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Community Structure of the Macrobenthos Associated with Seagrass of the Indian River Estuary, Florida

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Abstract

Effects of predation on community structure of the macrobenthos associated with dense stands of "alodule wrightii" in the Indian River estuary of east central Florida were studied using cages. The three study sites represented a stress gradient of temperature, salinity and tide. Major changes, as affected by caging, were measured by species diversity, species evenness and species richness, showing opposite effects at the sites representing two extremes of the environmental stress gradient. At the site characterized by a physically unstable and unpredictable environment, the increases of several species within the cage were in accord with predator-prey theory. At the other extreme, where the environment was more physically stable and predictable, increases in diversity of caged macrofauna were inconsistent with current hypotheses of biological interactions affecting community structure.

INTRODUCTION

The central ecological concept considered in this study is that changes in faunal diversity within a given habitat type along an environmental stress gradient can be related to physical environmental predictability and biological interactions in the establishment, organization and maintenance of marine benthic communities. One assumption commonly underlying this concept has been that species diversity is directly and perhaps causally related to community stability (Odum 1971). However, as Hurlbert (1971) and others have warned, species diversity should be regarded only as a "function of species richness and the evenness with which the individuals are distributed among these species". Therefore, in this study species diversity, species richness and species evenness were measured to gain initial insight into the structure of macrobenthic communities associated with one

species of seagrass of the Indian River estuary of east central Florida. Interpretations regarding densities of organisms are beyond the scope of this paper and will be reported elsewhere.

Effects of predation on the structure of macrobenthos associated with the seagrass <code>Halodule</code> (=Diplanthera) wrightii were studied by field experimentation with cages at three study sites representing a stress gradient of temperature, salinity and tide. Currently proposed hypotheses of effects of predator-prey interactions, within-community interactions and environmental factors were considered in an attempt to explain differences in community structure as affected by the cages.

As Sanders (1968, 1969), Dayton (1972), Dayton et al. (1974) and others (see reviews by Buzas 1972; Pianka 1966) have suggested, biological interactions become increasingly important as environmental predictability increases. Biological interactions of the benthos from temperate to tropical marine shallow waters to the deep sea may include such factors as trophic diversification, e.g., specializations of feeding (Kohn 1968); niche diversification, e.g., biochemical and microhabitat specializations (Grassle and Sanders 1973); biological disturbances (Dayton and Hessler 1972); and predation effects (Paine Other factors affecting community structure of the softbottom benthos include substratum selection by settling larvae (Gray 1974), competition for space (Woodin 1974) and sediment stability (Rhoads and Young 1970). Combinations of all these factors are likely to occur within a diverse, soft-bottom, benthic community and the relative importance of each would be expected to vary depending upon the particular community and the environment.

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STUDY AREA

The Indian River

The long, narrow body of water bounded on the east by a continuous chain of offshore barrier islands along 190 km of the east central coast of Florida is locally known as the "Indian River" (Fig.

1). The Indian River is a bar-built estuary typical of the Southeastern United States and Gulf of Mexico coastlines. The barrier island is bisected by three inlets (St. Lucie, Fort Pierce and Sebastian) along the southern half of the estuary, all of which have been dredged within the last 40 years and are maintained artificially (Walton 1974a, b). At the northern terminus of the estuary a narrow dredged channel (Haulover Canal) connects the Indian River with Mosquito Lagoon, which opens to the Atlantic Ocean at Ponce de Leon Inlet 40 km to the north. With recorded history, as is typical for bar-built estuaries, natural breaching of the barrier island has occurred during storm events.

The Indian River has an average depth of 1.5 m. The relative effect of tides, surface runoff, wind mixing and evapotranspiration varies locally within the estuary and is highly variable. The majority of rainfall occurs during the months from May through October, and November through April are normally dry (Thomas 1970). "blind" northern end of the Indian River, the flushing time of the water is in excess of 150 days (Carter and Okubo 1965) and astronomical tidal effects are dampened by the shallowness and constrictions (natural and artificial) of the estuary. Wind-induced currents and wind tides become increasingly influential in movement and mixing of water in that part of the estuary north of Sebastian Inlet (80 km south of Haulover Canal). In general, there is a trend toward wider ranges of physical environmental variables and greater unpredictability of tides as one progresses from the influences of the Atlantic Ocean through the inlets to those regions where flushing times are slowest.

