	0.0	0.0	0.0
4	031873	38.	3.	0.0	0.0	0.18	0.0	0.0
4	031873	39.	3.	0.03	0.0	0.0	0.54	0.0
4	031873	40.	3.	0.0	0.06	0.0	0.30	0.0
4	031873	41.	3.	0.0	0.0	0.0	0.27	0.0
4	031873	42.	3.	0.0	0.0	0.0	0.0	0.0
4	031873	43.	3.	0.0	0.0	0.0	0.20	0.03
4	031873	44.	3.	0.03	0.0	0.0	0.13	0.16
4	031873	45.	3.	0.0	0.0	0.0	0.37	0.0
4	031873	46.	3.	0.0	0.0	0.0	1.28	0.07
4	031873	47.	3.	0.0	0.0	0.0	0.68	0.82
4	031873	48.	3.	0.0	0.0	0.0	0.0	0.89
4	031873	49.	3.	0.10	0.0	0.41	0.0	0.0
4	031873	50.	3.	0.06	0.0	0.09	0.0	0.0
6	040873	2.	0.	0.0	0.0	0.0	0.0	0.0
6	040873	19.	0.	0.0	0.0	0.0	0.0	0.0
6	040873	20.	0.	0.0	0.0	0.0	0.0	0.0
6	040873	9.	5.	0.0	0.0	0.11	0.0	0.0
6	040873	10.	5.	0.0	0.0	0.22	0.11	0.0
6	040873	17.	5.	0.0	0.14	0.10	0.29	0.0
6	040873	18.	5.	0.0	0.23	0.0	0.06	0.0
6	040873	7.	10.	0.24	0.0	0.71	0.19	0.0
6	040873	8.	10.	0.11	0.0	0.28	0.23	0.0
6	040873	13.	10.	0.0	0.0	0.30	0.0	0.0
6	040873	14.	10.	0.0	0.0	0.0	0.0	0.0
6	040873	5.	15.	0.04	0.0	0.0	0.0	0.0
6	040873	6.	15.	0.0	0.0	0.0	0.06	0.0
6	040873	15.	15.	0.0	0.0	0.06	0.0	0.0
6	040873	16.	15.	0.0	0.0	0.08	0.0	0.0
6	040873	3.	20.	0.04	0.0	0.0	0.0	0.0
6	040873	4.	20.	0.0	0.0	0.0	0.06	0.0
8	051173	1.	2.	0.62	0.0	6.66	0.0	0.0
8	051173	2.	2.	1.20	0.0	28.33	0.28	0.0
8	051173	3.	5.	0.08	0.08	2.60	0.0	0.0
8	051173	4.	5.	0.0	0.0	0.72	0.05	0.0
8	051173	5.	10.	0.0	0.25	3.29	0.76	0.0
8	051173	6.	10.	0.18	0.54	3.77	1.08	0.0
8	051173	7.	15.	0.20	0.60	0.20	1.60	0.0
8	051173	8.	15.	0.0	0.0	0.11	0.46	0.0
8	051173	11.	20.	0.04	0.18	0.0	0.0	0.0
8	051173	12.	20.	0.0	0.04	0.0	0.07	0.04
9	051573	9.	2.	1.85	0.0	6.46	1.23	0.0
9	051573	10.	2.	0.30	0.40	5.20	0.0	0.0
9	051573	3.	5.	0.10	0.30	0.05	0.0	0.0
9	051573	4.	5.	0.0	0.55	0.16	0.48	0.0
9	051573	1.	10.	0.0	0.0	0.0	0.11	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	CALCARINA CALCAR	CALCARINA HISPICA	CALCARINA SPLENGLERI	HETEROSTEGINA DEPRESSA	NUMMULITES AMMONOIDES
9	051573	2.	10.	0.0	0.0	0.0	0.49	0.0
9	051573	5.	15.	0.0	0.08	0.0	0.15	0.0
9	051573	6.	15.	0.15	0.0	0.0	0.29	0.0
9	051573	7.	20.	0.0	0.24	0.0	0.12	0.86
9	051573	8.	20.	0.0	0.33	0.0	1.32	0.66
10	051573	19.	1.	1.07	0.27	0.0	0.0	0.0
10	051573	20.	1.	0.38	0.29	0.29	0.0	0.0
10	051573	11.	5.	0.0	1.27	0.0	0.0	0.0
10	051573	12.	5.	0.23	0.23	0.0	0.46	0.0
10	051573	13.	10.	0.09	0.0	0.0	0.0	0.09
10	051573	14.	10.	0.0	0.0	0.0	0.22	0.0
10	051573	15.	15.	0.0	0.0	0.0	0.05	0.0
10	051573	16.	15.	0.0	0.08	0.0	0.08	0.0
10	051573	17.	20.	0.0	0.0	0.0	0.85	1.80
10	051573	18.	20.	0.0	0.08	0.0	0.62	1.17
11	060573	23.	0.	0.0	0.0	0.0	0.0	0.0
11	060573	24.	0.	0.49	0.23	0.0	0.0	0.0
11	060573	21.	1.	0.40	1.25	0.24	0.0	0.0
11	060573	22.	1.	1.71	7.26	0.24	0.11	0.0
11	060573	1.	2.	0.0	1.29	0.0	0.0	0.0
11	060573	2.	2.	0.0	2.66	0.0	0.24	0.0
11	060573	3.	5.	0.0	0.18	0.0	0.09	0.0
11	060573	4.	5.	0.0	0.0	0.0	0.06	0.06
11	060573	5.	10.	0.0	0.20	0.0	0.12	0.0
11	060573	6.	10.	0.0	1.25	0.0	0.06	0.22
11	060573	7.	15.	0.0	0.14	0.0	0.42	0.76
11	060573	8.	15.	0.0	0.20	0.0	0.19	0.26
