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COMMUNITIES, JAMAICA, WEST INDIES.

Yale University, Ph.D., 1971
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THE ECOLOGY OF THE MOLLUSCS OF <u>THALASSIA</u>

COMMUNITIES, JAMAICA, WEST INDIES

Jeremy Bradford Cook Jackson

A Dissertation Presented to the Faculty of

the Graduate School of Yale University

in Candidacy for the Degree of

Doctor of Philosophy

1971

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ABSTRACT

Lucinacean bivalves dominate the infauna of Caribbean intertidal and shallow water environments, especially those covered by the angiosperms (Hydrocharitaceae) Diplanthera and Thalassia, but are of lesser importance in deeper waters. Experiments show that this distribution is primarily due to the very great physiological tolerance of lucinaceans to temperature and salinity fluctuations and to stagnant conditions. Feeding processes are also important. There is abundant food present in most shallow water environments but this consists primarily of microbial populations on plant detrital particles which are larger than those normally accomodated by suspension feeders. The Lucinacea generally lack complex ctenidial sorting mechanisms and are able to accept and process large detrital particles. They therefore exploit food supplies not available to most other suspension feeding bivalves.

Investigation of five Caribbean lucinids shows these species co-occur frequently but are not correlated in their distributions. The eurytopic species do, however, occur more frequently and in a wider range of environments than their comparatively stenotopic lucinid relatives. Differential physiological tolerance is therefore a primary factor in the niche specificity of individual lucinid species.

Four homogeneous areas within beds of the marine angiosperm Thalassia were selected along a composite onshore-offshore gradient for detailed study. Eleven environmental variables and molluscan and echinoderm abundance were sampled at monthly intervals for one year. Environmental conditions were generally more extreme, and their variance greatest, nearshore and decreased significantly with distance from shore. Environmental predictability and cumulative diversity (H) increased with distance from shore, whereas abundance was greatest in the more high stress environments. Over the year population stability was at least as great in the unpredictable, low diversity environments as in the more predictable, high diversity environments.

Bivalves collected from the low diversity environments were markedly eurytopic forms (mostly Lucinidae) whereas the highest diversity area contained predominantly stenotopic taxa. Typical suspension feeders were dominant only in the most diverse area, whereas more generalized feeders dominated the higher stress environments. There was no correlation between bivalve diversity and the total quantity of food available, but bivalve diversity increased with the variety of food.

In multivariate regression analyses, the environmental variables as a set were highly significant in "explaining" the population variables in any one area but subsets, or individual variables, were not significant. Between areas, the environmental set alone was not significant and a full 31 parameter model was required to "explain" the distributions. It is suggested that catastrophes, and other long term phenomena, and biological factors, such as predation, are of great importance in determining the differences in fauna between these areas.

ACKNOWLEDGEMENTS

computer programs and in other ways greatly assisted in the diversity calculations. Dr. H. Seal provided the regression programs and advice in their applications. R. Rowen and W. Sacco prepared the drawings and plates.

Finally, I wish to offer my deepest thanks and appreciation to my wife Elisabeth for her continued help, patience and encouragement throughout all aspects of this study.

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PART 1. PHYSIOLOGICAL TOLERANCE AND DISTRIBUTION OF

CARIBBEAN SHALLOW WATER LUCINACEA (MOLLUSCA, BIVALVIA)

I. ABSTRACT

Lucinacean bivalves dominate the infauna of Caribbean intertidal and shallow water environments, especially those covered by the angiosperms (Hydrocharitaceae) Diplanthera and Thalassia, but are of lesser importance in deeper waters. Experiments show that this distribution is primarily due to the very great physiological tolerance of lucinaceans to temperature and salinity fluctuations and to stagnant conditions. Feeding processes are also important. There is abundant food present in most shallow water environments but this consists primarily of microbial populations on plant detrital particles which are larger than those normally accomodated by suspension feeders. The Lucinacea generally lack complex ctenidial sorting mechanisms and are able to accept and process large detrital particles. They therefore exploit food supplies not available to most other suspension feeding bivalves.

Investigation of five Caribbean lucinids shows these species co-occur frequently but are not correlated in their distributions. The eurytopic species do, however, occur more frequently and in a wider range of environments than their comparatively stenotopic lucinid relatives. Differential physiological tolerance is therefore a primary factor

in the niche specificity of individual lucinid species.

Median shell length of 21 Caribbean lucinids is very different between shallower and deeper environments and greatly decreases with increasing depth. Large size allows shallow water lucinids to burrow deeply and thereby escape adverse seawater conditions which greatly decrease with increasing depth into the sediment.

II. INTRODUCTION

Most efforts to discern niche differentiations between similar sympatric species have emphasized differences in resource utilization, habitat range and predation among active organisms with distinctive behavioral patterns (Hutchinson, 1965). Many benthic marine organisms lack obvious behavioral patterns and, for any one feeding type (deposit feeding, suspension feeding, etc.), one is often forced to postulate feeding specificities of remarkable subtlety if competitive exclusion is to be maintained on this basis. This is especially true in shallow tropical waters or in the deep sea where very large numbers of similar species (low densities) co-occur over vast areas (Hessler and Sanders, 1967).

There are two additional sources of niche diversification which may be of great importance in aquatic environments. These are:
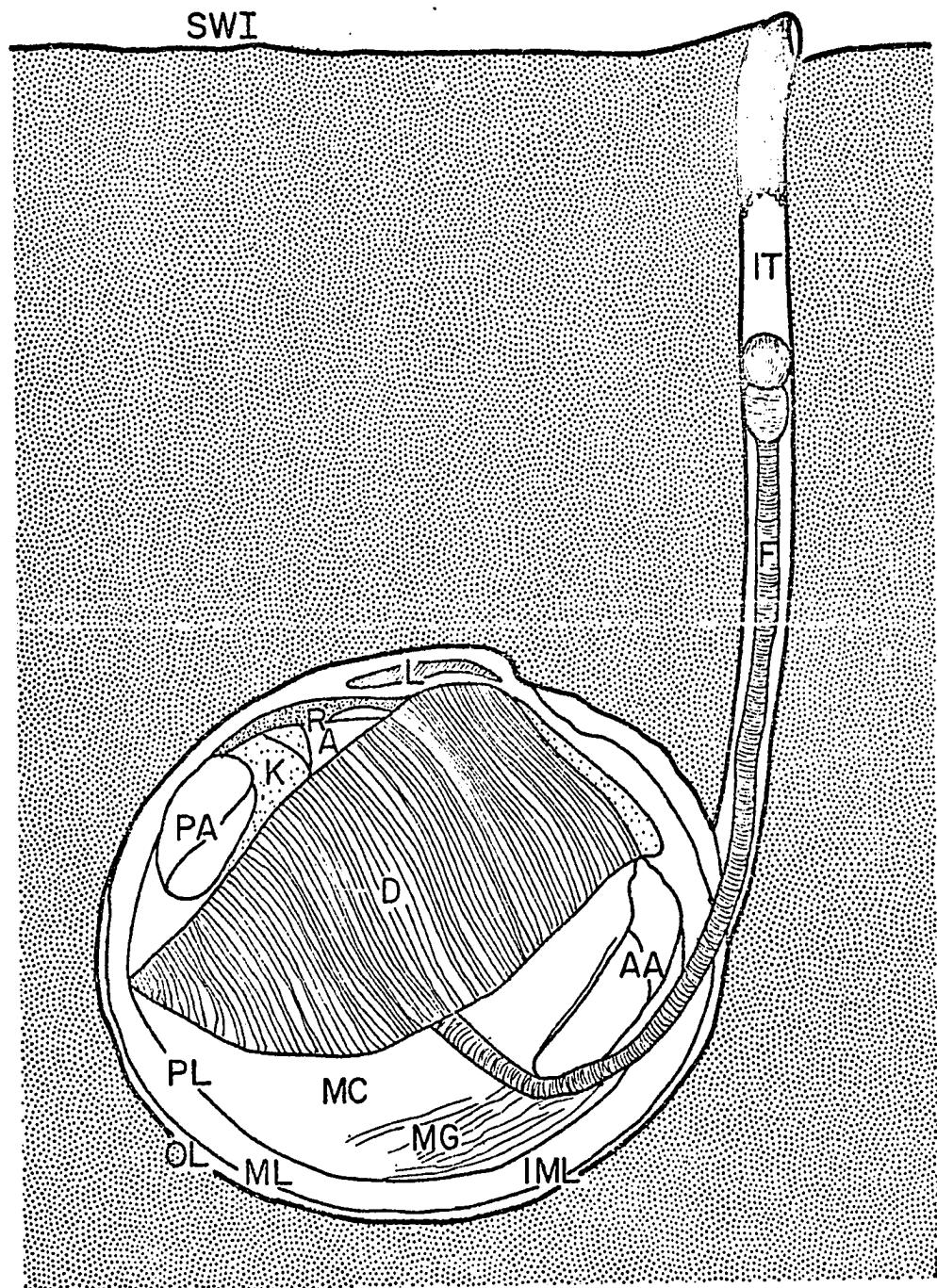
1. comparative physiological requirements and tolerances of different species (Hutchinson, 1970) and

2. biogenically generated habitat complexity in
otherwise monotonous environments (Rhoads and Young, 1970
and 1971).

The first factor is of greatest importance in shallow water,
high stress environments. There species distributions and
diversity are largely dependent on the physical and chemical
diversity of the environment. The second factor dominates
in somewhat deeper areas. In this case the number of species
and trophic types can be very different for areas similar in
physical and chemical conditions. These differences result
from the interactions between organisms and sediments. It
is the purpose of this study to compare the relative im-
portance of these two factors in determining the distributions
of shallow water lucinacean bivalves.

The Lucinacea are a taxonomically and ecologically well
defined group of burrowing eulamellibranch bivalves charac-
terized by the possession of an elongated anterior adductor
muscle and a long, vermiform foot which is used in the con-
struction of an anterior inhalent feeding tube (Figure 1).
The functional anatomy of the Lucinacea has been studied in
detail by Allen (1958), who paid particular attention to
the structures related to feeding, and all details of lucina-
cean internal anatomy presented here are based on his account.
Bretsky (1969) has recently completed an exhaustive system-
atic study of the American Lucinidae in which she has also
reviewed much of the evolutionary and ecological literature
concerning the Lucinacea.

Figure 1. General anatomy and life position of <u>Codakia</u>

<u>orbicularis</u> (Linne) modified after Allen, 1958 and

Kauffman, 1967. Right valve and mantle removed. Key:

A, auricle; AA, anterior adductor muscle; D, right

demibranch (gill); F, foot; IML, inner mantle lobe;

IT, inhalent tube; K, kidney; L, ligament; MC, mantle

cavity; MG, mantle gills; ML, middle mantle lobe; OL,

outer mantle lobe; PA, posterior adductor muscle; PL,

pallial line; R, rectum.

SWI

IT

F

L

R

K

PA

D

AA

PL

MC

MG

OL ML

IML

There are three families of the Lucinacea. These are the Ungulinidae, Thyasiradae and Lucinidae, of which the first and third are most common in tropical and subtropical waters, particularly in association with the marine angiosperms _Diplanthera_ and _Thalassia_. Shallow flats (intertidal to 1 m) covered by these plants commonly contain abundant populations of from two to four large, approximately similar-sized lucinid species (Moore, et al., 1968; Jackson, 1971).

Much of the present work was carried out in connection with a one year study of molluscan population variability and diversity in four Jamaican shallow water _Thalassia_ environments (Jackson, 1971). Lucinacea abundant in these areas were examined in greater detail than those most important in other environments. Tolerance experiments were used to determine the nature of the physiological tolerance of the common shallow water Lucinacea to high temperatures, low salinity and stagnation and to compare their tolerance to that of other common infaunal bivalves. The results were used to evaluate the importance of physiological tolerance in determining local bivalve distributions and to compare the importance of physiological tolerance with other factors (size, feeding and biogenic alteration of the environment) in establishing niche differentiations between individual lucinacean species.

III. MATERIALS AND METHODS

Animals for experimentation were collected at a variety of localities (Figure 2) but the great majority were from the Discovery Bay - Runaway Bay area or Kingston Harbor. Samples were collected using a pitch fork and were sieved as soon as possible, generally on location. The animals were kept in running seawater (25 to 30°C, 30 to 35°/oo salinity) for one to two weeks before use in the experiments. Five lucinacean species were sufficiently common to be available for systematic experimental analyses of all four factors considered, whereas others were examined for one or two of these only. Species of other groups were not examined in a regular fashion and were only used in experiments as sufficient individuals became available from samples collected for Lucinacea.

A. Lucinacea Examined

The shells of eight Caribbean Lucinacea commonly found in Diplanthera or Thalassia environments are pictured in Figures 3 and 4. All are Lucinidae except for the two Diplodonta which are members of the family Ungulinidae. The life habits of most of these species have been described by Allen (1958) and Stanley (1970) and their environmental distributions are summarized by Newell, et al., (1959), Tabb and Manning (1962), O'Gower and Wacassey (1967), Moore, et al., (1968) and Jackson (1971).

Figure 2. Map of Jamaica showing collection localities

for animals used in experiments.

Bloody Bay

Montego Bay

Falmouth

Discovery Bay

Runaway Bay

Half Moon Bay

Kingston Harbor

KINGSTON

Port Morant

Prospect

Kingston Harbor

18°   18°30'

78°

77°30'

77°

76°30'

0   25
kilometers
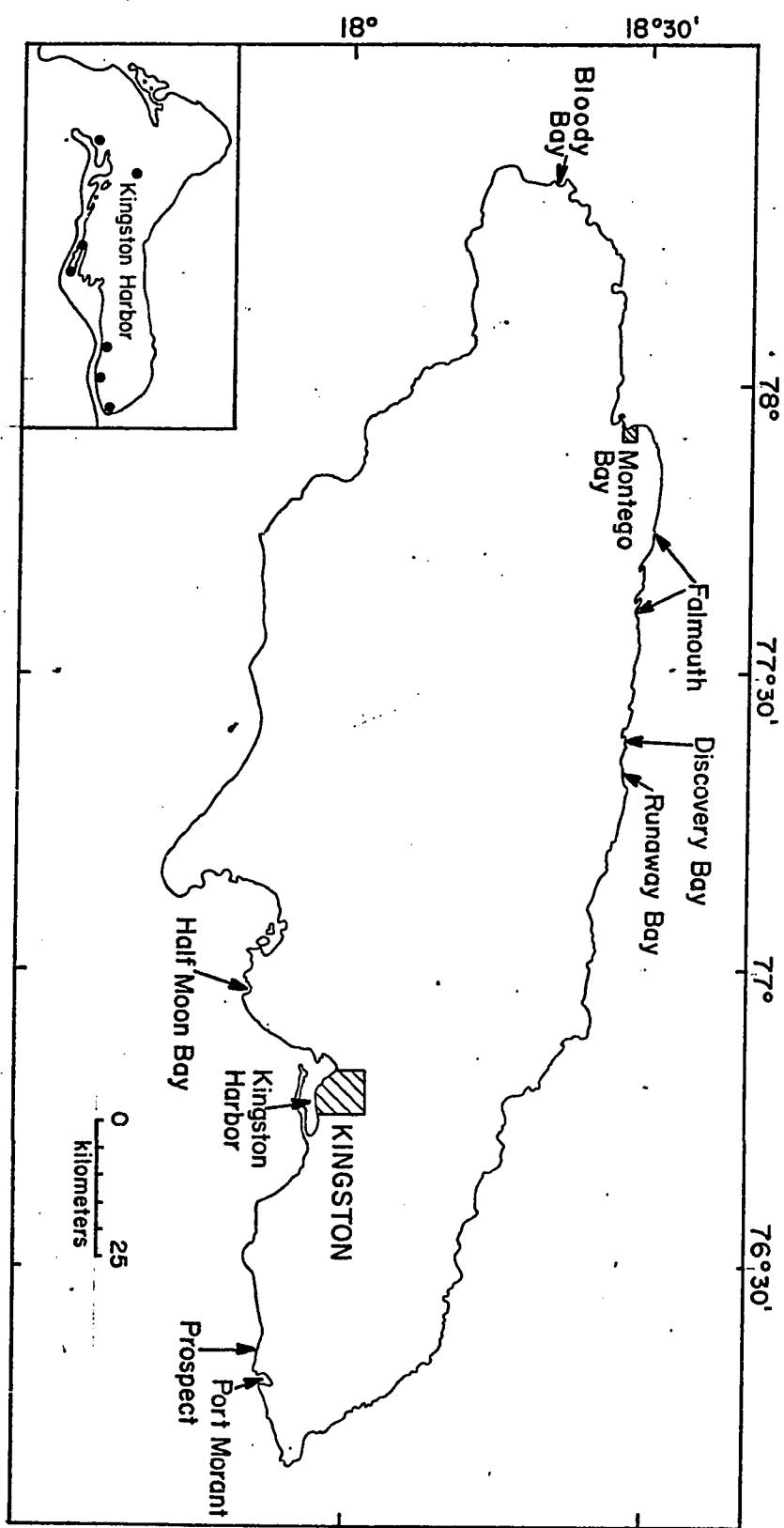
Figure 3. Interior and exterior lateral views of shells of four Caribbean Lucinacea studied. A, _Codakia_ _orbicularis_ (Linne);, B, _Ctena_ _orbiculata_ (Montagu); C, _Parvilucina_ _costata_ (d'Orbigny); D, _Lucina_ _pensylvanica_ (_Linne_).
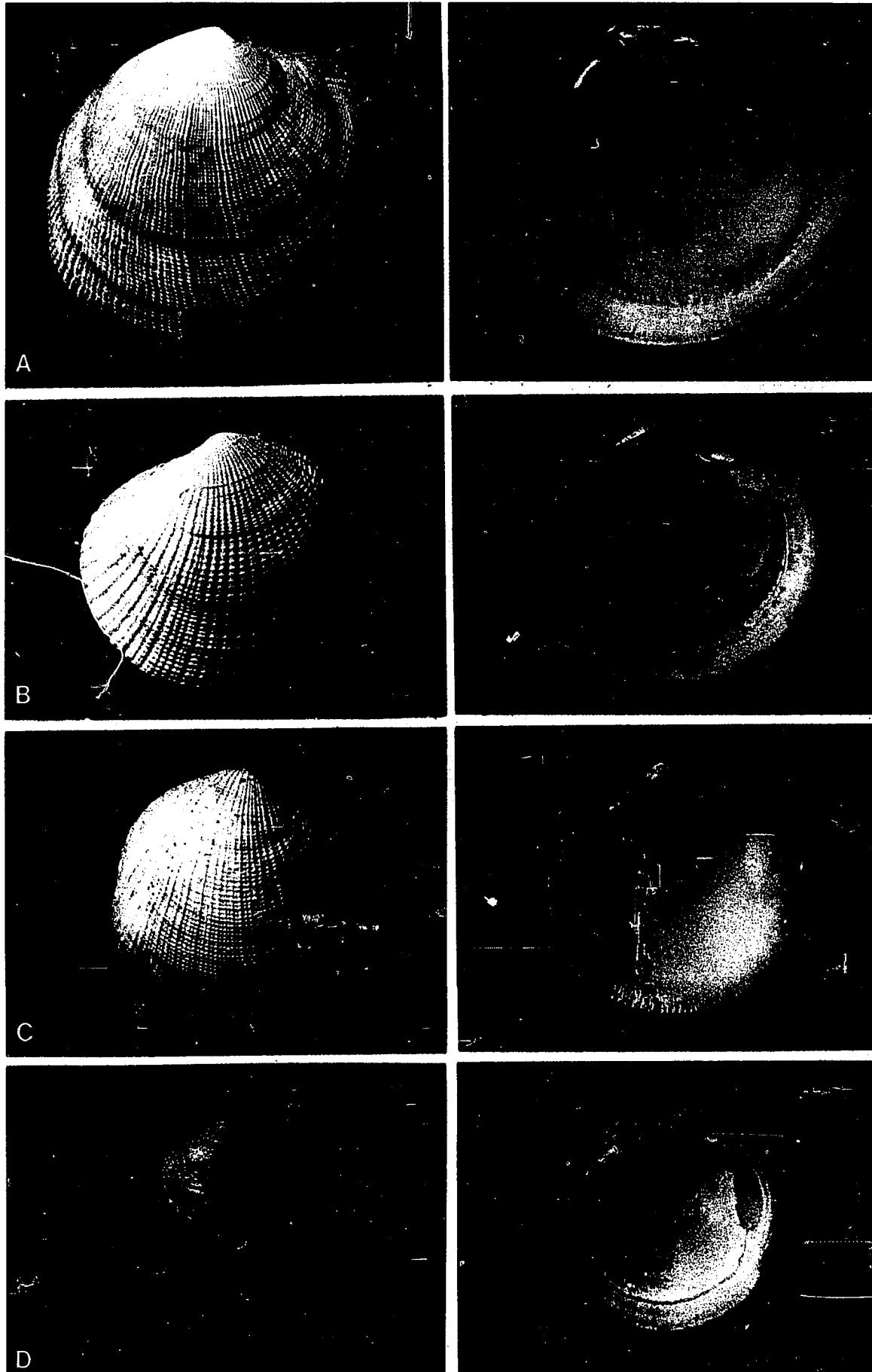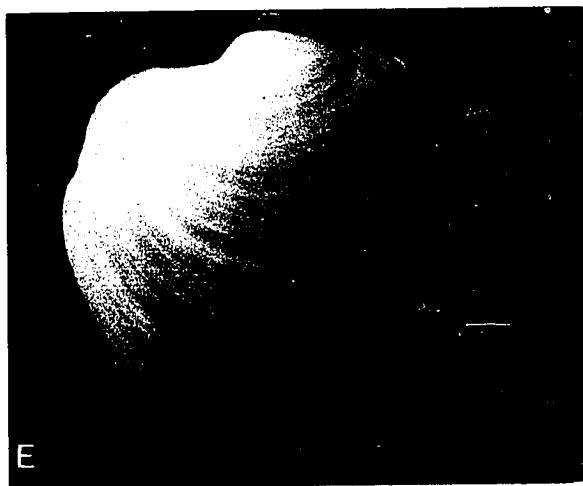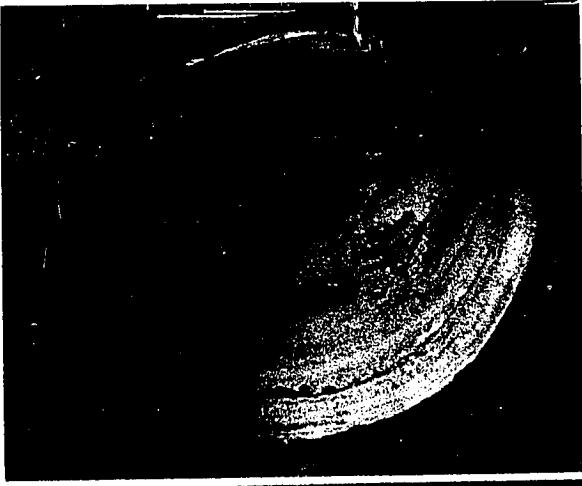
Figure 4. Interior and exterior lateral views of shells of four Caribbean Lucinacea studied. E, _Anodontia alba_ (Link); F, _Phacoides pectinata_ (Gmelin); G, _Diplodonta punctata_ (Say); H, _Diplodonta semiaspera_ (Phillippi).
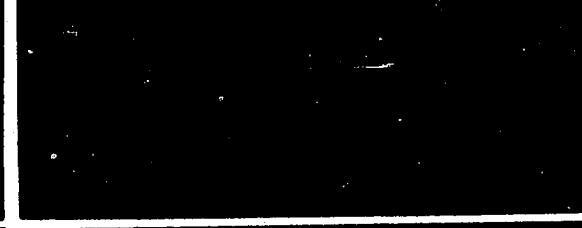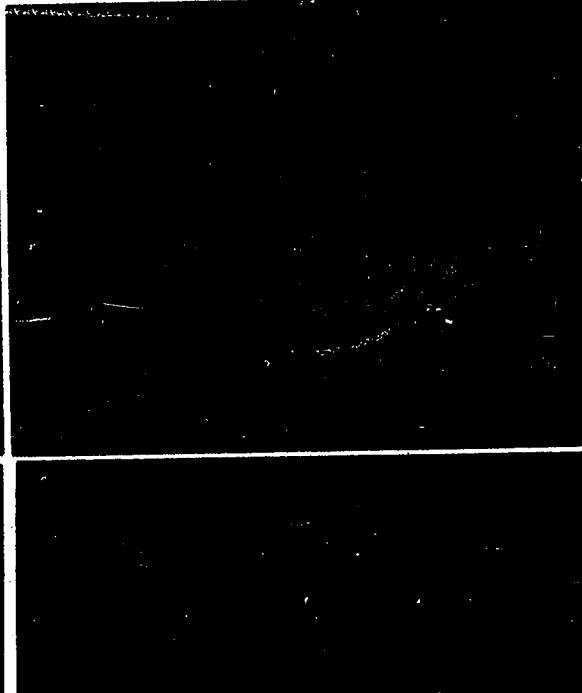
Ctena orbiculata (Montagu) is found abundantly in a great variety of shallow water environments, especially intertidal Thalassia flats and semi-enclosed bays like Kingston Harbor. Among or near mangroves, C. orbiculata is often the only infaunal bivalve present. It is also found in deeper bays and shelf areas to depths of more than 200 m. Although it is most common in muddier sands, C. orbiculata tolerates a very wide range of sediment types with or without vegetation. It is a moderate sized lucinid, reaching just 3 cm in length, and a shallow burrower.

Codakia orbicularis (Linné) is most common in somewhat protected flats behind reefs or in shallow bays. It is most abundant just below the low tide mark and was not collected live below 4 m. This species is found in much the same size range of sediments as C. orbiculata but appears to require greater sediment stability. It is therefore most abundant in areas where the Thalassia root network is particularly thick. Codakia orbicularis is a shallow burrower for its large size (to 8 or 9 cm) and is rarely found more than 5 cm below the sediment surface.

Phacoides pectinata (Gmelin) is a moderately large species (to 7 cm) which exhibits a strong preference for mangrove dominated environments but is also found in intertidal grass flats. As does C. orbiculata, it occurs alone at a number of localities but is apparently more specialized in its restriction to grassy bottoms or firm peats and muds

and to depths less than 1 m. It normally burrows to about 10 cm in grass flats but has been found as deep as 50 cm in muddy peats. Suitable localities for P. pectinata tend to be more abundant along mainland or large island coastlines where, due to more mature drainage patterns and greater volumes of runoff, vast areas of mangroves are commonly developed. Where such conditions are not present, as off small limestone islands like Grand Cayman, or are only poorly developed, as along the north coast of Jamaica, P. pectinata may be completely absent or rare.

Anodontia alba (Link) prefers protected intertidal and shallow subtidal environments covered by Diplanthera or Thalassia. It is most common just above the low tide mark and was not collected live below 5 m. Maximum adult size is about 5 cm. It is a deep burrower (to about 20 cm) and although found in a variety of sediment types shows a strong preference for fine, muddy sands.

Parvilucina costata (d'Orbigny) is the smallest lucinid studied (to 1.5 cm) and a shallow burrower. It prefers shallow, Thalassia covered areas deeper than 1 m, where it is often the most common lucinacean, but is common from the lower intertidal to about 10 m. This species exhibits little sediment preference. It occurs most frequently in medium to coarse sands but is also found in considerable numbers in very muddy areas.

Lucina pensylvanica (Linné) is a moderate sized lucinid (to 5 cm) which may be quite common in areas of good water

movement from the intertidal to depths as great as 50 m. It prefers medium to coarse, clean sands, with or without Thalassia cover, where it burrows to between 5 and 10 cm. Lucina pensylvanica is most common in shallow Thalassia covered bays where it is often found with the similar-sized lucinid Divaricella quadrisulcata (d'Orbigny). The latter species is a deep burrower (to about 20 cm) and is only found in areas of good water circulation. It was not studied experimentally as very few live individuals were collected in any of the areas regularly sampled.

Diplodonta punctata (Say) is not found intertidally. It is most abundant in shallow Thalassia covered environments with good water movement between about 1 to 5 m depth but has been collected live from depths of 250 m. This species is large for an ungulinid (to 2.5 cm) and is a shallow burrower. It prefers fairly muddy sands.

Diplodonta semiaspera (Phillippi) is a smaller species (maximum size just over 1 cm) which seems to prefer less muddy sands than D. punctata. It is found from the lower intertidal to about 40 m and shows a strong preference for Thalassia covered environments. It is a shallow burrower.

B. Lucinacean Occurrences

Table 1 is a listing of 42 localities at which one or more of the nine above Lucinacea are known to occur. The table is based on my own data from a number of Caribbean

Table 1. Occurrence data for nine lucinacean species from 42 Caribbean shallow water to intertidal localities. References given for data from other workers. Environments: A, intertidal to 1 m with seagrasses or mangroves (†); B, shallow (1-10 m) sandy, frequently grass covered bays and open waters; C, shallow (1-20 m), somewhat restricted bays or harbors with muddy to sandy bottoms. Species: 1, _C. orbicularis_; 2, _C. orbiculata_; 3, _P. costata_; 4, _L. pensylvanica_; 5, _A. alba_; 6, _P. pectinata_; 7, _D. quadrisulcata_; 8, _D. punctata_; 9, _D. semiaspera_. *=quantitative data used in correlation (Figure 11).

NO.	LOCALITY	ENVIRONMENT	SPECIES
* 1.	Runaway Bay, Jamaica, area I (Jackson, 1971)	A	1,2,3
* 2.	Runaway Bay, Jamaica, area II (Ibid)	A	1,2,3,4
3.	Discovery Bay, Jamaica, area III (Ibid)	B	1,2,3,4,5,7,8
4.	Discovery Bay, Jamaica, area IV (Ibid)	B	1,2,3,4,8
* 5.	Four miles west of Falmouth, Jamaica	A	1,2
* 6.	Reef flat just northwest Discovery Bay, Jamaica	A	1,2
* 7.	Bloody Bay, Jamaica	A	1,2,3,4,5
* 8.	Plumb Point Lagoon, Kingston Harbor, Jamaica	A	2,3,5,8,9
* 9.	Upper Basin, Kingston Harbor, Jamaica	A	2,3,5,8,9
*10.	Middle Ground, Kingston Harbor, Jamaica	A	2,3,8,9
*11.	Off coaling station, Outer Kingston Harbor	A	2,3,9
*12.	Half Moon Bay, Jamaica	A	1,2,3
*13.	Prospect, Jamaica	A	1
*14.	Southwest Port Morant Harbor, Jamaica	A	1,9
*15.	Island off la Parguera, Puerto Rico (locality BI)	A	1,2,3,8
*16.	Island off La Parguera, Puerto Rico (locality PR)	A	1,2,3
*17.	Runaway Bay, Jamaica (locality PTB)	A	1,2
*18.	East of Galeta Island, Panama (locality PAN 1)	A+	6
*19.	Atlantic side Islamorada Key, Florida (locality IS)	A	1,2,5
20.	Key Biscayne, Florida (Moore et al, 1968)	A	1,2,4,5,6,7,9
*21.	Key Biscayne, Florida (O'Gower and Wacassey, 1967)	A	1,4,5,7,8
*22.	Key Biscayne, Florida, _Thalassia_ (Ibid)	A	1,5,7
23.	Key Biscayne, Florida, sand (Ibid)	A	1,5,7
*24.	Virginia Key, Florida, _Diplanthera_ (Ibid)	A	1,4,5,8

Table 1. continued

NO.	LOCALITY	ENVIRONMENT	SPECIES
*25.	Virginia Key, Florida, Thalassia (Ibid)	A	1,5
26.	Virginia Key, Florida, sand (Ibid)	A	5
27.	North Sound, Grand Cayman (Abbott, 1958)	A,B,C	1,2,3,5
28.	Portete, Costa Rica (Houbrick, 1968)	A	1,5,6
29.	Playa Vega Baja, Puerto Rico (Arnow et al, 1963)	B,C	1,2
30.	Fresh drift near river mouth, Port Morant, Jamaica	A	5,6
31.	Mangroves, La Parguera, Puerto Rico	A +	6
32.	Oyster Bay, Florida (Tabb and Manning, 1961)	C	6
33.	West Whitewater Bay, Florida (Ibid)	C	2
34.	Margarita Island, Venezuela (Rodriguez, 1959)	A	2
*35.	East of Galeta Island, Panama (locality PAN 2)	A +	6
36.	Walsingham Pond, Bermuda (Gould, 1968)	C +	2
37.	East of Biostation, Bermuda (Ibid)	C +	2
38.	Great Bahama Bank, Strombus samba community (Newell et al, 1959)	B	4,7
39.	Great Bahama Bank, stable sand and Thalassia (Ibid)	A,B	1,4,5
40.	Great Bahama Bank, marshes and creeks (Ibid)	A +	2
41.	Bimini, Bahamas (Craig, 1967)	A,B	1,2,4,7
*42.	Two miles east of Falmouth Harbor, Jamaica	A	2,3
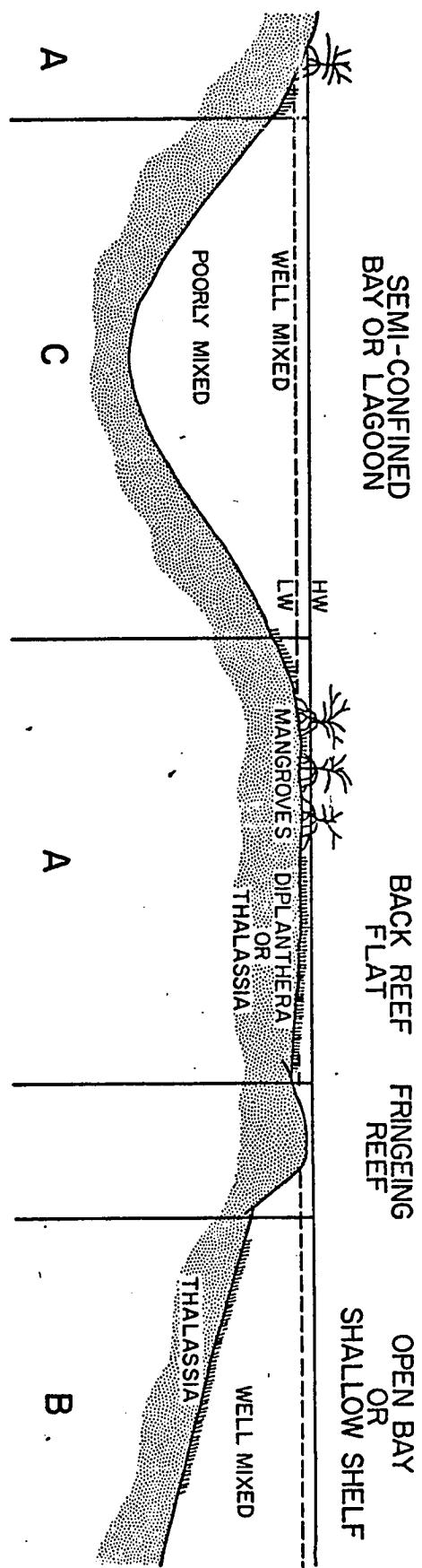
localities and from various reports in the literature for the same biogeographic area. Data from the southeastern United States (except the southern tip of Florida) and the Gulf of Mexico have not been included. Each of the localities was assigned to one of three fairly natural environmental divisions (Figure 5). Environment A includes areas from the shoreline to approximately 1 m depth covered by _Thalassia_ or _Diplanthera_ and/or among mangroves. It is the environment of all the Kingston Harbor localities and most of the other collecting areas shown in Figure 2. Environment B includes sandy, frequently _Thalassia_ covered bottoms in bays or shallow shelf areas with good water circulation between about 1 to 10 m depth. Environment C includes semi-confined bays or harbors with muddy to sandy bottoms in from 1 to 20 m. With the single exception of locality 30, which had large numbers of fresh, undamaged shells, all listings are for live animals only. Species are simply listed as being present or absent. Quantitative data, either as numbers/m^2, or relative abundances, were available from 23 of the environment A localities and are indicated by * in Table 1.

C. Methods Used

Temperature tolerances were determined by subjecting groups of usually a dozen individuals of a species to a

Figure 5. Diagrammatic cross section of environmental divisions represented in Table 1. Vertical scale greatly exaggerated.