Six species of seagrass (Halodule wrightii, Syringodium filiforme, Thallasia testudinum, Ruppia maritima, Halophila engelmannii and Halophila sp.) are found in the Indian River estuary (N. Eiseman, personal communication). Halodule wrightii was selected as the species characteristic of the study habitat because this species is widely distributed throughout the estuary and occurs in the shallowest water where the greatest environmental stresses are to be expected. In the United States this species has been reported along the Atlantic coast nearly continuously from North Carolina south to Florida and along the Gulf of Mexico coastline (Phillips 1960). Of the seagrasses, Halodule wrightii has been found to be the most tolerant of high salinities, both in the laboratory and in the field conditions of hypersaline Texas lagoons (McMillan and Mosely 1967).

Three study sites in *H. wrightii* seagrass areas within the Indian River estuary at St. Lucie Inlet, Link Port and Haulover Canal illustrate spatial extremes and extremes in ranges of physical environmental variables. Only the macrobenthos co-occurring with *H. wrightii* were studied. Sampling is biased toward 100% cover of seagrass and similar water depth. The sediments of the *H. wrightii* study sites can be broadly classified as well-sorted fine sand containing substantial amounts of clay-silt-sized sediment intermixed with shell hash. Anaerobic conditions characterized by dark, sulfurrich sediments prevail below 1 cm.

St. Lucie Study Site

The southernmost study site is in an area of extensive H. wrightii cover on the barrier island side (east) of the estuary, immediately north of St. Lucie Inlet (Fig. 1). A small amount of S. filiforme is present and isolated patches of T. testudinum are seen occasionally. There is extensive and periodic flushing of the area by tidal currents that follow the north side of the inlet during flood and ebb tides (Walton 1974a).

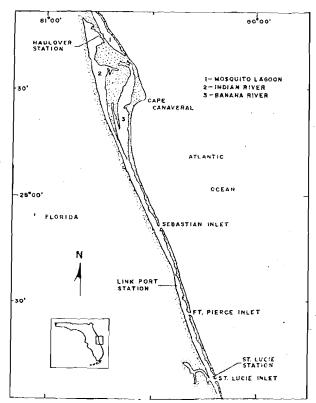
Link Port Study Site

This study site is located on the mainland (west) side of the estuary immediately north of a dredge-spoil finger of Link Port channel, and approximately 9.5 km north of Fort Pierce Inlet (Fig. 1). A typical transect perpendicular to the natural shoreline of red mangrove at this site shows H. wrightii extending 4 to 70 m or more from shore into T. testudinum and S. filiforme seagrass stands. Currents and semi-diurnal tides are influenced by wind to a greater extent at this site than at St. Lucie. Current velocities usually range up to 10 cm/sec on the channel (east) side of the seagrass areas (Wilcox, unpublished manuscript).

Haulover Study Site

The northernmost site studied is within a cove immediately north of the spoil bank formed from the dredging of the Haulover Canal at

Fig. 1. Map of the Indian River Estuary, Florida, showing locations of the Haulover, Link Port and St. Lucie sampling sites.



the northern terminus of the Indian River estuary (Fig. 1). The inner part of the cove supports a dense stand of *H. wrightii* intermixed with sparse *R. maritima*. Patchy stands of *S. filiforme* and *H. engelmannii* occur in deeper water, starting 100 m or more from shore. The tide, currents and water mixing at this site are dominated by winds. The water height is free of any astronomical tidal influences to an accuracy of 0.30 cm (Browne 1970).

METHODS

Benthic samples were collected with a coring device operated on the principle of a post-hole digger (Baird et al. 1971), which obtains an undisturbed plug of seagrass (including roots and rhizomes) and sediment (15 cm x 15 cm x 20 cm deep = 4500 cm³). Samples were washed through a 1.0 mm mesh screen, transferred to a solution of rose bengal and 0.15% propylene phenoxytol in sea water (McKay and Hartzband 1970) for 20-30 minutes, and finally into a 5-10% solution of formalin in sea water. After 24-72 hr, epifauna was separated from seagrass blades and infauna was sorted from debris. All specimens were stored in 70% ethyl alcohol. There was no attempt to analyze epifauna separately from infauna because many macrobenthic species associated with H. wrightii clearly overlap these categories.