11	060573	9.	20.	0.0	0.0	0.0	0.37	2.11
11	060573	10.	20.	0.0	0.0	0.0	0.10	1.41
12	060573	11.	1.	0.0	0.08	0.0	0.16	0.04
12	060573	12.	1.	0.0	0.0	0.0	0.0	0.0
12	060573	13.	5.	0.0	0.0	0.0	0.08	0.0
12	060573	14.	5.	0.0	0.0	0.0	0.03	0.0
12	060573	15.	10.	0.0	0.02	0.0	0.14	0.0
12	060573	16.	10.	0.0	0.03	0.0	0.10	0.03
12	060573	17.	15.	0.0	0.05	0.0	0.27	0.09
12	060573	18.	15.	0.0	0.06	0.0	0.25	0.09
12	060573	19.	20.	0.0	0.0	0.0	0.70	0.43
12	060573	20.	20.	0.0	0.0	0.0	0.69	0.46
13	060573	33.	1.	0.0	0.0	0.0	0.0	0.0
13	060573	34.	1.	0.0	0.0	0.0	0.07	0.0
13	060573	25.	5.	0.0	0.0	0.0	0.0	0.0
13	060573	26.	5.	0.0	0.0	0.0	0.0	0.0
13	060573	27.	10.	0.0	0.0	0.0	0.33	0.11
13	060573	28.	10.	0.0	0.0	0.0	0.20	0.13
13	060573	29.	15.	0.0	0.06	0.0	0.27	0.25
13	060573	30.	15	0.0	0.0	0.0	0.09	0.14
13	060573	31.	20.	0.0	0.0	0.0	0.42	0.75
13	060573	32.	20.	0.0	0.0	0.0	0.58	0.36
14	060673	57.	1.	0.0	0.0	0.0	0.0	0.0
14	060673	58.	1.	0.0	0.09	0.0	0.0	0.0
14	060673	59.	1.	1.04	3.13	0.26	1.04	0.0
14	060673	60.	1.	0.20	3.74	0.0	1.57	0.0
14	060673	47.	2.	0.0	0.09	0.0	0.0	0.0
14	060673	48.	2.	0.07	0.52	0.0	0.0	0.0
14	060673	49.	2.	0.06	0.0	0.0	0.06	0.0
14	060673	50.	2.	0.0	0.47	0.0	0.07	0.0
14	060673	41.	5.	0.0	0.0	0.0	0.0	0.0
14	060673	42.	5.	0.0	0.0	0.0	0.0	0.0
14	060673	51.	5.	0.0	0.06	0.0	0.11	0.0
14	060673	52.	5.	0.0	0.0	0.0	0.0	0.0
14	060673	43.	10.	0.06	0.50	0.0	0.0	0.0
14	060673	44.	10.	0.0	0.66	0.0	0.0	0.0
14	060673	53.	10.	0.0	0.0	0.0	0.0	0.0
14	060673	54.	10.	0.0	0.0	0.0	0.0	0.0
14	060673	45.	15.	0.0	0.16	0.0	0.0	0.0
14	060673	46.	4.	0.0	0.0	0.0	0.08	0.0
14	060673	55.	15.	1.47	0.0	0.0	0.0	0.0
14	060673	56.	15.	0.0	0.0	0.0	0.74	0.0
16	031773	1.	5.	0.0	0.0	0.0	0.68	0.0
16	031773	2.	5.	0.0	0.0	0.0	0.38	0.0
16	031773	3.	10.	0.0	0.0	0.0	0.43	0.0
16	031773	4.	10.	0.0	0.0	0.0	0.68	0.0
16	031773	5.	15.	0.0	0.0	0.0	1.50	0.0
16	031773	6.	15.	0.0	0.0	0.0	1.67	0.0
16	031773	7.	20.	0.28	0.0	0.0	2.79	0.0
16	031773	8.	20.	0.0	0.0	0.0	1.18	0.0
17	062972	16.	3.	1.23	0.0	2.05	0.04	0.0
17	062972	17.	2.	13.27	0.32	7.42	0.0	0.0
17	100372	9.	3.	0.33	0.22	1.57	0.16	0.0
17	100372	10.	3.	0.07	0.04	0.52	0.04	0.0
8	050573	17.	0.	58.29	0.0	21.21	0.0	0.0
8	050573	18.	0.	25.53	0.0	13.54	0.0	0.0
8	050573	19.	0.	189.49	0.0	113.06	3.18	0.0
15	032473	1.	1.	0.27	0.0	0.04	0.0	0.0
15	032473	2.	1.	0.0	0.0	0.0	0.0	0.0
15	032473	3.	1.	0.0	0.0	0.04	0.0	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	CALCARINA CALCAR	CALCARINA HISPICA	CALCARINA SPLENGLERI	HETEROSTEGINA DEPRESSA	NUMMULITES AMMONOIDES
16	C50672	2.	2.	0.24	0.0	0.96	0.96	0.0
16	050672	4.	2.	0.48	0.0	1.92	0.0	0.0
16	C50672	6.	2.	0.14	0.0	1.14	0.29	0.0
16	062172	1.	2.	0.68	0.0	1.14	0.68	0.0
16	062172	5.	2.	0.65	0.0	2.26	1.29	0.0
16	062172	6.	2.	0.48	0.0	1.68	0.48	0.0
16	062172	7.	2.	0.96	0.0	2.40	0.96	0.0
16	070772	1.	2.	0.35	0.35	3.90	1.06	0.0
16	C70772	6.	2.	0.34	0.34	1.02	0.68	0.0
16	070772	7.	2.	0.67	0.0	3.35	1.12	0.0
16	081072	2.	2.	1.38	0.0	2.30	0.23	0.0