CLASSIFICATION OF ENVIRONMENTS

SEMI-CONFINED
BAY OR LAGOON

WELL MIXED

POORLY MIXED

A

C

HW
LW

MANGROVES DIPLANTHERA
OR
THALASSIA

BACK REEF
FLAT

FRINGEING
REEF

A

OPEN BAY
OR
SHALLOW SHELF

THALASSIA

WELL MIXED

B

30 minute high temperature shock in aerated seawater and then immediately returning the animals to normal running seawater. Temperatures in the experimental container did not vary by more than $\pm 0.1^\circ C$. Following temperature shock the animals were examined daily and the percent mortality noted after one week. Death in all tolerance experiments was defined as an inability of gaping individuals to close their valves.

Salinity tolerance was determined by placing up to a dozen individuals of a species in a large aerated tank containing $15.0 \pm 0.1^\circ/oo$ salinity seawater maintained at $25 \pm 0.5^\circ C$ for varying periods and noting survival percentages one week after the end of the immersal. The $15^\circ/oo$ seawater was prepared by dillution of normal seawater by tap water as measured by a Beckman electrodeless field salinometer.

For determination of stagnation tolerance individual bivalves were placed, one to a container, in 115 ml screw top jars containing freshly aerated seawater and these jars were tightly sealed under seawater to avoid trapping air bubbles. The jars were then placed in a $25 \pm 0.5^\circ C$ water bath for the duration of the stagnation period. After suitable intervals the jars were opened, the surviving clams placed in normal running seawater and percent mortality noted one week after the opening of the jars.

Fifty percent mortality levels (LD 50's) were determined for each species by calculation of regression lines using the

Probit transformation. Goodness of fit was determined by comparison with χ^2 and the variance of the estimated 50% death point and observed variance were applied in the calculation of the standard error. When use of a standard error was not justified, fiducial limits of the 50% death point were calculated. The entire procedure is discussed in detail in Fisher and Yates, 1963.

In preliminary field tests for the presence of respiratory pigments a column was constructed using a 10 ml graduated pipette and Sephadex 100 gel. Ctenidia were excised, homogenized in a glass homogenizer in 5 ml pH 7.2 phosphate buffer and centrifuged in a small clinical centrifuge. The supernatant was filtered with a 0.45μ glass filter and passed through the column in a 0.1M NaCl solution. The colored fraction was analyzed in a 5 $m\mu$ intervals on a Bausch and Lomb Spectronic 20 spectrophotometer. Deoxygenation was achieved by adding a small amount of sodium dithionite.

Subsequent analyses were run following the procedures of Read (1962) in the laboratories of the Department of Biochemistry, University of the West Indies, Kingston, Jamaica. Ctenidia were homogenized as before, centrifuged at 8,000 x g for 10 minutes and the resulting supernatant was further centrifuged at 100,000 x g for one hour. This supernatant was pipetted off and analyzed on a Carl Zeiss PM QII auto-slit spectrophotometer at 5 $m\mu$ intervals or more frequently in the peak regions. Deoxygenation was achieved as before; no attempt was made to determine the quantity of pigment present

in the analyses.

All non-parametric methods are from Campbell (1967). Product moment correlations were obtained on the IBM 7094-7040 system of the Yale Computer Center.

IV. EXPERIMENTAL RESULTS

A. Resistance to High Temperature Shock

Temperature tolerance experiments were carried out using Codakia orbicularis, Ctena orbiculata, Parvilucina costata and Diplodonta punctata only from Discovery Bay and only from Kingston Harbor. These showed no variations in tolerance between the animals from the different areas and it is therefore assumed that temperature, salinity and stagnation tolerance are not greatly dependent on sampling area within Jamaica. The data presented in Tables 2, 3 and 4 are for animals collected throughout Jamaica as shown in Figure 1. The results from the temperature tolerance experiments are graphed in Figure 6. LD 50's are listed in Table 2 for the five species for which complete data are available and Table 3 gives temperature tolerance data for a number of other shallow water bivalves including the lucinid Lucina pensylvanica.

Larger bivalves were more tolerant of high temperature shock than were juveniles of the same species. Experiments using juvenile and adult Ctena orbiculata yielded differences

Table 2. Fifty percent mortality values (LD 50's) for exposure to high temperature shock, 15°/oo salinity and stagnation for five Jamaican Lucinacea. Temperature values those for which 50% of the animals survived a thirty minute shock. Salinity and stagnation values the number of hours 50% of the animals survived 15°/oo salinity or stagnant conditions at 25 $\pm$ 0.5°C. The number of animals used in each set of experiments is given in parentheses.

SPECIES	TEMPERATURE	SALINITY	STAGNATION
Codakia orbicularis	39.1±0.1 (142)	95-126 (60)	307±20 (48)
Ctena orbiculata (adult)	39.6±0.1 (67)	79-105 (58)	1270±170(35)
(juvenile)	39.4±0.1 (100)		
Parvilucina costata	38.6-39.2 (135)	43±3 (68)	320? (58)
Diplodonta punctata	38.1±0.1 (68)	50±4 (35)	460-550(48)
Diplodonta semiaspera	40.0±0.1 (60)	69±6 (33)	490±110(54)
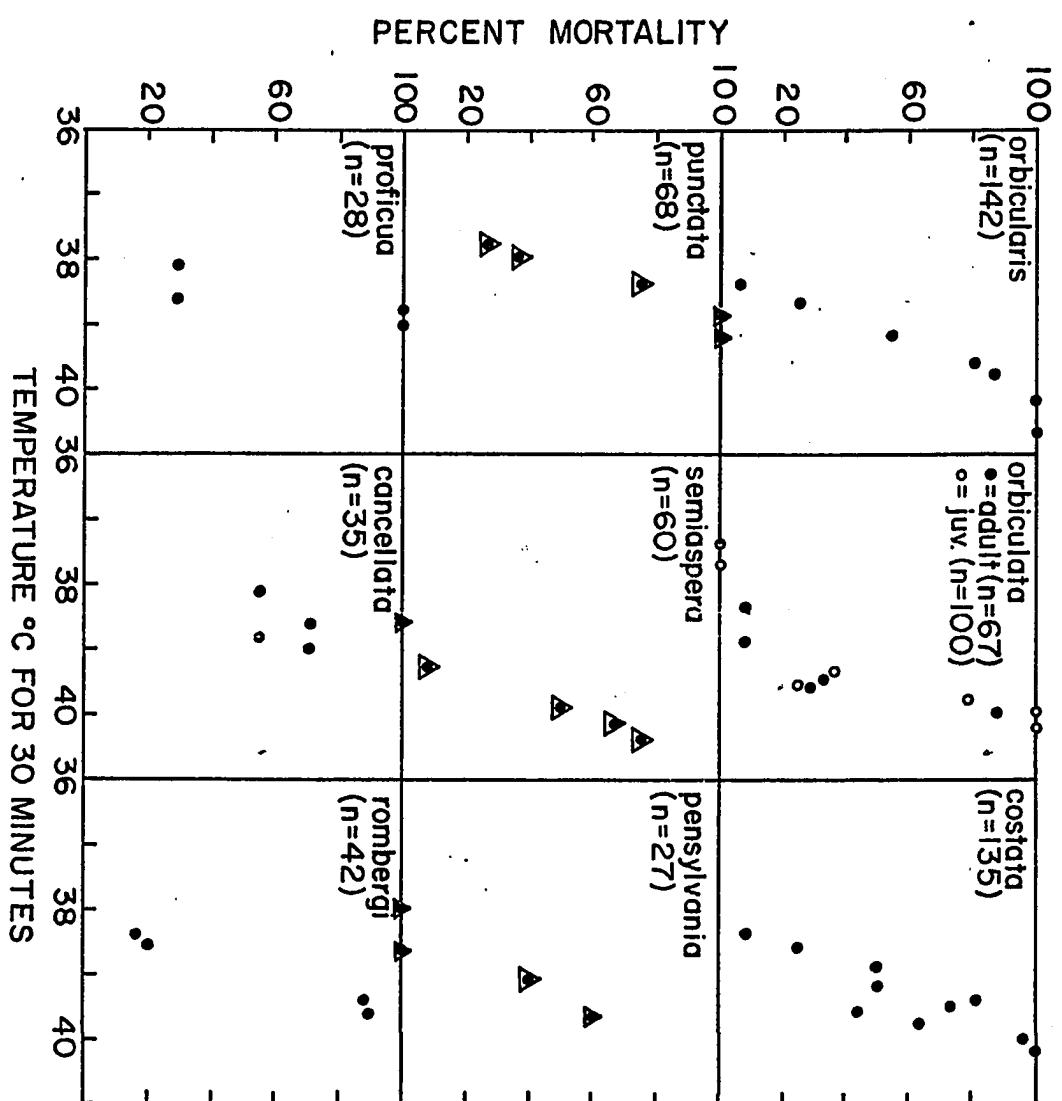
Table 3. LD 50's and approximate tolerances to 30 minute high temperature shocks for nine Jamaican infaunal bivalves. The number of animals used is given in parentheses.

SPECIES	TEMPERATURE
Lucina pensylvanica	39.5±0.3 (27)
Strigilla rombergi	38.9±0.1 (42)
Chione cancellata	38.8±0.3 (35)
Corbula caribaea	39 (20% mortality at 38.6°C for 5 animals and 60% mortality at 39.0°C for 5 animals)
Transennella conradina	38.7 (100% mortality for 6 animals)
Gouldia cerina	38.7 (100% mortality for 6 animals)
Anadara notabilis	(38.6)(50% mortality at 38.6 for 8 animals and 11.1% for 9 at 37.5)
Modiolus americanus	37.7 (100% mortality for 12 animals at 38.4 and 80% for 10 at 37.7)
Semele proficua	35.3-38.6 (28)

Table 4. Comparative tolerance of adult and juvenile Codakia orbicularis to 30 minute high temperature shocks.

NUMBER AND SIZE	TEMPERATURE $^{\circ}$C	PERCENT MORTALITY
12 large adults	39.6	75.0
9 juveniles	39.6	88.9
12 large adults	39.2	50.0
12 juveniles	39.2	58.3

Figure 6. Mortality-temperature curves for nine Jamaican infaunal bivalves. Exposure time to indicated temperature was 30 minutes.

PERCENT MORTALITY

TEMPERATURE °C FOR 30 MINUTES

orbicularis
(n=142)

punctata
(n=68)

proficua
(n=28)

orbiculata
●=adult(n=67)
o= juv.(n=100)

semiaspera
(n=60)

cancellata
(n=35)

costata
(n=135)

pensylvania
(n=27)

rombergi
(n=42)

in LD 50's at P≤ .05 (Table 2). Similar results were obtained in two pairs of experiments using <u>Codakia</u> <u>orbicularis</u> at 39.2 and 39.6°C (Table 4). The average difference between juvenile and adult mortality was 8.6% which is equivalent to a temperature difference of nearly 0.2°C. Among adults larger than 1 to 2 cm there was no observed difference in mortality with difference in size.

B. <u>Resistance</u> <u>to</u> <u>15°/oo</u> <u>Salinity</u>

The results from the salinity tolerance experiments are graphed in Figure 7 and the LD 50's given in Table 2. Table 5 is a ranking of salinity tolerance of nearshore Lucinacea based on the experiments and field collection data from areas of known salinities. The values are an approximation of minimal salinities tolerated by adults over extended periods. <u>Phacoides</u> <u>pectinata</u> is alone among the Caribbean Lucinacea in its tolerance of very brackish (and also hypersaline) conditions.

C. <u>Resistance</u> <u>to</u> <u>Stagnation</u>

The results of the stagnation tolerance experiments are graphed in Figure 8 and the LD 50's given in Table 2. Read (1964) has demonstrated the great temperature sensitivity of the stagnation tolerance of tropical bivalves. His data indicate a maximum decrease in tolerance of about

Figure 7. Mortality-15°/oo salinity curves for five Jamaican Lucinacea.
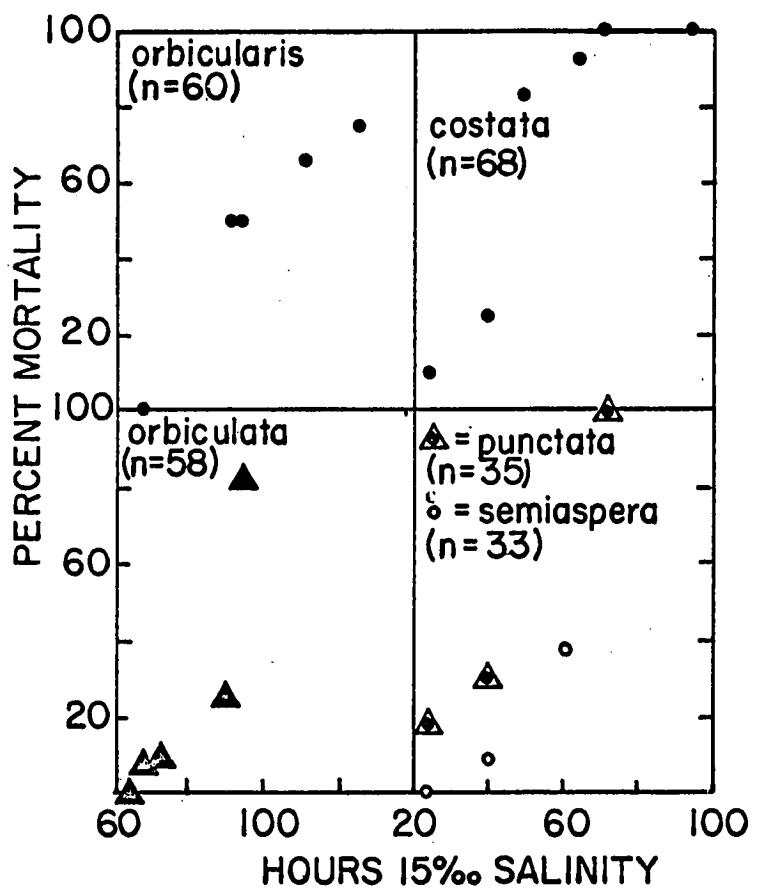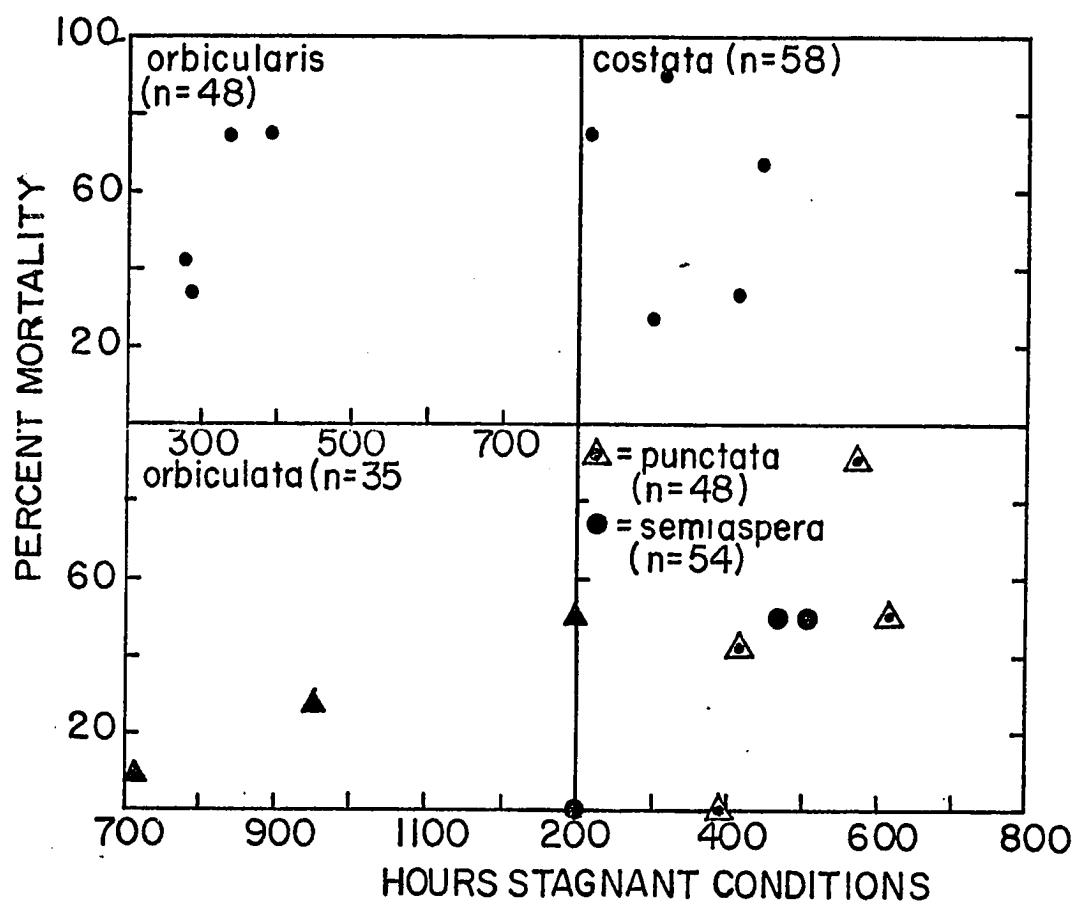
Table 5. Comparative low salinity tolerance of eight Caribbean Lucinacea.

SALINITY^{o}/oo	SPECIES	SOURCE
10 to 15	pectinata	Tabb and Manning, 1961
>15, <18	orbicularis	Slightly greater tolerance than orbiculata in experiments
18	orbiculata	Tabb and Manning, 1961
20?	semiaspera	Lower tolerance than orbiculata but higher tolerance than following species in experiments
>20, <28	alba costata punctata pensylvanica	Present in numerous localities where the salinity is commonly as low as 28o/oo for periods of more than a month including flat at Pear Tree Bottom, Jamaica (Jackson, 1971)

Figure 8. Mortality-stagnation curves for five Jamaican
Lucinacea.

two thirds for each 5°C rise in temperature. On this basis, the stagnation tolerance of P. pectinata (Read's experiments) at 25°C is probably in the vicinity of 600 hours. Similarly, tolerances for all species examined here except C. orbiculata may be as low as 35 to 40 hours at 35°C and 10 to 15 hours at 40°C.

Information on stagnation tolerance was obtained from a variety of incidental sources besides the regular experiments. While collecting samples for a one year survey of molluscan and echinoderm populations in Jamaican Thalassia environments (Jackson, 1971), samples were stored in buckets with fresh seawater until sieved and counted. During this processing time a number of bivalves died and these were all individuals of five species of cardiids (Table 6). In 13 samples for which accurate records of mortality were maintained, 19 or 21 cardiids died, but none of the 51 individuals of the remaining 12 species suffered mortality.

In an accident where the running seawater was cut off in a small holding tank for about 24 hours, the seawater became foul and 15 of 20 of the shallow infaunal arcid Anadara notabilis died, whereas only one of the over 200 C. orbicularis in the same tank died. Thus, the stagnation tolerance of A. notabilis lies between that of all the Lucinacea tested and that of the cardiids.

In a similar situation, a large holding tank containing hundreds of individuals became stagnant for about one week. Numerous C. orbicularis and P. costata died, whereas none of

Table 6. Survival of stagnant conditions in 13 sample buckets by 17 species of Discovery Bay, Jamaica infaunal bivalves.

SURVIVORS	DEAD
13 _Codakia orbicularis_	7 _Trachycardium muricatum_
10 _Parvilucina costata_	6 _Americardia media_
7 _Modiolus americanus_	3 _Laevicardium laevigatum_
6 _Transennella conradina_	2 _Papyridea soleniformis_
3 _Diplodonta punctata_	1 _Trachycardium isocardia_
2 _Ctena orbiculata_	
2 _Anadara notabilis_	
1 _Anodontia alba_	
1 _Diplodonta nucleiformis_	
1 _Lucina pensylvanica_	
1 _Gouldia cerina_	
1 _Chione paphia_	
1 _Trachycardium isocardia_	
1 _Americardia media_	

---

the C. orbiculata or A. alba suffered mortality. Thus,
A. alba is probably more tolerant of stagnation than any
of the lucinids except C. orbiculata and P. pectinata.
One last unplanned experiment of stagnation tolerance
(Table 7) involved prolonged storage (3 days) in plastic
bags of a group of bivalves during a delayed return to
Discovery Bay from the south coast of Jamaica. The temp-
erature in the bags at the end of this period was 30°C.

D. Presence of Respiratory Pigments

The absorption spectra for centrifuged ctenidial
homogenates of seven Lucinacea are shown in Figure 9 and are
summarized in Table 8. Haemoglobin is known from the gills
of P. pectinata (Read, 1962). The gills of that species
are a dark purplish color and it was the presence of similar
coloration in the gills of C. orbicularis, C. orbiculata and
P. costata which suggested these investigations. The gills of
the remaining four shallow water species investigated range
from a brownish cream for the lucinids L. pensylvanica and A.
alba to a cream in the two species of Diplodonta. Histo-
logical investigations by Allen (1958) and Read (1962) have
shown the darker coloration is due to the presence of brown
pigment granules. Read has further demonstrated that "par-
ticles of similar size, shape and structure take the charac-
teristic green color of iron with....ferrocyanide stain"
which indicates that all species containing the yellow-brown

Table 7. Percent survival of stagnant conditions by 10 species of Kingston Harbor, Jamaica infaunal bivalves for 3 days in plastic bags.

SPECIES	NUMBER	PERCENT MORTALITY
Anodontia alba	1	0.0
Anadara notabilis	2	0.0
Chione cancellata	9	0.0
Labiosa lineata	7	14.3
Pitar albida	1	0.0
Pinna carnea	2	50.0
Semele bellastriata	2	0.0
Semele proficua	39	25.6
Semele purpurascans	7	85.7
Trachycardium muricatum	7	85.7

Figure 9. Absorption spectra for centrifuged ctenidial homogenates of seven Jamaican Lucinacea.

ABSORPTION

WAVELENGTH (mμ)

Parvilucina costata

Lucina pensylvanica

Anodontia alba

Diplodonta punctata

Codakia orbicularis

Diplodonta semiaspera
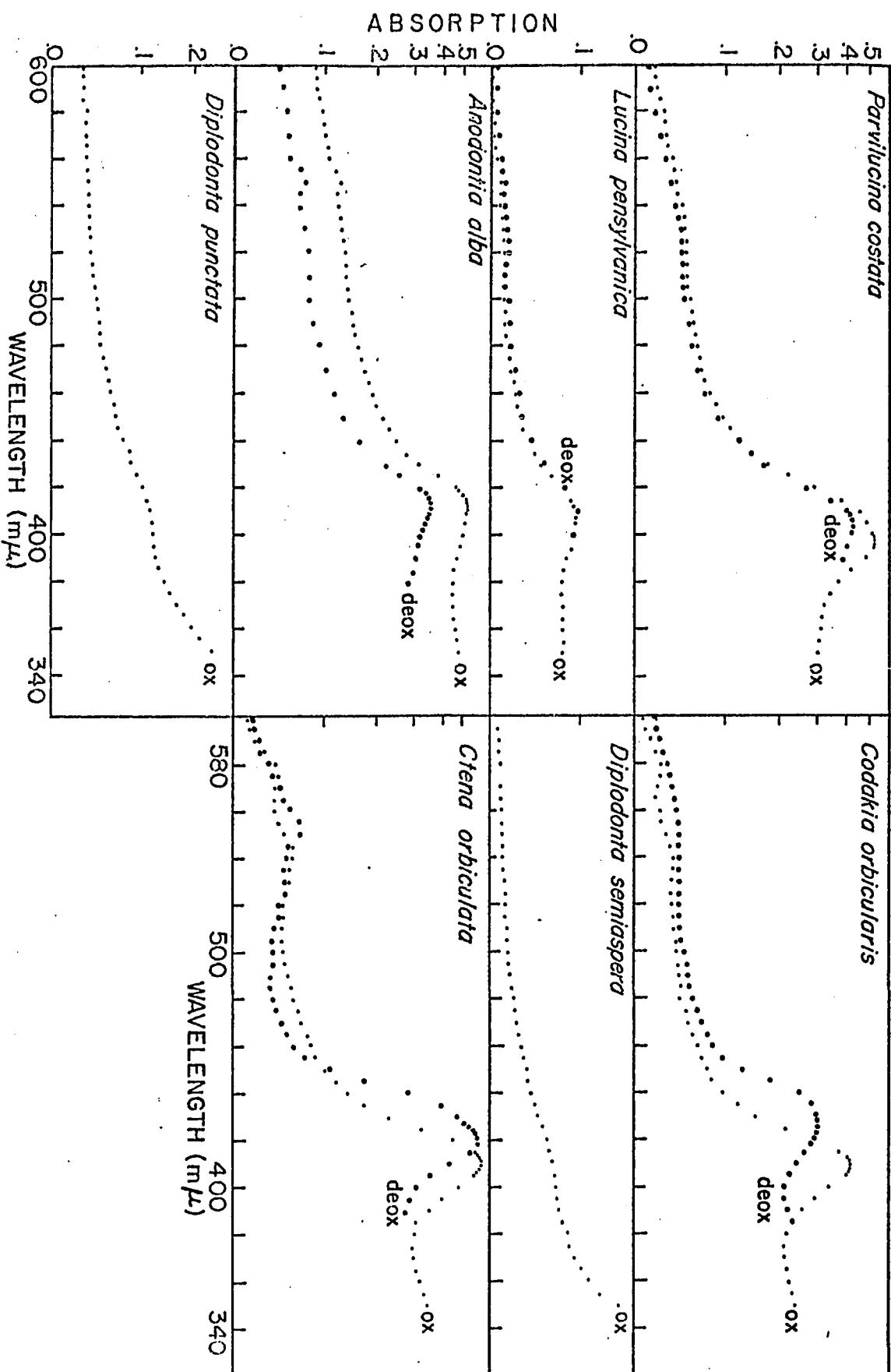
Ctena orbiculata

Table 8. Absorption spectra of centrifuged ctenidial homogenates of eight Jamaican Lucinacea. Peak values in mμ.

SPECIES		SORET	BETA	ALPHA
P. pectinata (Read, 1962)	ox.	416	543	579
	deox.	433.5	558	
C. orbicularis	ox.	409	535-540	575-580
	deox.	425	550	
C. orbiculata	ox.	409	540	575
	deox.	420-421	550-555	
P. costata	ox.	396-397	?	?
	deox.	405		
L. pensylvanica	ox.	407-410	?	?
	deox.	no shift obtained		
A. alba	ox.	411	?	?
	deox.	no shift obtained		
D. punctata	ox.	no peaks		
D. semiaspera	ox.	no peaks		

ctenidial granules contain respiratory pigments (presumably haemoglobins) including the one thyasirid investigated by Allen, Thyasira flexuosa. Allen did not find such granules in any of the ungulinids he examined and this agrees with the apparent lack of respiratory pigments in Diplodonta indicated by this study.

The shifts on deoxygenation in the Soret peaks for C. orbicularis, C. orbiculata and C. costata are quite distinct and were repeated twice each with similar results. The peaks for C. orbicularis and C. orbiculata are similar to those obtained by Read for P. pectinata but the peak for P. costata is very different from reported values. The deoxygenated curves for A. alba and L. pensylvanica are based on only one analysis each and thus the failure to obtain any shift is not conclusive. However, the deep purple coloration of the ctenidia of P. pectinata, C. orbicularis, C. orbiculata and P. costata and the superior quality of the spectra obtained for these species indicate the presence of far more respiratory pigment than for A. alba and L. pensylvanica.

E. Physiological Tolerance Ranks

The results of the experiments were summarized (Table 9) by ranking each species for which complete data were available on the basis of its tolerance to high temperature shock, $15^{o}/oo$ salinity, stagnation and the presence or absence of respiratory pigments. Any overlapping tolerances

Table 9. Ranks of LD 50 physiological tolerance levels for five Jamaican Lucinacea.

SPECIES	HIGH TEMPERATURE	15°/oo SALINITY	STAGNATION	RESPIRATORY PIGMENT	AVERAGE RANK
C. orbiculata	2	1.5	1	2	1.63
D. semiaspera	1	3	2.5	4.5	2.75
C. orbicularis	3.5	1.5	4.5	2	2.88
P. costata	3.5	4.5	4.5	2	3.63
D. punctata	5	4.5	2.5	4.5	4.13

were considered as ties and given the same rank corres-
ponding to their positions in a single ordered sequence.
The ranks were then summed and divided by four to give the
average tolerance rank for each of the five species.

Data from both experiments and field occurrences were
used in constructing a similar salinity-stagnation toler-
ance ranking for the six nearshore lucinids examined in
comparative detail in this study (Table 10). Salinity
data used are taken from Table 5 and the stagnation ranking
of P. pectinata and A. alba have already been discussed.
The stagnation tolerance of L. pensylvanica is not known
but was arbitrarily assumed to be roughly that of C. orbicu-
laris and P. costata. Other stagnation tolerance data are
from experimental data of this study.

V. DISCUSSION AND CONCLUSIONS

A. The Relation of Lucinacean Physiological Tolerance to
   Local Environmental Distributions.

Mayer (1914), Broekhuysen (1940), Fraenkel (1966) and
Foster (1969, 1971) have found close correlations between
the positions of organisms (corals, gastropods and barnacles)
on the shore and their physiological tolerance. Their work
has also demonstrated that many invertebrates are killed by
conditions not far from those commonly occurring in their

Table 10. Salinity-stagnation tolerance ranks for six
Caribbean Lucinidae.

SPECIES	LOW SALINITY	STAGNATION	AVERAGE RANK
P. pectinata	1	2	1.50
C. orbiculata	2.5	1	1.75
C. orbicularis	2.5	5	3.75
A. alba	5	3	4.00
P. costata	5	5	5.00
L. pensylvanica	5	5	5.00

natural environments. The results of this study are similar.

1. Temperature

On _Thalassia_ and _Diplanthera_ flats the occurrence of low tides on hot clear days may commonly produce water temperatures of 37 to 38°C and sediment temperatures (about 2 cm deep) of 34 to 36°C. At periods of abnormally low tides water and sediment temperatures may exceed 40°C and 38°C respectively. Such temperatures may develop quite rapidly. For example, a series of measurements were made at low tide early in the afternoon of 12 October 1970 at two back reef flats at Pear Tree Bottom, Jamaica. Water temperatures rose at rates of up to 2°C/hour and sediment temperatures in excess of 1°C/hour in the different localities.

The differences in high temperature tolerance between _D. punctata_ and _D. semiaspera_ are sufficiently great to explain the restriction of the former species to subtidal environments whereas the latter is common on the lower reaches of many intertidal _Thalassia_ flats in areas of good water movement. In addition, since sediment temperatures above about 39°C are likely to be quite rare, the slight differences in temperature tolerance between _C. orbicularis_ and _C. orbiculata_ could be important in determining distribution patterns in areas subject to extremely high temperatures. _Codakia_ _orbicularis_, however, occurs nearly up to the

shoreline on most intertidal flats yet this species is the
least tolerant of high temperature shock of all the lucinids
tested. Apparently the differences in temperature tolerance
between these lucinids are not of primary significance in
differential species survival. This result is similar to
that of Broekhuysen (1940) and in agreement with Read (1963)
who suggested that the resistance of bivalve enzyme activity
to destruction by heat "is correlated with the extremes of
the chemical environment that the animal can withstand [such
as stagnant conditions within its mantle cavity] rather than
the environmental temperature."

2. Salinity

Extreme low salinities at a given nearshore locality
are very variable and, although usually seasonal, may occur
at any time of year. The very great low salinity tolerance
of P. pectinata, C. orbicularis and C. orbiculata is correlated
with their dominance and frequent solitary occurrence in
mangroves and back reef areas of highly variable salinity.
The somewhat less tolerant D. semiaspera is often found in
such localities as well. In contrast, the comparatively
poor tolerance to low salinities of the other Lucinacea
appears to be responsible for restricting them from many
euryhaline nearshore environments. The experiments indicate
that these species (P. costata, A. alba, L. pensylvanica and

<u>D</u>. <u>punctata</u>) should regularly be killed by exposure of only a few days to salinities of about 15°/oo. Thus, the wide range of low salinity tolerance among the Lucinacea appears to be a primary factor in determining the distributions of the individual species. Low salinities may be of further importance in that they tend to decrease tolerance to high temperatures by a variety of marine invertebrates (Kinne, 1970).

3. Stagnation

Stagnation tolerance is considerably decreased by increase in temperature (Read, 1964; Theede, <u>et</u> <u>al</u>., 1969). However, even at 40°C, the stagnation tolerance of all the lucinaceans examined (greater than 10 hours) exceeds that of a reasonable period of stress likely to be caused by irregular tidal or temperature events. It is therefore probable that such exceptional tolerance is more frequently of importance in resisting periods of anoxic bottom conditions, often of considerable duration, in environments with poorly circulating waters.

In addition to their considerable low salinity tolerance, <u>P</u>. <u>pectinata</u> and <u>C</u>. <u>orbiculata</u> survive stagnant conditions for more than twice as long as any of the other Lucinacea investigated. This exceptional stagnation tolerance is correlated with their common occurrence in various mangrove environments where other euryhaline species (particularly

C. orbicularis and D. semiaspera) are not found (Table 1).
Similarly, C. orbiculata is the most abundant species in
the restricted Upper Basin of Kingston Harbor, whereas in
the more freely circulating waters of the Middle Ground of
that Harbor (Goodbody, 1970), P. costata tends towards
dominance. Clearly, differential stagnation tolerance is
a primary factor among the Lucinacea in limiting the en-
vironmental distributions of the individual species.

4. Respiratory Pigments

Among the Lucinacea the apparent species differences
in the amounts of presumptive haemoglobin are not obviously
correlated to their stagnation tolerances or distributions.
For example, both species of Diplodonta are more tolerant
of stagnation than are C. orbicularis and P. costata, yet
the former apparently do not have respiratory pigments.
The presence of such pigments may simply be related to the
small ctenidial respiratory surface area available to these
bivalves, especially in the Lucinidae which possess unpaired
gills. The mantle gills (Figure 1) found in many lucinids
(Allen, 1958) are probably respiratory in function. These
structures are restricted to larger species of the family
implying that the respiratory surface area of these forms
is not otherwise adequate. The presence of respiratory pig-
ments must be highly advantageous in these circumstances.
As discussed above, the thyasirids most probably have
respiratory pigments. The thyasirid outer demibranch is

relatively smaller than in the ungulinids. Thyasirids
may also reach considerable size. The lack of respira-
tory pigments in the ungulinids, perhaps secondary, may
be related to the absence of large species and the
presence of well developed paired gills in this family.

Seawater oxygen concentrations over Thalassia flats
commonly fluctuate from below saturation at night to more
than 200% of saturation in daytime (Odum, 1957; Jackson,
1971). The respiratory pigments may therefore allow
oxygen to be taken up at low environmental concentrations
(Jones, 1954) and act as oxygen buffers to maintain
reasonably uniform oxygen concentrations in the blood
(reviewed by Newell, 1970).

5. Frequency of Occurrence and Physiological
   Tolerance Rank

The three environments illustrated in Figure 5 are
very unequally represented in the data of Table 1. Environ-
ment A comprises 34 of the 42 localities but only four of
these were dominated by mangroves. Therefore, for analysis
of distributions, these data are only useful for species
found most commonly in Thalassia and Diplanthera covered areas
of environment A. Three or more of the nine species were
present together at 52% of the localities with an average of
2.83 species/locality. However, as seen in Figure 10, there
were only six of a possible 36 significant ($P \leq 0.05$) positive

Figure 10. Correlation matrix (presence/absence data) for
nine lucinacean species at 42 Caribbean shallow water to
intertidal localities (Table 1). N=42. For r=.30 P$\leq$ 0.05.

	C. orbicularis	C. orbiculata	P. costata	L. pensylvanica	A. alba	P. pectinata	D. quadrisulcata	D. punctata
C. orbiculata	.05							
P. costata	.07	.56						
L. pensylvanica	.35	-.02	.08					
A. alba	.25	-.29	-.04	.26				
P. pectinata	-.28	-.44	-.32	-.10	.04			
D. quadrisulcata	.24	-.18	-.18	.50	.31	-.03		
D. punctata	.03	-.13	.43	.30	.24	-.22	.11	
D. semiaspera	-.22	.18	.29	-.07	.10	.00	.00	.32

correlations between the occurrences of these species. Figure 11 is a similar matrix for the five species present at more than 20% of the localities in Table 1, all lucinids, at localities for which relative abundance data were available (*in Table 1). There are no significant positive correlations and five significant negative correlations ($P \leq 0.05$) between these species. Thus, although frequently co-occurring, the distributions of each of these Lucinacea are very different and must be controlled by different combinations of factors.