Cages of 1/2-inch mesh (12 mm x 12 mm) hardware cloth, 2 m on a side (4 m 2), and 2 m high were constructed at each sampling site. The cage penetrated the sediment by approximately 5 cm and extended above highest stages of flood tide. The mesh was cleaned as required.

No previous cage experiments in subtropical seagrass habitats have been reported. Our supposition was that caging off areas of intensive cover of *H. wrightii* found in a range of environmental extremes would provide a means of assessing the relative importance of predation on community structure of the macrobenthos. Several factors were taken into consideration to account for potential disruptive influences due to the presence of the cage structures.

First, we predicted that there might be changes in current velocities and directions. These changes in turn, might affect (1) rate of sedimentation and (2) changes of physical and chemical characteristics of the sediment within the cages. Both factors were indirectly measured and observed during the course of the study (see Methods) and were deemed more meaningful ecologically than direct short-term measurements of current velocities and directions.

Second, we predicted that there might be changes in species occurrences and numbers of individuals in each species owing to the following factors: (1) preclusion of transient and resident predators such as finfishes, rays, large decaped crustaceans and horseshoe crabs, (2) preclusion or selection of passively drifting larva, and (3) post-larval biological interactions such as within-community predation and competition for requisites such as space and food. It was originally postulated that changes in community structure as

affected by the cages would be influenced primarily by the preclusion of transient and resident predators (defined here as being too large to pass through 1/2-inch mesh).

A set of 5 pilot replicates was taken from each sampling site at the time of construction of the cages on 29 August 1974 at Haulover Station, on 12 September 1974 at St. Lucie Station and on 16 September 1974 at Link Port Station. Analyses of these data indicated that 4 replicates per sample were sufficient for the purposes of this study (see Results). Thereafter, 4 replicates from inside and outside of the cage at each site were taken at 4 sampling periods during 8-17 October 1974, 14-22 November 1974, 13-19 December 1974 and 24-27 February 1975.

During sampling, measurements were made of surface water salinity, surface water temperature, water depth and range of sediment-water interface temperatures (with a maximum-minimum thermometer). Flux of seston (living and dead components of suspended matter in mg dry wt/cm 2 /day) was measured by gravimetrically analyzing seston collected in 0.5-1 jars with 22 cm 2 openings at 16 cm above the sediment surface inside and outside the cages at each site.

Data were analyzed using Shannon's information function,

$$[H' = -\sum_{i=1}^{s} p \quad ln \quad p \quad] \quad (Pielou \quad 1966),$$

where p_i is the proportion of the ith species and s is the total number of species. Species evenness was measured by E', where E' = eH'/s (Buzas and Gibson 1969). Species richness was measured by S-1/lnN (Margalef 1968) in order to relate the number of species to the number of individuals. Use of parametric statistical tests of differences for these indices is questionable here (see Hutcheson 1970; Lloyd et al. 1968) and numbers of samples that would justify nonparametric tests are impractical. All three indices have inherent mathematical weaknesses (Peet 1975; Heip and Engels 1974), but are used here for comparison with the literature and to provide a convenient means of determining major trends of change in community structure as affected by this field experimental approach.

RESULTS

Means and ranges of selected measurements at the three sites during the period of study are summarized in Table 1. As expected, the ranges of water temperature, water salinity, sediment-water

Table 1. Tidal characteristics, ranges of surface water temperature, sediment-water interface temperature, surface water salinity and water depth at Haulover, Link Port and St. Lucie sites.

Condition	Haulover	Link Port	St. Lucie
Surface water temperature, °C (at time of sampling)	11 - 32.5	18.5 - 31.5	19.5 - 30
Sediment-water interface temperature, °C (maxmin.)	8 ~ 34	14 - 32	14 - 33
Surface water salinity, ^o /oo (at time of sampling)	22 - 42	25 - 35	32 - 34
Water depth, cm (at time of sampling)	22 - 100	30 - 60	34 - 65
Tide	Mixed-wind dominated	Semidiurnal- wind influenced	Semidiurnal

interface temperature and water depth increase progressively from the St. Lucie to the Haulover site. Data are not available on predictability of tidal stages at the three sites, but predictability is probably less at Haulover relative to the other two sites because the tides there are wind-dominated (Table 1).