16	C81072	3.	2.	0.0	0.0	0.71	0.12	0.0
16	081072	5.	2.	2.40	0.0	3.60	0.80	0.0
16	091072	1.	2.	1.26	0.0	2.84	0.63	0.0
16	091072	4.	2.	1.79	0.0	6.25	1.34	0.0
16	C91072	6.	2.	0.83	0.0	1.65	0.0	0.0
16	101472	1.	2.	1.29	0.0	3.66	0.0	0.0
16	101472	4.	2.	2.29	0.66	6.89	1.97	0.0
16	101472	5.	2.	6.22	0.0	14.98	0.0	0.0
16	110672	1.	2.	1.08	0.0	3.42	0.72	0.0
16	110672	4.	2.	1.29	0.0	2.21	0.37	0.0
16	110672	5.	2.	2.26	0.38	11.70	0.0	0.0
16	120572	1.	2.	0.0	0.0	1.79	0.40	0.0
16	120572	3.	2.	0.80	0.0	2.50	0.10	0.0
16	120572	5.	2.	0.22	0.0	1.22	0.0	0.0
16	010973	1.	2.	0.18	0.0	1.17	2.25	0.0
16	010973	3.	2.	0.65	0.0	2.28	0.0	0.0
16	010973	5.	2.	0.23	0.0	0.35	0.92	0.0
16	020673	2.	2.	2.10	0.0	5.10	1.80	0.0
16	020673	4.	2.	0.23	0.0	1.38	0.23	0.0
16	020673	6.	2.	1.51	0.0	4.52	1.01	0.0
16	C31773	9.	2.	0.88	0.0	1.76	0.44	0.0
16	C31773	18.	2.	0.0	0.0	1.55	0.52	0.0
16	041573	3.	2.	0.55	0.0	0.55	1.82	0.0
16	041573	4.	2.	0.26	0.0	0.52	0.26	0.0
16	C41573	5.	2.	0.67	0.0	1.33	1.67	0.0
16	052473	11.	2.	0.0	0.0	0.15	0.0	0.0
16	052473	12.	2.	1.74	0.0	1.16	0.58	0.0
16	052473	13.	2.	0.18	0.0	1.09	0.36	0.0
16	062573	22.	2.	0.74	0.0	0.74	0.74	0.0
16	062573	24.	2.	0.58	0.0	2.31	1.73	0.0
16	062573	16.	2.	0.05	0.0	0.75	0.55	0.0
17	040872	1.	1.	122.40	0.0	0.80	0.0	0.0
17	C40872	3.	1.	47.60	5.60	2.40	2.00	0.0
17	040872	9.	1.	164.80	0.0	0.0	0.80	0.0
17	050472	2.	1.	10.13	0.0	7.55	0.0	0.0
17	050472	3.	1.	1.93	0.15	6.77	0.0	0.0
17	050472	8.	1.	0.07	0.0	0.10	0.0	0.0
17	062572	11.	1.	3.26	0.0	0.63	0.0	0.0
17	062572	12.	1.	4.30	0.0	3.55	0.0	0.0
17	062572	12.	1.	0.27	0.0	2.00	0.0	0.0
17	071372	4.	1.	7.06	0.0	2.98	0.0	0.0
17	071372	6.	1.	131.18	0.0	2.52	0.10	0.0
17	071372	7.	1.	55.38	0.0	2.57	0.71	0.0
17	081672	1.	1.	0.75	0.0	0.48	0.0	0.0
17	081672	2.	1.	6.49	0.0	2.08	0.0	0.0
17	081672	5.	1.	8.65	0.0	0.68	0.0	0.0
17	090172	1.	1.	2.30	0.0	3.21	0.0	0.0
17	090172	2.	1.	2.36	0.0	2.95	0.0	0.0
17	090172	3.	1.	3.87	0.0	2.94	0.0	0.0
17	100372	1.	1.	55.10	0.0	4.31	0.0	0.0
17	100372	3.	1.	29.41	0.0	4.02	0.0	0.0
17	100372	4.	1.	287.79	0.56	25.00	1.11	0.0
17	110272	1.	1.	7.26	0.0	3.54	0.0	0.0
17	110272	2.	1.	2.41	0.0	2.74	0.0	0.0
17	110272	5.	1.	0.09	0.0	1.47	0.0	0.0
17	12307	2.	1.	26.48	0.0	5.14	0.15	0.0
17	12307	3.	1.	36.73	0.0	3.84	0.0	0.0
17	12307	4.	1.	139.64	0.0	3.05	0.0	0.0
17	012573	11.	1.	75.72	0.0	8.10	0.0	0.0
17	012573	13.	1.	121.76	0.0	5.84	0.0	0.0
17	012573	15.	1.	34.46	0.0	1.50	0.0	0.0
17	022373	1.	1.	1.11	0.0	0.71	0.0	0.0
17	022373	2.	1.	7.85	0.0	1.46	0.05	0.0
17	022373	3.	1.	1.04	0.0	1.56	0.0	0.0
17	033173	1.	1.	48.66	0.0	5.34	0.0	0.0
17	033173	2.	1.	9.30	0.0	1.33	0.0	0.0
17	033173	3.	1.	3.70	0.0	0.57	0.0	0.0
17	C42773	1.	1.	14.29	0.0	4.32	0.0	0.0
17	042773	3.	1.	134.84	0.0	2.02	0.0	0.0
17	042773	4.	1.	22.08	0.0	2.12	0.0	0.0
17	052273	1.	1.	47.08	0.0	4.07	0.0	0.0
17	052273	2.	1.	12.30	0.0	0.46	0.0	0.0
17	052273	3.	1.	15.38	0.0	1.85	0.0	0.0
17	062573	12.	1.	244.13	0.0	7.59	0.0	0.0