These differences in distribution are often evident on a local scale in the distinctive zonation of individual lucinid species. For example, three large lucinids show very little overlap in distribution where they co-occur on a large Diplanthera-Thalassia flat at Key Biscayne, Florida (Figure 12, Stanley, 1970). Phacoides pectinata occurs abundantly in the upper reaches of the flat whereas C. orbicularis is most abundant farther from shore. Anodontia alba is present throughout almost the entire area but burrows more deeply than either of the other species. On a similar flat in Jamaica, C. orbiculata is most common about 20 m from shore whereas the abundance of C. orbicularis progressively increases outwards from shore for som 80 m. Such differences in distributions are in agreement with the comparative physiological tolerances of the individual species.

The percent occurrence by locality of the nine Lucinacea is given in Table 11. The percent occurrence for the three lucinids for which complete experimental data are available

Figure 11. Correlation matrix (relative abundance data)

for five lucinid species at 23 shallow water to intertidal

Caribbean localities (* in Table 1). N=23. For r=.40 P≤0.05.

	C. orbiculata	_C. orbicularis_	_P. costata_	_A. alba_
C. orbicularis	-.54			
P. costata	.26	-.52		
A. alba	-.31	-.07	-.27	
L. pensylvanica	-.23	.15	-.09	.16

Figure 12. Depths of burial of three lucinid species
in an intertidal flat, Key Biscayne, Florida (from Stanley,
1970). Open circles=Phacoides pectinata; solid circles=
Codakia orbicularis; crosses=Anodontia alba. Depths
measured to uppermost points on shells.
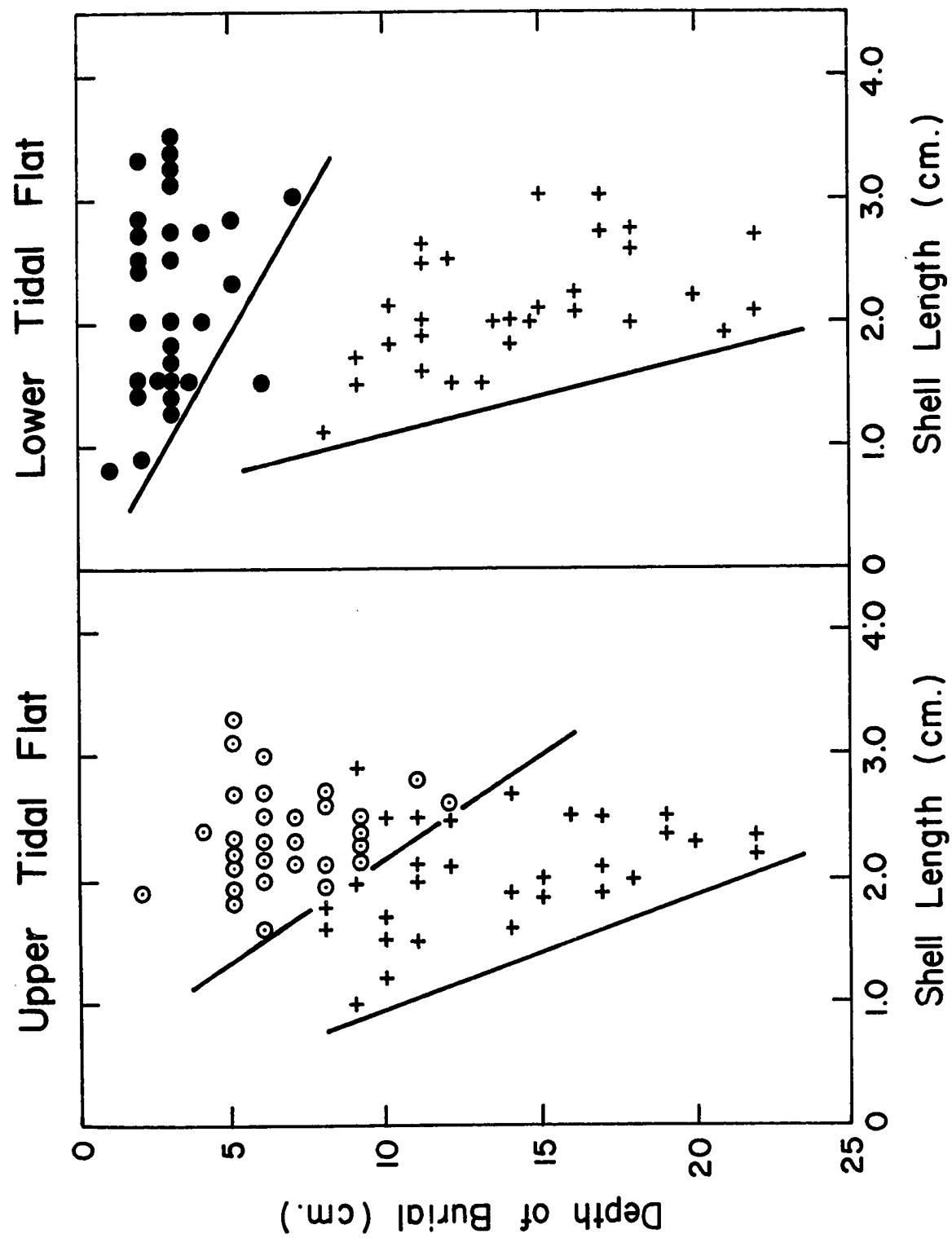
Table 11. Percent occurrence (presence/absence) of nine Lucinacea at 42 Caribbean shallow water to intertidal localities.

SPECIES	PERCENT
Ctena orbiculata	61.9
Codakia orbicularis	59.5
Anodontia alba	38.1
Parvilucina costata	33.3
Lucina pensylvanica	23.8
Diplodonta punctata	19.1
Phacoides pectinata	16.7
Divaricella quadrisulcata	16.7
Diplodonta semiaspera	14.3
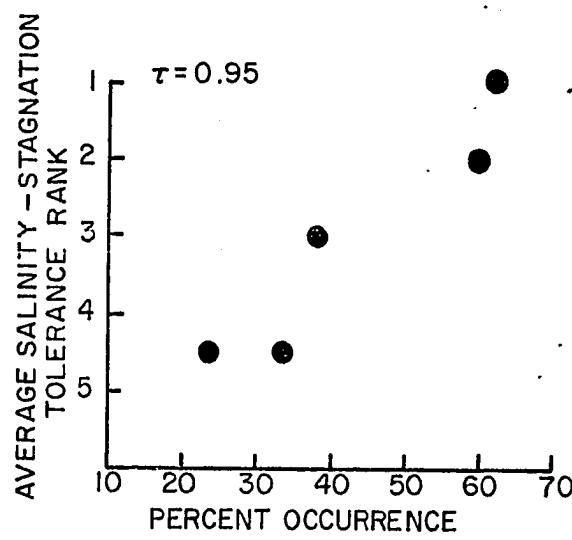
(C. orbiculata, C. orbicularis and P. costata) is exactly
the same as their average tolerance ranking in Table 9.
There is also a strong positive correlation between per-
cent occurrence and average salinity-stagnation tolerance
for the five lucinids whose normal environments are ade-
quately represented by the 42 localities (Figure 13).
Phacoides pectinata was not included because of its strong
preference within the Caribbean area of mangrove dominated
environments. No tolerance data were available for D. quad-
risulcata. The Kendall coefficient of rank correlation
(S=9, n=5) is 0.95 which is significant at approximately
P=0.05. Clearly, variations in physiological tolerance,
especially to lowered salinities and stagnant conditions,
are of major importance in determining the distributions
of nearshore lucinid species.

Just as for other organisms (Broekhuysen, 1940; Fraenkel,
1966; Foster, 1969, 1971), however, even the most eurytopic
lucinids investigated can be killed by environmental condi-
tions not very far from the normal range of variation charac-
teristic of their habitats. Indeed, many cases of mass kills
due to very high temperatures, flood rains or stagnant water
conditions have been documented from tropical shallow water
environments (Vaughan, 1918; Hodgkin, 1959; Slack-Smith,
1960; Goodbody, 1961; Tabb and Jones, 1962; Goreau, 1964;
Banner, 1968; Glynn, 1968). This supports the view (Slobod-
kin and Sanders, 1969) that unpredictable or catastrophic
events are of major importance in determining the composition

Figure 13. Correlation of percent occurrence and low salinity-stagnation tolerance rank for five Caribbean lucinid species. γ =Kendall coefficient of rank correlation.

of shallow marine communities.

The infrequent occurrence of the very eurytopic D. semiaspera strongly suggests that factors other than comparative physiological tolerance are of primary importance in determining ungulinid distributions. Most apparent is the restriction of both D. semiaspera and D. punctata to areas of good water circulation. These species were considerably more tolerant of stagnant conditions than either of the lucinids C. orbicularis or P. costata which regularly occur in areas of poor water movement. Therefore, the restricted ungulinid distributions must reflect other requirements.

6. Areas Outside the Caribbean

a. Gulf of Mexico

Just north of the Caribbean in the southern Gulf of Mexico, the shallow water associations of eurytopic lucinids tend to break down. This is not due to significantly different patterns of sedimentation, salinity variation or stagnant conditions since the ranges of these variables observed in the Gulf occur in numerous parts of the Caribbean and adjacent mainland areas. The major difference between the areas is their overall temperature range and, most importantly, the influence of very low seawater temperatures on the distributions of the different species. For example,

shallow (less than 1 m) grass flats in lagoons and shallow
bay margins in the Rockport area of Texas show a normal
annual temperature for circulating water ranging from 3 to
36°C (Parker, 1959) whereas the waters over similar environ-
ments in southern Florida around Miami and in Jamaica ap-
parently do not fall much below about 18°C (Smith, et al.,
1950) and 24°C respectively. The Texas flats support abun-
dant populations of P. pectinata and A. alba but C. orbicu-
laris, C. orbiculata and L. pensylvanica are absent. These
environments undergo considerable salinity fluctuations, in-
cluding moderate hypersalinity, but not in excess of values
both C. orbicularis and C. orbiculata survive in the Carib-
bean. Thus the important factor in the exclusion of these
species is most likely related to the much lower winter
temperatures characteristic of the Texas bay coastal waters.

b. Seychelles, Indian Ocean

In tropical and subtropical areas beyond the Western
Atlantic, shallow Thalassia flats and mangrove environ-
ments are frequently dominated by lucinacean faunas similar
to those described in this paper. Taylor's (1968) investi-
gations of the fauna of the predominantly intertidal Thalassia
flats and other shallow environments at Mahé, Seychelles, pro-
vides a basis for detailed comparisons (Table 12). The
Thalassia infauna is dominated by two very large species of
Codakia (tigerina and punctata), the smaller Ctena divergens

Table 12. Environmental distribution of seven Seychelles Lucinacea (Taylor, 1968).

SPECIES	MANGROVES	EX-MANGROVE FRINGES	THALASSIA BEDS	SAND AND COBBLE RIDGES	OUTER REEF ENVIRONMENT
Diplodonta lateralis				rare	
Divaricella ornata			abundant	rare	
Anodontia edentula		present	abundant		present
Ctena divergens	present	present	abundant		present
Codakia interrupta		present		rare	rare
Codakia punctata				common	present
Codakia tigerina				common	present

and a large tellinid. Codakia tigerina is very similar to C. orbicularis and the two have been considered to be the same species by some authors (see Bretsky, 1969). Like C. orbicularis in Jamaica, it is the most abundant infaunal bivalve on the Seychelles back reef Thalassia flats.

The occurrence of Ctena divergens in practically the entire range of soft bottom environments studied by Taylor (Table 12) indicates that, as for Ctena orbiculata in the Caribbean, this species must be the most eurytopic of the Seychelles lucinids. In the "ex-mangrove fringes" environment C. divergens tolerates long periods of complete exposure at low tides and highly reducing conditions. There and within the mangrove environment salinities may be very low and fluctuate considerably. Unlike the Caribbean case, C. divergens may be more tolerant of low salinities than C. tigerina or C. punctata.

The presence of a second, albeit much less abundant, intertidal species of Codakia is different from the Caribbean situation as is the absence of Lucina or Phacoides in the Thalassia flat environment at Mahé. A fourth lucinid, Anodontia edentula does occur. This species is also found in the "ex-mangrove fringe" environment. Like A. alba in the Caribbean, A. edentula must be very tolerant of stagnant conditions.

The presence and composition of the more diverse, although less abundant, lucinacean fauna seaward of the fringing reefs at Mahé closely parallels the differences between back reef

and shallow bay and shelf faunas in the Caribbean (Abbott, 1958; Jackson, 1971). The limitation of both Diplodonta lateralis and Divaricella ornata to areas of freely circulating waters is similar to the distributions of the corresponding Caribbean species. One important difference, however, is the absence outside the Mahé reefs of any counterpart to P. costata.

All of the Indian Ocean lucinids except the smaller C. divergens were found deeply buried (15 to 20 cm) into the sediment (Taylor, 1968; Taylor and Lewis, 1970). This depth is comparable to that occupied by A. alba and P. pectinata but is considerably greater than that reached by C. orbicularis and other Caribbean lucinids. The greater burial depth of Seychelles Codakia is most likely a function of the greater frequency of very hot temperatures (38.5 to 40.7°C) at Mahé in comparison to the Caribbean environments examined in this study.

B. The Relation of Physiological Tolerance to Local Environmental Distributions in Other Infaunal Bivalve Groups

1. Temperature

The species of other bivalve groups examined in temperature tolerance experiments are often very common in shallow subtidal Thalassia environments but are only

rarely found on intertidal flats. Comparison of their high temperature tolerance with that of the Lucinacea is hampered by the limited nature of the data. Examination of Table 3 nevertheless suggests that few, if any, of these non-lucinaceans are likely to show 50% survival at temperatures as high as $39^{\circ}C$ whereas the LD 50's of at least four of the Lucinacea are greater than this temperature (Table 2). These differences should be sufficient to at least partially explain the far greater abundance of the Lucinacea on shallow to intertidal, back reef flats and other high temperature environments (Moore, et al., 1968 and Jackson, 1971).

2. Salinity

The range of salinity tolerance shown by the Lucinacea is no greater than that of other common shallow water bivalve groups in the Caribbean like the venerids and tellinids which also contain numerous euryhaline as well as stenohaline species (Tabb and Manning, 1961).

3. Stagnation

Although not confirmed in controlled experiments, the very low stagnation tolerance of the cardiids (Tables 6 and 7) seems well established and is correlated with their dominant occurrence in predominantly sandy environments with continually moving waters (Abbott, 1958; Stanley, 1970; Jackson,

1971). Working with North and Baltic Seas invertebrates, Theede, et al., (1969) likewise found that the cardiid Cardium edule had the lowest resistance (whole animal and cellular) of all bivalves tested to both oxygen defficiency and H_2S toxicity. The data for the three species of Semele (Table 7) are of interest for they indicate that differential stagnation tolerance is also important in determining the distributions of individual tellinacean species. This is tentatively confirmed by the distributions of S. proficua and S. purpurascans in Kingston Harbor which parallel those of C. orbiculata and P. costata mentioned above. Finally, the venerid Chione cancellata appears to be quite tolerant of stagnant conditions (Table 8). This species also survives salinities at least as low as $18^o/oo$ for extended periods (Tabb and Manning, 1961) and is very tolerant of high temperature shock (Table 5). This considerable eurytopy correlates well with C. cancellata's more frequent occurrence in shallow water, high stress environments than any other non-lucinacean observed.

C. The Relations of Lucinacean Distributions to Other Factors

While physical and chemical environmental factors are very important in limiting the shoreward distribution of infaunal bivalves, biological factors dominate in generally lower stress offshore environments. The most important to

the Lucinacea appear to be of four sorts related to the presence or absence of sea grasses (or other sediment binding agents), interference by other organisms, food supply and predation. The effects of predation have been briefly discussed elsewhere (Jackson, 1971).

1. Presence or Absence of Sea Grasses

The anterior inhalent tube through which the Lucinacea feed is a fragile structure and is often found adhering to the roots of sea grasses, especially Thalassia. This provides stabilization and protection against destruction by more mobile burrowers. In the absence of such plants otherwise similar sediments tend to be more mobile. Therefore, given similar current conditions, there is a greater probability of disenterrment of infaunal bivalves in grass free environments. Under such conditions, slow burrowing becomes a liability. This is particularly true for larger bivlaves which, other things being equal, take longer to bury themselves than smaller bivalves (Stanley, 1970). The Lucinacea are generally very slow burrowers (Ibid; personal observations) and adults of C. orbicularis, L. pensylvanica and other species often seem incapable of reburrowing in natural environments. Their great vulnerability in naked sediments must therefore have been a major factor in the evolution of the lucinacean preference for sea grass dominated environments. In addition, both the sediments and overlying waters of Diplanthera and Thalassia

environments are characterized by abundant supplies of large-sized organic particles. This is important to lucinacean feeding as will be discussed below.

2. Interference by Other Organisms

Suspension feeding and deposit feeding invertebrates regularly show non-overlapping distributions in offshore, muddy sediments (Rhoads and Young, 1970). Feeding activities and faecal pellet production of protobranch and tellinacean bivalves and other deposit feeders disturb the sediment-water interface and promote high bottom water turbidity (Ibid). Consequently, suspension feeders can neither maintain their burrows nor feed properly due to excessive ctenidial clogging. The overall simplicity in the morphology and function of the lucinacean feeding system (Allen, 1958) makes the group far less susceptible to ciliary clogging than are other eulamelli-branch suspension feeders. The Lucinacea, however, may still be excluded from biogenically unstable deposits by the vul-nerability of their anterior inhalent tube.

Suspension feeders do co-occur in abundance with deposit feeders over a wide area of offshore muds in Cape Cod Bay (Rhoads and Young, 1971; Young and Rhoads, 1971). The sus-pension feeders are able to survive due to the presence of sediment mounds produced by the abundant (2 to 6/m^2) deposit feeding holothurian Molpadia oolitica. The mounds are pro-duced by the feeding activities of the holothurian, are

composed of comparatively coarse sediments and are further stabilized by the abundant presence of the tube dwelling polychaete Euchone incolor. In cross section these worms give the environment the appearance of a miniature sea grass bed. Significantly, the small lucinacean Thyasira gouldi commonly occurs in the holothurian mound microenvironment but is not found in the surrounding valleys which are charac-terized by deposit feeding bivalves and unstable sediments.

Whereas protobranchs are uncommon in the tropics except at great depths, tellinaceans are tremendously diverse and abundant. Observations with SCUBA in the center (30 to 60 m) of Discovery Bay, Jamaica, have revealed the presence of an unstable, reworked carbonate mud interface, an abundance of tellinaceans and the virtual absence of lucinaceans and other suspension feeding bivalves. Clearly sediment alteration by deposit feeders is an important limiting factor in lucinacean distributions.

3. Food Supply

The morphology and ciliary sorting mechanisms of the lucinacean feeding and digestive tract are considerably simpler than the complex systems characteristic of most bivalves (Allen, 1958). In relation to this simplicity the Lucinacea process larger particles than do typical eulamellibranch suspension feeders (Ibid). The amount of such organic detritus, either suspended or on the bottom, is

always considerable in <u>Diplanthera</u> and <u>Thalassia</u> environ-
ments. The great majority of this material is derived
from the leaching and partial breakdown of the vegetation.
The detrital particles provide a vast surface area for the
growth of very large populations of bacteria and other micro-
organisms (Fenchel, 1970). The bacteria metabolize cellu-
lose and other common forms of detrital carbon characteristic
of marine sediments which are not directly utilizeable by
most invertebrates. Such populations of microorganisms are
used as food by many deposit and suspension feeding inverte-
brates (R. Newell, 1965; Reid and Reid, 1968; Fenchel, 1970;
Longbottom, 1970) and are presumably the basis of the lucina-
cean diet as well. In contrast, plankton populations may be
limited in waters over shallow to intertidal back reef flats
(Jackson, 1971). This may explain the absence of typical
suspension feeding bivalves in many of these environments.

Allen's work preceded recognition of the nutritional
importance of detrital microbial populations. He concluded
that the general absence of Lucinacea from environments with
a diverse infauna and their abundance in sulfide rich muds
implied competitive inferiority in relation to other infaunal
bivalves and stated that "the Lucinacea have successfully
adapted themselves to conditions in which food is at a mini-
mum and where the oxygen content of the substratum is very
low." Far from being competitively inferior, however, the
Lucinacea have maintained a dominant position in nearshore,
food-rich environments in the face of the tremendous

evolutionary explosion of siphonate, infaunal suspension feeding bivalves during the Mesozoic and Cenozoic (Stanley, 1968; Bretsky, 1969). Their considerable tolerance of physiological stress has simply extended the range of environments in which the Lucinacea can exploit rich detrital food sources.

The feeding structures in the Ungulinidae are more complex than in the Lucinidae and show more similarities to the typical eulamellibranch condition (Allen, 1958). Lucinids are also able to use larger and more variously-sized particles than ungulinids (Ibid). Therefore, differences between the nature of the food material used by the two families and typical eulamellibranchs must be greater for lucinids than ungulinids. Such differences in diet appear to be the primary reason for the absence of D. semiaspera and D. punctata from reef flats with restricted water movement despite the considerable stagnation tolerance of both of these species. This suggests that plankton are a major component of the ungulinid diet.

Since the lucinid feeding process is one of simplification and generalization, feeding behavior may not be an important aspect of niche differentiation within the family. Hutchinson (1959, 1965) has emphasized the importance of simple differences in size in niche separation and it is reasonable to assume that the median size of particles ingested by lucinids is correlated with overall animal size or the dimensions of the anterior adductor. Thus, both young

and old individuals of the same species, and adults of different sized species, may use different size fractions of detritus and thereby not compete for food resources.

Because of the vast amounts of detritus available, especially on _Thalassia_ and _Diplanthera_ flats or among mangroves, most populations of nearshore Lucinidae are probably rarely, if ever, food limited. For this reason, and by their occurrence in high stress environments, nearshore lucinids are opportunists as characterized by Levinton (1970). In areas examined for any length of time, however, these species did not undergo frequent population fluctuations as is presumably typical of opportunistic species.

Ctena orbiculata has many opportunistic traits. Besides its wide environmental distribution and correlated high physiological tolerance, this species is highly polymorphic (Dall, 1901; Bretsky, 1969). Variations in proportions and ornamentation, such as heavier ribbing and thicker shells in shallow water environments, seem well correlated with the greatly different conditions individual C. _orbiculata_ must contend with over the vast environmental range of this species. _Ctena orbiculata_ also has a remarkably high and constant reproductive activity in comparison with other lucinids collected in monthly samples from the Jamaican north coast (Jackson, 1971). Juveniles (2 to 4 mm) of all the common lucinids were observed in small to moderate numbers during most months of the year. Whereas the number of juveniles of these species never outnumbered that of adults, the

opposite was true for C. orbiculata, generally by an order of magnitude. Such a continuously high reproductive rate should allow this species to quickly and successfully colonize any normally unfavorable environment (such as one made unsuitable by the activities of deposit feeders) in an advantageous period. It should also be the first lucinid to recolonize areas devastated by hurricanes and other catastrophes. Thus, C. orbiculata is an opportunist in much the same way as Mulinia lateralis in more northern waters (Levinton, 1970).

D. The Relations of Lucinacean Physiological Tolerance to Species Size

The environmental distributions and shell lengths of 21 Caribbean shallow water and shelf Lucinidae are shown in Table 13. Environments A, B and C are as illustrated in Figure 5. Environment D includes shelf sands and muds from 20 to about 200 m. The shell lengths are near maximum adult values. There is a considerable size range among these species. Nearly half (10) are one cm or less, whereas six range from more than one to three cm and only five are greater than three cm in length.

Median lucinid shell length is very different (Mann Whitney U Test) between the shallower and deeper environments and greatly decreases with increasing depth. A similar size distribution was observed on a local scale in Jamaica

Table 13. Environmental distributions and shell lengths of 21 Caribbean shallow water and shelf Lucinidae. Environments as illustrated in Figure 5 plus D=shelf (20 to 200 m) sands and muds. Data from references in Table 1 and Abbott, 1954; McLean, 1951; McNulty, et al., 1962; Stanley, 1970 and Warmke and Abbott, 1961. Taxonomy from Bretsky, 1969 except for *. Key: +++=abundant, ++=common and +=rare.

SPECIES	SHELL LENGTH (mm)	ENVIRONMENT A	B	C	D
LUCINA					
(Lucina) pensylvanica	50	+++	+++		
(Cavilinga) trisulcata	10	+		+	+
(Bellucina) amiantus	5		+	+++	++
(Parvilucina) multilineata	5		+	+++	+++
(P.) costata	15	+++	+++	+++	
(P?) portoricana	7			++	+
(Pleurolucina) sombrerensis	5				++
(P.) leucomya	5			++	++
(Phacoides) pectinata	70	+++		+	
(Lucina) muricatus	10			++	+
(L.) nassula	10	++		++	++
(Callucina) radians	15			+	++
*("Codakia") pectinella	4			+	+
ANODONTIA					
(Anodontia) alba	50	+++	++	+	
(A.) philippiana	50			+	+
(A.) phenax	10			+	+
CODAKIA					
(Codakia) orbicularis	80	+++	+++	+	
(C.) cubana	18				+
(Ctena) orbiculata	25	+++	+++	++	+
DIVARICELLA					
(Divalinga) quadrisulcata	25	+++	+++		+
(Egracina) dentata	30		+		
Number of Species		9	9	16	15
Median Species Length (mm)					
presence/absence		25	25	10	10
abundance weighted		25-50	25	10	7-10

(Jackson, 1971). The significance levels of the size differences between lucinids in environment A and deeper habitats (C, D) are shown in Table 14 using both presence/absence and abundance weighted data. In abundance weighted tests, each species was counted once, twice or three times depending on whether it was listed as rare, common or abundant in Table 13. Size differences are greatest between environments A and D but are also highly significant between environments A and C in the abundance weighted comparison. The smaller species occur in a variety of environments but only one species smaller than two cm occurs abundantly in environment A and all of the species one cm or smaller are most characteristic of more offshore environments.

In order to feed and survive in a reducing sedimentary environment infaunal suspension feeders must maintain contact with the overlying seawater. Therefore, body size (or siphon length, lucinid foot length, etc.) strongly controls how deeply an organism can burrow and, in general, large bivalves burrow deeper than small bivalves (Stanley, 1970). In very shallow to intertidal environments deep burrowing allows escape from high temperatures, extreme salinity fluctuations and other sea water variations which greatly decrease with increasing depth into the sediment. In addition, large bivalves are usually more eurytopic than are small bivalves.

Large size also decreases gastropod predation. For example, on back reef Thalassia flats the percentage of

Table 14. Significance levels of difference in median lucinid length between environment A and deeper environments (C, D).

	ENVIRONMENT PAIRS	
	A-C	A-D
presence/absence	not significant	P_.05
abundance weighted	P_.001	P_.001

drilled valves of C. orbicularis was found to be consistently less than for the much smaller C. orbiculata. When different species are of roughly similar size, however, the shallowest burrowers suffer the heaviest predation. Thus, in similar environments the percentage of drilled C. orbicularis was found to be greater than for the deeper burrowing A. alba and P. pectinata. This is especially noteworthy since shells of C. orbicularis are appreciably thicker than those of A. alba. Presumably, other sorts of predation are also affected. Large size certainly reduces predation by water birds and fish and deeply burrowing bivalves are less accessible to excavation and attack by fishes and rays.

There are as well numerous disadvantages to large size in burrowing bivalves and these are, most importantly, a lower surface to mass ratio and the greater time required for completion of reburrowing if disinterred (Stanley, 1970). The former, as a function of gill area, is important in both food collecting and respiration. In the large lucinids, the decreased surface to mass ratio is offset by the presence of respiratory pigments and mantle gills. It is of little consequence to feeding efficiency due to the comparative insignificance of the ctenidia in the lucinid feeding process. The large lucinids studied tend to live in stable sediments and disinterrment is only likely to occur during catastrophic events such as the destruction of entire Thalassia beds by hurricanes. In

addition, the ventral peripheral regions of all lucinid shells examined are up to two times as thick, and therefore two times as heavy, as compared to the area of the umbo. Unlike most other infaunal bivalves which apparently do not show such shell thickening, most lucinids live with their dorsal area upwards as shown in Figure 1. Thus, the differential shell weighting must provide a stabilizing effect within the substrate.

In the shelf environment (D), there are generally neither large temperature and salinity fluctuations nor extensive growths of sediment binding plants. Thus large size is likely to be more of a liability and this is confirmed by the significantly smaller size of the offshore lucinids. The importance of the holothurian mound microenvironments in Cape Cod Bay (Rhoads and Young, 1971) demonstrates the much smaller scale of the environmental mosaic which controls the distributions of soft bottom infauna in deeper waters. Clearly, the preponderance of smaller lucinids in the finer sediments of bays and shelf areas must reflect a far greater variety of suitable microenvironments for bivalves less than one cm in length than for larger forms.

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Part 2. MOLLUSCAN POPULATION VARIABILITY AND DIVERSITY

IN MARINE THALASSIA COMMUNITIES, JAMAICA, WEST INDIES

I. ABSTRACT

Four homogeneous areas within beds of the marine angio-
sperm Thalassia were selected along a composite onshore--
offshore gradient for detailed study. Eleven environmental
variables and molluscan and echinoderm abundance were
sampled at monthly intervals for one year. Environmental
conditions were generally more extreme, and their variance
greatest, nearshore and decreased significantly with dis-
tance from shore. Environmental predictability and cumula-
tive diversity (H) increased with distance from shore,
whereas abundance was greatest in the more high stress en-
vironments. Over the year, population stability was at
least as great in the unpredictable, low diversity environ-
ments as in the more predictable, high diversity environments.

Bivalves collected from the low diversity environments
were markedly eurytopic forms whereas the highest diversity
area contained predominantly stenotopic taxa. Typical sus-
pension feeders were dominant only in the most diverse area,
whereas more generalized feeders dominated the higher stress
environments. There was no correlation between bivalve diver-
sity and the total quantity of food available, but bivalve
diversity increased with the variety of available food.

In multivariate regression analyses, the environmental

variables as a set were highly significant in "explaining" the population variables in any one area but subsets, or individual variables, were not significant. Between areas, the environmental set alone was not significant and a full 31 parameter model was required to "explain" the distributions. It is suggested that catastrophes, and other long term phenomena, and biological factors, such as predation, are of great importance in determining the differences in fauna between these areas.

II. INTRODUCTION

Diversity patterns and distributions within the oceans and coastal waters have been described for a great many level bottom environments. A variety of theories have been put forth to explain these distributions, but comparatively few studies have been attempted (see most notably the early work of Sanders, 1956, 1958, 1960) in which detailed information on the environment, biology of the dominant taxa and distribution patterns have been combined so as to allow evaluation of these different proposals.

This study was designed as a within habitat comparison of the annual individual and total species variability along a composite onshore-offshore environmental stress gradient in four Jamaican marine angiosperm (Thalassia) communities. The purpose was to:

1. characterize the individual environments in terms

of the variability of factors known or suspected to be of ecological importance. Eleven such factors were measured on a regular (monthly) basis and observations made on numerous others.

2. characterize the environments in terms of the nature, distributions and variability of their biota. Monthly observations were made on a number of groups but primary attention was given the molluscs and echinoderms with particular emphasis on the infaunal and semi-infaunal bivalves.

3. determine the variety of dominant bivalve taxa and establish their range of tolerance to a number of stress conditions. Detailed studies were carried out on the physiological tolerance, distributions and general adaptive strategies of numerous species of the Lucinacea and other important bivalve taxa and are reported elsewhere (Jackson, 1971).

4. determine the environmental variables most responsible for the nature of the fauna and their distributions. This has been attempted through use of experimental physiological data, correlations between individual environmental factors and population variations and through multivariate regression analysis.

5. evaluate these results in terms of theories regarding the origins of diversity patterns and their distributions.
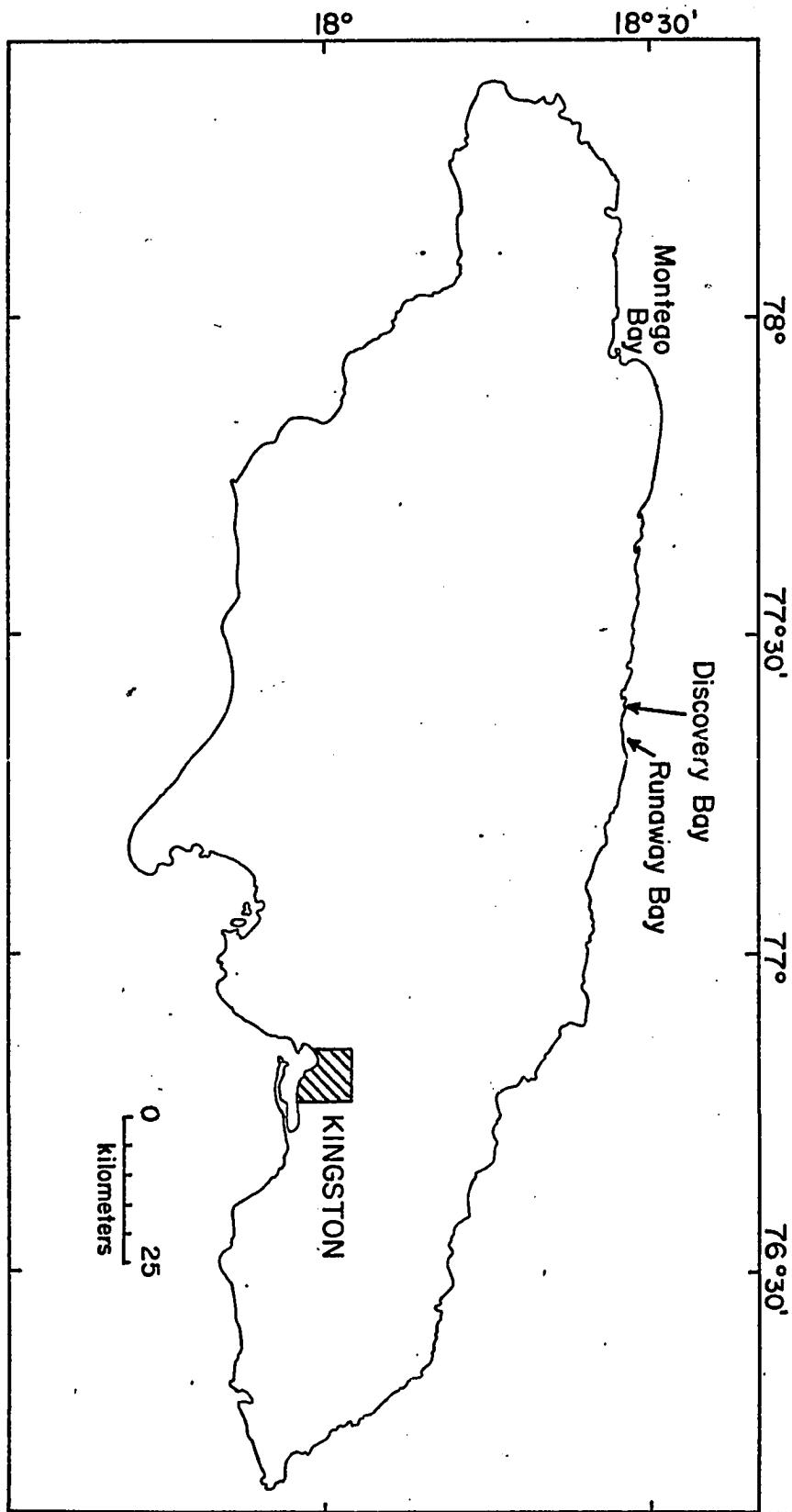
III. METHODS AND STUDY AREAS

A. Sampling

A pilot study was carried out in Florida, Puerto Rico, Curaçao, Panama and Jamaica in July and August of 1968 in order to gain some knowledge of the range of population densities and diversities commonly found in Caribbean shallow water Thalassia beds. On the basis of these findings, two study areas were chosen between Discovery Bay and Runaway Bay on the north coast of Jamaica, West Indies (Figure 1). The first of these is a back reef flat at a locality known as Pear Tree Bottom (Figure 2). Sampling areas (designated I and II) of 5 by 7 m were laid out, long axis parallel to the shore, at distances of 20 and 35 m from the mean high water mark (Figure 3). The other locality chosen was the southeastern corner of Discovery Bay (Figures 4 and 5) where two similar sized areas (III and IV) were laid out at approximately 60 and 120 m from shore (75 m apart) to the west of the old Discovery Bay Marine Laboratory site.