Measurements of water temperature and salinity over a 2 1/2 year period (June 1972 - November 1974) near the Link Port site (Wilcox, unpublished manuscript) demonstrate a wider range of salinity (17-370/00) and temperature (11.5-32°C) than measured during the relatively short period of this study. Greater ranges of these variables probably occur over the long-term at the Haulover site also.

Tides are known to vary greatly within the Indian River estuary during periods of spring tides, high winds and high precipitation (Walton $1974\underline{a}$). It is unlikely, in any case, that the seagrass sites studied ever become dry or remain so over long periods of time because of the sensitivity of H. wrightii to dessication (Phillips 1960).

No obvious changes in the sediments were observed within the cages during the experiment. Drift grasses, algae and debris were trapped against the mesh of the cages only at the level of high water stages at each site, so that blockage of water currents through the mesh was minimal. No significant differences (Student's t, 99% confidence) of seston flux ($mg/cm^2/day$) were measured inside and outside of cages at all three sites.

Polychaetes (53.5%) and molluscs (16.9%) comprised over 70% of the total number of 24,288 specimens representing 230 taxa (listed in Appendix 1). Species identification and trophic information were also most complete for these dominant groups. For these reasons, analyses based on polychaetes and molluscs from the sites studied were assumed to be representative of responses at the community level of organization. Analyses of the 5 pilot replicates taken prior to the field experiment at each of the three study sites indicated that 90% or more (Gaufin et al. 1956) of the expected species of molluscs

and polychaetes would be found in four of the replicates of each sample representing an area of 900 cm². The greater amount of time and effort necessary to sample and process additional replicates was deemed unprofitable in terms of the probable increase in new (unsampled) species; therefore the number of replicates per sample for the experiment was reduced to four.

Table 2 summarizes indices of species diversity, species evenness and species richness for polychaetes and molluscs from all monthly samples at the three sites and shows the trend of changes (Fig. 2) of these three indices by month and treatment (inside and outside cages). The relative dependence of species diversity, H', on species evenness, E', and species richness, S-1/lnN, is readily apparent between sites and treatments.

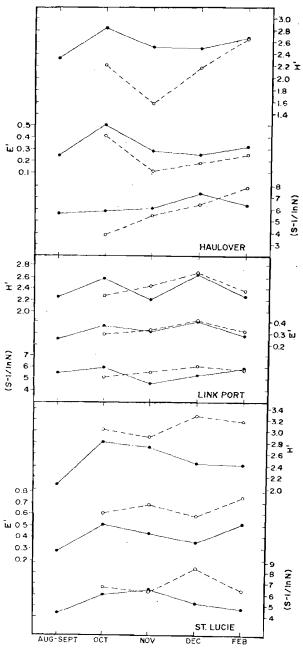
Table 2. Species diversity (H'), species evenness (E') and species richness (S-1/1nN) of polychaetes and molluscs at Haulover, Link Port and St. Lucie sites during August-September (A) for pilot replicates, and October (B), November (C), December (D), and February (E) for outside and inside cage samples. N is number of replicates for each sample.