17	062573	13.	1.	86.58	0.0	4.03	0.34	0.0
17	062573	14.	1.	119.61	0.0	4.23	0.77	0.0

APPENDIX C. HAWAII SAMPLE SITES

Site #	Location	Bottom type	Setting
1, 2, 12	Kahe Point	Predominantly rubble	West facing (leeward) fringing reef
3	Kahuku Beach Park	Rubble and sand	Permanent sand bottom tidepool on east facing (windward) fringing reef
4	Hauula Beach Park	Rubble	East facing fringing reef
5	North Kahana Bay	Rubble	East facing fringing reef
6	Punaluu Beach	Rubble	East facing fringing reef
7	Diamond Head Beach	Rubble	South facing fringing reef
8	Magic Island	Rubble and sand	South facing fringing reef
9	Queen's Surf	Rubble and sand	South facing fringing reef
10	Hanauma Bay	Predominantly algal veneer on coralline pavement	Southeast facing fringing reef, partially enclosed bay
11	Pupukea	Algal veneer on coralline pavement	Northwest facing fringing reef
13	Makapuu Tidepool	Algal veneer	Large tidepool on basalt bench, east facing
14	Outside Kaneohe Bay	**	East facing "barrier" reef
15	Waikiki	Rubble and sand	South facing fringing reef
16	Offshore Honolulu	**	South facing fringing reef

** Dredge samples

Remarks: Rubble was generally covered by thin algal veneer.

APPENDIX D. STANDING CROP DATA (#/CM²) FOR 9 SPECIES OF FORAMINIFERA FROM 159 SAMPLES FROM OAHU

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	MARGINOPORA VERTEBRALIS	PENEROPUS PERTUSUS	SOFITES MARGINALIS	SPIROLINA APERTINA
1	120575	19	8.0	0.06	0.31	0.0	0.0
1	120575	20	8.0	0.19	2.72	0.19	0.29
1	120575	23	8.0	0.04	0.96	0.0	0.18
1	012276	09	8.0	0.47	1.42	0.0	0.35
1	012276	10	8.0	0.13	1.15	0.0	0.13
1	012276	19	8.0	0.0	0.50	0.0	0.75
1	022676	03	8.0	0.35	0.59	0.0	0.47
1	022676	04	8.0	0.0	1.50	0.64	0.64
1	022676	05	8.0	0.0	0.79	0.0	0.11
1	032476	24	8.0	0.10	0.79	0.20	0.30
1	032476	25	8.0	0.0	0.59	0.12	0.12
1	032476	26	8.0	0.10	0.30	0.0	0.10
1	041976	04	8.0	0.31	4.50	0.0	0.0
1	041976	05	8.0	0.0	2.88	0.0	0.0
1	041976	06	8.0	0.27	1.73	0.0	0.0
1	052076	14	8.0	0.0	0.93	0.0	0.0
1	052076	15	8.0	0.0	1.19	0.0	0.0
1	052076	16	8.0	0.0	2.89	0.0	1.16
2	120575	24	8.0	0.0	1.09	0.05	0.41
2	120575	27	8.0	0.10	0.0	0.0	0.30
2	120575	28	8.0	0.12	0.43	0.06	0.0
2	012276	C1	8.0	0.16	0.11	0.0	0.11
2	012276	03	8.0	0.17	0.35	0.0	0.17
2	012276	C4	8.0	0.24	0.97	0.0	0.61
2	022676	C6	8.0	0.0	0.31	0.0	0.31
2	022676	07	8.0	0.0	0.0	0.0	0.33
2	022676	C8	8.0	0.0	0.13	0.0	0.13
2	032476	14	8.0	0.0	0.0	0.0	0.75
2	032476	15	8.0	0.24	2.13	0.0	0.0
2	032476	16	8.0	0.0	0.50	0.0	0.0
2	041976	11	8.0	0.25	0.25	0.0	0.0
2	041976	12	8.0	0.29	2.01	0.0	0.0
2	041976	13	8.0	0.40	1.20	0.0	0.0
2	052076	02	8.0	0.43	0.86	0.0	0.43
2	052076	03	8.0	0.0	1.38	0.0	0.92
2	052076	05	8.0	0.0	0.78	0.0	0.0
3	052774	01	0.0	0.34	0.0	0.0	1.35
3	052774	03	0.0	0.31	0.0	0.0	0.94
4	082574	C5	2.0	0.0	0.0	0.0	0.27
4	082574	06	2.0	0.23	0.11	0.0	0.29
5	092274	C1	2.0	0.0	0.0	0.0	0.06
5	092274	02	2.0	0.56	0.0	0.0	0.56
6	092274	C5	1.0	1.73	0.31	0.0	0.82
6	092274	06	1.0	0.30	0.05	0.05	0.45