At each of the four sample areas a grid was constructed using four stakes and marked lines to delimit 5 by 7 m rectangles divided into 100 0.5 by 0.7 m rectangular sample cells. A reference corner point (0, 0) was chosen and the adjacent axes noted as 1,2,...9, thereby assigning cell numbers 00 to 99. At each area, 48 cells were chosen in a
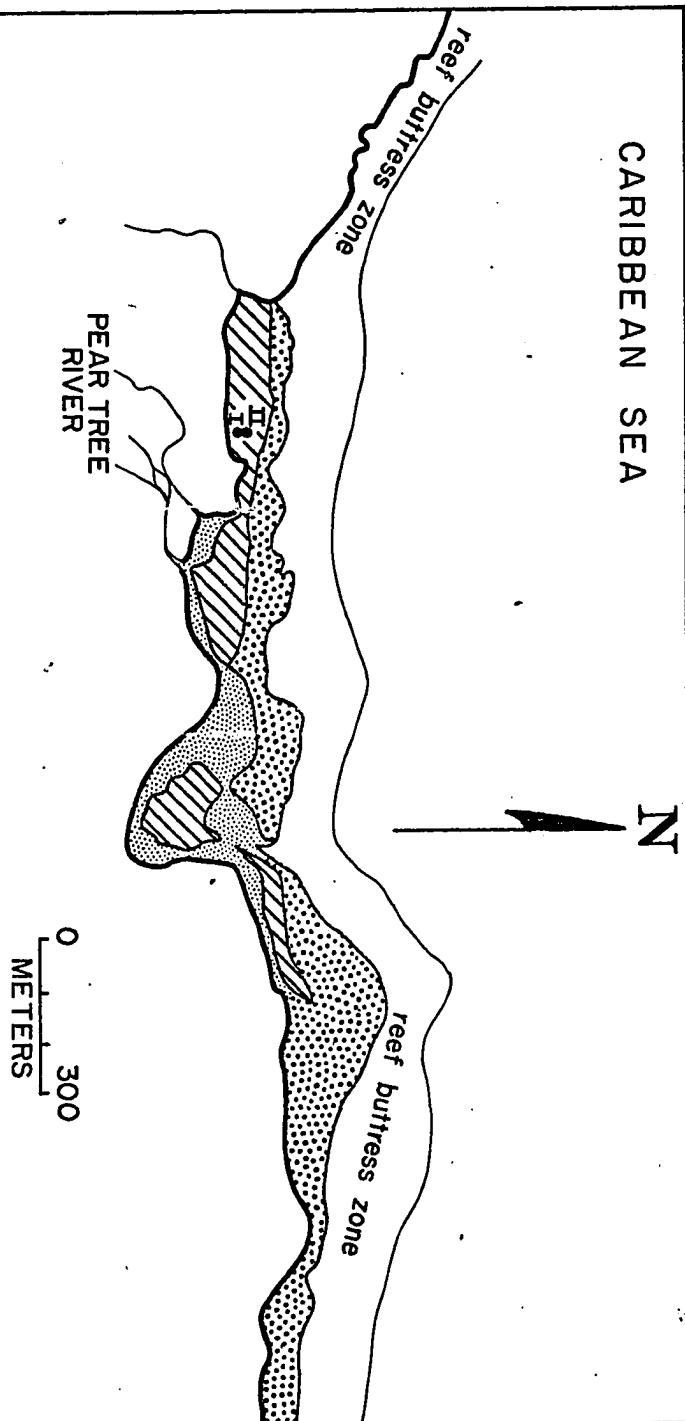
Figure 1. Map of Jamaica with location of sample areas.

Montego Bay

Discovery Bay

Runaway Bay

KINGSTON

0

25

kilometers

18°

18°30'

78°

77°30'

77°

76°30'

Figure 2. Environmental map of the Pear Tree Bottom area

drawn from an aerial photograph showing location of

sample areas I and II.

CARIBBEAN SEA

PEAR TREE BOTTOM SAMPLE AREAS & ENVIRONMENTS

PEAR TREE RIVER

reef buttress zone

reef buttress zone

N

0 300
METERS

Thalassia

Reef crest, rubble, bare rock

Sand

Sample areas I and II

Figure 3. Diagrammatic map of Pear Tree Bottom back reef flat showing location of sample areas I and II.

BUTTRESS ZONE

BOULDER REEF CREST

ROCK AND THALASSIA

THALASSIA

II

THALASSIA & DIPLANTHERA

I

DIPLANTHERA

BARE SAND

SAND BEACH

THIN SEDIMENTS

~80 METERS

THICK SEDIMENTS

0   10   20   30   40   50
METERS
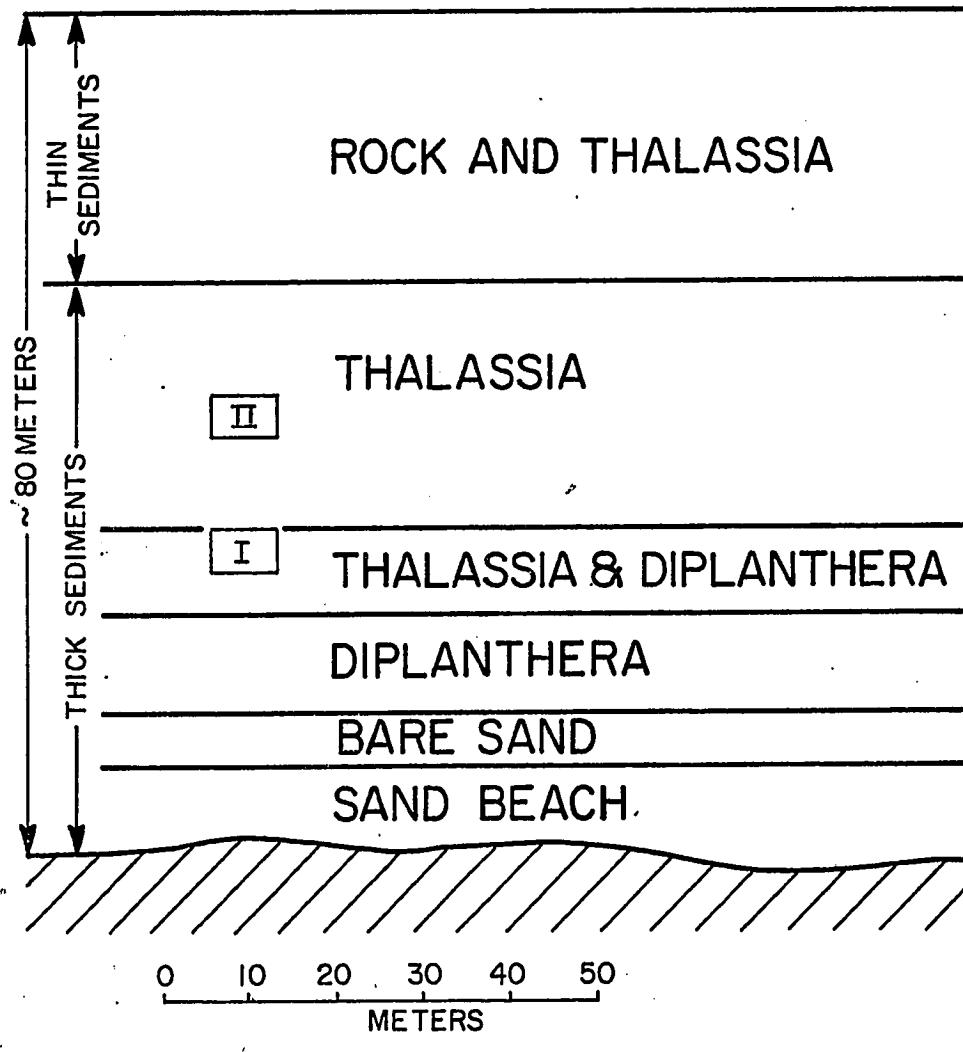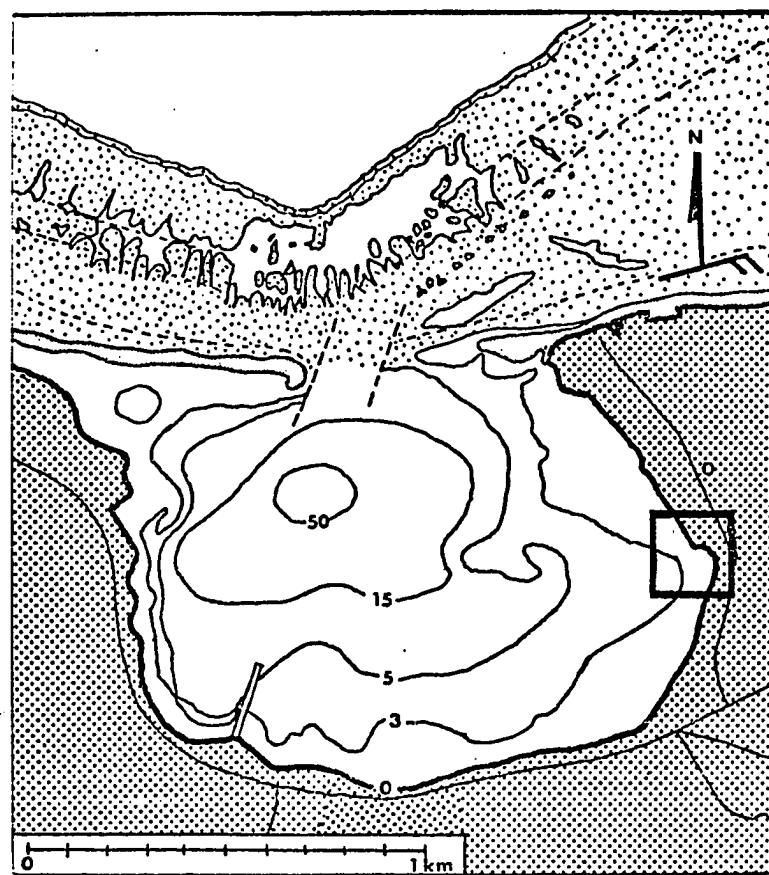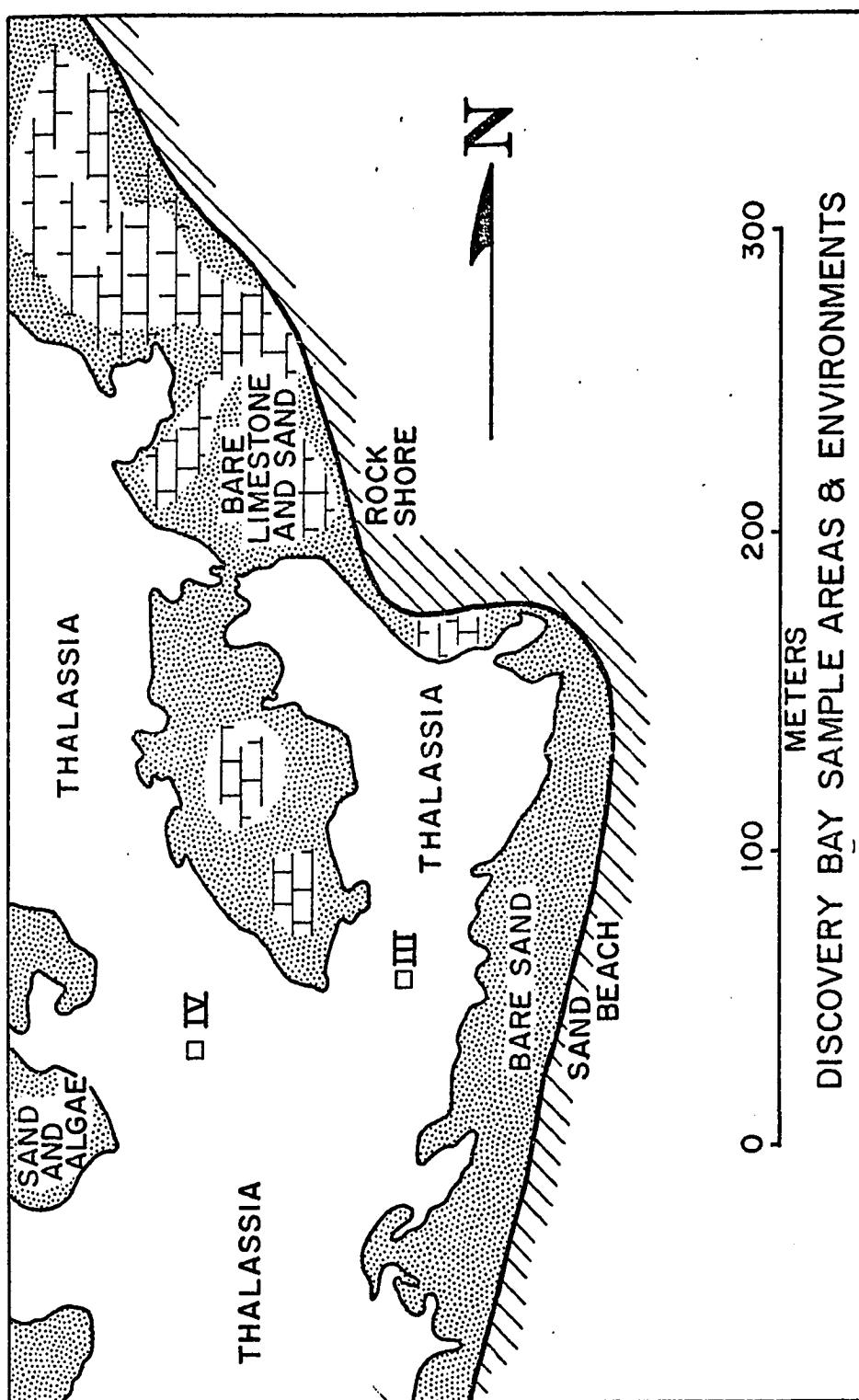
Figure 4. Map of Discovery Bay. Box defines area of detail map of Figure 5.

Figure 5. Environmental map of southeastern Discovery
Bay drawn from an aerial photograph showing location of
sample areas III and IV.

DISCOVERY BAY SAMPLE AREAS & ENVIRONMENTS

THALASSIA

SAND AND ALGAE

THALASSIA

□ IV

□ III

THALASSIA

BARE SAND

SAND BEACH

THALASSIA

BARE LIMESTONE AND SAND

ROCK SHORE

N

0   100   200   300
METERS

random sequence for sampling at monthly intervals, four replicates per month, for one year.

The sample areas were located in as homogeneous localities as possible from surficial examination. However, in anticipation of encountering cells which could not be properly sampled, the four peripheral rows outside the lines were designated as alternative cells. In the event that a sample could not be taken in the proper cell (due to the presence of a large rock, etc.) it was collected from the same point in the nearest peripheral row. Thus, in each area a total of 48 of a possible 140 cells were sampled at random over a one year period. This intensive sampling of approximately 34% of the available area was a necessary compromise between maximal environmental homogeneity and minimal environmental disturbance due to sampling.

Because of the widely disparate sizes of the organisms present, three kinds of samples were collected from each cell including one 0.25 m^2, one of 0.10 m^2 and a one inch (2.54 cm) internal diameter core. The core was obtained from the center of the area from which the 0.25 m^2 sample was to be removed and the 0.1 m^2 from the remaining area of each cell. No quantitative sampler is available that will effectively penetrate the thick _Thalassia_ root mat and produce repeatedly similar samples of adequate size not only in wadeable depths but also in deeper areas. Therefore, the following sampling procedure was used for the larger samples.

A grid the same size as the area to be removed was placed in the cell and a knife was used to cut out the shape of the sample. Then, a heavy pronged garden pitch fork was used to loosen the root mat and substrate to a depth of approximately 20 cm as determined by the length of the prongs. In the shallow areas at Pear Tree Bottom the samples were then lifted out by hand. The 0.25 m^2 samples were sieved on location, away from the sample areas, using a 0.64 mm (=¼ inch) mesh. The 0.1 m^2 samples were placed in large plastic cans for subsequent sieving with a one mm mesh at the Laboratory. In the deeper sampling areas at Discovery Bay the samples were cut out and loosened as above but were immediately lifted by the SCUBA diver into large garbage containers fitted with lids to prevent the loss of floatable material, especially _Thalassia_ leaves. These samples were sieved in the same manner as those from Pear Tree Bottom. Sample volumes varied by as much as 15 to 20% but largely due to the presence of large buried rocks, which prevented uniform excavation to 20 cm. The cores were preserved in buffered formalin within a few hours of collection and the top 2 to 3 cm sieved with a 0.63μ screen. These samples were then preserved in alcohol and are presently being examined for foraminifera, micro-molluscs (including juveniles) and other microfauna.

Both live animals and unbroken dead shell material were saved from the 0.25 m^2 samples. All live molluscs and most echinoderms were identified and counted and all

the live infaunal and semi-infaunal bivalves were measured
(shell length) with calipers to 0.1 mm. These length data
were used for an estimate of biomass. The same methods
were used for the 0.10 m^2 samples except that the _Thalassia_
leaves and roots were saved to be dried and weighed. In
each area, all 48 of each of the three sample types were
successfully collected over the one year period of study.

Sampling was carried out from November, 1969 to October,
1970. Sampling was begun between the 27th and 29th of each
month and required between four days and one week for com-
pletion. All sampling at Pear Tree Bottom was completed in
a single day. Collections of the physical-chemical samples
and the cores and measurements of the environmental variables
at Discovery Bay were generally carried out on the following
day, weather permitting. For comparative purposes, collec-
tions and observations were made at mid-morning, usually at
10 to 10:30 A.M.

The environmental variables were measured or sampled
in each area by the following procedures:

1. Before the areas had been disturbed, separate water
samples were collected for measurements of "turbidity" and
particulate organic carbon. The samples were collected in
screw-top jars which were opened about 10 cm above the
sediment-water interface; they were stored under refrigera-
tion until the analyses were performed in the laboratory.
A single approximately 600 ml sample was collected for
particulate organic carbon analysis in each area. Five

hundred ml were poured off during vigorous mixing and filtered through precombusted 4.25 cm Reeve Angel #934 AH glass fiber filters. These were analysed by the standard "wet ashing" acid dichromate method (Strickland and Parsons, 1965). Extinction was measured on a Bausch and Lomb Spectronic 20 spectrophotometer and particulate organic carbon calculated in mg C/m^3. Although this method is subject to considerable questioning, it was considered adequate for this comparative environmental study with all measurements carried out in the same laboratory.

The variety of suspended particulate organic matter present was not regularly determined. Reiswig (1971) has provided considerable data on the variety and amount of $> 0.22 \mu$ visible particulate organic matter present in the immediate vicinity of the Discovery Bay sample areas. For purposes of comparison, two similar samples were collected at Pear Tree Bottom in the summer, 1970. The filters were stained and examined qualitatively in order to obtain a rough estimate of the dominant material present.

2. Single "turbidity" water samples were collected in each area by the above procedures. These were vigorously shaken and 225 ml filtered through a 25 mm 0.22μ Millipore type GS membrane filter at low suction. The resulting material was scraped from the filter and resuspended in 10 ml of distilled water. Extinction of the constantly mixed sample was measured on a Bausch and Lomb Spectronic 20 in 50 mμ intervals from 350 to 800 mμ. The average

extinction for all frequencies was used as the measure of "turbidity."

3. Additional water samples were collected by the above methods in glass jars above each cell to be sampled and these were stored in shade until return to the laboratory. Water pH and dissolved oxygen were measured immediately on opening the jars. The pH was measured using a Beckman Expandomatic laboratory meter and oxygen was measured using a Yellow Springs Model 50 oxygen meter. In these and the other sediment and water chemistry analyses performed each month, comparative measurements _in situ_ and in samples stored up to a few hours before measurement in the laboratory showed no significant differences in the values obtained.

4. Bottom water salinity was measured with a Beckman portable electrodeless salinometer of the CBI type.

5. Bottom water and sediment (3 to 4 cm below the sediment-water interface) temperatures were measured with a calibrated thermometer accurate to $\pm 0.1^{\circ}C$.

6. A sediment sample was collected in each cell using a screw-top jar. These were immediately sealed and stored in the shade until returned to the laboratory. Pore water pH was measured immediately on opening the jars by probing the sample with the pH electrode. Replicate measurements were made for all samples and the meter recalibrated at frequent intervals during the measurements. Sulfide ion activity was also measured using a Keithley electrometer and a silver-silver sulfide electrode by the

methods of Berner (1963).

7. Size analyses were performed on the same sediment samples. After removal of all _Thalassia_ material, the sediments were oven dried at $105^{\circ}C$, weighed and wet sieved into seven fractions including silt plus clay. The fractions were dried, weighed and subtracted from the total weight for the percent silt plus clay fraction. The data were analyzed according to the standard procedures of Krumbein and Pettijohn (1938).

B. Statistical Methods

The variance/mean ratio $(s^2/\bar{x})$ has been used in all cases as an approximate measure of spatial (or spatial-temporal) distributions. Values not significantly different from one are considered random, less than one regular (=uniform, infradispersed) and greater than one aggregated (=clumped). Pielou (1969) and Greig-Smith (1964) have discussed the applications and deficiencies of this procedure. In cases when a collection is not too large for all its members to be identified and counted it is appropriate to use the Brillouin uncertainty measure, H, as an index of diversity and this has been done in this study (see Pielou, 1966, 1969). This is given by:

$$H = \frac{1}{N} \log \frac{N!}{N_1! \, , \, N_2! \ldots N_s!}$$

where N is the total number of individuals in the sample and N_1, N_2...N_S is the number of individuals in each of S species. Stirling's approximation was used in the computer calculations of the factorials and logarithims were taken to the base 2.

In the calculation of cumulative diversity, the diversity is first calculated for a single sample, then the animals of a second sample are added to those of the first and the diversity is recalculated and so on throughout the entire number of samples available. This procedure was carried out using all 48 samples (0.25 and 0.10 m^2 combined) from each area. Calculations were made for three different bivalve groups (defined below) using both abundance and length abundance data. For calculations of length diversity the data (measured to 0.1 mm) were multiplied by 10 and rounded to the nearest whole number. Calculations were made twice for each of these groups, once in the sequence in which the samples were collected throughout the year, and secondly in an arbitrary random sequence (same random sequence for each set of calculations).

A set of samples can be considered a reasonable representative of the community or association under study if its cumulative diversity curve starts to level off well before the information from the last samples has been included in the calculations. Besides the number of species and their relative abundances, such a pattern is dependent on two major factors: sample size and the distributions of the

different taxa (both in kinds and abundance) in both space and time.

It is not the purpose of this paper to review the vast literature on the subject of sample size in field collections (see Greig-Smith, 1964; Pielou, 1969). Clearly, the sample size should be sufficient to guarantee a number of individuals in most samples. Below a mean population density of about two, especially in cases where there are a large number of samples with one's and zero's, the variance to mean ratio ($s^2/\bar{x}$) breaks down as an estimate of spatial distribution (Taylor, 1961). In this case it is no longer possible to make significant statements regarding the presence or absence of individual taxa within any group of samples.

Even if the sample size is adequate, randomness or aggregation in time or space will produce variations in the smoothness of the cumulative diversity curve proportional to this inherent inhomogeneity in the populations. Finally, besides all these possible variations in the states of the populations, H is itself dependent on sample size since, especially for large numbers, N! of the total population increases more rapidly than for the smaller populations of any individual species.

For comparing variances, limits of the interval estimate of F were obtained by dividing the sample ratio by tabulated values of F (P $\leq$ .05). The null hypothesis that the two variances are equal is rejected at 5% if the sample

ratio does not lie between these calculated values.

Because of demonstrated differences in variances, use of

the t-test was not justified and the Fisher-Behrens pro-

cedure was used for testing the significance between means

of these variables. The correlation matrices of environ-

mental and population variables were obtained by the pro-

duct moment procedure. The Kendall Rank-Order method was

also used. All these methods are discussed in Campbell

(1967).

An a priori multivariate linear model was constructed

on the plan of the univariate analyses of Buzas (1969).

The model simultaneously considers five dependent popula-

tion variables (number of species, number and length number

of bivalves, diversity and length diversity) for each of

three bivalve groups (the composition of which is discussed

below) in relation to the observed environmental variables,

station differences, periodicities and station difference-

periodicity interactions. Such a model is appropriate when

a number of dependent variables are known or suspected to be

correlated and is discussed at length by Seal (1964, chapter

5) under the title of the p-variate linear model.

Briefly, in matrix notation:

$$\underset{(N \times P)}{X} = \underset{(N \times q)}{Z'} \quad \underset{(q \times p)}{B} + \underset{(N \times p)}{E}$$

where X is a matrix of N observations on p dependent variables,

Z' is a matrix of the q observed environmental variables and

instrumental variates, $B\Omega$ is a matrix of q parameters to

"explain" the observations and $\underset{\sim}{E}$ is a matrix of residuals not accounted for by the model.

Following calculation of the matrix products $\underset{\sim}{Z}X$ and $\underset{\sim}{Z}Z'$ and the inversion of the latter, an estimate of $B\Omega$ is obtained from

$$\hat{\underset{\sim}{B}\Omega} = (\underset{\sim}{Z}Z')^{-1} \underset{\sim}{Z}X.$$

It is then appropriate to postulate a series of reduced models $\omega_1, \omega_2, \ldots \omega_n$ in which natural groups of beta's are set equal to zero and the calculations repeated. The significance of any reduced model ω is obtained by calculating the ratio U where

$$\frac{\left| (N-q) \hat{\underset{\sim}{\Sigma} \Omega} \right|}{\left| (N-s) \hat{\underset{\sim}{\Sigma} \omega} \right|} = U_{p, \, q-s, \, f}$$

where

$$-\left\{ f - \tfrac{1}{2}(p-q+s+1) \right\} \ln U_{p, \, q-s, \, f} \qquad f=N-q$$

is distributed approximately as chi-square with $p(q-s)$ degrees of freedom. Because of covariance of environmental variables, significance tests for individual variables were conducted following the methods of Scheffe (Seal, 1964).

The sampling program has already been discussed. For each set of population variables there are $i=1,2,\ldots12$ months, $j=1,2,3,4$ stations (=environments) and $k=1,2,3,4$ replicate samples. The number of observations, N, is 48 for the single station case and 192 for simultaneous analysis of all four areas. All values of the dependent variables were transformed to $\ln (x_{ijk}+1)$ before the analyses.

The composition of the matrix $\underset{\sim}{Z}'$ for any single dependent variable is shown in Tables 5 and 6 of Appendix A for the single station and combined station models respectively. z_0 is a vector of units such that by making all other vectors sum to zero, β_0 is the mean of all 48 or 192 observations. z_1 through z_{11} (or z_4 through z_{14} in the four station cases) are the observed environmental variables and z_{12} through z_{15} (or z_{15} through z_{18}) describe the periodicities as discussed by Buzas (1969). In the larger model, z_1 through z_3 account for station differences and z_{19} through z_{30} describe interactions between these station differences and the periodicities.

All computer analyses were run on the IBM 7094-7040 and IBM 360-85 systems of the Yale Computer Center.

IV. RESULTS

A. Environments

1. Pear Tree Bottom Back Reef Flat

The zonation of environments on the Pear Tree Bottom back reef flat site is shown in Figure 3. The correlation matrices for all eleven regularly measured environmental variables are given in Figures 16 and 17 of Appendix B. The boulder crest of the reef (Frontispiece) lies between 80 to

100 m from the mean high water mark. The crest is normally exposed in various places at all tides and is formed from reef material thrown up from the more seaward buttress zone during severe storms. The reef flat behind the crest is a constructional feature built up by the accumulation of reef rubble and biogenic calcareous sediments which are stabilized by the root networks of <u>Thalassia</u> <u>testudinum</u> and <u>Diplanthera</u> <u>wrightii</u> (Figure 6).

From the crest to about 50 to 60 m from shore, the unconsolidated sediment is a thin (maximum about 10 cm), irregular veneer lying over and between reef derived rubble. Shoreward of this point, however, sediment accumulation is fairly considerable and, where probed, appeared to be well in excess of 50 cm in thickness. In addition, the median grain size of the sediment increases away from shore (Table 10 of Appendix B). Both of these phenomena are due to the greater effect of storm waves in winnowing material near the region of the reef crest which usually forms a very effective barrier between the sea and the land in this area. When seas run as high as 2 m, the thin layer of water over the flat may be little disturbed except by wind or during very high tides.

On the ebb, the water behind the crest is almost entirely isolated from the sea and only a very limited current is maintained, most often as a weak counterclockwise circulation moving at from one to two cm per second. This

Figure 6. Pear Tree Bottom back reef flat with stakes showing location of sample areas I and II.

circulation is maintained by the strong N. E. Trade Winds which are regularly active in the area and drive the strong east to west longshore current on the north coast of Jamaica. At other times with no wind, almost the only water movement is that of very slight oscillations perpendicular to the shore which are generated by the occasional waves that carry over the crest. This process is only effective for a few hours around high tide when there may be comparatively open circulation of water between the back reef area and the sea.

Just to the east, and therefore upcurrent of the study area, are a pair of small inlets. The western one receives two of the channels of the Pear Tree River (Figure 2). Another channel empties into the sea at the western end of the back reef flat and is therefore downcurrent of the study area. During the study period these channels always contained flowing water, although the level fluctuated considerably, and often discharged vast amounts of reddish-brown, bauxite laden water during periods of a few days following heavy rains in the hills and mountains to the south. The reef crest generally formed a very effective barrier to this fresh water which floated out to sea in a long band past the reef and sometimes extended down shore for many km before becoming well mixed with the seawater. However, when such flows occurred during periods of exceptionally high tides the back reef flat was exposed to very brackish conditions for periods of a few hours or more, twice daily. This

condition was observed from 25 to 29 May, 1970. Unfortunately, the salinometer available was not operational at the time, but by most conservative estimates, salinities were well below 15°/oo on every high tide. During this time considerable amounts of silt and clay settled out over the back reef flat with each tidal influx of bauxite laden water.

As already seen, the back reef flat at Pear Tree Bottom is characterized by unpredictable environmental variations of generally very high variance. The tidal pattern is semidiurnal with the usual spring and neap events with a normal range of about 25 cm. However, this pattern is commonly overshadowed by irregular fluctuations generated by storms, shifts in circulation patterns, etc. Of specific interest in this context, organisms living within 30 to 50 m from shore may be exposed at any time of the year in an apparently random fashion. The normal low tide depth at I is from 10 to 15 cm and at II about 20 cm. Area I may be exposed 10 or more times a year whereas Area II was only observed to be fully exposed at low tides over a single three day period in 1970.

Diurnal fluctuations in water temperature, and less frequent salinity, may be almost as great as the entire annual range of these parameters. Figures 8 and 9 give the average values of all but the sediment environmental variables throughout the year at the time of the monthly samplings. The yearly means and standard deviations are also given in these figures. When low tides occur in the

afternoons of hot, sunny days, water temperatures may rise as fast as $2^{o}C$ per hour, reaching maxima of about $41^{o}C$. Sediment temperatures rise more slowly, usually no more than $1^{o}C$ per hour, and reach maxima of about $39^{o}C$. Such high temperatures may occur at almost any time of year but are more common during summer months when surface temperatures of freely circulating seawater average about $30^{o}C$. Nocturnal low temperatures were not measured with any regularity but apparently do not drop more than two or three degrees below surface seawater temperatures which may fall to about $25^{o}C$ during winter months. The slightly lower $(0.1^{o}C)$ mean water temperature at I as compared to II resulted from a procedural oversight whereby the temperatures at I were almost always measured before those at II. The approximately 15 minutes between the sets of measurements at mid-morning was sufficient for a significant change in temperature.

As seen in Figure 8, the longest period of generally low salinities occurred from April to September. This was quite unexpected since this period is the dry season on the north coast of Jamaica and 1970 was not an unusual year in this regard. However, these low salinities were not due to local events at all but were the result of river discharge as a result of the heavy rains which regularly occur in the mountains of central Jamaica at this season. Besides these fluctuations, local heavy rains, especially during winter months, may pour up to 5 or 10 cm of fresh water onto the

back reef flat in only a few hours. If this occurs during an unusually low tide, salinities of only a few parts per thousand may be present over the flat for the duration of the low tidal cycle.

In relation to both rapid fresh water influx and prevailing sea and wind conditions, "turbidity" was observed to fluctuate very considerably over the flat (Figure 8). Turbid water conditions were often limited to only a little longer than a single high tide period but occasionally lasted up to a week or more during periods of especially strong river outflow or continually heavy rains.

The particulate organic carbon in the seawater was always high and fluctuated wildly (Figure 8). The 4117 mg C/m^3 for Area I should be correct in order of magnitude and was due to the presence of great amounts of visible Thalassia derived detritus present suspended in the water at the time of collecting. Why this was true at Area I and not at II is not known. Qualitative examination of the filter samples indicated that the great majority of the suspended visible particulate organic matter on the reef flat consists of Thalassia derived detritus rather than plankton.

Daytime oxygen saturation values (Figure 9) were very high and had already reached near peak values (upwards to 200% saturation) by mid-morning, the time of the monthly collections and observations. Such values are the result of the high photosynthetic activity of the Thalassia and

the semi-confined nature of the water mass. Comparatively low oxygen saturation generally corresponded to similarly low water temperatures. This correlation is not direct, however, but results from the similar effect of heavy cloud cover on both these variables. Oxygen was not measured at night but presumably decreased well below saturation in response to the high respiratory demand of both the Thalassia and animal community.

On the back reef flat the environmental gradient across the sediment water interface is extreme. Sulfide ion activities in excess of -0.5 volt were present in almost all samples within one or two cm of the sediment surface. The resulting daytime gradient from as much as 200% oxygen saturation to such actively reducing conditions within one or two cm is among the harshest natural environmental boundaries known. The pH gradient across the interface was correspondingly great (Figure 9) with sediment values ranging from 0.8 to 1.4 pH units below that of the overlying bottom water.

Also of ecological importance is the considerable gradient between daytime sediment and water temperatures (Figure 9) with the latter averaging a full degree warmer than the former over the one year period. This difference was infrequently less than $0.5^{\circ}C$, even in winter months, and was commonly more than $3.0^{\circ}C$ on excessively hot sunny days. This considerable increase in temperature gradient with rising temperature was highly significant ($P \leq .001$) and points out the considerable environmental buffering maintained

by the sediments in such environments. This effect was always greater in finer grained sediments.

Diplanthera is the only marine angiosperm present from the narrow bare sand zone at the beach to about 10 m from shore. At this point Thalassia begins to appear and rapidly becomes the dominant plant (Figure 3). At 20 m from shore, at the point of the shoreward border of Area I, Thalassia comprises about 90% of the angiosperm biomass and within a further 5 to 10 m Diplanthera drops out completely. Thalassia is short-leaved on the back reef flat, especially towards the shore. This is common in such areas, as the leaves do not survive long periods of complete exposure. The total Thalassia biomass increased significantly with distance from shore up to the point where the sediment thickness decreases to a thin veneer and cover becomes less than complete. Throughout this range, although leaf length increased greatly, the rhizome-root biomass was well in excess of 90% of the total Thalassia dry weight. There was a slight but consistent increase in dry weight from the winter low to August at II but there was no such apparent seasonal component at I (Figure 9).