Samp1	ing Site, Times	and Treatments	н'	E'	S-1/1nN
1. H	aulover				
A	Pilot replica	ites (N=5)	2.32	0.24	5.66
В	Outside cage Inside cage	(N=4) (N=4)	2.84 2.21	0.50 0.41	5.83 3.82
С	C. Outside cage	(N=4)	2.51	0.28	6.09
	Inside cage	(N=4)	1.56	0.11	5.46
D	Outside cage	(N=4)	2.49	0.25	7.29
	Inside cage	(N=4)	2.16	0.18	6.36
Е	. Outside cage	(N=4)	2.68	0.32	6.31
	Inside cage	(N=4)	2.68	0.25	7.82
2. L A	ink Port . Pilot replica	etes (N=5)	2.26	0.25	5.50
В	. Outside cage	(N=4)	2.58	0.36	5.97
	Inside cage	(N=4)	2.28	0.29	5.17
С	. Outside cage	(N=4)	2.21	0.31	4.58
	Inside cage	(N=4)	2.45	0.32	5.56
D	Outside cage	(N=4)	2.54	0.40	5.30
	Inside cage	(N=4)	2.57	0.40	6.09
E	. Outside cage	(N=4)	2.27	0.27	5.88
	Inside cage	(N=4)	2.36	0.31	5.81
3. S	t. Lucie				
A	. Pilot replica	ites (N=5)	2.08	0.28	4.45
В	. Outside cage	(N=4)	2.82	0.51	6.05
	Inside cage	(N=4)	3.03	0.61	6.69
С	C. Outside cage	(N=4)	2.73	0.43	6.46
	Inside cage	(N=4)	2.90	0.68	6.25
D	Outside cage	(N=4)	2.44	0.35	5.24
	Inside cage	(N=4)	3.27	0.58	8.32
E	E. Outside cage	(N=4)	2.42	0.51	4.70
	Inside cage	(N=4)	3.17	0.74	6.33

Fig. 2. Species diversity (H'), species evenness (E') and species richness (S-1/lnN) of polychaetes and molluscs at Haulover, Link Port and St. Lucie sites during August-September for pilot replicates, and October, November, December and February for outside and inside cage samples. Dashed line indicates inside cage samples and solid line indicates outside cage samples.

At the Haulover site there is a good relationship between the curves describing diversity and evenness. The indices of diversity and evenness are consistently lower for inside versus outside cage samples, except during February when the diversity indices are the same value (H'=2.68) and reflect an increase in richness of the cage sample.

The trends are similar and the differences are small between all three indices at the Link Port site. There appears to be little effect of the cage on community structure of the macrobenthos as measured by these indices.



All values of diversity, evenness and richness are higher for samples inside versus outside the cage at the St. Lucie site, with the exception of a lower value for richness in November. An inverse relationship exists between the curves of diversity and evenness for within-cage samples. The richness values show a similar pattern as shown by diversity indicating that the richness component has a relatively greater effect on diversity than evenness.

The curves describing diversity, evenness and richness components show a progressive trend from the Haulover to Link Port to St.

Lucie sites. The indices for caged versus uncaged samples are lower at Haulover, higher at St. Lucie and similar at Link Port. Diversity and evenness values are highest for the cage samples at the St. Lucie site (Table 2).

Percentages of numbers of polychaetes and molluscs representing various feeding types from inside and outside of cages at the three sites are given in Table 3. Percent composition of feeding types was more similar at St. Lucie and Haulover than at Link Port. Deposit feeders which were dominant at all stations outside cages increased greatly inside cages at St. Lucie and Haulover, with no percentage change at Link Port. Similarly, carnivores decreased within cages at St. Lucie and Haulover, but increased at Link Port. Suspension feeders increased slightly at St. Lucie while decreasing at Link Port The feeding type termed "others" (herbivores, scavenand Haulover. gers, parasites, etc.) represents the lowest percentage of polychaetes and molluscs from all sites, a bias resulting from the inclusion of species from those feeding types assumed to have greatest ecological importance in the community. This bias was intentional because most benthic invertebrates encompass several of these "types" and would certainly be classified as omnivores. The ranking of feeding types outside cages at all sites (deposit feeders > carnivores > suspension feeders > others) is changed within cages only at the St. Lucie and Haulover sites, where suspension feeders > carnivores.

Table 4 ranks the ten most numerous species from inside and outside cages at all three sites. No species represents more than 21% of the total numbers of individuals at any site outside the cages. Percent dominance of the top-ranked species within cages drops to 10% at St. Lucie and 15% at Link Port, but increases to 45% at Haulover. The top-ranked species outside cages at both St. Lucie and Link Port, a polychaete (Clymenella mucosa), is displaced in dominance inside cages at those sites by an amphipod (Grandidierella sp. A). The large increase in percent dominance of a top-ranked species at Haulover (from 17% outside the cage to 45% inside the cage) is due to the same species of polychaete (Polydora ligni) in both instances. Some changes in the rank of species undoubtedly results from differences in total numbers of individuals relative to the distribution of species abundances inside and outside cages at the same site. However, large increases of particular species within cages are

Table 3. Percentage abundances of major feeding types of polychaetes and molluscs at Haulover, Link Port and St. Lucie sites (DF=deposit feeders; SF=suspension feeders; C=carnivores; O=other).