6	092274	07	1.0	0.0	0.0	0.0	0.14
7	062575	C5	2.0	0.56	0.0	0.0	1.06
7	062575	06	2.0	0.98	0.0	0.0	0.58
8	100874	04	0.0	0.18	0.0	0.0	0.91
8	100874	C5	0.0	0.08	0.0	0.0	0.25
9	102874	01	2.0	0.0	0.0	0.0	0.09
9	102874	02	2.0	0.0	0.0	0.0	0.0
9	102874	05	1.0	0.44	0.0	0.0	0.61
9	102874	06	1.0	0.96	0.21	0.0	1.28
9	102874	C3	3.0	0.04	0.0	0.0	0.21
9	102874	C4	3.0	0.07	0.0	0.0	0.35
10	122374	11	0.0	0.0	0.0	0.0	0.15
10	122374	12	0.0	0.06	0.0	0.0	0.19
10	122374	13	2.0	0.13	0.0	0.0	0.38
10	122374	14	2.0	0.12	0.0	0.0	0.31
10	122374	15	2.0	0.0	0.0	0.0	0.26
11	080474	25	2.0	0.0	0.0	0.0	0.56
11	080474	26	2.0	0.20	0.20	0.0	0.86
11	032175	15	3.0	0.06	0.32	0.0	0.38
1	032175	16	3.0	0.07	0.20	0.07	0.20
12	120575	25	1.0	0.0	0.0	0.0	0.03
12	041976	01	1.0	0.14	0.69	0.14	0.41
12	041976	02	1.0	0.0	0.0	0.0	1.24
12	041976	03	1.0	0.17	0.0	0.0	0.84
13	103170	01	1.0	3.04	0.46	0.0	0.16
13	012171	C1	1.0	6.04	1.51	0.0	0.30
13	030175	11	1.0	2.63	1.72	0.0	1.21
4	082574	C1	5.0	0.22	0.0	0.0	1.11
4	062574	C2	5.0	0.12	0.0	0.0	0.23
4	082574	03	5.0	0.30	0.0	0.0	0.70
4	082574	04	5.0	0.94	0.0	0.0	0.16
10	122374	01	5.0	0.15	0.07	0.0	0.59
10	122374	02	5.0	0.25	0.0	0.0	0.17
10	122374	03	5.0	0.07	0.0	0.07	0.22
1	032175	05	5.0	0.0	0.19	0.0	0.51
1	032175	06	5.0	0.0	0.08	0.08	0.61
2	032175	09	5.0	0.0	0.16	0.0	0.33

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	MARGINOPORA VERTEBRALIS	PENEOPLIS PERTUSUS	SOFITES MARGINALIS	SPIPOLINA APIETINA
2	032175	10	5.0	0.0	0.0	0.0	0.0
2	032175	11	5.0	0.08	0.0	0.08	0.08
11	080474	13	5.0	0.0	0.0	0.17	0.34
11	080474	14	5.0	0.13	0.0	0.0	0.51
11	080474	21	5.0	0.09	0.18	0.0	0.18
14	052974	01	10.0	0.0	0.20	0.0	0.51
14	052974	02	10.0	0.0	0.22	0.0	1.29
14	090474	21	10.0	0.12	0.24	0.12	0.60
14	090474	22	10.0	0.0	0.0	0.0	0.97
14	090474	23	10.0	3.25	0.75	0.0	5.25
15	073174	07	10.0	0.0	0.08	0.0	0.40
15	073174	09	10.0	0.12	0.0	0.0	0.36
15	073174	10	10.0	0.0	0.0	0.0	0.84
10	122374	04	10.0	0.04	0.0	0.0	0.17
10	122374	05	10.0	0.04	0.04	0.0	0.30
10	122374	06	10.0	0.12	0.0	0.12	0.52
11	080474	11	10.0	0.0	0.43	0.0	0.95
11	080474	12	10.0	0.33	0.66	0.0	1.31
11	080474	15	10.0	0.44	1.00	0.0	1.89
11	080474	16	10.0	0.0	0.0	0.0	1.70
2	032175	13	10.0	0.0	0.48	0.06	0.30
2	032175	14	10.0	0.0	0.32	0.0	0.16
11	080474	17	15.0	0.05	0.0	0.0	0.18
11	080474	18	15.0	0.06	0.11	0.0	0.11
11	080474	19	15.0	0.14	0.19	0.0	0.61
11	080474	20	15.0	0.15	0.15	0.0	0.87
10	122374	10	15.0	0.17	0.17	0.0	0.68
10	122374	16	15.0	0.0	0.0	0.0	0.56
10	122374	17	15.0	0.24	0.0	0.0	1.67
15	073174	03	15.0	0.24	0.0	1.69	0.48
15	073174	04	15.0	0.08	0.0	0.0	0.08
15	073174	06	15.0	0.07	0.0	0.0	0.43
14	052974	20	20.0	0.36	0.18	0.09	1.16
15	073174	01	20.0	0.15	0.0	0.0	0.07
15	073174	02	20.0	0.10	0.0	0.10	0.20
2	032175	01	20.0	0.0	0.0	0.04	0.0
2	032175	02	20.0	0.0	0.0	0.0	0.0
2	032175	03	20.0	0.0	0.07	0.0	0.0
2	032175	04	20.0	0.0	0.0	0.0	0.0
2	062076	21	25.0	0.06	0.18	0.0	0.06
2	062076	22	25.0	0.0	0.0	0.0	0.0
14	052974	14	30.0	0.42	1.09	0.0	0.55