2. Discovery Bay

An environmental map of the southeastern portion of Discovery Bay is shown in Figure 5. The correlation matrices for all eleven regularly measured environmental variables are given in Figures 18 and 19 of Appendix B. The Bay is slightly
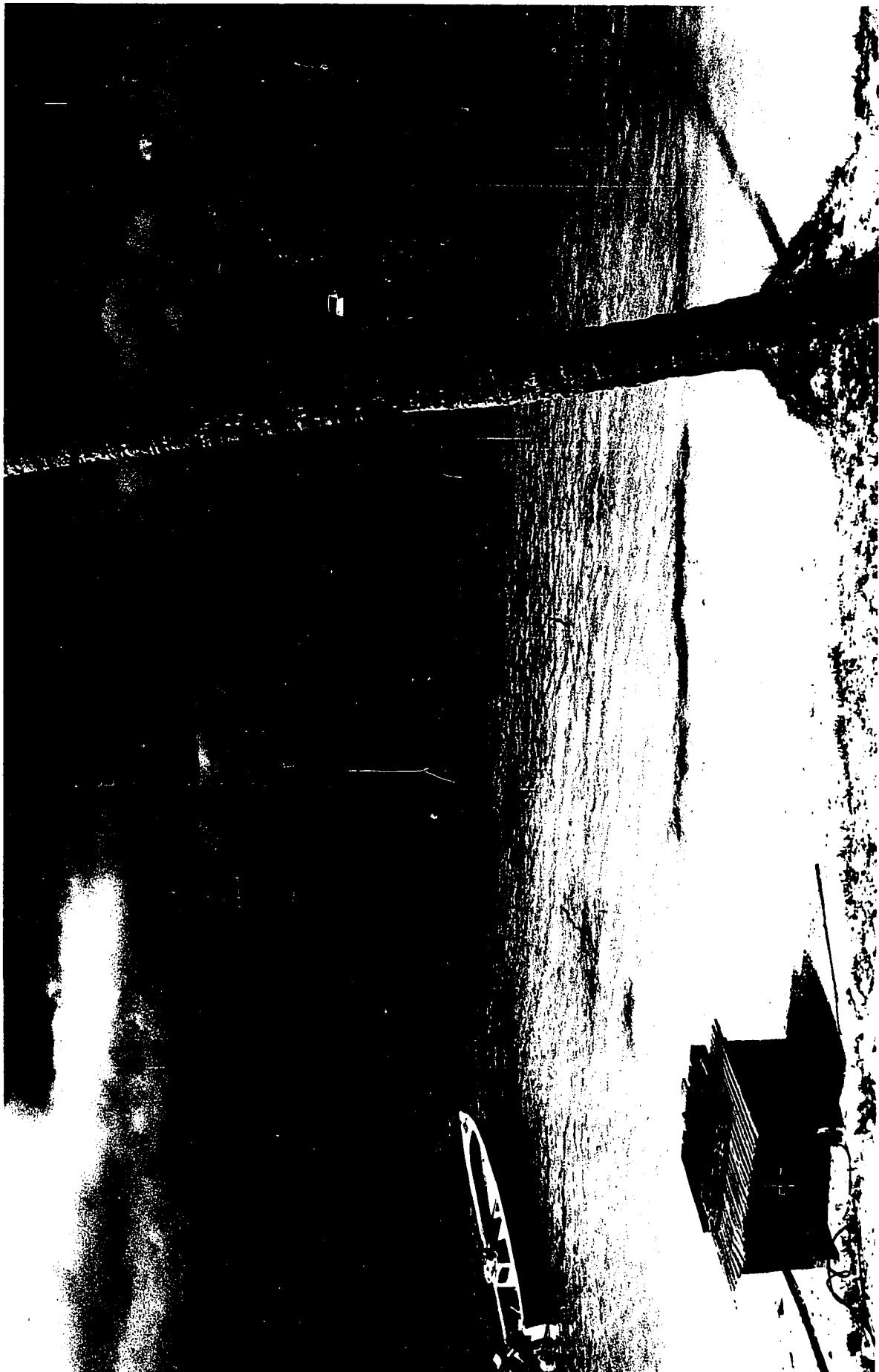
greater than one km in its north-south dimension and 1.5 km wide. It is most likely a solution feature in origin. Discovery Bay is separated from the sea by a continuation of the fringeing reef which is present all along this coast. The reef forms a barrier which comes within 0.5 m or less of the surface all along its course except in the recently con-structed 150 m wide, 12 m deep ship channel. Previous to the opening of this channel a natural passage only two to three m deep was present.

The eastern third of Discovery Bay (Figures 4 and 7) consists of a shallow (0 to 8 m) lagoonal shelf extending from the northeast corner to the south central portion of the Bay. This area lies within the lee of the land and receives comparatively little effect from the prevailing N. E. Trade Winds. Consequently there has been considerable sand accumu-lation and fairly complete sediment binding by angiosperms and calcareous algae over large patches of the shelf. Between these are numerous areas of accumulations of bare sand and erosional limestone bench surfaces. The little sediment binding in these latter areas is accomplished by various calcareous green algae which are apparently the major sedi-ment contributors in this region of Discovery Bay.

The contact between Thalassia patches and neighboring environments is unstable and is often distinguished at its shallower end by erosional ridges of Thalassia root net-works projecting some 20 to 30 cm above the adjacent bare sand or limestone surface. Wave scour erosion during storms

Figure 7. **Thalassia** patch where Discovery Bay samples were collected.

may have become more effective in this area since the opening of the ship channel. If so, the total area of Thalassia coverage in the Bay may be consequently decreasing.

The sediments (Table 10 of Appendix B) in the Thalassia patch studied consist of poorly sorted medium to coarse calcareous sands. Silt and clay contents varied widely, ranging from almost zero to about 30%, but averaging near 12% at III and 10% at IV. These sediments are predominantly algal in origin with a very large component of molluscan shell debris as the second most important component. The decrease in median grain size closer to shore, in spite of the greater power of storm waves in these shallower depths, is due to the significantly thicker Thalassia cover at Area III.

There is a general clockwise circulation of surface waters in the Bay generated by the Trade Winds during the day, but this pattern ceases by nightfall. There are also wave generated oscillatory movements perpendicular to the shore. These waves are greatest in winter and are primarily the result of long period swells reaching the coast from the north to northeast. The oscillatory motion was observed to slowly build up during the day prior to the arrival of winter storms and divers could anticipate such storms up to a day before their arrival. During such storms, which occur frequently from early November into April, the Bay becomes highly turbid from the shoreline to near the edge of the lagoonal shelf demonstrating effective wave erosion and/or turbulence to from 5 to 8 m depth. The water was especially

cloudy from approximately the three meter contour to the shore and at the height of storm activity this zone is characterized by the frequent appearance of geyser-like sediment eruptions which extend to the surface in defined narrow columns before mixing by the next wave.

Violent as the storm activity is in its effect on the Bay, it is markedly seasonal and therefore fairly predictable in nature. Naturally enough, "turbidity" as measured in this study closely parallels the seasonal storm pattern and Discovery Bay is beautifully clear throughout the remainder of the year with visibility in 2 to 4 m depth in excess of 15 m. During storms visibility was zero and often remained less than 5 m for days afterwards.

Variation in all other non-sediment environmental variables at the Discovery Bay sample areas was either markedly seasonal or practically insignificant. Regular diurnal variations in all of these, except probably oxygen saturation, are slight in comparison to the annual range. This is due to the effective current mixing within the Bay and the entirely sublittoral position of the sample areas. This general result and the frequently rigorous oceanographic conditions are the most significant differences between the Discovery Bay sample areas and those at Pear Tree Bottom.

The water temperature range shown in Figure 8 is almost as great at Discovery Bay as on the Pear Tree Bottom

Figure 8. Monthly variations (1969-1970) in water temperature, salinity, "turbidity" and particulate organic carbon at all sample areas.

MEAN MONTHLY WATER TEMPERATURE VARIATIONS

I • x̄ = 29.2 ± 1.4
II ○ x̄ = 29.3 ± 1.4

III • x̄ = 28.2 ± 1.1
IV ○ x̄ = 28.1 ± 1.1

MEAN WATER TEMPERATURE (°C)

32
30
28
30
28
26

N D J F M A M J J A S O
1969   1970

MONTHLY SALINITY VARIATIONS

I • x̄ = 31.5 ± 2.5
II ○ x̄ = 31.7 ± 2.3

III • x̄ = 34.9 ± 0.4
IV ○ x̄ = 34.8 ± 0.4

36
34
32
30
28
36
34

N D J F M A M J J A S O
1969   1970

MONTHLY "TURBIDITY" VARIATIONS

I • x̄ = 0.108 ± 0.088
II ○ x̄ = 0.091 ± 0.074

III • x̄ = 0.049 ± 0.044
IV ○ x̄ = 0.031 ± 0.032

"TURBIDITY" (AVERAGE EXTINCTION)

.360
.280
.200
.120
.040
.160
.080

N D J F M A M J J A S O
1969   1970

MONTHLY PARTICULATE ORGANIC CARBON VARIATIONS

I • x̄ = 786 ± 1012
II ○ x̄ = 487 ± 195

III • x̄ = 316 ± 100
IV ○ x̄ = 308 ± 116

PARTICULATE ORGANIC CARBON (Mg c/M³)

800
600
400
200
600
400
200

N D J F M A M J J A S O

Figure 9. Monthly variations (1969-1970) in dissolved

oxygen, pH and temperature gradients (water minus sedi-

ment) and _Thalassia_ dry weight at all sample areas.

MEAN MONTHLY % OXYGEN SATURATION

I • x̄ = 154 ± 25
II o x̄ = 161 ± 29

III • x̄ = 118 ± 8
IV o x̄ = 119 + 8

MEAN PERCENT OXYGEN SATURATION

N D J F M A M J J A S O
1969 1970

MEAN MONTHLY WATER pH
MINUS SEDIMENT pH VARIATIONS

I • x̄ = 1.09 ± 0.21
II o x̄ = 1.13 ± 0.19

III • x̄ = 0.79 ± 0.18
IV o x̄ = 0.62 ± 0.14

MEAN pH GRADIENT

N D J F M A M J J A S O
1969 1970

MEAN MONTHLY WATER TEMPERATURE
MINUS SEDIMENT TEMPERATURE

I • x̄ = 1.0 ± 0.7
II o x̄ = 1.1 ± 0.7

III • x̄ = 0.2 ± 0.2
IV o x̄ = 0.2 ± 0.2

MEAN TEMPERATURE GRADIENT (°C)

N D J F M A M J J A S O
1969 1970

MEAN MONTHLY THALASSIA
DRY WEIGHT VARIATIONS

I • x̄ = 256 ± 100
II o x̄ = 302 ± 73

III • x̄ = 239 ± 73
IV o x̄ = 196 ± 81

MEAN THALASSIA DRY WEIGHT (g/0.1M²)

N D J F M A M J J A S O
1969 1970

reef flat. As already discussed, however, this is decep-
tive as no sampling occurred on a very hot day during low
tide. The seasonal pattern is markedly constant at Dis-
covery Bay and diurnal variations averaged only about $1^{o}C$
(Reiswig, 1971 and my own observations).

Salinity variations over the entire year (Figure 8)
were less than $2^{o}/oo$ despite heavy rains and very consider-
able surface and underground drainage into various parts of
the Bay. No significant stratification was observed in the
sample areas even just after heavy rains.

The curves for suspended particulate organic carbon
(Figure 8) are similar at III and IV and the annual means
identical within the errors of the analyses. Reiswig's
(1971) results showed naked cells (predominantly naked
flagellates), diatoms and bacteria to be the most impor-
tant components, comprising roughly 70 to 80% of the total
material by volume in both seasons. Visible detritus was
always less than 10% of the total particulate organic matter
available in his samples. However, the total visible par-
ticulate organic matter was always less than 7% of the or-
ganic material retained by glass fiber filters in his chemi-
cal analyses for particulate organic carbon. Reiswig has
extensively discussed the significance and possible nature
of this unidentified material. My own observations (Figure
8), using the same reagents, standards and similar methods
as Reiswig, have shown the material to be markedly biannual
in abundance. If, as Reiswig suggests, this unidentified

material is reef derived then the winter peak may represent release due to storm damage whereas the summer peak could represent truly increased productivity at the source. Whatever the case, the bulk of the visible material is definitely not detritus as at Pear Tree Bottom.

Daytime oxygen saturation was essentially constant throughout the year (Figure 9). The lower values in comparison to Pear Tree Bottom are almost certainly due to lower photosynthetic rate due to lower light intensities at the greater depths. In addition, the more effective circulation patterns within Discovery Bay mix the predominantly Thalassia derived oxygen with comparatively low oxygen waters from other environments.

The interface strength as measured by pH gradient was significantly greater ($P \leq .01$) at III than IV (Figure 9). This was due to the somewhat thicker Thalassia growth and finer grain size in the more nearshore area. During and just after winter storms there was practically no difference in water and sediment pH and the sediments showed little sulfide ion activity to depths as great as 3 or 4 cm. However, within a few days both the reducing conditions and pH gradient built up to their normal values. As at Pear Tree Bottom, sediment sulfide ion potentials of -0.5v were common after calm water periods during which time pH gradients as high as one full pH unit were commonplace. The water minus sediment temperature gradient was low and practically constant throughout the year (Figure 9), but

varied similarly in relation to storm disturbances.

The changes in _Thalassia_ biomass were markedly seasonal, varying by more than 200% over the year, and peaking in both areas in mid to late summer (Figure 9). This variation suggests that the August peak for area II is also truly seasonal and that such variation is characteristic of _Thalassia_ at Jamaica as well as more temperate waters to the north.

3. Distribution of Environmental Variability.

The variances for each of the "weather" (=salinity, temperature, etc.) and interface gradient (=pH gradient, $T^{o}C$ gradient) environmental variables were used in the calculation of F-ratios for the six possible two-sample comparisons of variance between sample areas. The results are shown in Table 1. Between Areas I and II, only the variances for particulate organic carbon are significantly different and between Areas III and IV only those for "turbidity." Between Pear Tree Bottom and Discovery Bay, however, the variances are significantly greater at the former locality for five of the seven different variables. As already discussed, observations other than the regular sampling data indicated that the diurnal and seasonal variations in water temperature are also greater at I than at II and very much greater at Pear Tree Bottom than at Discovery Bay. However, even without this additional information, the ranking of areas by the number of significant differences

Table 1. Environmental variables; significant differences in variances (P .05) between areas. F equals variance ratio.

	Variable	F Ratio
$s_I^2 > s_{II}^2$	particulate organic carbon	26.9
$s_I^2 > s_{III}^2$	salinity	40.8
	particulate organic carbon	103
	"turbidity"	3.91
	percent oxygen saturation	9.77
	water minus sediment temperature	16.0
$s_I^2 > s_{IV}^2$	salinity	36.7
	particulate organic carbon	76.2
	"turbidity"	11.0
	percent oxygen saturation	9.77
	water minus sediment temperature	18.1
$s_{II}^2 > s_{III}^2$	salinity	33.7
	particulate organic carbon	3.83
	"turbidity"	2.83
	percent oxygen saturation	13.1
	water minus sediment temperature	15.1
$s_{II}^2 > s_{IV}^2$	salinity	30.2
	particulate organic carbon	2.84
	"turbidity"	5.57
	percent oxygen saturation	13.1
	water minus sediment temperature	17.0
$s_{III}^2 > s_{IV}^2$	"turbidity"	2.75

in environmental variance shows that

$$s_I^2 > s_{II}^2 > s_{III}^2 > s_{IV}^2.$$

The means of none of these seven variables are sig-
nificantly different between I and II. Among the other
variables, however, the sediments are both finer and
better sorted at I than at II (P ≤ .01). Also, Thalassia
density is greater (P ≤ .05) at the more offshore of these
environments. In so protected a setting the significance
of these differences is not obvious but it did appear that
the sediment surface at I was somewhat more fluid and un-
stable than at II.

At Discovery Bay, the "turbidity" and pH gradients
are significantly greater at III than at IV (P ≤ .01).
This is due to the greater Thalassia biomass (P ≤ .05) and
resultant finer grain size and greater amounts of silt and
clay at the shallower locality (for both P ≤ .01).

The differences are more pronounced between the back
reef flat and Bay localities. Thus, at Pear Tree Bottom
the salinity is lower and the pH gradient, "turbidity,"
temperature gradient and oxygen saturation are higher (all
at P ≤ .01) than the corresponding values of these variables
at Discovery Bay.

As used in this study, stress is a collective term
for three aspects of environmental variability. For any
single environmental variable or set of variables these are:

    a. the mean value

b. the variance

c. the predictability of the variance.

Clearly, in all of these aspects, there is a significant decrease in the degree of environmental stress from the shallowest to deepest sample area.

B. Fauna

Both reef flat areas contained large numbers of comparatively few species with the complete absence of entire groups commonly found in shallow water Thalassia environments. Molluscs were by far the most abundant macroinvertebrates and were estimated to comprise well in excess of three quarters of the benthic invertebrate biomass. The Discovery Bay areas contained modest numbers of a great number of species including representatives of almost all important soft bottom groups. Echinoderms were the dominant members of the epifauna but no group appeared to dominate the infauna.

1. General Fauna

At Pear Tree Bottom the most common non-molluscan invertebrates were burrowing anemones and a heavily pigmented sipunculid. Only five kinds of polychaetes were noted. These were almost all very small, frequently pigmented and were not abundant. Hermit crabs were very abundant right along the shore but much less so only as

far seaward as Area I. Other common crustacea included a moderate variety of shrimps and crabs.

Small isolated growths of a variety of characteristically shallow water scleractinians and hydrocorals were found at both Discovery Bay areas, especially at III. The colonies were seldom greater than 5 or 6 cm in greatest dimension and were found on various dead projecting coral branches or on the dorsal surfaces of large semi-infaunal or epifaunal bivalves. A great variety of anemones were found but, as for corals, these were most abundant in nearby rockier areas of the Bay. These included a burrowing anemone occasionally found in the sample areas and a very common stinging form which grows on the leaves of _Thalassia_. Hydroids were also found on the _Thalassia_.

Polychaetes were much more diverse at Discovery Bay and were dominated by two very characteristic and abundant species of _Clymenella_ and _Diopatra_. The latter formed parchment-like tubes of agglutinated shell fragments which frequently exceeded 20 cm in length. Both species were present in almost every sample collected within Discovery Bay. Two large sipunculid species, including the one found at Pear Tree Bottom were common. Crustacea were very abundant and included a great variety of shrimps, crabs and stomatopods.

Echinoderms were almost entirely absent from the reef flat and included only a single uncommon burrowing holothurian. At Discovery Bay, the two _Thalassia_ grazers

Lytechinus variegatus and Tripneustes ventricosus were the
most abundant epifaunal echinoids. The abundance of both
these species was essentially constant throughout the year.
The small Brissus unicolor was the commonest infaunal
echinoid. Of the holothurians, one moderate sized species
averaging about 10 cm in relaxed length was a major compo-
nent of the infaunal biomass in both Discovery Bay areas.
Large epifaunal holothurians were always evident in the
Bay but in fairly small numbers. Various infaunal ophiuroids
were very common among the Thalassia roots, especially at IV,
and were noticed in almost every sample. Only one small
starfish was collected during the entire year. Starfish are
well known to be quite patchy in their distributions in
Jamaican waters and are very poorly represented at Discovery
Bay.

A variety of small fish, including a few mollusc-
feeding puffers, were observed on the reef flat, mostly
during high tides and seaward of the sample areas. The fish
fauna at the Discovery Bay areas was very diverse and, among
the carnivores, was dominated by a great variety of wrasses,
the spiney puffer Diodon holocanthus and the yellow spotted
stingray Urolophus jamaicensis. The latter two species are
voracious mollusc predators, the former feeding primarily
on gastropods and the latter on shallow burrowing bivalves
and other infauna (Randall, 1967). There was also consider-
able fish grazing of Thalassia, especially by parrotfishes.
Their feeding structurally weakens the leaves making them

more susceptible to detachment by gentle wave disturbance
and thereby contributing fresh Thalassia material to the
bottom during periods free from storms.

2. Gastropods

Gastropod abundances for the year are given in Table
11 of Appendix C. The most important group in numbers (and
probably in biomass) at Pear Tree Bottom were the tiny
epiphyton grazers Neritina virginea and Cerithium variabile.
These snails graze most commonly on the surfaces of Thalassia
leaves and numerous individuals of each species were usually
present on any single leaf of these plants. Both species
were more abundant nearer shore but fluctuated wildly in
abundance throughout the year. The three species of naticids
(Natica, Polinices) were the only gastropod predators ob-
served on the reef flat over the year.

There were no very common gastropod grazers on the
Thalassia in either Discovery Bay sample area and gastropods
in general, although moderately diverse, were not well repre-
sented. Gastropod predators were less abundant than on the
reef flat and Oliva reticularis, rather than naticids, was the
most common form. No muricids were collected live but their
dead shells were fairly common as were those of bivalves with
characteristic muricid drill holes.

3. Epifaunal Bivalves

Two species of epifaunal bivalves were collected in the Pear Tree Bottom samples (Appendix C, Table 13) but only _Arcopsis_ _adamsi_ was at all common. It is more abundant than would appear from these data as it favors somewhat rockier areas. Even under rocks, however, the variety and abundance of epifaunal bivalves was low.

Epifaunal bivalves were both more abundant and diverse in Discovery Bay (Appendix C, Table 13). Loosely attaching forms were rare. Of the two most abundant species _Chama_ _macerophylla_ was only found cemented to coral and other limestone debris whereas _Arca_ _zebra_ was most common attached to the tops of large semi-infaunal _Modiolus_ _americanus_ or to individuals of the same species.

4. Infaunal and Semi-infaunal Bivalves

Representatives of four somewhat arbitrary categories of infaunal and semi-infaunal bivalves were recognized on the basis of morphology, feeding behavior and positioning within the sediment. For a review of bivalve functional morphology see Purchon (1968) and Stanley (1970). In addition to these, Jørgensen (1966) and Stanley (1968) discuss bivalve feeding behavior and feeding types. The life habits of most of the species in this study have been described in detail by Stanley (1970).

The groups are:

      a. Lucinacea

The functional morphology of the Lucinacea was studied by Allen (1958). They are here represented by the two families Lucinidae (<u>Anodontia</u>, <u>Codakia</u>, <u>Ctena</u>, <u>Divaricella</u>, <u>Lucina</u> and <u>Parvilucina</u>) and Ungulinidae (<u>Diplodonta</u>). They are generally slow, deep burrowers and are often quite large. All lucinaceans feed by means of an anterior inhalent tube which is constructed by their unique vermiform foot. Their ctenidial apparatus is very simple and the food pathway from the mantle opening of the inhalent tube to the mouth uncomplicated. Their digestive tract is also quite simple and consequently the Lucinacea are able to feed on large, variably sized suspended particles. The ungulinids have secondarily developed rather more complex ctenidea than the lucinids and may therefore be intermediate in their diet between that of the lucinids and most infaunal eulamellibranch suspension feeders.

      b. Typical Infaunal Eulamellibranch Suspension
          Feeders

Most species in this group are fairly shallow burrowers. Most are siphonate and the siphons are usually considerably shorter than the shell length. All have well developed

ctenidea (eulamellibranch) with complex ciliary networks which are used in the selection of food particles and the rejection of inappropriate materials. They feed primarily on plankton (?also "dissolved" organic matter) and can not accomodate large particles. This group includes from this study the Cardiidae (Americardia, Laevicardium, Papyridea and Trachycardium), the Veneridae (Antigona, Chione, Gouldia and Pitar), Corbula and Labiosa. Tagellus is a suspension-feeding tellinacean. Crassinella lacks siphons and complex ctenidial sorting areas and feeds by means of an anterior inhalent current (Allen, 1968). Anadara is a non-siphonate infaunal to semi-infaunal suspension feeder.

c. Deposit-feeding Tellinacea

The Tellinacea are derived from the typical eulamellibranchs. They include quite mobile forms and deeper burrowers, for their size, than most species of the former group. Deposit-feeding tellinaceans of the families Semelidae (Semele) and Tellinidae (Arcopagia, Macoma and Tellina) utilize surface detritus which they collect by means of long, separate, flexible siphons. Many species can also double as suspension feeders. The Tellinacea retain the complex eulamellibranch ctenidial sorting mechanisms and are apparently limited to the use of comparatively small particles. Reid and Reid (1969) have discussed the significance of the varied nature of

tellinacean feeding behavior as seen in the genus _Macoma_.

d. Semi-infauna

Semi-infaunal bivalves are suspension feeders. The pen shells (Pinnidae) _Atrina_ and _Pinna_ and the mussel _Modiolus_ are very large forms which live about three-quarters buried within the sediment. They are held in position by means of their powerful byssus.

The total abundance , both number and length number (=sum of lengths in cm), for each infaunal and semi-infaunal species collected live in combined (=0.25 and 0.10 m^2) samples from Pear Tree Bottom is shown in Table 2. Comparable data for Discovery Bay are shown in Table 3. The total area sampled at each locality was 1.4 m^2/month or 16.8 m^2/year. The data from the two sample sizes were combined because the number of bivalves smaller than the effective mesh of the 0.25 m^2 samples (6 mm) proved insignificant except for two species. The first of these, _Ctena orbiculata_, was most abundant on the back reef flat throughout the year as juveniles. Therefore, the estimates of number (but not so much of length number) are quite low for this species. The same is true to a lesser degree for the smaller lucinid _Parvilucina costata_ and in all areas an estimated 20% of those trapped by the 1 mm mesh used for the 0.1 m^2 samples were lost through the larger screen. These combined data were used in all

Table 2. Total number and length number (cm) for one year of live infaunal and semi-infaunal bivalves from Pear Tree Bottom sample areas. For number/m² divide by 16.8. *=Lucinidae.

AREA I	NUMBER	LENGTH NUMBER	AREA II	NUMBER	LENGTH NUMBER
*Codakia orbicularis	315	1309.3	*Codakia orbicularis	980	3045.6
*Ctena orbiculata	219	99.8	*Ctena orbiculata	198	117.5
Arcopagia fausta	17	46.8	*Parvilucina costata	50	43.4
*Parvilucina costata	12	9.8	Arcopagia fausta	30	128.1
Chione pygmaea	1	0.9	Chione cancellata	1	0.7
Tellina caribaea	1	0.6	Chione pygmaea	1	1.0
			Corbula contracta	1	0.5
			*Lucina pensylvanica	1	1.2
			Semele proficua	1	1.2
TOTALS	565	1467.3		1263	3339.2
NUMBER SPECIES	6			9	

Table 3. Total number and length number (cm) for one year of live infaunal and semi-infaunal bivalves from Discovery Bay sample areas. For number/m² divide by 16.8. *=Lucinidae.

AREA III	NUMBER	LENGTH NUMBER	AREA IV	NUMBER	LENGTH NUMBER
*Parvilucina costata	249	222.9	Modiolus americanus	29	137.0
*Codakia orbicularis	176	453.2	Anadara notabilis	26	67.1
Diplodonta punctata	91	128.1	Pitar fulminata	23	21.9
Modiolus americanus	49	263.6	*Parvilucina costata	21	15.2
Anadara notabilis	37	123.6	Trachycardium muricatum	17	36.2
Americardia media	13	32.2	Diplodonta punctata	15	16.0
*Ctena orbiculata	13	24.0	Americardia media	14	33.6
*Anodontia alba	8	16.2	*Codakia orbicularis	10	9.9
*Lucina pensylvanica	6	11.0	*Ctena orbiculata	8	10.2
Tellina caribaea	6	7.0	Chione paphia	7	16.9
Pitar fulminata	6	5.9	Laevicardium laevigatum	6	13.7
Chione paphia	3	6.9	Trachycardium isocardia	6	13.0
Trachycardium muricatum	3	4.1	Lablosa anatina	5	15.0
Papyridea soleniformis	2	6.9	Pinna carnea	4	23.3
Lablosa anatina	2	6.1	Diplodonta nucleiformis	4	3.7
*Divaricella quadrisulcata	2	2.9	Arcopagia fausta	3	3.1
Crassinella lunulata	2	0.9	*Codakia sp (?portoricana)	3	2.6
Trachycardium isocardia	1	3.4	Tellina caribaea	3	2.1
Tagelus divisus	1	2.9	*Lucina pensylvanica	2	4.6
Macoma tageliformis	1	1.9	Atrina seminuda	1	7.5
*Codakia sp (?portoricana)	1	1.2	Papyridea soleniformis	1	2.6
Arcopagia fausta	1	1.2	Tagelus divisus	1	2.5
Chione cancellata	1	1.0	Chione cancellata	1	2.2
			Antigona listeri	1	2.0
			Laevicardium pictum	1	1.5
			Gouldia cerina	1	0.8
TOTALS	674	1327.1		213	462.5
NUMBER SPECIES	23			26	

subsequent analyses.

The Lucinidae comprise in excess of 96% of both the number and length number at both Pear Tree Bottom localities. By far the most abundant of these is the large (commonly to 5 cm) Codakia orbicularis which makes up more than 80% of the total abundance in both reef flat areas. The only non-lucinid of any importance is the large (to 6 or 7 cm) tellinacean Arcopagia fausta. This species was found deeply buried, below 5 to 10 cm, in the usual tellinacean sideways-down position.

At the shallower Discovery Bay locality, Area III, the Lucinidae are still the most abundant family. The small Parvilucina costata is the most numerous lucinid but the larger C. orbicularis still makes up the bulk of the lucinid biomass. No one species comprises more than one third of the total number of bivalves and five species, including two non-lucinids, are important components of the biomass.

No one species or family dominates the deeper Discovery Bay locality, Area IV, and the five most abundant species comprise less than 55% and 60% of the total number and length number respectively. For the first time, lucinids are not the most abundant family and only 20.7% of the number and 9.0% of the length number are species of that group. Three of the five most abundant species from III are of similar importance at IV. However, these include only one lucinid, P. costata, and the two others, Modiolus americanus

and <u>Anadara</u> <u>notabilis</u>, are less abundant than at III. The two new species, <u>Pitar</u> <u>fulminata</u> and <u>Trachycardium</u> <u>muricatum</u>, are members of two of the most diverse and abundant of families of Caribbean shallow water bivalves, the Veneridae and Cardiidae, which were absent or poorly represented in the other three sample areas. At IV, the cardiids comprise more than 21% of the total bivalve abundance and are the most abundant family in this environment. The venerids make up 15.5% and 9.3% of the total number and length number respectively.

Typical eulamellibranch suspension feeders dominate the infaunal and semi-infaunal bivalve assemblage only at Area IV. At Pear Tree Bottom this group made up only 0.2% of the total abundance and at III was only 17.5% of the total bivalve number. In contrast, at IV typical eulamellibranch suspension feeders include the three most abundant species and comprise 65.3% of the total number and 82.1% of the total length number of bivalves in the area. Throughout Jamaica it appears that this group tends to be most common and most diverse in comparatively low stress, low biomass environments.

There are clearly important differences between the different areas in the distributions and relative importance of the various families or functional groups of infaunal and semi-infaunal bivalves. The greatest contrast is that between the abundance of the lucinids and that of the other infaunal taxa. Therefore, three groups were defined for use

in the subsequent analyses. These were:

Group 1. All infaunal and semi-infaunal bivalves.

Group 2. All Lucinidae. The ungulinid genus Diplodonta was not included because of its possible intermediate feeding behavior between the Lucinidae and other infaunal suspension feeders.

Group 3. The total infaunal bivalves in categories (2) and (3) discussed above, that is, all other infaunal suspension and deposit feeders. The deposit feeding Tellinacea were not put into a separate group because of their varied feeding behavior and the lack of specific observations on many of these Jamaican species.

For brevity, these groups will often be referred to simply as Group 1, Group 2 and Group 3.

C. Population Variations and Distributions

1. Environmental Distributions and Diversity

Besides the abundances of the individual species, the values of five collective population variables were calculated for each sample area using combined sample (0.25 and 0.10 m^2) data. These variables are the number of species (S), the two abundance parameters bivalve number (X) and length number (X_L), diversity (H_X) and length diversity (H_{X_L}). The individual sample values for these variables for the three bivalve groups at each sample area are given

in Tables 14-25 of Appendix C.

The total number of infaunal and semi-infaunal bivalve species/sample area increases progressively with distance from shore and decrease in environmental stress. This is also true for Group 3 bivalves and for the lucinids as far as Area III. As for environmental stress, the faunal changes are greatest between Pear Tree Bottom and Discovery Bay rather than among the different reef flat or Bay localities.

Total bivalve abundance (both number and biomass) shows a more than two-fold increase in the 10 meters separating the reef flat Areas I and II. This is almost entirely due to the more than three-fold increase in number of the lucinid Codakia orbicularis. There is then a progressive decrease in lucinid abundance with decreased environmental stress and at Area IV lucinid abundance is well below 5% of its value at Area II. Because of the overwhelming dominance of the lucinids at the three shallowest localities, Group 1 abundance also decreases from II to III to IV. However, Group 3 abundance increases progressively with distance from shore.

Cumulative diversities were calculated for each bivalve group at each sampling locality and the resulting values and graphs are given in Table 4 and Figures 20-22 of Appendix C. Examination of these curves shows that in every case sampling was adequate and that the cumulative diversities may be considered reasonable estimates of the "true" diversities in each sample area. Cumulative diversity decreases

Table 4. Environmental distribution of cumulative diversity and cumulative length diversity.

BIVALVE GROUP	SAMPLE AREAS			
	I	II	III	IV
DIVERSITY				
1	1.28	1.04	2.58	3.81
2	1.09	0.87	1.36	1.70
3	0.46	0.60	2.36	2.96
LENGTH DIVERSITY				
1	0.63	0.57	2.75	3.60
2	0.43	0.33	1.37	2.07
3	0.22	0.21	2.11	3.08

slightly on the reef flat from I to II with decrease in environmental stress. This is due to the very great increase in dominance at II in relation to the much greater density of the C. orbicularis population at that sample area. However, from II, diversity greatly increases seaward with decrease in environmental stress.

Cumulative diversity generally increases quite markedly with the total number of species per area and decreases with an increase in the number or biomass of the bivalves. This is due to the overwhelming dominance of a few taxa in the high biomass areas as noted above for C. orbicularis. The effect is accentuated using length abundance data. Thus, length diversity is considerably lower than that based simply on the number of bivalves at the low diversity reef flat areas. In contrast, at Discovery Bay the differences are slight and, for some groups, consideration of biomass actually increases the cumulative diversity value.

Because of the great decrease in bivalve abundance going offshore, there are differences between the distributions of the cumulative and average sample values for species number and diversity. This is particularly evident at Area IV where, for Groups 1 and 2, average species number and diversity are much lower than at Area III whereas the cumulative values show just the opposite distribution. However, Group 3 bivalves do not exhibit these reversals in distributions.

Correlation coefficients were calculated between the five population variables for the three bivalve groups at each sample area and for all four areas combined (Figures 23-27 of Appendix C). The total number of species is always highly correlated with the number of species in the other groups and in all three groups to both measures of diversity. Total species number shows no correlation to either abundance measure for Groups 1 and 2 at Pear Tree Bottom but is positively correlated at Discovery Bay as it is in all areas to Group 3 abundance. Although they show no correlation at Pear Tree Bottom, Group 2 and Group 3 species number are negatively correlated at III and positively at IV.

The two Group 1 abundance parameters, number (X) and length number (X_L), are always highly correlated. In all four areas total bivalve and lucinid abundance are correlated. However, Group 3 abundance shows no significant relation to total abundance except at IV nor, generally, to lucinid (Group 2) abundance in any area. At Pear Tree Bottom there are generally no significant correlations between sample abundance and diversity except with Group 3. In contrast, in Discovery Bay there are significant correlations within all three groups.

For all areas taken together, Group 1 diversity is negatively correlated to length number. Length diversity shows a similar relation to both abundance indices. Group 1 diversity is, however, positively correlated to both Group 2

and Group 3 diversity in most areas individually and in all areas taken together. Finally, lucinid diversity is negatively correlated to both Group 3 diversity indices.

In summary:

a. Individual sample diversity is highly correlated to species number but variably correlated to abundance. In areas with high dominance by a few taxa, sample diversity and abundance may be negatively correlated.

b. At Area IV there is no dominance by any one species or species group. There is also moderately high mean sample diversity and low abundance. Consequently, between all 15 variables there are no negative correlations at any level of significance.

c. Bivalve number is positively correlated to length number (= biomass) in all three groups.

d. Except at IV taken alone there is generally no correlation or significant negative correlation between all Group 2 (lucinids) and Group 3 (non-lucinacean infauna) population variables.

2. Spatial-Temporal Distributions

The monthly averages for the five population variables over the year are plotted in Figures 10-12. The means and standard deviations for all 48 samples/area/bivalve group are given in these figures. Neither the number of species nor their abundance changed significantly at any of the four

sample areas during the entire year of observations. Species number was especially constant at both reef flat localities and was most variable, both in number and composition, at the 4 m deep Discovery Bay locality (Area IV). Abundance variation was greatest at the two most densely populated areas (II and III) and at all areas was greater for length number than for number. In none of these fluctuations is there suggestion of a seasonal pattern.

Examination of the tabulated sample data (Appendix C, Tables 14 to 25) shows that the variation within any one month is generally greater than the mean monthly variations. This strongly suggests that most of the observed variance is spatial rather than temporal. Variance/mean ratios ($s^2/\bar{x}$) were therefore calculated for the number of species and their abundance as a rough measure of spatial (more accurately spatial-temporal) distribution simply as a convenient means of comparing the different sample areas. Variance/mean ratios were also calculated for the commonest species at each sample area. The results are given in Tables 26 and 27 of Appendix C.