	Haulo	ver	Link	Port	St. 1	Lucie
Feeding Types	Outside Cage	Inside Cage	Outside Cage	Inside Cage	Outside Cage	Inside Cage
DF %	51	74	73	73	53	68
SF %	18	14	10	6	12	. 16
С %	28	9	16	20	29	11
0 %	. 3	3	<1	<1	6	4

are obvious, as in the case of the amphipod, isopod and tanaid crustaceans. Percentage dominance of the top 10 species ranges from 60 to 75% inside cages to 51 to 83% outside cages.

Table 4. Top-10 ranked species, number of individuals and percentage of total number of individuals at Haulover, Link Port and St. Lucie experimental stations (P=polychaet; G=gastropod; Pel.=pelecypod; A=amphipod; I=isopod; T=tanaid; E=echinoderm; S=sipunculid).

Rank Species Name						
Haulov	ver (outside cage)					
1	Polydora ligni (P)	896	17.48			
2	Exogone dispar (P)	606	11.82			
3	Phaseolion sp. (S)	563	10.99			
4	Paratanaidae A (T)	280	5.46			
5	Clymenella mucosa (P)	279	5.44			
6	Fabriciola sp. A (P)	206	4.02			
7	Cymadusa sp. A (A)	177	3.45			
8	Prionospio heterobranchia (P)	128	2.50			
9	Erichsonella filiformis		_			
	isabelensis (I)	125	2.44			
10	Nemertinea	116	2.26			
0	TOMOL CARGO	Total Number of Ind				
Haulov	ver (inside cage)	Total Hambel of File	21144415			
1	Polydora ligni (P)	3076	44.59			
2	Phascolion sp. (S)	420	6.09			
3	Paratanaidae A (T)	419	6.07			
4		416	6.03			
	Capitella capitata capitata (P)	255	3.70			
5	Cymadusa sp. A (A)					
6	Fabriciola sp. A (P)	237	3.44			
7	Synaptula hydriformis (E)	229	3.32			
8	Brachidontes exustus (Pel.)	224	3.25			
9	Exogone dispar (P)	222	3.22			
10	Terebella rubra (P)	221 Total Number of Ind	3.20 ividuals 6899			
Link F	ort (outside cage)					
1	Clymenella mucosa (P)	484	. 20.23			
2	Cerithium muscarum (G)	273	11.41			
3	Streblospio benedicti (P)	235	9.82			
4	Phaseolion sp. (S)	215	8.99			
5	Laeonereis culveri (P)	173	7.23			
6	Crepidula fornicata (G)	89	3.72			
7	Nemertinea	71	2.97			
8	Capitella capitata capitata (P)	69	2.88			
9	Polydora ligni (P)	63	2.63			
10	Erichsonella filiformis					
10	isabelensis (I)	58	2.42			
	Cymadusa sp. A (A)	58	2.42			
	cymuausa sp. K (K)	Total Number of Ind				
Timbe T	Cont (institutes)	Total Number of The	ividuals 2572			
	Port (inside cage)	476	15.30			
1	Grandidierella sp. A (A) Cerithium muscarum (G)	412	13.24			
2						
3	Melita nitida (A)	293	9.42			
4	Tharyx annulosus (P)	281	9.03			
5	Cymadusa sp. A (A)	210	6.75			
6	Clymenella mucosa (P)	133	4.27			
	Erichsonella filiformis	7.00	4 07			
	isabelensis (I)	133	4.27			

Table 4. (cont.)