14	052974	24	30.0	0.37	0.0	0.0	0.37
16	022676	21	30.0	0.03	0.24	0.08	0.03
16	022676	22	30.0	0.0	0.45	0.80	0.0
16	022676	23	30.0	0.03	0.22	0.36	0.03
16	022676	24	30.0	0.0	0.13	0.05	0.0
16	100675	03	30.0	0.0	0.0	0.0	0.0
16	121375	21	30.0	0.0	0.0	0.0	0.0
16	021976	23	35.0	0.0	0.40	0.10	0.0
14	052974	19	40.0	1.28	4.68	0.0	0.85
14	052974	25	40.0	0.0	0.0	0.0	0.0
14	090474	02	40.0	0.50	0.0	0.20	0.60
14	090474	22	40.0	0.0	0.22	0.0	0.22
16	121275	20	40.0	0.0	0.10	0.0	0.0
16	100775	04	45.0	0.0	0.10	0.0	0.0
14	090474	13	50.0	0.70	0.0	0.20	0.30
14	090474	14	50.0	1.40	0.0	0.0	0.10
16	100675	02	53.0	0.0	0.10	0.10	0.0
16	022676	25	50.0	0.0	0.10	0.10	0.0
14	090474	11	65.0	0.0	0.0	0.10	0.0
14	090474	12	65.0	0.0	0.0	0.0	0.20
16	110375	13	60.0	0.20	0.30	0.40	0.0
16	110375	12	70.0	0.20	0.0	0.0	0.0
16	102675	10	70.0	0.0	0.0	0.0	0.0
16	121175	18	70.0	0.0	0.0	0.0	0.0
16	121175	19	70.0	0.0	0.10	0.0	0.0
16	021976	24	70.0	0.0	0.10	0.10	0.0
14	052974	17	80.0	0.0	0.0	0.05	0.0
16	110275	11	80.0	0.0	0.0	0.0	0.0
16	121375	22	80.0	0.0	0.0	0.0	0.0
16	110675	15	90.0	0.10	0.0	0.0	0.0
16	100775	05	100.0	0.0	0.0	0.0	0.30
16	110775	17	100.0	0.0	0.0	0.0	0.0
16	110475	14	110.0	0.0	0.0	0.0	0.0
16	110675	16	110.0	0.0	0.0	0.20	0.0
16	121275	19	130.0	0.0	0.0	0.0	0.0
16	102575	07	120.0	0.0	0.0	0.0	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	AMPHISTEGINA BICIRCULATA	AMPHISTEGINA LESSONII	AMPHISTEGINA LOBIFERA	HETEROSTEGINA DEPRESSA	NUMMULITES AMMONOIDES
1	120575	19	8.0	0.0	3.91	1.12	2.19	0.0
1	120575	20	8.0	0.0	5.15	2.52	0.49	0.0
1	120575	23	8.0	0.0	1.27	1.32	0.31	0.0
1	012276	09	8.0	0.0	8.99	0.83	0.47	0.0
1	012276	10	8.0	0.0	3.21	0.90	0.13	0.0
1	012276	19	8.0	0.0	2.74	0.37	0.12	0.0
1	022676	03	8.0	0.0	3.05	1.17	0.12	0.0
1	022676	04	8.0	0.0	7.28	0.43	1.50	0.0
1	022676	05	8.0	0.0	3.62	0.68	0.23	0.0
1	032476	24	8.0	0.0	8.61	0.20	0.30	0.0
1	032476	25	8.0	0.0	2.24	0.12	0.24	0.0
1	032476	26	8.0	0.0	3.21	0.50	0.20	0.0
1	041976	04	8.0	0.0	10.22	1.24	0.31	0.0
1	041976	05	8.0	0.0	6.01	0.39	0.39	0.0
1	041976	06	8.0	0.0	2.53	0.27	0.0	0.0
1	052076	14	8.0	0.0	54.63	0.0	0.0	0.0
1	052076	15	8.0	0.0	20.24	1.19	0.79	0.0
1	052076	16	8.0	0.0	13.87	0.58	0.0	0.0
2	120575	24	8.0	0.0	1.23	0.50	0.36	0.0
2	120575	27	8.0	0.0	2.18	0.30	0.20	0.0
2	120575	28	8.0	0.0	1.59	0.24	0.24	0.0
2	012276	01	8.0	0.0	30.43	6.59	3.03	0.0
2	012276	03	8.0	0.0	9.25	2.49	0.69	0.0
2	012276	04	8.0	0.0	6.42	1.94	1.33	0.0
2	022676	06	8.0	0.0	8.40	0.47	0.93	0.0
2	022676	07	8.0	0.0	5.13	0.65	1.49	0.0
2	022676	08	8.0	0.0	4.31	2.09	1.31	0.0
2	032476	14	8.0	0.0	7.72	1.32	1.32	0.0
2	032476	15	8.0	0.0	10.19	1.42	1.18	0.0
2	032476	16	8.0	0.0	9.65	1.73	1.73	0.0
2	041976	11	8.0	0.0	12.47	1.50	0.50	0.0
2	041976	12	8.0	0.0	10.06	1.15	0.86	0.0
2	041976	13	8.0	0.0	10.36	2.99	0.60	0.0
2	052076	02	8.0	0.0	12.31	3.46	0.22	0.0
2	052076	03	8.0	0.0	50.69	2.76	1.38	0.0
2	052076	05	8.0	0.0	40.31	8.91	0.0	0.0
3	052774	01	0.0	0.0	0.45	0.34	0.0	0.0
3	052774	03	0.0	0.0	0.18	0.04	0.0	0.0