Bivalve number for all groups and the individual common species is either slightly aggregated ($s^2/\bar{x} > 1$) or random ($s^2/\bar{x} = 1$) in all areas. Length number, however, is always strongly aggregated. These aggregations of biomass result from aggregation of individual dominant species with the less abundant species dispersed throughout each area in an apparently random fashion.
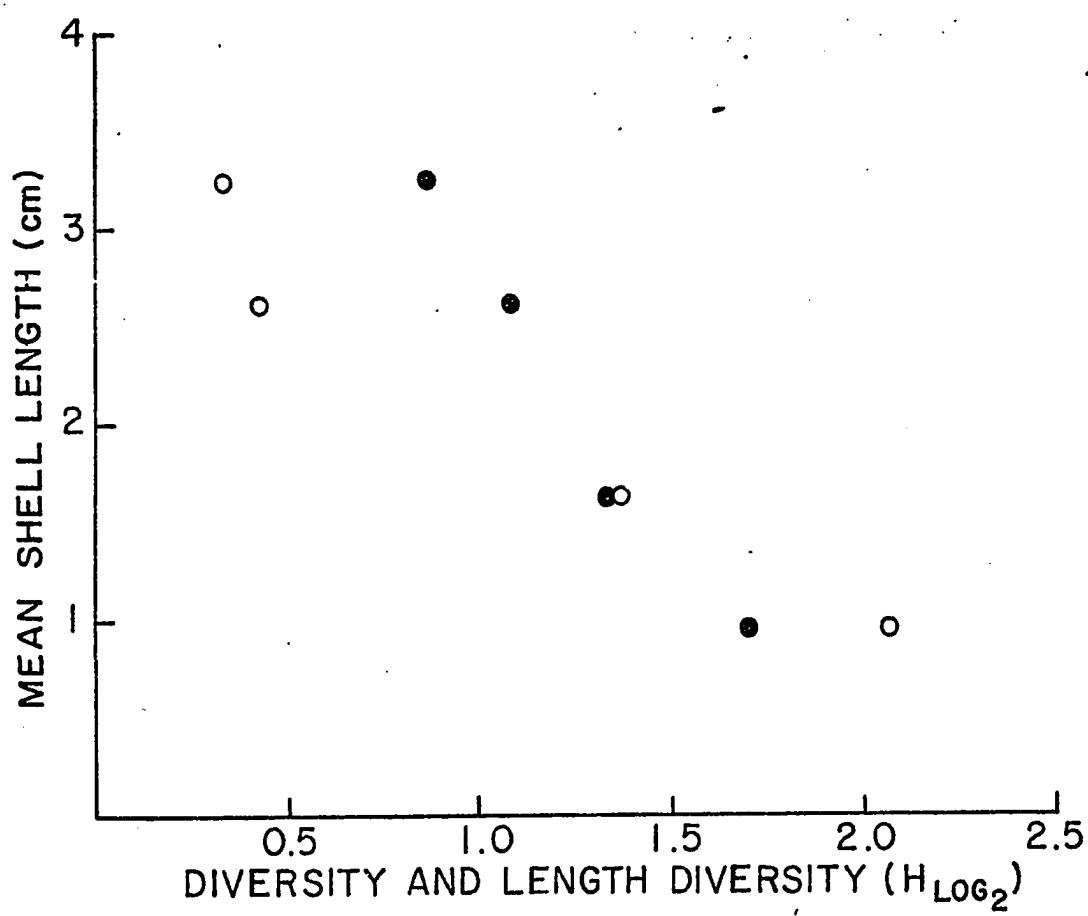
The distribution of the total number of species/ sample (Groups 1 and 2) is significantly regular ($s^2/\bar{x} < 1$) at all areas but IV where it is random. Increasing as it does from I to IV, the variance/mean ratio is apparently correlated to cumulative diversity.

3. Size and Size-frequency

As was implied from the correlation data, average size (for all species together) is greatest in areas of highest bivalve density. This is true for all three bivalve groups. Thus size and abundance are positively correlated and there is a marked decrease in size with increase in diversity and decrease in environmental stress. This is illustrated in Figure 13 for the lucinids. Lucinid cumulative diversity and mean shell length are perfectly negatively correlated (Kendall Rank Order Correlation = -1.00) within the four sample areas. The probability of this association by chance is .08 which is the maximum significance possible for only four observations. The relation between lucinid length diversity and abundance (not plotted) is the same. Group 3 bivalves generally show the same relation of size to diversity except at Area I where only 19 Group 3 individuals were present. In contrast, epifaunal bivalves and the gastropods show just the opposite size distribution with larger species dominating in the higher diversity, low stress environments.

Besides the trend of greater size with lower cumulative

Figure 13. Relation of lucinid cumulative diversity and mean lucinid shell length. Solid circles=diversity; open circles=length diversity.
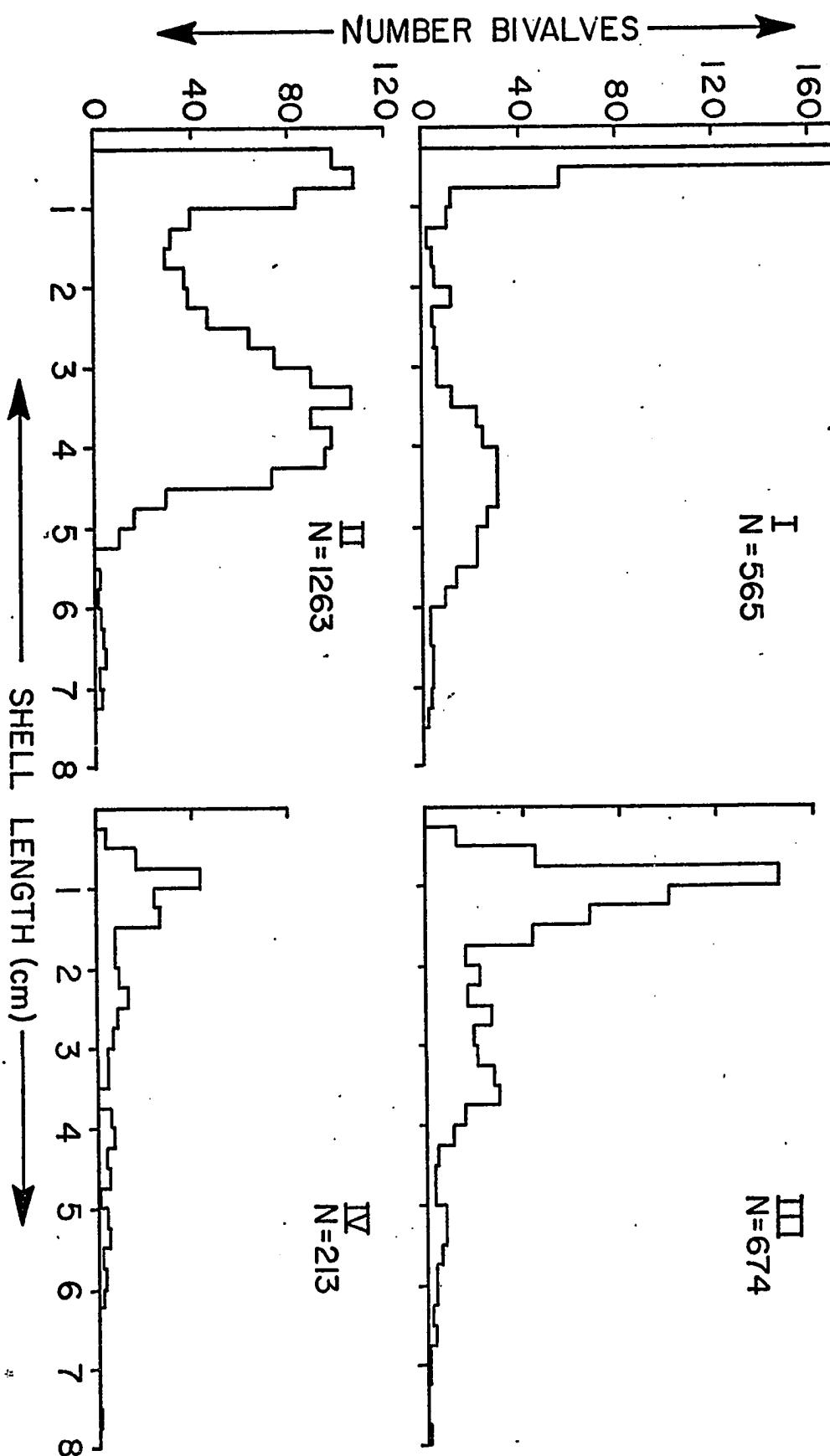
diversity, there is a very great change in the nature of the total live infaunal and semi-infaunal bivalve size-frequency distributions along the environmental gradient. These distributions for the combined 0.25 and 0.10 m^2 samples are shown in Figure 14. The bimodal curves for the reef flat localities result from the great preponderance of large adults and juveniles with very few moderate sized individuals of these large, near shore species. Very few of the smaller bivalves were adults of small species. The low abundance of large individuals at the Discovery Bay localities results from the great dominance of smaller species and the rarity of adults of the potentially larger species present. These size-frequency distributions appear to be well preserved in the dead shell size-frequency distributions from the same areas.

4. Predation

Because of their deep burrowing habits, the lucinids are apparently only occasionally taken by predators other than similarly deep burrowing gastropods, especially naticids. Lucinids are not common from the stomachs of speared fish (Randall, 1967). Moreover, rays (which normally do not swallow the shells of their prey) were not observed to excavate deeply during feeding except in bare sand. Because the naticids are drills it is possible to gain a rough knowledge of the relation between predation pressure (% drilled

Figure 14. Length-frequency distributions at each sample area for all live infaunal and semi-infaunal bivalves collected at Pear Tree Bottom and Discovery Bay (1969-1970).

LENGTH-FREQUENCY ALL SPECIES LIVE INFAUNAL AND SEMI-FAUNAL BIVALVES
NOVEMBER, 1969 - OCTOBER, 1970
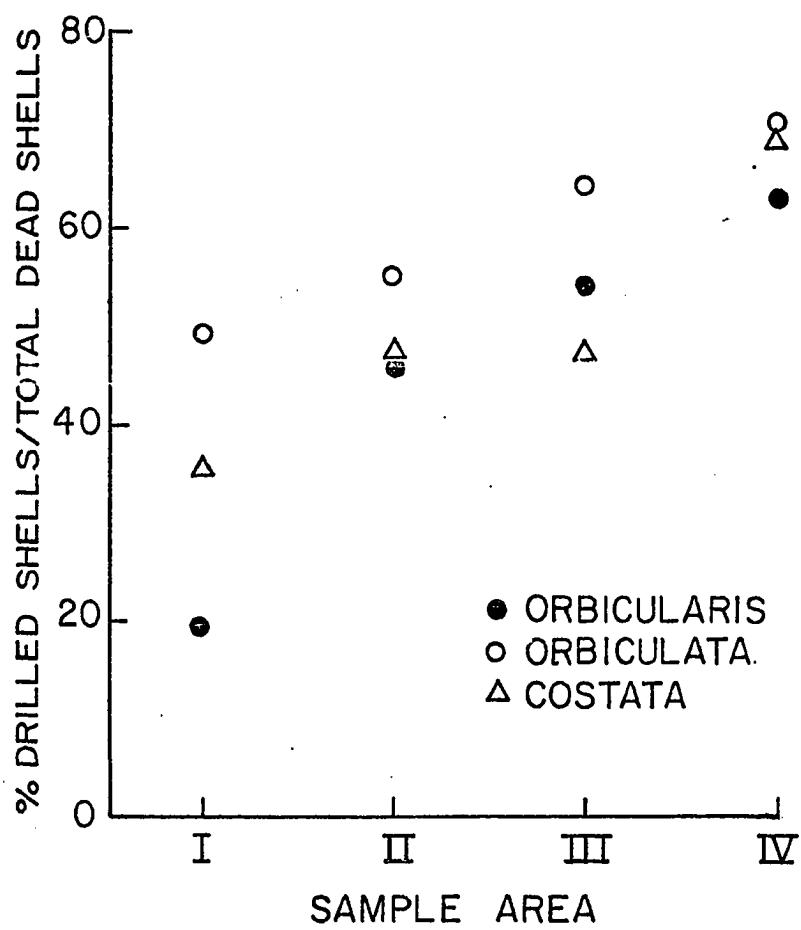
total dead shells/2) and lucinid diversity in these areas. The results for the three commonest lucinids from 12 0.25 m^2 samples/sample area are shown in Figure 15. The percent drilled for each species increases progressively with distance from shore. Note especially the great increase in predation in the 10 meters separating the reef flat areas I and II. From II to IV percent predation increases with diversity.

In all four areas there is greater drill predation on smaller individuals than on adults of the larger species (mean length drilled shells less than mean length undrilled shells). Also, the smaller species (e.g., Ctena orbiculata) tend to suffer greater drill predation than do the larger species (e.g., Codakia orbicularis). Parvilucina costata appears to be an exception but this species has a very thick shell for its small size.

Drills are far from being the dominant bivalve predators in the Discovery Bay areas and predation rates by fish, rays and other gastropods were not determined. However, the diversity of predators, especially fish (based on Randall, 1967), is greatest in those environments with highest bivalve diversity in spite of the fact that prey biomass is lower in such areas. In addition, Randall's data and that on the species distributions of both the numbers and types (muricid or naticid) of drill holes in dead shells from this study indicate that infaunal bivalve predators commonly show size preferences but not species preferences in their feeding

Figure 15. Environmental distribution of percent drill predation for C. orbicularis, C. orbiculata and P. costata at all sample areas.

behavior.

D. Multivariate Regression Analyses

For each of the individual areas, eight ω models were compared against the general Ω model (Table 7 of Appendix A). Separate runs were made for each bivalve group at each area except for Group 3 at Area I where only 19 individuals were present. For reasons of space, the results are shown in Table 9 of Appendix A only for those models demonstrated to be significant. In every case, the set of all environmental variables is highly significant and the periodicities are not. Thus, the variation of the population variables is adequately "explained" in each area without recourse to variables other than those measured in the monthly sampling. However, no natural subset of the environmental variables is significant alone nor is any one of these variables alone.

Separate runs for each bivalve group were also made for all areas combined and the hypotheses tested are given in Table 8 of Appendix A. Again, only those ω models shown to be significant are given in Table 9. The results are not rewarding. Neither the environmental variables nor the periodicities are significant by themselves. For significance of these factors of interest a 20 parameter model is required including all environmental variables and either of the periodicities and its interactions. Moreover, since in

this group sense either periodicity is significant, it is not appropriate to distinguish between them. Therefore, it can only be concluded that all environmental, periodicity and interaction variables are necessary to adequately "explain" the distributions.

The very high significance of the station differences for the Group 1 (total infaunal and semi-infaunal bivalves) and Group 2 (lucinids which are 84% of the Group 1 individuals) bivalves is very important. Clearly, when considered over the total range of environments, some property or set of properties of the individual areas, physical, chemical or biological, were more significant in determining the population distributions than were the factors measured during the year of study.

V. DISCUSSION AND CONCLUSIONS

The reef flat is obviously a very high stress environment in comparison to the Discovery Bay localities. In this environment organisms must be able to burrow deeper than two or three cm or be able to tolerate ambient temperatures in excess of 40°C. However, within the sediments organisms must be able to tolerate highly reducing conditons with great concentrations of hydrogen sulfide and very low pH. In addition, salinities are moderately low for months on end and may drop in a matter of hours to only a few parts per thousand.

The ability of bivalves to tolerate such conditions is largely related to their ability to isolate themselves as effectively as possible from their external environment for as long as is necessary for adverse conditions to reverse themselves. In order to do this successfully, bivalves must be able to survive long periods of stagnant conditions within their mantle cavities, often at elevated temperatures. It has been demonstrated elsewhere (Jackson, 1971) that temperature, salinity and stagnation tolerance are all significant factors in determining the distributions of shallow water Caribbean infaunal bivalves. Furthermore, salinity and stagnation tolerance are of primary importance, at least for the Lucinacea. Of all groups examined, only the Lucinacea exhibited high tolerance to all factors, alone or combined, and it is this eurytopic group which comprises greater than 96% of both the number and length number of total bivalves on the reef flat.

Environmental conditions at I are sufficiently more rigorous than at II for there to be a more than two-fold increase in abundance in the 10 meters separating the two localities. This is largely due to the increase in abundance of Codakia orbicularis. In contrast, Ctena orbiculata, which is significantly more tolerant of high temperature and stagnation stress than is C. orbicularis (Jackson, 1971) actually slightly increases in number, but not in length number, towards the shore. The greater fluidity of the sediment surface at I may also be important by decreasing larval and

juvenile survival in that area.

High physiological tolerance is of course necessary in the other invertebrate groups as well. The general importance of oxygen fluctuations on the reef flat is evident from the high frequency of pigmented polychaetes and the heavily pigmented sipunculid. Lucinids also have blood pigments (Read, 1962; Jackson, 1971). The epifaunal Neritina virginea, Cerithium variabile and Arcopsis adamsi are all capable of surviving water temperatures in excess of $41^{\circ}C$ and possess considerable salinity tolerance (Jackson, unpublished data). Naticids are not so tolerant but may avoid excessive temperatures and exposure by their deep burrowing habits. On occasion, however, large numbers of dead and dying Polinices lacteus have been observed on reef flats in water temperatures of about $39^{\circ}C$. This is the most probable reason for the nearly two times greater numbers of naticids at II than at I.

Area III is one of intermediate conditions, for although salinity and temperature stresses are insignificant, wave action is not. Although the Thalassia root mat is very thick and strong, wave action during storms still has a considerable erosive effect on the upper one to three cm. This is seen from the large amounts of sediment stirred up and in the breakdown in the chemical gradient across the sediment-water interface. This has at least two very important effects on the nature of the infaunal bivalve community.

First, bivalves must either be firmly attached to the

substrate, be buried sufficiently deeply to avoid uncovering or be rapid burrowers. About 81% of the infaunal and semi-infaunal bivalves (Group 1) at III, including the three most abundant species, are Lucinacea. All of these are deeply burrowing species and live from 3 or 5 to some 20 cm beneath the sediment surface. The fourth most abundant species is the large semi-infaunal mussel Modiolus americanus. This species possesses a very strong byssus by which it firmly attaches to Thalassia roots or other solid materials. As evidence of their stability in this environment, many individuals were observed to support two or even three generations of the large epifaunal Arca zebra. Finally, although the fifth most abundant species, Anadara notabilis, is a shallow burrower it is weakly byssate at this locality. Besides this anchoring, the species is large (8 to 9 cm) and very heavy shelled. The resultant great weight must certainly be an aid in stability. Thus, the life habits of these species are a definite indication of the importance of wave strength in determining the occurrence of bivalves in this locality.

The second factor associated with wave activity is that of the higher and more variable turbidity on the shallower parts of the lagoonal shelf within Discovery Bay. Not only are amounts of suspended material greater at III than IV during storms, but turbid conditions last far longer at the shallower locality. Moreover, during minor storms visibility may go to zero at III but not drop below one or two meters

at IV. Eulamellibranch bivalves are typically very sensitive to ctenidial clogging and must stop filtering during excessively turbid conditions. Two important exceptions are the Lucinacea and Tellinacea. The former commonly lack complex ctenidial sorting mechanisms and the latter have variously developed greater tolerance in relation to their highly modified selective deposit feeding behavior.

As noted previously, stormy weather and turbid water conditions may last for very long periods within the Bay. At III, turbid conditions sufficient to prevent filtering activity could easily last a week or more at a time almost every winter. In order to survive such conditions, suspension feeding bivalves must either be able to close down and survive self-imposed stagnant conditions within the mantle cavity or risk ctenidial clogging. Cardiids in Jamaica are particularly intolerant of stagnant conditions (Jackson, 1971) and this suggests that the greater turbidity at III could well be responsible for their lower diversity and abundance than at IV.

There are no such obvious stress factors to overcome for successful habitation at Area IV. Consequently, this area is most notable for the abundance of taxa not capable of surviving conditions at the other localities. Such a stenotopic group is the cardiids whose primary abundance is therefore one of the most diagnostic features of the Area IV assemblage.

The great diversity and abundance of echinoderms

provides additional evidence of the unimportance of the variation in temperature, salinity and the other "weather" variables at the Discovery Bay localities. Furthermore, the lower frequency of benthic species with blood pigments, especially at IV, is certainly related to the general absence of adverse conditions requiring regular and prolonged isolation from the water column. The low abundance of gastropods at III is probably due to shell breakage and abrasion by storms. This is supported by frequent observations of large densities of these species, especially *Cerithium literatum*, in more protected but otherwise similar localities within Discovery Bay. The opposite distribution of epifaunal bivalve abundance is not contradictory but results from the greater availability at III of small, relatively firm pieces of coral debris suitable for attachment by strongly byssate or cemented taxa.

The taxonomic distribution of physiological tolerance seen here is decidedly non-random. Highly developed eurytopy is limited to very few groups, particularly the Lucinidae. The dominance of these eurytopic taxa in low diversity, high stress environments is in complete agreement with the expectations of the stability-time hypothesis as most recently discussed by Slobodkin and Sanders (1969). However, although very much less abundant than at the shallower localities, the lucinids are still quite common at IV in comparison to the other bivalve groups. Thus, in this case, there is no evidence to indicate that the eurytopic taxa are competitively excluded

by the stenotopic taxa as proposed by Slobodkin and Sanders (1969).

The very high total bivalve diversity at IV is considerably greater than any value reported from temperate water marine angiosperm environments. Levinton's data (1971) from a subtidal _Zostera_ _marina_ bed in Massachusetts in a setting roughly comparable to Discovery Bay are particularly relevant. This increase in within habitat infaunal diversity towards the equator is in agreement with the work of Stanley (1970) on total bivalve species number and that of Sanders (1968) on benthic polychaete-bivalve communities from non-vegetated, soft-bottom environments.

Cumulative diversity at IV is also much higher than for Gorgonia on any of the reef zones just outside Discovery Bay (Kinzie, 1970). Gorgonians are dominant taxa of Caribbean reefs and at Discovery Bay are represented by a number of species comparable to the number of bivalve taxa present within _Thalassia_ environments. Comparisons between organisms so different as bivalves and gorgonians must be made with great caution. However, contrary to general opinion, coral reefs are often less diverse than are neighboring level-bottom environments.

The correlation of greater number and biomass per unit area with lower diversity appears to be quite general in marine environments. This is true both on a local scale, as in this study, and along traverses extending from coastal waters to abyssal depths (Hessler and Sanders, 1967; Sanders

and Hessler, 1969; Buzas and Gibson, 1968). In both cases there is a similar, but not proportional, decrease in faunal abundance and the amount of total organic carbon available. Thus, contrary to the theoretical expectations of Connell and Orias (1964) and the experimental observations of Hall et al (1970), there is generally in the seas a negative correlation between cumulative diversity and the total amount of food available.

It is, however, important to examine the types of food available in the different environments. Lucinids utilize fairly large suspended detrital particles, presumably for their bacterial flora (Allen, 1958; Jackson, 1971). Although there is a considerable decrease in the abundance of this material between the reef flat and Discovery Bay it is most unlikely that the lucinids are ever food limited in any of these environments. This is simply because the amount of Thalassia-derived detritus is always so great as to vastly exceed the amount being processed at any one time. Moreover, the kinetics of bacterial flora renewal on previously processed detritus may be on the order of only a few days (Fenchel, 1970; Newell, 1965). If this is the case, any relation between lucinid diversity and variation in food supply in such environments is of little or no significance.

Such may not be the case for the more typical eulamellibranch suspension feeders. As already discussed, qualitative comparisons indicate a far greater variety and abundance of plankton at the Discovery Bay localities as compared to Pear

Tree Bottom. If such Group 3 bivalves as the cardiids and venerids utilize only this fraction of the available particulate organic carbon then both their abundance and diversity increase with the abundance and diversity of their food supply. However, if as is quite possible (see Jørgenson, 1966), they utilize other material such as the "unresolved" particulate organic carbon of Reiswig (1971) then abundance and diversity decrease with food abundance but increase with the diversity of the available food supply.

Reiswig showed that the "unresolved" fraction comprised more than 90% of the particulate organic carbon in our analyses. Therefore, if such bivalves utilize only plankton they may at times be food limited in the Thalassia environments. However, if they can also utilize the "unresolved" fraction (as do sponges in this area) then it is most unlikely that these suspension feeding bivalves are ever limited by their food supply. The complexity of these relations indicates the great danger in generalizing on the relations of food supply to diversity until the nutritional strategies of many more groups are understood. Reiswig's work (1971) on Jamaican sponges has provided a most important first step in this direction.

The relation between predation and molluscan diversity in Thalassia communities is still under study and will be dealt with in a subsequent paper. However, certain general observations can be made at this time. In predator-prey interactions, the observed aggregations of biomass of the

dominant species must tend to strongly favor moderate to low density, random or regularly distributed species. This is true because, having entered a particular concentration, the probability that a predator will continue to encounter and feed on the dominant species is greater than the percentage of that dominant species in the total population. Thus, even without preferential feeding behavior, as may be the case in these _Thalassia_ communities, increased predation should tend to decrease dominance and thereby increase diversity. Paine (1966, 1969), Harper (1969) and Hall, _et al._, (1970), have all demonstrated the positive role of increased predation pressure on the total species number or diversity of a variety of communities including the marine intertidal, grasslands and artificial ponds. The present observations and the positive correlation of lucinid diversity and drill predation are in agreement with these studies.

As a group, the three reef flat naticids prey on a wide variety of molluscs. Predominant among these appear to be the readily available, small epifaunal gastropods _Neritina virginea_ and _Cerithium variabile_ whose dead shell populations may show almost complete mortality by drilling. However, as already noted, the abundance of these snails fluctuates very greatly and may rapidly drop by more than an order of magnitude. This may be due either to intense naticid predation or some unknown seasonal aspect of the gastropod life cycles. In either case, the large lucinid biomass must be of great importance in allowing stability

of predator populations over these periods.

The indications from field evidence of the greater physiological tolerance of the lucinid prey relative to at least one of the naticids helps to explain the considerable decrease in drill predation on the reef flat from I to II throughout the year of observations. The continually lower lucinid density, in the face of simultaneously lower levels of predation, appears to confirm the argument that environmental stress is sufficiently greater at Area I to severely limit settlement and juvenile survival of even this eurytopic group. Finally, the mass death of only one naticid species, and that the one which was more common at II than I, implies the existence of significant differences in the tolerances and behavior of these gastropods. However, their possible nature or importance to the bivalve populations are not known.

The relation of body size to environment has been investigated by many workers (Hutchinson, 1959; Slobodkin, 1968; Miller, 1969) and in particular for bivalves by Stanley (1970) and Jackson (1971). Briefly, infaunal bivalves from high stress environments tend to be comparatively large in comparison to those from lower stress environments. This is the case for at least two reasons. First, greater size allows an infaunal organism to burrow more deeply below the sediment-water interface, thereby increasing the distance between itself and most adverse environmental events. Second, larger bivalves tend to be physiologically

more tolerant than smaller bivalves either of the same or different species.

Increased size does not help epifaunal invertebrates to protect themselves from most adverse environmental effects such as very high water temperatures. In addition, smaller species of most organisms tend to mature more rapidly than larger species (Slobodkin, 1968 from Bonner, 1965). Thus, other factors being equal, smaller species are capable of more rapid recolonization of areas where local extinction has been caused by extreme environmental stress. As already noted, epifaunal molluscs from high stress environments (Arcopsis adamsi, Cerithium variabile) tend to be much smaller than their more stenotopic relatives (Arca zebra, Cerithium literatum, C. eburneum). Thus, where increased size allows significant isolation from stress conditions, then species living in high stress environments tend to be larger than their relatives living in comparatively low stress environments. In contrast, where large size does not afford such an advantage, then selection in high stress environments strongly favors small size and the ability for rapid increase. Exactly these sorts of molluscan size patterns were observed between the four areas examined in this study.

The size-frequency distributions are, of course, strongly influenced by these factors. Predation is also very important because, in all environments, increased predation lowers the percentage of organisms which reach

adult size. On the reef flat, predation rates are comparatively low and a large number of the infaunal bivalves reach full adult size. Recruitment is continuous for most species and juvenile and small adult mortality is quite high. However, having reached full adult size, the life expectancy for the larger species is much increased and there is an accumulation of large individuals of a variety of ages. It is these bivalves which give the reef flat size-frequency distributions their markedly bimodal appearance. At Discovery Bay, predation pressure is so high that very few individuals of the larger species reach full adult size. There is also a greater relative abundance of smaller species. Other collections made during the pilot study and from around Jamaica showed the same distributions.

These two sorts of size-frequency distributions appear to be quite general. Large infaunal bivalves are regularly found in intertidal and shallow subtidal sediments in both tropical and temperate seas but are uncommon to rare in deeper environments. Deep sea bivalves are especially small (Hessler and Sanders, 1967). This trend is strongly evident for Caribbean Lucinidae (Jackson, 1971). Decreased predation in comparatively low stress environments may allow a shift to a greater mean size but should not affect the unimodality of the curve. In high stress environments, greatly increased predation could reduce mean size and suppress the bimodality. However, this is not possible unless the predators are as physiologically tolerant as their prey which was

not the case in this study. Also, there is likely to be strong selection for more rapid bivalve growth rates in such high stress environments and this will increase the percentage of individuals which reach full adult size.

It is apparent that the size-frequency distribution of all the individuals in an infaunal community may be an excellent indicator of the average physiological tolerance of the component species and the degree of environmental stress. Epifaunal communities may also show consistent (opposite) relations. Such distributions appear to be well preserved in the dead shell assemblages from the same areas. Thus, analysis of total community size-frequency distributions may provide insights into the nature of ancient communities and environments.

In the regression analyses, the high significance of the station differences relative to the factors measured during the year of study suggest the following:

1. The choice of variables was incomplete. It is certain that one or more physical or chemical factors of general significance was not among those measured. One variable already demonstrated to be very important is wave action, at least within Discovery Bay. Although this variable was definitely covariant with turbidity within Discovery Bay, this was not necessarily the case at Pear Tree Bottom. Therefore, some measure of wave action would have added significant information to the general model and undoubtedly there were other such factors. However, the

fact that the individual area models were so highly significant for the set of environmental variables in every case suggests that the addition of even a great variety of meaningful variables would not materially affect the total analyses. As already seen, this is not true for certain biological factors such as predation and inclusion of predation rates may well have proved significant.

2. It is likely that the variables measured were on the whole among the most significant environmental factors but that the time scale of the observations was not adequate. This is especially probable for two reasons:

a. Although reproduction is fairly continuous for many of the species, their generation times are probably at least as great as one year. Just as spatial replication is absolutely essential, seasonal replication must also be necessary for adequate analysis of periodic variations, both biological and environmental.

b. It is probable that the most significant environmental events, especially at Pear Tree Bottom,are catastrophes. In Jamaica, the most important catastrophic events of interest in this context, both for their tremendous physical power and associated flood rains, are hurricanes. The marine biological effects of these disturbances in the Caribbean have been described by Tabb and Jones (1962) and Goreau (1964). For over twenty years no hurricane has directly hit Jamaica although the island has suffered excessively heavy rains associated with at least one such storm

that passed within the vicinity. This is unusual, for a great many times in Jamaica's written history hurricanes of very great force have struck various parts of the island about once a year for a number of consecutive years (Black, 1965). Considering other catastrophic events, Glynn (1968) has discussed the effects and frequency of very high reef flat temperatures coincident with exposure at Puerto Rico. From his data it is clear that water temperatures sufficiently great to have a serious effect on large numbers of nearshore lucinids ($>40^{\circ}$C) are likely to be rare events indeed. These conclusions are entirely in accord with those of Slobodkin and Sanders (1969) regarding the importance of unpredictable events in high stress environments. However, the time scale of such catastrophes is perhaps greater than is often appreciated.

The results of the regressions are similar to those of Buzas (1969) and strongly suggest that, except for events of catastrophic proportions, only entire sets of environmental variables are likely to be significant in determining species or community distributions. However, for the purpose of understanding the observed faunal distributions, the models were only useful in the context of large amounts of experimental and environmental information not obtained as a result of the sampling program.

Even more serious is the lack of significant generality of the environmental variable models between areas and the great significance of the station differences. These problems

could only be resolved by occupying for many years a far greater number of sample areas than investigated in this study. It is questionable whether the results would be greatly more informative than those already obtained and the expense and labor would be excessive. Population and environmental variables should continue to be monitored, especially in tropical and subtropical environments for which we have so little information. However, it is apparent that for resolution beyond the level of this study, multivariate methods can be most profitably employed not through passive observations but in the design and monitoring of experimental communities either through the use of artificial communities or by perturbation analysis.

Information diversity is a measure of the uncertainty in an assemblage; high diversity areas being ones of low faunal predictability and low diversity areas the opposite. The spatial distribution analyses for species number suggest that this faunal predictability is spatial as well as taxonomic. Levinton (1971) has suggested that the temporal stability of populations might be approximated by their variability in space. If this is true then the reef flat communities should be more stable than those in Discovery Bay, especially at IV.

Samplings in numerous Jamaican localities visited in previous years by myself and other collectors have indicated that the constancy of population levels and diversity at Pear Tree Bottom may be fairly typical of tropical and

subtropical high stress environments for the periods between catastrophic events. For example, Allen's (1958) brief description of the bivalves from the Palisadoes Road-Port Royal Mangroves area (Kingston Harbor) indicates little faunal change to the present (Jackson 1968 to 1970, unpublished data) despite the catastrophic rains and mass deaths of 1963 associated with the near passage of hurricane Flora (Goreau, 1964). If this community was severely affected, its reestablishment must have been extremely rapid. Allthis implies a bimodality whereby varyingly great periods of faunal constancy are broken by some sudden event which destroys most or all of the population but is followed by a rapid return to approximately the original conditions. During the more favorable periods, equilibrium may result from the continual recruitment of the dominant taxa as balanced against predation and moderate mostly juvenile, mortality due to physiological stress.

Fager (1968) observed the faunal density and species composition of a low diversity, high stress sand bottom community off La Jolla, California, for six years. His results showed the community to be remarkably constant over that period. In a recent review, Castenholz (1967) has also emphasized the considerable stability of a variety of intertidal rocky shore communities. Large lucinid bivalves have dominated low diversity molluscan communities of a distinctively modern aspect in nearshore marine environments similar to those examined in this study

since at least the Cretaceous (Bretsky, 1969; Waage,
personal communication). Moreover, the Paleozoic lucinid
Paracyclas has been found in life position in low diversity,
nearshore Devonian deposits in New York (Thayer, personal
communication). Thus, description of low diversity communi-
ties as immature may often be unwarrented and low diversity
marine communities may be at least as stable as are high
diversity communities.

VI. SUMMARY

1. Four homogeneous areas within beds of the marine
angiosperm Thalassia were selected along a composite
onshore-offshore gradient for detailed study. Eleven
environmental variables and molluscan and echinoderm
abundance were sampled at monthly intervals for one
year (1969-1970).

2. The two shallower areas are situated on an occas-
ionally intertidal back reef flat characterized by unpre-
dictable environmental variability of very high variance.
Diurnal variations in environmental variables are almost
as great as their entire yearly range and the chemical
gradient across the sediment-water interface is extreme.
Water conditions are quiet. The two deeper areas are
located completely subtidally in a large, semi-enclosed
bay characterized by predictable (seasonal) environmental

variability of very low variance except for wave action and associated factors. Diurnal variations of almost all factors are far lower than the observed annual variations and the chemical gradient across the interface comparatively moderate.

3. The variances of all but one of the environmental variables (not including sediment size parameters) are very different between the four sample areas and there is a significant decrease in environmental variance going offshore. There are also significant differences in the means of many of these variables. The result is a major decrease in the degree of environmental stress from the shallowest to deepest sample area.

4. Both back reef flat areas contain large numbers of comparatively few species with the complete absence of entire groups commonly found in shallow water Thalassia environments. Molluscs are by far the most abundant macroinvertebrates and are estimated to comprise well in excess of three quarters of the benthic invertebrate biomass. The bay areas contain modest numbers of a great variety of species including representatives of almost all important soft-bottom groups. Echinoderms are the dominant epifauna but no group appears to dominate the infauna.

5. Lucinidae comprise in excess of 96% of the back reef flat infaunal bivalve number and biomass. One species, Codakia orbicularis, makes up more than 80% of the total abundance. This is due to the very high tolerance of these bivalves to high temperatures, low salinity and stagnation as compared to other infaunal bivalve groups. At the shallower bay locality the Lucinidae are still the most abundant family but no one species comprises more than one third of the bivalve abundance. Heavy wave action and related excessive turbidity during winter storms here excludes many shallow burrowers and typical eulamellibranch suspension feeders due to ctenidial clogging. There are no such obvious stress factors at the deeper bay area and no one species or family is dominant. Both the Cardiidae and Veneridae are here more abundant than the Lucinidae.