Rank	Species Name	# individuals	% of total # individu	als
7	Laeonereis culveri (P)	131	4.21	
8	Phascolion sp. (S)	100	3.21	
9	Cymodoce faxoni (I)	94	3.02	
10	Crepidula formicata (G)	68	2.19	
St. L	ucie (outside cage)	Total Number of	Individuals	3112
1	Clymenella mucosa (P)	254	17.66	
2	Nemertinea	92	6.40	
3	Diastoma varium (G)	88	6.12	
4	Phascolion sp. (S)	81	5.63	
5	Fabricia sabella (P)	75	5.22	
6	Cymadusa sp. A (A)	68	4.73	
7	Paratanaidae A (T)	62	4.31	
8	Streblospio benedicti (P)	59	4.10	
9	Polydora socialis (P)	53	3,69	
10	Aricidea sp. A (P)	47	3.27	
St. Lı	ucie (inside cage)	Total Number of	Individuals	1438
1	Grandidierella sp. A (A)	112	9.77	
2 🔍	Nemertinea	111	9,69	
3	Cymadusa sp. A (A)	86	7.50	
4	Phasicolion sp. (S)	56	4.89	
5	Fabricia sabella (P)	44	3.84	
6	Erichsonella filiformis	. ,	3.04	
	isabelensis (I)	43	3.75	
7	Streblospio benedicti (P)	39	3.40	
8	Clymenella mucosa (P)	35	3.05	
9	Cymodoce faxoni (0)	33	2.88	
10	Tharyx annulosus (P)	27	2.36	
		Total Number of		1146

DISCUSSION AND CONCLUSIONS

When the selected environmental variables measured at the three study sites are ranked in order of increasing ranges, an environmental stress gradient is clearly evident: Haulover > Link Port > St. Lucie. The ranges of temperature, salinity and tidal height reported in this study are greater than those measured by Jackson (1972) in his study of Thalassia communities in Jamaica. Jackson (1973) later defined environmental stress in relation to distribution and occurrence of selected molluscs according to their physiological tolerances. While no direct correlations of stress and tolerance per se were examined in this study, it was assumed that dominant macrobenthic species associated with H. wrightii would respond differently to caging in relation to varying degrees of environmental stress, and that the effects of their responses would be seen at the community level of organization.

Contrary to temperate marine and estuarine environments, where diversity of benthos is higher in stenohaline than euryhaline zones

(Boesch 1972), the seagrass-associated macrobenthos of the subtropical Indian River estuary is equally diverse in areas of narrow and wide ranges of salinity. This study also presents an apparent paradox to the stability-time hypothesis of Sanders (1968), in that species diversity of the seagrass-associated macrobenthos does not decrease along a gradient of environmental stress in the Indian River estuary, as Sanders' hypothesis would predict. High diversity of macrofauna occurs at both extremes of the gradient at the Haulover and St. Lucie sites.

The stability-time hypothesis (Sanders 1968) states that physical instability and unpredictability of an environment prevents the establishment of diverse benthic communities, but rather communities which he defined as "physically controlled" and characterized by low diversity. Conversely, in a physically stable and predictable environment, benthic communities, given sufficient time, will become more diverse through biological interactions or "biological accommodation." To explain occurrences of diverse benthic communities in habitats characterized by environmental stress, Slobodkin and Sanders (1969) refined the original hypothesis of Sanders by contrasting "shortterm, non-equilibrium or transient high diversity" with "long-term or evolutionary high diversity". Grassle and Sanders (1973) have emphasized that, "...the two contrasting types of diversity cannot be set forth as simple alternatives". They further stated that shortterm high diversity can be expected to be progressively less important along a gradient from physically controlled to biologically accommodated conditions influencing community structure. If one speculates that the diverse macrobenthic community at the Haulover site results from short-term high diversity, this apparent paradox of the stability-time hypothesis can be clarified by the caging experiment.

Interactions of predation and community structure have been elucidated by caging experiments in the field for rocky intertidal communities (Dayton 1971), subtidal sponge communities (Dayton et al. 1974), subtidal fouling communities (Sutherland 1974) and intertidal soft-bottom communities (Woodin 1974). These experimental studies were prompted, in part, by the classical predator-prey study by Paine (1966) which hypothesized that, "Local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major requisites by one species". As predicted by Paine's hypothesis, species diversity decreased inside the cage at the Haulover site. Species evenness also decreased inside the cage, due primarily to an explosive increase of the polychaetes Polydora ligni (17-45% increase) and Capitella capitata capitata (<1-6% increase) (Table 4). These polychaete species have been described as "opportunistic species" by Grassle and Grassle (1974) or rstrategists, "adapted for life in a short-lived unpredictable habitat" The question, therefore, remains: What (Wilson and Bossert 1971). factors are responsible for the increases of these opportunistic species within the cage at Haulover?