4	082574	05	2.0	0.0	0.18	0.76	0.04	0.0
4	082574	06	2.0	0.0	0.91	2.63	0.14	0.0
5	092274	01	2.0	0.0	0.12	0.19	0.1	0.0
5	092274	02	2.0	0.0	0.78	0.33	0.0	0.0
6	092274	05	1.0	0.0	0.10	0.51	0.0	0.0
6	092274	06	1.0	0.0	0.40	0.15	0.0	0.0
6	092274	07	1.0	0.0	0.0	0.22	0.0	0.0
7	062575	05	2.0	0.0	0.25	0.45	0.0	0.0
7	062575	06	2.0	0.0	0.35	0.81	0.0	0.0
8	100874	04	0.0	0.0	0.0	0.0	0.0	0.0
8	100874	05	0.0	0.0	0.0	0.0	0.0	0.0
9	102874	01	2.0	0.0	0.0	0.0	0.0	0.0
9	102874	02	2.0	0.0	0.0	0.0	0.0	0.0
9	102874	05	1.0	0.0	0.0	0.0	0.0	0.0
9	102874	06	1.0	0.0	0.0	0.0	0.0	0.0
9	102874	03	3.0	0.0	0.04	0.0	0.0	0.0
9	102874	04	3.0	0.0	0.0	0.57	0.0	0.0
10	122374	11	0.0	0.0	0.0	0.0	0.0	0.0
10	122374	12	0.0	0.0	0.0	0.0	0.0	0.0
10	122374	13	2.0	0.0	0.13	0.19	0.0	0.0
10	122374	14	2.0	0.0	0.31	0.35	0.28	0.0
10	122374	15	2.0	0.0	0.0	0.59	0.07	0.0
11	080474	25	2.0	0.0	1.27	2.19	0.0	0.0
11	080474	26	2.0	0.0	1.45	2.24	0.0	0.0
1	032175	15	3.0	0.0	1.88	2.49	0.45	0.0
1	032175	16	3.0	0.0	0.53	0.86	0.66	0.0
12	120575	25	1.0	0.0	3.00	3.70	0.70	0.0
12	041976	01	1.0	0.0	6.34	3.72	1.10	0.0
12	041976	02	1.0	0.0	3.10	0.31	0.15	0.0
12	041976	03	1.0	0.0	3.52	0.67	0.33	0.0
13	103170	01	1.0	0.0	3.52	10.24	0.0	0.0
13	012171	01	1.0	0.0	7.55	36.86	0.30	0.0
13	030175	11	1.0	0.0	6.87	4.95	0.0	0.0
4	082574	01	5.0	0.0	0.49	0.40	0.09	0.0
4	082574	02	5.0	0.0	0.46	0.75	0.0	0.0
4	082574	03	5.0	0.0	0.80	1.70	0.60	0.0
4	082574	04	5.0	0.0	1.72	2.34	0.31	0.0
10	122374	01	5.0	0.0	0.67	0.96	0.67	0.0
10	122374	02	5.0	0.0	0.67	0.34	0.17	0.0
10	122374	03	5.0	0.0	0.36	0.72	0.22	0.0
1	032175	05	5.0	0.0	3.21	1.60	0.51	0.0
1	032175	06	5.0	0.0	6.44	2.50	0.30	0.0
2	032175	09	5.0	0.0	4.88	2.03	0.08	0.0

SITE NUMBER	DATE	SAMPLE NUMBER	DEPTH (M)	AMPHISTEGINA BICIPICULATA	AMPHISTEGINA LESSONII	AMPHISTEGINA LOBIFERA	HETEROSTEGINA DEPRESSA	NUMMULITES AMMONOIDES
2	032175	10	5.0	0.0	2.81	2.26	0.27	0.0
2	032175	11	5.0	0.0	5.33	2.58	0.50	0.0
11	050474	13	5.0	0.0	5.69	6.72	0.0	0.0
11	080474	14	5.0	0.0	3.01	3.01	0.06	0.0
11	080474	21	5.0	0.0	1.34	2.05	0.0	0.0
14	052974	01	10.0	0.0	7.48	2.63	0.0	0.0
14	052974	02	10.0	0.0	25.16	10.32	0.0	0.0
14	090474	21	10.0	0.0	2.65	2.05	0.0	0.0
14	090474	22	10.0	0.0	2.26	0.32	0.0	0.0
14	090474	23	10.0	0.0	3.25	7.00	0.25	0.0
15	073174	07	10.0	0.0	2.38	0.65	0.81	0.0
15	073174	09	10.0	0.0	5.66	1.57	1.33	0.0
15	073174	10	10.0	0.0	3.36	1.09	1.51	0.0
10	122374	C4	10.0	0.0	4.09	1.01	1.01	0.0
10	122374	C5	10.0	0.0	3.13	1.74	1.35	0.0
10	122374	06	10.0	0.0	3.06	0.98	1.39	0.0
11	080474	11	10.0	0.0	20.17	11.47	3.09	0.0
11	080474	12	10.0	0.0	15.25	6.72	0.33	0.0
11	080474	15	10.0	0.0	10.33	6.89	0.11	0.0
11	080474	16	10.0	0.0	16.22	11.62	0.24	0.0
2	032175	13	10.0	0.0	7.83	1.57	0.36	0.0
2	032175	14	10.0	0.0	6.72	0.64	0.16	0.0
11	060474	17	15.0	0.0	3.72	1.24	0.18	0.0
11	060474	18	15.0	0.0	4.33	0.89	0.22	0.0
11	060474	19	15.0	0.0	3.74	0.98	0.75	0.0
11	080474	20	15.0	0.0	7.44	1.59	0.21	0.0
10	122374	10	15.0	0.0	4.03	1.70	1.59	0.0