6. Cumulative Brillouin diversity of both the lucinids and other infaunal and semi-infaunal bivalves greatly increases from the back reef flat to the bay localities with decreasing environmental stress. Cumulative diversity is strongly dependent on total species number but is frequently inversely correlated to abundance and size. Similarly, in individual samples, diversity is positively correlated to the number of species but variably or negatively correlated to abundance. This is due to the overwhelming abundance of a few species in the high stress,

low diversity environments. Lucinids and other infaunal bivalves are larger in areas where they are most abundant. These groups, however, show no correlation or are negatively correlated in their co-occurrence due to their distinctive differences in physiological tolerance and feeding behavior. All of these relations are in agreement with the predictions of the stability-time hypothesis (Slobodkin and Sanders, 1969).

7. The Lucinidae feed on large particles such as _Thalassia_ derived detritus. Due to the abundance of such material it is most unlikely that these bivalves are ever food limited in sea grass and neighboring environments. The decrease in lucinid abundance with depth is more likely a result of increased predation in the bay environments. Typical eulamellibranch suspension feeders dominate only at the deepest bay area and comprise well under 1% of the back reef flat infaunal bivalve fauna where food supplies may be inadequate. The diversity of suspension feeders increases with the diversity of their available food supply but their relation to the abundance of suitable food is not known.

8. Average infaunal bivalve size is greatest in areas of highest population density and there is a distinctive decrease in size with decrease in environmental stress.

This is because large size allows substantial isolation from stress conditions for infaunal organisms. Epifaunal bivalves and gastropods show the opposite distributions. Total infaunal and semi-infaunal bivalve size-frequency distributions are strongly bimodal on the back reef flat but unimodal in the bay localities. This distribution results from the differences in physiological stress and predation pressure in these areas. All of these patterns appear to be well preserved in the dead shell distributions from the same samples.

9. Increased predation pressure appears to exert a positive role in determining the diversity of the four bivalve communities. The lucinids are only occasionally taken by predators other than deep burrowing, drilling, naticid gastropods. The percent drilled for each species generally increases with water depth and the diversity of the lucinid assemblage. In all sample areas, drill predation is greater for smaller than for larger bivalves. Naticids are by far the dominant predators of bivalves on the back reef flat but not in the bay where other gastropods, fish and rays are also important. Overall predator diversity is greatest in environments with highest bivalve diversity in spite of the fact that prey biomass is lower in such areas.

10. In multivariate regression analyses, the measured environmental variables as a set are highly significant in"explaining" bivalve population variations over the year in any one area. Three different natural subsets of these or individual environmental variables, however, were not significant. Between areas, the environmental variable set alone is not significant but the arbitrary station differences are highly significant. Thus, some property or set of properties of the individual areas, physical, chemical or biological, are more significant in determining population distributions between areas than are the eleven factors measured during the year of study. It is probable that the most important of these are catastrophes, especially those related to hurricanes.

11. Neither the number of species nor their abundance changed significantly at any of the four sample areas during the entire year of observations and variations within any one month were generally greater than the mean monthly variations. This strongly suggests that most of the observed variance is spatial rather than temporal. Variance/mean ratios of total infaunal and semi-infaunal bivalve species number/sample increases with depth and is apparently correlated to cumulative diversity. The low diversity communities may be at least as stable as the high diversity communities.

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VIII. APPENDIX A. MULTIVARIATE REGRESSION ANALYSES

Table 5. Composition of matrix $\underset{\sim}{Z}'$ for single station analyses.

z_0 = vector of units

z_1 = observed salinity ^{o}/oo

z_2 = observed water temperature ^oC

z_3 = observed water pH minus sediment pH

z_4 = observed particulate organic carbon mg C/M^3

z_5 = observed "turbidity" as percent extinction

z_6 = observed sediment median grain size in mm

z_7 = observed sediment sorting

z_8 = observed dry weight _Thalassia_ in g

z_9 = observed silt plus clay weight percent

z_{10} = observed water temperature minus sediment temperature ^oC

z_{11} = observed percent oxygen saturation

z_{12} = sin (m x π/6) m=1,2,...12

z_{13} = cos (m x π/6) m=1,2,...12

z_{14} = sin (m x π/3) m=1,2,...12

z_{15} = cos (m x π/3) m=1,2,...12

Table 6. Composition of matrix $\underset{\sim}{Z}{}'$ for combined station analyses.

z_0 = vector of units

z_1 = -1 for Area I observations, +1 for II, -1 for III and +1 for IV

z_2 = -1 for Areas I and II observations and +1 for III and IV

z_3 = +1 for Areas I and IV observations and -1 for II and III

z_4 = observed salinity $^o/oo$

z_5 = observed water temperature ^oC

z_6 = observed water pH minus sediment pH

z_7 = observed particulate organic carbon mg/M^3

z_8 = observed "turbidity" as percent extinction

z_9 = observed sediment median grain size in mm

z_{10} = observed sediment sorting

z_{11} = observed dry weight Thalassia in g

z_{12} = observed silt plus clay weight percent

z_{13} = observed water temperature minus sediment temperature ^oC

z_{14} = observed percent oxygen saturation

z_{15} = sin (m x π/6) m=1,2,...12

z_{16} = cos (m x π/6) m=1,2,...12

z_{17} = sin (m x π/3) m=1,2,...12

z_{18} = cos (m x π/3) m=1,2,...12

z_{19} = z_1 x z_{15}

z_{20} = z_2 x z_{15}

z_{21} = z_3 x z_{15}

z_{22} = z_1 x z_{16}

z_{23} = z_2 x z_{16}

z_{24} = z_3 x z_{16}

z_{25} = z_1 x z_{17}

z_{26} = z_2 x z_{17}

z_{27} = z_3 x z_{17}

z_{28} = z_1 x z_{18}

z_{29} = z_2 x z_{18}

z_{30} = z_3 x z_{18}

Table 7. ω model hypotheses for individual areas.

	Hypothesis ($B_i=0$)	Effect
1	$i=1,\ldots 15$	environmental variables and overall periodicity
2	$i=12, 13$	$\pi/6$ periodicity
3	$i=14, 15$	$\pi/3$ periodicity
4	$i=12,\ldots 15$	overall periodicity
5	$i=6,7,9$	sediments
6	$i=3, 10$	interface gradient
7	$i=1, 2, 4, 5, 11$	"weather" variables
8	$i=1,\ldots 11$	overall environmental variables

Table 8. ω model hypotheses for all areas combined.

	Hypothesis ($B_i = 0$)	Effect
1	i=4,...30	environmental variables, overall periodicity and interactions
2	i=4,...16	environmental variables and $\pi/6$ periodicity
3	i=4,...16,19,...24	environmental variables, $\pi/6$ periodicity and interactions
4	i=4,...14,17,18	environmental variables and $\pi/3$ periodicity
5	i=4,..14,17,18, 25,...30	environmental variables, $\pi/3$ periodicity and interactions
6	i=4,...18	environmental variables and overall periodicity
7	i=19,...24	$\pi/6$ interactions
8	i=25,...30	$\pi/3$ interactions
9	i=15,16,19,...24	$\pi/6$ periodicity and interactions
10	i=17,18,25,...30	$\pi/3$ periodicity and interactions
11	i=15,...30	overall periodicity and interactions
12	i=9,10,12	sediments
13	i=6,13	interface gradient
14	i=4,5,7,8,14	"weather" variables
15	i=4,...14	overall environmental variables
16	i=1,...3	station differences

Table 9. Significant ω models.

AREA	HYPOTHESIS $B_1=0$	VARIABILITY ON ACCOUNT OF:	df	(N-q)	(N-s)	U	SIGNIFICANCE LEVEL
		Group 1					
I	i=1,...11	environmental variables	25	0.286	1.89	59.5	.005
II	i=1,...11	environmental variables	25	0.159	0.541	38.5	.05
III	i=1,...11	environmental variables	25	0.162	0.643	43.4	.025
IV	i=1,...11	environmental variables	25	0.790	4.64	55.7	.005
I-IV	i=4,...30	environmental variables, overall periodicities	20	4.30×10^3	1.11×10^4	151.6	.005
I-IV	i=4,...16, 19,...24	environmental variables, $\pi/6$ periodicity and interactions	60	4.30×10^3	8.43×10^3	106.4	.005
I-IV	i=4,...14,17, 18,25,...30	environmental variables, $\pi/3$ periodicity and interactions	60	4.30×10^3	8.36×10^3	105.1	.005
I-IV	i=1,...3	station differences	140	4.30×10^3	1.90×10^4	258.6	.005

Table 9. continued

AREA	HYPOTHESIS $B_i=0$	VARIABILITY ON ACCOUNT OF:	df (N-q)	(N-s)		U	SIGNIFICANCE LEVEL
		Group 2					
I	i=1,...11	environmental variables	25	5.25×10^{-2}	0.452	67.8	.005
II	i=1,...11	environmental variables	25	1.16×10^{-2}	5.35×10^{-2}	48.0	.005
III	i=1,...11	environmental variables	25	0.402	2.740	60.5	.005
IV	i=1,...11	environmental variables	25	5.08×10^{-3}	3.01×10^{-2}	56.1	.005
I-IV	i=4,...30	environmental variables, overall periodicities and interactions	20	6.16×10^{3}	1.39×10^{4}	184.2	.005
I-IV	i=4,...16, 19,...24	environmental variables, $\pi/6$ periodicity and interactions	60	6.16×10^{3}	1.13×10^{4}	99.5	.005
I-IV	i=4,...14,17, 18,25,...30	environmental variables, $\pi/3$ periodicity and interactions	60	6.16×10^{3}	1.18×10^{4}	102.4	.005
I-IV	i=1,...3	station differences	140	6.16×10^{3}	3.63×10^{4}	304.9	.005

Table 9. continued

AREA	HYPOTHESIS $B_i=0$	VARIABILITY ON ACCOUNT OF:	df (N-q)	(N-s)	U	SIGNIFICANCE LEVEL
		Group 3				
II	$i=1,\ldots11$	environmental variables	25	5.98×10^{-2}	0.273	47.8	.005
III	$i=1,\ldots11$	environmental variables	25	0.324	2.342	62.3	.005
IV	$i=1,\ldots11$	environmental variables	25	0.648	3.40	52.2	.005
I-IV	$i=4,\ldots30$	environmental variables, overall periodicities and interactions	20	2.99×10^{3}	8.45×10^{3}	166.1	.005
I-IV	$i=4,\ldots16,$ $19,\ldots24$	environmental variables, $\pi/6$ periodicity and interactions	60	2.99×10^{3}	6.53×10^{3}	123.2	.005
I-IV	$i=4,\ldots14,17,$ $18,25,\ldots30$	environmental variables, $\pi/3$ periodicity and interactions	60	2.99×10^{3}	5.91×10^{3}	107.7	.005

IX.   APPENDIX B.   ENVIRONMENTAL VARIABLES

Figure 16. Correlation matrix of environmental variables measured monthly at Pear Tree Bottom (Area I) for year 1969-1970. N = 48. For r = 0.29 P≤ 0.05. Key: 1 = salinity ^{o}/oo, 2 = water temperature ^{o}C, 3 = pH gradient (water minus sediment), 4 = water particulate organic carbon, 5 = turbidity, 6 = sediment median, 7 = sediment sorting, 8 = _Thalassia_ dry weight, 9 = % silt and clay, 10 = temperature gradient (water minus sediment), 11 = % oxygen saturation.

	1	2	3	4	5	6	7	8	9	10
2	-.72									
3	-.13	.51								
4	-.27	-.23	-.40							
5	-.48	.50	.15	.17						
6	-.01	-.14	-.06	.12	-.22					
7	.22	-.12	.17	-.13	-.15	.52				
8	-.03	-.11	.10	.05	-.21	.19	-.13			
9	.28	-.08	.13	-.11	.15	-.37	.36	.01		
10	-.46	.83	.48	-.26	.42	-.26	-.12	-.11	.05	
11	.10	.47	.57	-.54	.15	.04	.02	-.09	.13	.46

Figure 17. Correlation matrix of environmental variables
measured monthly at Pear Tree Bottom (Area II) for year
1969-1970. N = 48. For r = 0.29 P ≤ 0.05. Key as in
Figure 16.

	1	2	3	4	5	6	7	8	9	10
2	-.79									
3	-.46	.54								
4	-.09	.12	.18							
5	.06	.38	-.42	-.13						
6	-.22	.06	-.05	.11	-.05					
7	-.06	.01	-.20	.05	.04	.34				
8	-.39	.34	.23	-.06	-.29	-.06	-.03			
9	.38	-.35	-.34	.11	.32	-.43	.41	-.21		
10	-.65	.80	.41	.23	-.13	-.03	-.02	.15	-.18	
11	-.39	.76	.60	.08	-.59	-.06	-.03	.19	-.23	.62

Figure 18. Correlation matrix of environmental variables measured monthly at Discovery Bay (Area III) for year 1969-1970. N = 48. For r = 0.29 P≤0.05. Key as in Figure 16.

	1	2	3	4	5	6	7	8	9	10
2	-.09									
3	.27	.17								
4	-.52	.12	-.38							
5	.07	-.54	-.36	.11						
6	-.28	.09	-.02	.08	-.20					
7	.01	.13	.30	-.06	-.13	.40				
8	-.28	.13	-.06	.37	-.33	.05	-.21			
9	.41	-.17	.29	-.28	.08	-.68	.16	-.22		
10	-.10	.34	.07	.30	.08	-.01	.08	-.04	.04	
11	-.16	-.19	-.02	-.21	-.10	.03	.15	-.27	.06	-.41

Figure 19. Correlation matrix of environmental variables measured monthly at Discovery Bay (Area IV) for year 1969-1970. N = 48. For r = 0.29 P≤ 0.05. Key as in Figure 16.

	1	2	3	4	5	6	7	8	9	10
2	.26									
3	.03	.19								
4	-.19	.12	-.16							
5	-.14	-.52	-.33	.45						
6	-.35	-.14	-.11	-.05	.12					
7	-.22	-.04	.19	-.25	-.03	.44				
8	-.26	.39	.14	.37	-.12	-.03	-.07			
9	-.01	-.07	-.11	-.10	-.02	-.38	.42	-.11		
10	.18	.39	.06	.11	-.04	-.21	-.23	.33	.10	
11	.13	-.22	-.20	.02	.01	.17	-.06	-.21	-.31	-.46

Table 10. Environmental distribution of sediment properties.
Values are means and standard deviations for all 48 samples
in each sample area.

	I	II	III	IV
Median (mm)	0.169±0.016	0.237±0.054	0.248±0.059	0.322±0.069
Sorting	1.63±0.23	2.18±0.48	2.11±0.74	2.22±0.40
Percent silt plus clay	10.61±5.16	9.92±5.66	12.60±5.01	10.40±3.75

X. APPENDIX C. POPULATION VARIABLES

Table 11. Total gastropod abundance in monthly samples from Pear Tree Bottom for year 1969-1970. The average number/m^2 is given in parentheses.

	AREA I
0.10 m^2 samples	2498 Neritina virginea (521)
	2081 Cerithium variabile (434)
	38 Colubraria swifti (7.92)
0.25 m^2 plus	10 Natica livida (0.60)
0.10 m^2 samples	4 Polinices lacteus (0.24)
	AREA II
0.10 m^2 samples	1916 Neritina virginea (400)
	918 Cerithium variabile (191)
	57 Colubraria swifti (11.9)
	3 Hyalina avena (0.18)
0.25 m^2 plus	14 Polinices lacteus (0.83)
0.10 m^2 samples	7 Polinices hepaticus (0.42)
	2 Natica livida (0.12)
	1 Acmaea antillarum (0.06)
	1 Tegula fasciata (0.06)

Table 12. Total gastropod abundance in combined monthly samples from Discovery Bay for year 1969-1970. Number/m^2 in parentheses.

III	IV
10 *Turbo castanea* (0.60)	9 *Oliva reticularis* (0.54)
4 *Cerithium literatum* (0.24)	8 *Cerithium literatum* (0.48)
	5 *Turbo castanea* (0.30)
	3 *Polinices lacteus* (0.18)
	2 *Tegula fasciata* (0.12)
	2 opisthobranchs (0.12)

Table 13. Total epifaunal bivalve abundance in combined monthly samples from Pear Tree Bottom and Discovery Bay for year 1969-1970. Number/m^2 in parentheses.

Pear Tree Bottom

I	II
1 Arcopsis adamsi (0.06)	21 Arcopsis adamsi (1.25)
1 Barbatia domingensis (0.06)	

Discovery Bay

III	IV
79 Chama macerophylla (4.75)	5 Arca zebra (0.30)
25 Arca zebra (1.50)	3 Chama macerophylla (0.18)
2 Arcopsis adamsi (0.12)	2 Arcopsis adamsi (0.12)
2 Aequipecten muscosus (0.12)	1 Pinctata radiata (0.06)
1 Pecten ziczac (0.06)	1 Lima pellucida (0.06)
1 Lima pellucida (0.06)	

Figure 10. Group 1 (total infaunal and semi-infaunal)

bivalves monthly population variable means at all sample

areas (1969-1970).

MONTHLY POPULATION MEANS, GROUP I BIVALVES

Figure showing monthly population means for Group I Bivalves across four areas.

AREA I
- •$\bar{s} = 2.42 \pm 0.61$
- •$\bar{x} = 11.7 \pm 4.24$
- ○$\bar{x}_L = 30.57 \pm 13.77$
- •$\bar{H}_x = 0.810 \pm 0.251$
- ○$\bar{H}_{XL} = 0.504 \pm 0.295$

AREA II
- •$\bar{s} = 3.06 \pm 0.78$
- •$\bar{x} = 26.31 \pm 8.05$
- ○$\bar{x}_L = 69.57 \pm 22.76$
- •$\bar{H}_x = 0.752 \pm 0.274$
- ○$\bar{H}_{XL} = 0.463 \pm 0.250$

AREA III
- •$\bar{s} = 5.08 \pm 1.37$
- •$\bar{x} = 14.04 \pm 6.11$
- ○$\bar{x}_L = 27.65 \pm 14.02$
- •$\bar{H}_x = 1.481 \pm 0.366$
- ○$\bar{H}_{XL} = 1.875 \pm 0.417$

AREA IV
- •$\bar{s} = 3.42 \pm 1.73$
- •$\bar{x} = 4.44 \pm 2.59$
- ○$\bar{x}_L = 9.64 \pm 6.85$
- •$\bar{H}_x = 0.987 \pm 0.519$
- ○$\bar{H}_{XL} = 1.265 \pm 0.671$

Y-axis labels: NUMBER SPECIES; NUMBER AND LENGTH NUMBER; DIVERSITY (H_{LOG_2})

X-axis: N D J F M A M J J A S O
1969 1970

Figure 11. Group 2 (Lucinidae) bivalves monthly population variable means at all sample areas (1969-1970).

MONTHLY POPULATION MEANS, GROUP 2 BIVALVES

AREA I: $\bar{s} = 2.15 \pm 0.41$; $\bar{x} = 11.38 \pm 4.14$, $\bar{x}_L = 29.56 \pm 12.92$; $\bar{H}_x = 0.736 \pm 0.206$, $\bar{H}_{XL} = 0.416 \pm 0.231$

AREA II: $\bar{s} = 2.56 \pm 0.57$; $\bar{x} = 25.60 \pm 7.95$, $\bar{x}_L = 66.83 \pm 20.88$; $\bar{H}_x = 0.650 \pm 0.266$, $\bar{H}_{XL} = 0.310 \pm 0.166$

AREA III: $\bar{s} = 2.42 \pm 0.81$; $\bar{x} = 9.48 \pm 4.57$, $\bar{x}_L = 15.26 \pm 8.62$; $\bar{H}_x = 0.736 \pm 0.340$, $\bar{H}_{XL} = 0.861 \pm 0.416$

AREA IV: $\bar{s} = 0.71 \pm 0.82$; $\bar{x} = 0.92 \pm 1.10$, $\bar{x}_L = 0.87 \pm 1.20$; $\bar{H}_x = 0.100 \pm 0.252$, $\bar{H}_{XL} = 0.148 \pm 0.369$

NUMBER SPECIES · NUMBER AND LENGTH NUMBER · DIVERSITY (H_{LOG_2})

N D J F M A M J J A S O
1969 1970
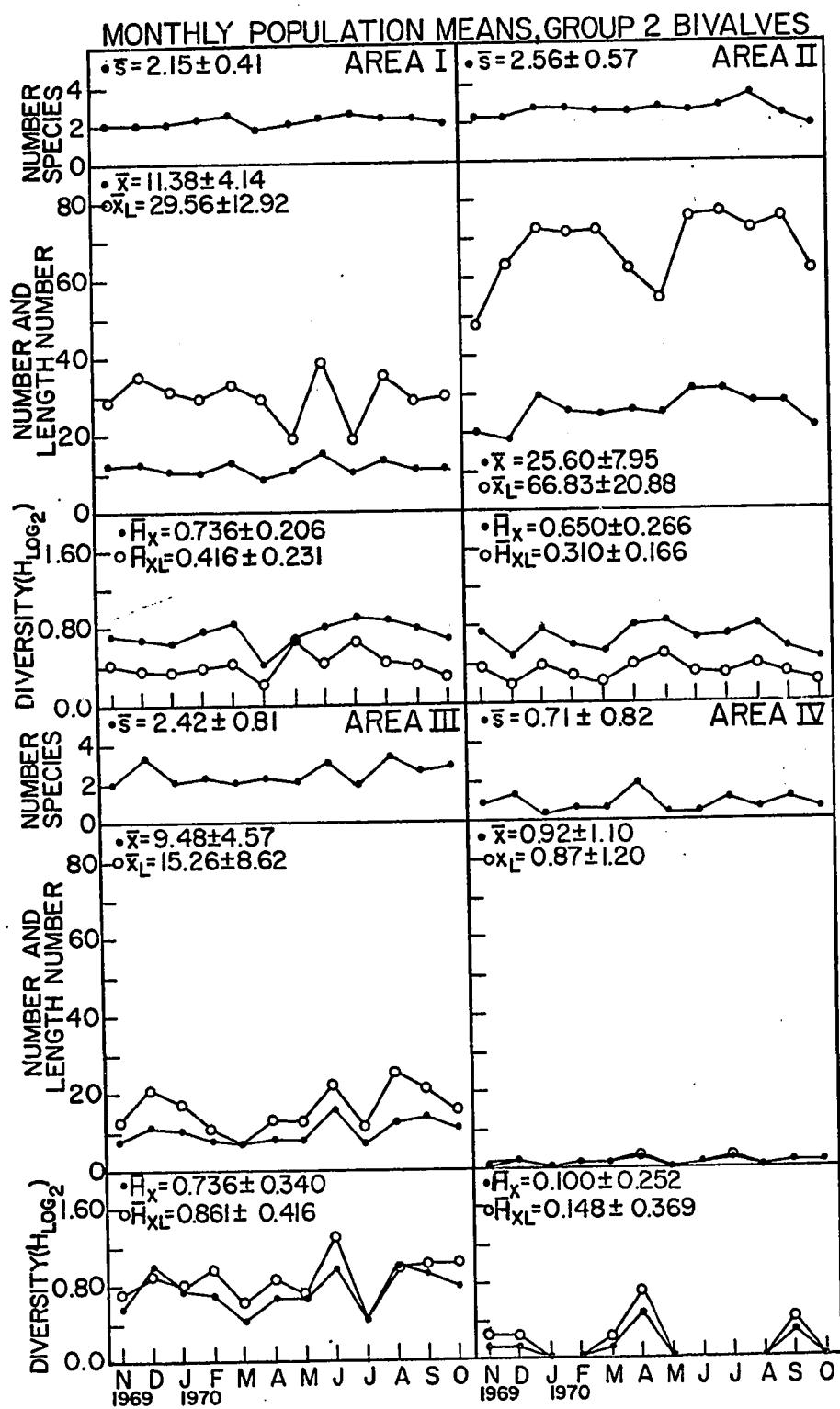
Figure 12. Group 3 (all infaunal suspension and deposit feeders except Lucinacea) bivalves monthly population variable means at all sample areas (1969-1970).

MONTHLY POPULATION MEANS, GROUP 3 BIVALVES

$\bullet \bar{s} = 0.27 \pm 0.49$ AREA I

$\bullet \bar{s} = 0.50 \pm 0.58$ AREA II

$\bullet \bar{x} = 0.40 \pm 0.91$ $\circ \bar{x}_L = 1.01 \pm 2.77$

$\bullet \bar{x} = 0.71 \pm 0.94$ $\circ \bar{x}_L = 2.74 \pm 4.50$

$\bullet \bar{H}_X = 0.012 \pm 0.084$ $\circ \bar{H}_{XL} = 0.008 \pm 0.052$

$\bullet \bar{H}_X = 0.024 \pm 0.116$ $\circ \bar{H}_{XL} = 0.017 \pm 0.084$

$\bullet \bar{s} = 1.29 \pm 1.15$ AREA III

$\bullet \bar{s} = 1.90 \pm 1.05$ AREA IV

$\bullet \bar{x} = 1.65 \pm 1.45$ $\circ \bar{x}_L = 4.17 \pm 3.97$

$\bullet \bar{x} = 2.42 \pm 1.63$ $\circ \bar{x}_L = 4.83 \pm 3.29$

$\bullet \bar{H}_X = 0.258 \pm 0.407$ $\circ \bar{H}_{XL} = 0.359 \pm 0.558$

$\bullet \bar{H}_X = 0.483 \pm 0.427$ $\circ \bar{H}_{XL} = 0.659 \pm 0.584$

Y-axis labels: NUMBER SPECIES (4, 2, 0); NUMBER & LENGTH NUMBER (20, 10, 0); DIVERSITY (H_{LOG_2}) (1.20, 0.80, 0.40, 0.0)

X-axis: N D J F M A M J J A S O   N D J F M A M J J A S O

1969   1970   1969   1970

Figure 20. Group 1 bivalves cumulative diversity at all areas for year 1969-1970.

CUMULATIVE DIVERSITY–GROUP I BIVALVES
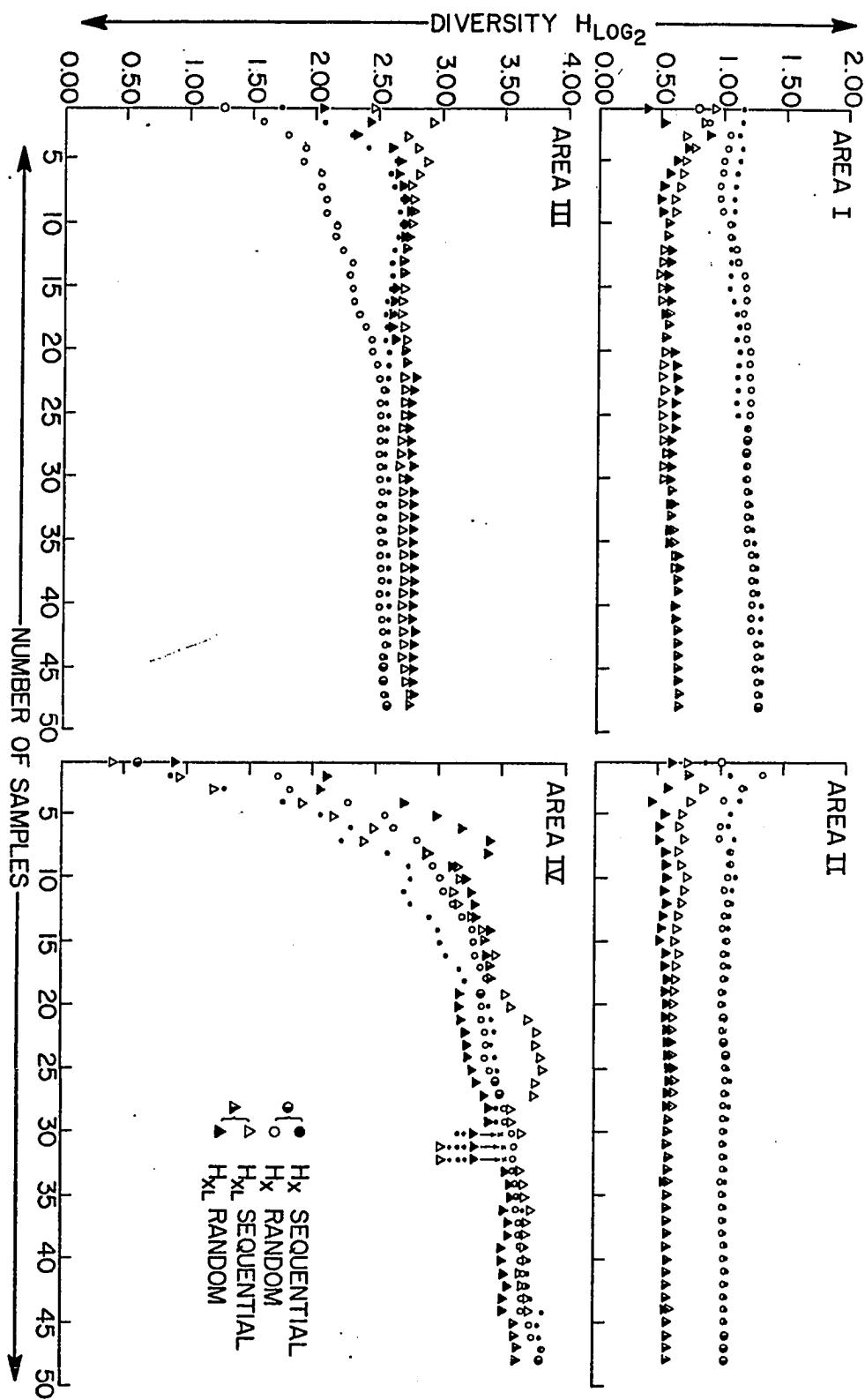
Figure 21. Group 2 bivalves cumulative diversity at all areas for year 1969-1970.

CUMULATIVE DIVERSITY - GROUP 2 BIVALVES
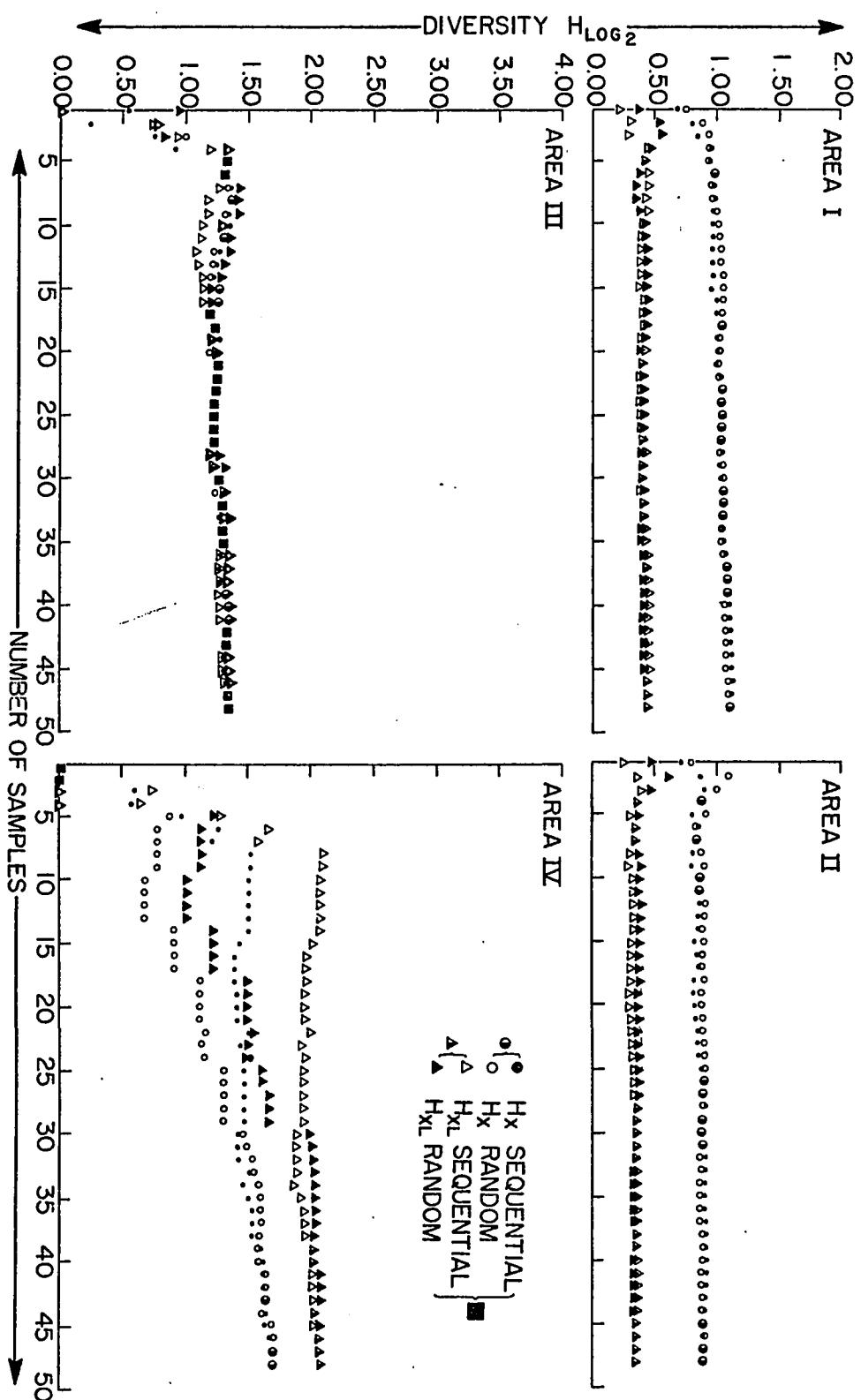
Figure 22. Group 3 bivalves cumulative diversity at all
areas for year 1969-1970.

CUMULATIVE DIVERSITY–GROUP 3 BIVALVES

Table 14. Group 1 bivalve population variables for individual 0.25 and 0.10 m^2 samples from Pear Tree Bottom (Area I) for year 1969-1970.

SAMPLE NUMBER	SPEICES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	4	13	42.8	1.15	0.91
2	2	10	22.3	0.78	0.37
3	2	10	31.4	0.78	0.27
4	2	17	24.7	0.66	0.76
5	2	11	45.0	0.67	0.37
6	2	23	44.8	0.89	0.52
7	2	8	23.1	0.77	0.41
8	2	8	27.7	0.39	0.10
9	2	11	20.9	0.76	0.58
10	2	13	52.9	0.49	0.13
11	2	7	16.2	0.74	0.43
12	2	11	35.2	0.53	0.19
13	2	9	28.8	0.72	0.31
14	2	8	19.1	0.77	0.43
15	2	10	37.0	0.56	0.14
16	3	13	32.9	1.05	0.60
17	3	15	31.3	1.05	1.04
18	3	14	35.5	0.96	0.40
19	2	15	52.1	0.59	0.15
20	3	8	18.0	1.04	0.69
21	2	9	36.7	0.37	0.08
22	1	4	19.5	0.00	0.00
23	2	8	16.9	0.73	0.57
24	2	13	42.7	0.63	0.19
25	2	10	15.6	0.70	0.66
26	3	13	25.4	1.25	0.99
27	3	18	30.5	1.05	0.53
28	2	7	7.6	0.42	0.90
29	2	17	53.5	0.74	0.22
30	2	20	55.2	0.81	0.28
31	4	16	46.1	1.37	1.21
32	3	11	13.3	0.96	0.95
33	2	7	18.7	0.74	0.29
34	3	8	13.6	1.04	0.88
35	3	10	20.1	1.05	0.55
36	3	16	21.6	1.06	1.02
37	3	17	48.6	1.01	0.37
38	3	18	55.4	1.03	1.01
39	3	10	23.1	1.05	0.55
40	3	10	21.8	1.14	0.59
41	2	10	35.7	0.78	0.28
42	2	16	34.7	0.84	0.46
43	3	6	17.8	0.86	0.44
44	3	12	25.7	1.05	0.63
45	2	7	19.3	0.64	0.23
46	2	10	34.8	0.70	0.22
47	2	7	7.2	0.74	0.67
48	3	21	64.7	0.80	0.67

Table 15. Group 1 bivalve population variables for individual 0.25 and 0.10 m^2 samples from Pear Tree Bottom (Area II) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	3	26	64.7	0.86	0.71
2	4	19	50.2	0.98	0.61
3	3	14	27.3	1.11	1.09
4	3	26	63.7	0.86	0.40
5	3	21	67.0	0.43	0.39
6	2	28	65.1	0.81	0.43
7	5	32	83.9	1.04	0.82
8	2	16	50.6	0.26	0.06
9	4	32	104.9	0.71	0.71
10	4	26	57.5	1.17	1.02
11	2	36	88.4	0.74	0.34
12	3	26	58.1	0.79	0.39
13	2	24	70.1	0.39	0.22
14	3	14	43.2	0.73	0.31
15	3	36	97.9	0.50	0.26
16	4	30	86.7	1.12	0.84
17	4	26	66.1	1.02	0.37
18	3	31	109.7	0.45	0.60
19	2	20	63.8	0.22	0.11
20	3	24	61.5	0.82	0.34
21	2	30	73.1	0.75	0.41
22	3	22	45.7	0.92	0.45
23	3	22	61.5	0.68	0.32
24	3	29	73.0	0.96	0.72
25	4	20	31.5	1.21	0.87
26	3	27	49.1	1.01	0.61
27	2	27	75.0	0.32	0.14
28	3	25	60.6	0.93	0.43
29	2	18	53.0	0.24	0.06
30	2	39	106.6	0.56	0.20
31	3	27	64.5	0.73	0.36
32	3	37	77.6	1.08	0.59
33	4	58	141.2	0.92	0.62
34	3	21	59.7	0.58	0.53
35	3	24	66.1	0.74	0.28
36	3	20	50.1	0.72	0.34
37	3	36	95.9	0.88	0.35
38	3	25	66.4	0.63	0.23
39	5	27	83.9	0.84	0.78
40	4	23	49.2	1.21	0.62
41	4	25	62.8	1.16	0.86
42	2	41	100.9	0.65	0.32
43	2	12	42.3	0.31	0.11
44	3	36	118.6	0.78	0.74
45	2	25	86.6	0.19	0.27
46	4	21	62.4	0.63	0.25
47	3	21	59.1	0.73	0.28
48	3	18	42.5	0.76	0.46

Table 16. Group 1 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Discovery Bay (Area III) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	8	20	25.9	1.73	2.49
2	5	8	14.3	1.52	1.98
3	5	13	33.9	1.52	1.80
4	5	11	31.1	1.67	2.08
5	7	21	49.5	2.08	2.25
6	3	9	19.3	1.20	1.32
7	6	12	34.6	1.70	2.04
8	8	22	42.2	1.83	2.05
9	4	10	16.4	1.44	1.81
10	6	13	26.3	1.83	2.04
11	6	15	29.7	1.73	2.19
12	6	25	50.9	1.73	2.02
13	4	15	32.7	1.37	1.70
14	6	8	22.3	1.73	2.25
15	4	7	8.8	1.15	1.67
16	5	16	27.2	1.57	2.10
17	1	2	2.1	0.00	0.00
18	5	11	18.5	1.38	1.97
19	4	11	13.4	0.94	1.44
20	8	14	19.5	1.90	2.77
21	5	10	18.2	1.50	1.89
22	4	15	39.7	1.46	1.58
23	5	12	16.2	1.17	1.91
24	4	7	13.3	1.29	1.69
25	6	11	26.0	1.74	2.31
26	4	15	32.4	1.55	1.86
27	4	11	20.7	1.28	1.39
28	3	7	7.3	0.80	1.21
29	6	36	79.8	1.92	2.15
30	6	11	25.2	1.78	2.18
31	7	17	27.2	1.85	2.27
32	4	22	29.2	1.25	1.79
33	3	6	9.6	0.86	1.48
34	5	23	51.3	1.67	1.84
35	5	8	17.6	1.52	1.89
36	5	9	15.2	1.59	1.81
37	5	13	35.1	1.43	1.58
38	5	20	40.0	1.57	1.87
39	5	19	43.7	1.56	1.81
40	6	16	38.2	1.74	1.75
41	6	18	45.0	1.90	2.05
42	6	20	39.6	1.47	2.19
43	5	12	26.4	1.58	2.01
44	4	23	26.5	1.27	1.80
45	3	10	12.5	0.67	1.26
46	5	11	20.0	1.47	1.90
47	6	10	20.8	1.55	2.27
48	6	19	31.9	1.62	2.32

Table 17. Group 1 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Discovery Bay (Area IV) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	2	3	3.2	0.57	0.38
2	2	3	8.6	0.57	0.87
3	3	4	4.3	0.90	1.15
4	3	3	4.9	0.86	1.01
5	4	4	7.6	1.26	1.60
6	2	2	3.3	0.59	0.72
7	2	3	3.8	0.57	0.72
8	5	7	9.4	1.54	2.11
9	2	2	6.2	0.59	1.47
10	1	1	0.6	0.00	0.00
11	1	1	1.8	0.00	0.00
12	1	1	0.8	0.00	0.00
13	5	5	10.0	1.49	1.98
14	2	2	3.1	0.59	0.89
15	3	4	6.4	0.90	1.13
16	2	2	3.1	0.50	0.69
17	4	6	18.6	1.21	1.20
18	3	3	6.8	0.97	1.12
19	6	9	11.7	1.78	2.22
20	3	3	6.8	0.97	1.36
21	3	3	15.8	0.97	1.27
22	5	6	9.4	1.50	2.09
23	3	4	6.4	0.96	1.44
24	6	6	7.7	1.70	2.24
25	4	4	6.6	1.26	1.51
26	2	3	9.5	0.57	0.91
27	3	3	6.6	0.86	1.16
28	3	6	23.8	0.82	0.44
29	0	0	0.0	0.00	0.00
30	5	7	10.5	1.54	2.36
31	5	7	25.2	1.46	1.48
32	3	4	10.0	0.96	0.87
33	7	13	17.4	1.99	2.41
34	5	6	11.6	1.50	1.99
35	2	3	3.6	0.57	0.92
36	5	5	14.1	1.49	2.17
37	3	5	12.6	0.91	1.19
38	2	3	9.9	0.57	0.81
39	4	4	8.6	1.26	1.32
40	4	6	11.5	1.21	1.43
41	4	5	15.2	1.26	1.26
42	2	2	4.8	0.59	0.94
43	6	7	19.2	1.70	2.08
44	9	13	26.7	2.14	2.51
45	2	6	30.1	0.45	0.56
46	4	5	5.4	1.26	1.88
47	5	5	13.8	1.49	1.99
48	2	4	6.1	0.53	0.94

Table 18. Group 2 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Pear Tree Bottom (Area I) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	2	11	35.1	0.67	0.22
2	2	10	22.3	0.78	0.37
3	2	10	31.4	0.78	0.27
4	2	17	24.7	0.66	0.76
5	2	11	45.0	0.67	0.37
6	2	23	44.8	0.89	0.52
7	2	8	23.1	0.77	0.41
8	2	8	27.7	0.39	0.10
9	2	11	20.9	0.76	0.58
10	2	13	52.9	0.49	0.13
11	2	7	16.2	0.74	0.43
12	2	11	35.2	0.53	0.19
13	2	9	28.8	0.72	0.31
14	2	8	19.1	0.77	0.43
15	2	10	37.0	0.56	0.14
16	3	13	32.9	1.05	0.60
17	2	14	26.3	0.84	0.50
18	3	14	35.5	0.96	0.40
19	2	15	52.1	0.59	0.15
20	3	8	18.0	1.04	0.70
21	2	9	36.7	0.37	0.08
22	1	4	19.5	0.00	0.00
23	2	8	16.9	0.73	0.57
24	2	13	42.7	0.63	0.19
25	2	10	15.6	0.70	0.66
26	2	8	22.8	0.73	0.59
27	2	17	29.9	0.86	0.40
28	2	7	7.6	0.42	0.90
29	2	17	53.5	0.74	0.22
30	2	20	55.2	0.81	0.28
31	3	13	31.4	0.99	0.48
32	2	10	12.8	0.70	0.77
33	2	7	18.7	0.74	0.29
34	3	8	13.6	1.04	0.88
35	2	9	19.7	0.78	0.44
36	3	16	21.6	1.06	1.02
37	2	16	48.0	0.81	0.29
38	2	17	48.3	0.84	0.53
39	2	9	22.2	0.80	0.34
40	3	10	21.8	1.14	0.59
41	2	10	35.7	0.78	0.28
42	2	16	34.7	0.84	0.46
43	2	5	17.1	0.49	0.21
44	3	12	25.7	1.05	0.63
45	2	7	19.3	0.64	0.23
46	2	10	34.8	0.70	0.22
47	2	7	7.2	0.74	0.67
48	2	20	57.2	0.61	0.17

Table 19. Group 2 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Pear Tree Bottom (Area II) for year 1969-1970.

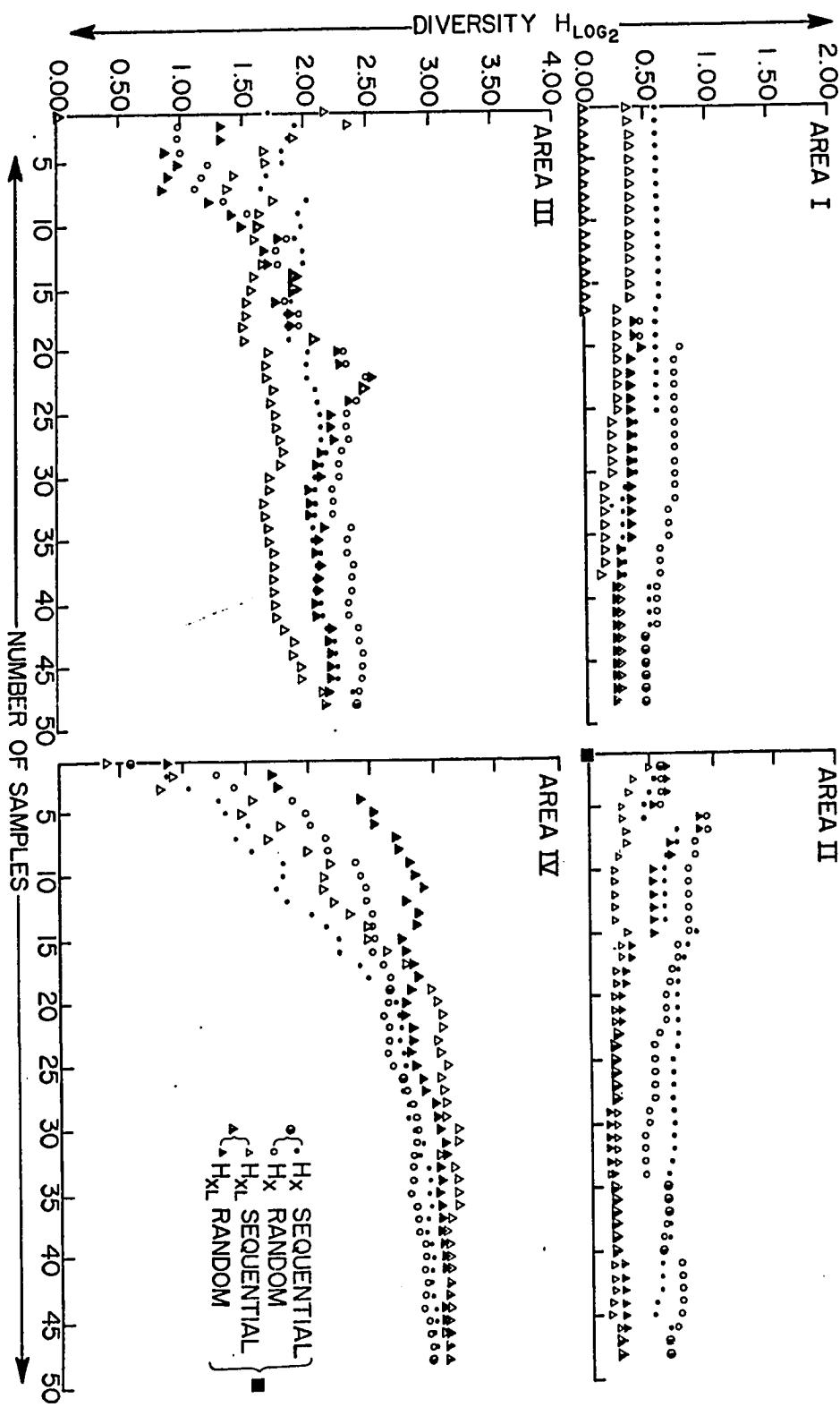| SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	2	25	57.6	0.70	0.24
2	3	18	49.2	0.79	0.48
3	2	12	21.7	0.75	0.47
4	2	25	62.1	0.70	0.24
5	2	20	63.1	0.22	0.08
6	2	28	65.1	0.81	0.43
7	3	29	74.0	0.67	0.31
8	2	16	50.6	0.26	0.06
9	3	30	92.4	0.46	0.23
10	3	25	50.4	1.03	0.55
11	2	36	88.4	0.74	0.34
12	3	26	58.1	0.79	0.39
13	3	24	70.1	0.39	0.22
14	3	14	43.2	0.73	0.31
15	2	35	97.2	0.36	0.20
16	3	28	74.8	0.88	0.31
17	3	25	65.7	0.87	0.33
18	2	29	96.3	0.17	0.08
19	2	20	63.8	0.22	0.11
20	3	24	61.5	0.82	0.34
21	2	30	73.1	0.75	0.41
22	3	22	45.7	0.92	0.45
23	3	22	61.5	0.68	0.32
24	2	28	67.2	0.81	0.35
25	3	19	31.2	1.04	0.80
26	3	27	49.1	1.01	0.61
27	2	27	75.0	0.32	0.14
28	3	25	60.6	0.93	0.43
29	2	18	53.0	0.24	0.06
30	2	39	106.6	0.56	0.20
31	3	27	64.5	0.73	0.36
32	3	37	77.6	1.08	0.59
33	3	57	134.6	0.83	0.36
34	2	20	54.5	0.38	0.12
35	3	24	66.1	0.74	0.28
36	3	20	50.1	0.72	0.34
37	3	36	95.9	0.88	0.35
38	3	25	66.4	0.63	0.23
39	4	26	77.8	0.68	0.43
40	3	21	48.0	0.94	0.47
41	3	23	57.8	0.90	0.49
42	2	41	100.9	0.65	0.32
43	2	12	42.3	0.31	0.11
44	2	32	98.2	0.38	0.10
45	1	24	82.6	0.00	0.00
46	2	19	60.8	0.23	0.08
47	3	21	59.1	0.73	0.28
48	3	18	42.5	0.76	0.46

Table 20. Group 2 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Discovery Bay (Area III) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	1	11	9.4	0.00	0.00
2	2	4	6.5	0.53	0.94
3	2	9	19.9	0.72	0.50
4	3	6	13.5	1.02	1.36
5	5	14	28.5	1.54	1.59
6	2	6	7.6	0.73	0.87
7	3	8	19.6	0.95	0.74
8	3	15	26.7	0.84	0.63
9	2	6	6.6	0.66	1.02
10	2	6	13.9	0.66	0.53
11	2	10	15.9	0.80	0.76
12	2	18	32.0	0.86	0.80
13	2	10	13.4	0.56	1.00
14	3	4	9.1	0.96	1.27
15	2	5	4.2	0.49	0.68
16	2	11	15.5	0.76	0.96
17	1	2	2.1	0.00	0.00
18	3	9	8.8	0.91	1.13
19	2	9	8.7	0.37	0.41
20	2	7	6.2	0.42	0.86
21	3	8	14.9	1.04	1.32
22	2	9	19.2	0.58	0.45
23	2	9	8.2	0.37	0.77
24	2	5	8.2	0.68	0.81
25	2	6	10.8	0.66	0.60
26	2	9	15.9	0.78	0.82
27	2	9	16.9	0.78	0.71
28	2	6	6.0	0.45	0.70
29	3	25	40.1	1.14	1.29
30	3	5	5.9	0.91	1.51
31	4	13	20.4	1.26	1.52
32	2	17	19.3	0.56	0.86
33	1	4	4.1	0.00	0.00
34	2	11	25.0	0.76	0.54
35	3	6	11.2	1.02	1.11
36	1	3	2.4	0.00	0.00
37	3	10	24.0	0.87	0.79
38	3	9	18.9	0.91	0.81
39	3	15	23.7	1.04	1.16
40	4	13	31.7	1.30	1.15
41	3	10	17.9	1.05	1.13
42	3	17	29.3	0.96	1.38
43	2	8	15.2	0.77	0.73
44	2	18	18.7	0.65	0.94
45	2	9	8.9	0.37	0.59
46	4	10	19.2	1.26	1.74
47	2	6	7.3	0.45	0.42
48	3	15	21.8	1.00	1.49

Table 21. Group 2 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Discovery Bay (Area IV) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	0	0	0.0	0.00	0.00
2	0	0	0.0	0.00	0.00
3	2	2	1.4	0.59	0.95
4	1	1	0.6	0.00	0.00
5	1	1	1.3	0.00	0.00
6	1	1	0.8	0.00	0.00
7	1	1	0.9	0.00	0.00
8	2	3	3.2	0.57	0.91
9	0	0	0.0	0.00	0.00
10	1	1	0.6	0.00	0.00
11	0	0	0.0	0.00	0.00
12	0	0	0.0	0.00	0.00
13	0	0	0.0	0.00	0.00
14	0	0	0.0	0.00	0.00
15	1	2	1.1	0.00	0.00
16	1	1	0.7	0.00	0.00
17	0	0	0.0	0.00	0.00
18	0	0	0.0	0.00	0.00
19	2	3	2.6	0.57	0.90
20	0	0	0.0	0.00	0.00
21	0	0	0.0	0.00	0.00
22	3	4	6.0	0.96	1.40
23	1	2	2.0	0.00	0.00
24	3	3	2.8	0.97	1.35
25	1	1	0.7	0.00	0.00
26	0	0	0.0	0.00	0.00
27	0	0	0.0	0.00	0.00
28	0	0	0.0	0.00	0.00
29	0	0	0.0	0.00	0.00
30	1	2	1.6	0.00	0.00
31	0	0	0.0	0.00	0.00
32	0	0	0.0	0.00	0.00
33	1	3	3.6	0.00	0.00
34	1	2	1.4	0.00	0.00
35	1	1	1.2	0.00	0.00
36	1	1	1.4	0.00	0.00
37	0	0	0.0	0.00	0.00
38	0	0	0.0	0.00	0.00
39	1	1	0.8	0.00	0.00
40	1	1	1.3	0.00	0.00
41	0	0	0.0	0.00	0.00
42	0	0	0.0	0.00	0.00
43	2	3	2.4	0.57	0.81
44	2	2	1.5	0.59	0.77
45	0	0	0.0	0.00	0.00
46	1	1	0.9	0.00	0.00
47	1	1	0.9	0.00	0.00
48	0	0	0.0	0.00	0.00

Table 22. Group 3 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Pear Tree Bottom (Area I) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	2	2	7.7	0.59	0.36
2	0	0	0.0	0.00	0.00
3	0	0	0.0	0.00	0.00
4	0	0	0.0	0.00	0.00
5	0	0	0.0	0.00	0.00
6	0	0	0.0	0.00	0.00
7	0	0	0.0	0.00	0.00
8	0	0	0.0	0.00	0.00
9	0	0	0.0	0.00	0.00
10	0	0	0.0	0.00	0.00
11	0	0	0.0	0.00	0.00
12	0	0	0.0	0.00	0.00
13	0	0	0.0	0.00	0.00
14	0	0	0.0	0.00	0.00
15	0	0	0.0	0.00	0.00
16	0	0	0.0	0.00	0.00
17	1	1	5.0	0.00	0.00
18	0	0	0.0	0.00	0.00
19	0	0	0.0	0.00	0.00
20	0	0	0.0	0.00	0.00
21	0	0	0.0	0.00	0.00
22	0	0	0.0	0.00	0.00
23	0	0	0.0	0.00	0.00
24	0	0	0.0	0.00	0.00
25	0	0	0.0	0.00	0.00
26	1	5	2.6	0.00	0.00
27	1	1	0.6	0.00	0.00
28	0	0	0.0	0.00	0.00
29	0	0	0.0	0.00	0.00
30	0	0	0.0	0.00	0.00
31	1	3	15.8	0.00	0.00
32	1	1	0.5	0.00	0.00
33	0	0	0.0	0.00	0.00
34	0	0	0.0	0.00	0.00
35	1	1	0.5	0.00	0.00
36	0	0	0.0	0.00	0.00
37	1	1	0.6	0.00	0.00
38	1	1	7.1	0.00	0.00
39	1	1	0.9	0.00	0.00
40	0	0	0.0	0.00	0.00
41	0	0	0.0	0.00	0.00
42	0	0	0.0	0.00	0.00
43	1	1	0.6	0.00	0.00
44	0	0	0.0	0.00	0.00
45	0	0	0.0	0.00	0.00
46	0	0	0.0	0.00	0.00
47	0	0	0.0	0.00	0.00
48	1	1	7.4	0.00	0.00

Table 23. Group 3 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Pear Tree Bottom (Area II) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	1	1	2.1	0.00	0.00
2	1	1	1.0	0.00	0.00
3	1	2	5.6	0.00	0.00
4	1	1	1.6	0.00	0.00
5	1	1	4.0	0.00	0.00
6	0	0	0.0	0.00	0.00
7	2	3	9.9	0.57	0.26
8	0	0	0.0	0.00	0.00
9	1	2	12.6	0.00	0.00
10	1	1	7.1	0.00	0.00
11	0	0	0.0	0.00	0.00
12	0	0	0.0	0.00	0.00
13	0	0	0.0	0.00	0.00
14	0	0	0.0	0.00	0.00
15	1	1	0.7	0.00	0.00
16	1	2	11.9	0.00	0.00
17	1	1	0.5	0.00	0.00
18	1	2	13.4	0.00	0.00
19	0	0	0.0	0.00	0.00
20	0	0	0.0	0.00	0.00
21	0	0	0.0	0.00	0.00
22	0	0	0.0	0.00	0.00
23	0	0	0.0	0.00	0.00
24	1	1	5.8	0.00	0.00
25	1	1	0.3	0.00	0.00
26	0	0	0.0	0.00	0.00
27	0	0	0.0	0.00	0.00
28	0	0	0.0	0.00	0.00
29	0	0	0.0	0.00	0.00
30	0	0	0.0	0.00	0.00
31	0	0	0.0	0.00	0.00
32	0	0	0.0	0.00	0.00
33	1	1	6.5	0.00	0.00
34	1	1	5.2	0.00	0.00
35	0	0	0.0	0.00	0.00
36	0	0	0.0	0.00	0.00
37	0	0	0.0	0.00	0.00
38	0	0	0.0	0.00	0.00
39	1	1	6.0	0.00	0.00
40	1	2	1.2	0.00	0.00
41	1	2	4.9	0.00	0.00
42	0	0	0.0	0.00	0.00
43	0	0	0.0	0.00	0.00
44	1	4	20.4	0.00	0.00
45	1	1	4.0	0.00	0.00
46	2	2	1.6	0.59	0.53
47	0	0	0.0	0.00	0.00
48	0	0	0.0	0.00	0.00

Table 24. Group 3 bivalve population variables for individual 0.25 and 0.10 m^2 combined samples from Discovery Bay (Area III) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	6	7	13.7	1.70	2.15
2	1	2	0.9	0.00	0.00
3	1	2	6.9	0.00	0.00
4	2	5	17.6	0.68	0.91
5	0	0	0.0	0.00	0.00
6	1	3	11.6	0.00	0.00
7	2	3	10.0	0.57	0.83
8	3	3	4.7	0.97	1.37
9	1	2	7.2	0.00	0.00
10	3	4	7.8	0.96	1.24
11	2	3	8.8	0.57	0.84
12	2	2	3.8	0.59	0.67
13	0	0	0.0	0.00	0.00
14	1	2	6.8	0.00	0.00
15	1	1	3.5	0.00	0.00
16	1	1	3.7	0.00	0.00
17	0	0	0.0	0.00	0.00
18	1	1	3.9	0.00	0.00
19	1	1	3.1	0.00	0.00
20	4	4	7.9	1.26	1.76
21	1	1	1.9	0.00	0.00
22	0	0	0.0	0.00	0.00
23	1	1	0.9	0.00	0.00
24	2	2	5.1	0.59	0.66
25	2	2	6.9	0.59	0.94
26	0	0	0.0	0.00	0.00
27	2	2	3.9	0.59	0.89
28	1	1	1.3	0.00	0.00
29	1	1	2.4	0.00	0.00
30	1	3	10.7	0.00	0.00
31	2	2	3.5	0.59	0.79
32	1	2	5.0	0.00	0.00
33	2	2	5.5	0.59	0.94
34	1	1	1.0	0.00	0.00
35	0	0	0.0	0.00	0.00
36	2	3	3.4	0.57	0.00
37	0	0	0.0	0.00	0.00
38	0	0	0.0	0.00	0.00
39	0	0	0.0	0.00	0.00
40	0	0	0.0	0.00	0.00
41	1	1	3.0	0.00	0.00
42	2	2	4.8	0.59	0.90
43	1	1	3.0	0.00	0.00
44	1	1	3.3	0.00	0.00
45	1	1	3.6	0.00	0.00
46	0	0	0.0	0.00	0.00
47	3	3	8.1	0.97	1.47
48	1	1	1.1	0.00	0.00

Table 25. Group 3 bivalve population variables for individual 0.25 and 0.10 m² combined samples from Discovery Bay (Area IV) for year 1969-1970.

SAMPLE NUMBER	SPECIES NUMBER	ABUNDANCE	LENGTH ABUNDANCE	DIVERSITY	LENGTH DIVERSITY
1	2	3	3.2	0.57	0.38
2	2	3	8.6	0.57	0.87
3	1	2	2.9	0.00	0.00
4	2	2	4.4	0.59	0.71
5	2	2	4.7	0.59	0.55
6	1	1	2.5	0.00	0.00
7	1	2	2.9	0.00	0.00
8	2	2	3.7	0.59	0.77
9	1	1	1.8	0.00	0.00
10	0	0	0.0	0.00	0.00
11	1	1	1.8	0.00	0.00
12	1	1	0.8	0.00	0.00
13	3	3	6.7	0.97	1.28
14	1	1	2.2	0.00	0.00
15	0	0	0.0	0.00	0.00
16	1	1	2.4	0.00	0.00
17	3	3	5.1	0.97	1.38
18	2	2	2.3	0.59	0.73
19	4	6	9.1	1.30	1.65
20	2	2	5.6	0.59	0.83
21	2	2	5.8	0.59	0.94
22	2	2	3.4	0.59	0.79
23	2	2	4.5	0.59	0.96
24	3	3	4.9	0.97	1.33
25	2	2	5.0	0.59	0.73
26	1	2	3.5	0.00	0.00
27	2	2	2.2	0.59	0.86
28	1	1	1.0	0.00	0.00
29	0	0	0.0	0.00	0.00
30	3	4	8.1	0.96	1.42
31	3	3	8.6	0.97	1.47
32	1	2	8.1	0.00	0.00
33	4	8	12.0	1.37	1.72
34	3	3	5.7	0.97	1.31
35	1	2	1.7	0.00	0.00
36	3	3	8.3	0.97	1.55
37	1	3	7.5	0.00	0.00
38	2	3	9.9	0.57	0.81
39	2	2	2.0	0.59	0.85
40	2	4	9.3	0.53	0.70
41	2	2	3.5	0.59	0.78
42	2	2	4.8	0.59	0.94
43	1	1	2.7	0.00	0.00
44	5	8	16.0	1.40	1.60
45	1	1	4.1	0.00	0.00
46	3	4	4.4	0.96	1.45
47	3	3	8.3	0.97	1.35
48	2	4	6.1	0.53	0.94

Figure 23. Correlation matrix of bivalve population

variables at Pear Tree Bottom (Area I). N=48. For

r=0.29 P$\leq$.05. Key: S=species number; X=abundance; X_L=

length abundance; H_Y=diversity; H_{Y_L}=length diversity. For

explanation of bivalve groups, see text.

GROUP 1

	S	X	X_L	H_X
X	.31			
X_L	.12	.73		
H_X	.86	.39	.05	
H_XL	.71	.26	-.19	.05

GROUP 2

	S	X	X_L	H_X	H_XL			
X	.19	.98	.72	.27	.14	.13		
S	.60	.13	-.07	.62	.71			
H_XL	.32	.05	-.51	.47	.77	.53	.04	
H_X	.56	.34	-.02	.84	.50	.79	.34	.72
X_L	-.01	.70	.98	-.05	-.33	.13		

GROUP 3

	S	X	X_L	H_X	H_XL	S	X	X_L	H_X	H_XL	S	X	X_L	H_X
X	.61	.22	.13	.56	.54	.01	.01	-.00	.08	.06	.06	.75	.64	.35
S	.74	.28	.20	.55	.52	-.09	.13	.07	.04	-.04		.66	.26	.35
H_XL	.32	.05	-.51	.47	.77	.53	.04	-.53	.58			.52	.26	
H_X	.63	.36	.40	.46	.57	.14	.23	.21	.13	-.02	-.12	.52		
X_L	.38	.04	.13	.20	.20	-.05	-.01	-.05	.06	-.05	-.12			
H_X	.38	.04	.13	.20	.20	-.05	-.01	-.05	.06	-.05	-.12	.52	.26	1.00

Figure 24. Correlation matrix of bivalve population variables at Pear Tree Bottom (Area II). N=48. For r=0.29 P≤.05. Key as in Figure 23.

Group	Var	S	X	X_L	H_X	H_{XL}	S	X	X_L	H_X	H_{XL}	S	X	X_L	H_X
GROUP 1	X	.09													
	X_L	.04	.88												
	H_X	.65	.17	-.14											
	H_{XL}	.66	.16	.03	.78										
GROUP 2	S	.67	.01	-.15	.57	.31									
	X	.02	.99	.86	.14	.08	.02								
	X_L	-.04	.90	.98	-.19	-.11	.89	-.14							
	H_X	.39	.16	-.22	.89	.65	.18	-.21	.89						
	H_{XL}	.40	.06	-.32	.83	.57	.61	.08	.91	.91					
GROUP 3	S	.68	.11	.20	.31	.58	.09	.02	-.31	-.21	-.07				
	X	.57	.16	.30	.32	.64	.08	.04	.15	-.13	-.10	.85			
	X_L	.40	.29	.50	.17	.62	.08	.20	.33	-.18	-.20	.62	.86		
	H_X	.39	.00	.03	.06	.06	.03	.04	.01	-.16	-.15	.54	.40	.34	
	H_{XL}	.32	-.04	-.00	.01	-.02	-.08	-.08	-.02	-.21	-.19	.85	.14	.07	.95

Figure 25. Correlation matrix of bivalve population

variables at Discovery Bay (Area III). N=48. For r=0.29

P≤.05. Key as in Figure 23.

Correlation matrix (lower triangular):

	S	X	X_L	H_X	H_{X_L}	S	X	X_L	H_X	H_{X_L}	S	X	X_L	H_X
GROUP 1														
X	.48													
X_L	.48	.88												
H_X	.86	.53	.64											
H_{X_L}	.88	.43	.39	.87										
GROUP 2														
S	.34	.30	.44	.50	.35									
X	.44	.92	.76	.34	.29	.37								
X_L	.40	.83	.89	.49	.27	.57	.86							
H_X	.40	.40	.57	.60	.40	.92	.45	.68						
H_{X_L}	.30	.27	.32	.45	.40	.83	.37	.42	.86					
GROUP 3														
S	.53	.07	-.10	.26	.46	-.35	-.04	-.18	-.37	-.36				
X	.44	-.03	-.12	.28	.42	-.32	-.17	-.26	-.31	-.26	.90			
X_L	.26	-.12	-.11	.21	.33	-.21	-.22	-.27	-.16	-.11	.67	.89		
H_X	.54	.06	-.04	.29	.42	-.25	-.06	-.10	-.29	-.35	.93	.81	.59	
H_{X_L}	.53	.03	-.05	.28	.42	-.26	-.08	-.11	-.30	-.36	.92	.80	.59	.99

Figure 26. Correlation matrix of bivalve population variables at Discovery Bay (Area IV). N=48. For r=0.29 $P \leq .05$. Key as in Figure 23.

	GROUP 1					GROUP 2					GROUP 3			
	S	X	X_L	H_X	H_{X_L}	S	X	X_L	H_X	H_{X_L}	S	X	X_L	H_X
GROUP 1														
X	.90													
X_L	.59	.72												
H_X	.98	.85	.55											
H_{X_L}	.91	.76	.41	.94										
GROUP 2														
S	.59	.46	.02	.56	.59									
X	.64	.57	.08	.62	.65	.59								
X_L	.59	.54	.09	.59	.63	.87	.93							
H_X	.52	.43	.14	.48	.48	.83	.74	.94						
H_{X_L}	.51	.42	.12	.47	.47	.75	.32	.73	1.00					
GROUP 3														
S	.81	.74	.45	.79	.76	.28	.32	.74	.25	.87				
X	.71	.80	.40	.67	.64	.25	.32	.32	.21	.20	.86			
X_L	.65	.70	.53	.62	.59	.12	.16	.17	.12	.10	.78	.80		
H_X	.76	.67	.37	.76	.74	.27	.33	.33	.21	.20	.96	.80	.71	
H_{X_L}	.71	.62	.36	.73	.73	.23	.29	.31	.17	.16	.93	.75	.69	.98

Figure 27. Correlation matrix of bivalve population variables at Pear Tree Bottom and Discovery Bay sample areas combined. N=192. For r=0.15 P≤.05. Key as in Figure 23.

Correlation matrix (lower-triangular) for three groups.

Group	Var	S	X	X_L	H_X	H_{X_L}	S	X	X_L	H_X	H_{X_L}	S	X	X_L	H_X
GROUP 1	X	.12													
	X_L	-.01	.94												
	H_X	.91	.04	-.13											
	H_{X_L}	.87	-.18	-.33	.89										
GROUP 2	S	.34	.56	.48	.32	.06									
	X	-.07	.97	.93	-.15	-.36	.57								
	X_L	-.18	.90	.97	-.29	-.50	.49	.95							
	H_X	.28	.47	.35	.40	.09	.88	.47	.36						
	H_{X_L}	.54	.16	-.02	.61	.53	.68	.09	-.07	.76					
GROUP 3	S	.63	-.23	-.29	.52	.64	-.36	-.38	.09	-.40	-.08				
	X	.57	-.19	-.23	.50	.60	-.31	-.34	-.12	-.35	-.38	.76			
	X_L	.47	.01	.04	.39	.48	-.17	-.12	-.11	-.21	-.03	.69	.90		
	H_X	.56	-.26	-.31	.48	.57	-.32	-.38	-.39	-.35	-.11	.91	.79	.55	
	H_{X_L}	.55	-.27	-.33	.47	.58	-.34	-.40	-.41	-.37	-.11	.90	.77	.53	.99

Table 26. Environmental distribution of variance/mean ratios for species number (S), bivalve number (X) and length number (X_L). 1.00 ± 0.48 is random at $P \leq .05$.

<u>Values in parentheses are for ratios calculated on means 1.</u>

VARIABLE AND GROUP	I	II	III	IV
Group 1				
S	0.15	0.20	0.37	0.88
X	1.53	2.46	2.66	1.51
X_L	6.20	7.45	7.11	4.86
Group 2				
S	0.08	0.13	0.27	(0.94)
X	1.50	2.47	2.21	(1.31)
X_L	5.65	6.52	4.86	(1.66)
Group 3				
S	(0.88)	(0.67)	1.03	0.58
X	(2.08)	(1.23)	1.28	1.10
X_L	7.62	7.39	3.79	2.24

Table 27. Variance/mean ratios for common Pear Tree Bottom and Discovery Bay infaunal and semi-infaunal bivalves. Values in parentheses are for ratios calculated on means < 1.

PEAR TREE BOTTOM

I	ABUNDANCE	LENGTH ABUNDANCE
Codakia orbicularis	1.51	6.13
Ctena orbiculata	1.63	0.81
Parvilucina costata	(1.42)	(1.05)
Arcopagia fausta	(2.18)	(7.73)

II	ABUNDANCE	LENGTH ABUNDANCE
Codakia orbicularis	2.30	6.60
Ctena orbiculata	2.30	1.33
Parvilucina costata	1.00	(0.92)
Arcopagia fausta	(1.24)	7.62

DISCOVERY BAY

III	ABUNDANCE	LENGTH ABUNDANCE
Anadara notabilis	(1.14)	4.11
Codakia orbicularis	1.89	5.69
Diplodonta punctata	2.07	3.04
Parvilucina costata	2.20	2.16
Modiolus americanus	1.20	7.39

IV	ABUNDANCE	LENGTH ABUNDANCE
Anadara notabilis	(1.23)	3.54
Parvilucina costata	(1.23)	(0.97)
Modiolus americanus	(2.05)	11.38
Pitar fulminata	(1.20)	(1.22)