10	122374	16	15.0	0.0	6.11	2.08	0.69	0.0
10	122374	17	15.0	0.0	11.90	6.43	2.14	0.0
15	073174	C3	15.0	0.0	5.78	1.81	0.36	0.0
15	073174	C4	15.0	0.0	1.65	0.39	0.71	0.0
15	073174	C6	15.0	0.0	5.68	1.44	0.50	0.0
14	052974	20	20.0	0.0	13.57	6.79	0.62	0.0
15	073174	01	20.0	0.0	2.91	0.28	0.02	0.0
15	073174	02	20.0	0.0	4.36	0.79	0.0	0.0
2	032175	C1	20.0	0.0	0.55	0.0	0.0	0.0
2	032175	02	20.0	0.0	0.60	0.0	0.0	0.0
2	032175	03	20.0	0.0	1.68	0.15	0.18	0.0
2	032175	04	20.0	0.0	0.88	0.11	0.0	0.0
2	062076	21	25.0	0.0	5.91	0.06	0.47	0.0
2	062076	22	25.0	0.0	3.25	0.0	0.05	0.0
14	052974	14	30.0	0.0	3.09	1.21	0.24	0.0
14	052974	24	30.0	0.16	7.51	2.33	0.20	0.0
16	022676	21	30.0	0.0	0.34	0.0	0.0	0.11
16	022676	22	30.0	0.0	0.92	0.0	0.02	0.20
16	022676	23	30.0	0.0	4.57	0.0	0.14	0.55
16	022676	24	30.0	0.03	1.36	0.0	0.0	0.08
16	100675	03	30.0	0.0	0.10	0.0	0.0	0.0
16	121375	21	30.0	0.0	1.00	0.0	0.10	0.0
16	021976	23	35.0	0.0	0.20	0.0	0.0	0.0
14	052974	19	40.0	0.85	21.28	2.55	1.28	0.0
14	052974	25	40.0	0.0	0.0	0.0	0.0	0.0
14	090474	02	40.0	0.0	8.00	2.50	0.10	0.0
14	090474	22	40.0	0.0	10.44	2.22	0.0	0.0
16	121275	20	40.0	0.0	0.30	0.0	0.0	0.0
16	100775	04	45.0	0.0	0.10	0.0	0.10	0.30
14	090474	13	50.0	3.50	4.00	0.50	0.70	0.90
14	090474	14	50.0	5.50	3.70	0.70	1.20	0.50
16	100675	02	50.0	0.0	0.20	0.0	0.10	0.40
16	022076	25	50.0	0.0	0.10	0.0	0.0	1.60
14	090474	11	65.0	1.80	2.60	0.0	0.10	0.20
14	090474	12	65.0	1.80	3.40	0.10	0.50	0.10
16	110375	13	60.0	0.0	0.40	0.0	0.0	0.60
16	110375	12	70.0	0.0	0.0	0.0	0.0	0.10
16	102675	10	70.0	0.0	0.10	0.0	0.20	1.20
16	121175	18	70.0	0.10	0.10	0.0	0.20	0.30
16	121175	19	70.0	0.10	0.0	0.0	0.10	0.30
16	021976	24	70.0	0.0	0.10	0.0	0.0	1.60
14	052974	17	80.0	0.0	0.05	0.0	0.50	0.20
16	110275	11	80.0	0.0	0.0	0.0	0.0	0.10
16	121375	22	80.0	0.0	0.0	0.0	0.0	0.0
16	110575	15	90.0	1.40	0.0	0.0	0.10	0.0
16	110775	05	100.0	9.70	0.0	0.0	1.00	0.10
16	110775	17	100.0	1.00	0.0	0.0	0.30	0.0
16	110475	14	110.0	4.20	0.0	0.0	0.10	0.0
16	110675	16	110.0	0.0	0.0	0.0	0.20	0.10
16	121275	19	130.0	0.0	0.0	0.0	0.0	0.0
16	102575	C7	120.0	0.0	0.0	0.0	0.0	0.0

APPENDIX E. Secchi depths from off Honolulu Harbor away from Sand Island
outfall influence
(Courtesy of Blue Water Marine Laboratory)

Date	Secchi Depth (m)	k (f = 1.7)
5 Oct.75	15	.113
6 Oct.75	18	.0944
6 Oct.75	32	.0531
7 Oct.75	23	.0739
25 Oct.75	32	.0531
25 Oct.75	12	.142
25 Oct.75	26	.0654
25 Oct.75	29	.0586
26 Oct.75	29	.0586
26 Oct.75	18	.0944
26 Oct.75	20.5	.0829
26 Oct.75	22.5	.0755
26 Oct.75	38.5	.0442
26 Oct.75	29.0	.0586
2 Nov.75	21	.0810
3 Nov.75	15	.113
3 Nov.75	10	.170
4 Nov.75	30	.0567
6 Nov.75	30	.0567
6 Nov.75	27	.0630
7 Nov.75	23	.0739
7 Nov.75	24	.0708
7 Nov.75	26	.0654
7 Nov.75	26	.0654
12 Dec.75	20	.0850
12 Dec.75	28.5	.0596
12 Dec.75	21	.0810
12 Dec.75	32	.0531
13 Dec.75	15	.113
13 Dec.75	13	.131
13 Dec.75	12	.142
$\bar{x}$	23.2	.0822
S.D.	7.16	.0313

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