A contributing condition which may help to explain these increases is the "year-class" phenomenon noted by Sanders (1968), by which extreme environmental variations at Haulover may have

facilitated rapid population growth of these particular species. Polydora ligni and Capitella capitata capitata show no such increases in numbers within the cages at St. Lucie and Link Port, so that potentially disruptive influences of the cage structure can be discounted in explaining the population increases of these same species at Haulover. These species apparently were able to increase in numbers inside the cage at Haulover in the relative absence of fish and other transient predators as though the macrobenthic community at this site were responding to a reduction of predation pressure. Grassle and Sanders (1973) suggested that in physically unpredictable and unstable environments, the removal or exclusion of a predator results in increased numbers of prey species with high reproductive rates.

Subtidal, benthic field experiments in Chesapeake Bay (Virnstein, personal communication) have shown large increases inside cages of the pelecypod *Mulinea lateralis*, an opportunistic species. A high susceptibility to predation might explain the rapid decrease of opportunistic species with environmental stabilization following a disruptive influence (e.g., oil spill—Sanders et al. 1972; dredging—Reish 1963; pollution—Rosenberg 1972, Dean and Haskin 1964). Such fluctuations in numbers of opportunistic species have been suggested as features of genetic variability (Grassle 1972; Levinton 1973) or poor competitive ability (Grassle and Grassle 1974).

This caging study suggests that susceptibility to predation may be an important factor in regulating population sizes of opportunistic species, as indicated by results from pollution abatement studies. In this regard, pollution or other such environmental disturbances may exclude predators in the same way that some cages allowed opportunistic species to increase population sizes rapidly. According to the stability-time hypothesis, these increases would be expected to be greatest in physically controlled communities.

In order to meet the requisites of the short-term diversity hypothesis of Slobodkin and Sanders (1969), a community must be studied over a period of years rather than months. Over the longer term the macrobenthos at Haulover might experience far greater fluctuations in species and numbers of individuals than observed in the relatively short time span of this study. As presently planned, future sampling at the Haulover site should provide necessary information about frequencies of occurrence of selected species from the macrobenthic community over the longer term in order to determine if a temporary non-equilibrium situation exists. The December 1974 and February 1975 samples suggest that this may be the case since the rapid influx of species resulted in increasing richness and diversity.

Similar trends and small differences between diversity, evenness and richness of macrobenthos at the Link Port site are shown in Figure 2. The fact that environmental stress at this site is between the extremes measured at the Haulover and St. Lucie sites implies that physical and biotic factors are in some way "balanced" at this location, and preclusion of predators does not markedly affect community structure as measured by diversity, evenness and richness.

Similarly, at Link Port there are small differences of percentage of feeding types as affected by the cage (Table 3). In contrast, the percentage dominance of individual taxa has been greatly altered by the cage (Table 4). Internal or within-community regulation apparently maintains a "structural stability" (Boesch 1972) of the macrobenthos at this site. This effect by a caging experiment upon a macrobenthic community has not previously been reported in the literature.

The increases in diversity, evenness and richness of the macrobenthos within the cage at the St. Lucie site (Fig. 2) might not be predicted by the predator-prey hypothesis of Paine (1966). Predators intensively cropping prey populations would be expected to reduce competition among prey species by allowing more prey species to coexist. As Grassle and Sanders (1973) state, the effects of predators on community structure have been well demonstrated in environments that are primarily physically controlled. In contrast, predation effects in more physically predictable and stable environments require further study.

Whether or not the within-habitat macrobenthic communities studied here conform exactly to definitions of physically controlled or biologically accommodated communities in the sense of Sanders (1968) is not important. According to trends of diversity, evenness and richness, these communities responded in three clearly different ways to preclusion of predators: (1) decrease (Haulover site), (2) little or no effect (Link Port site), and (3) increase (St. Lucie site). Opposite effects of caging are seen at the sites representing the two extremes of the environmental stress gradient. caging studies of the macrobenthos are required in environments characterized by stability and predictability of environmental vari-Internal (within-community) regulation may play a greater role than predation by transient predators in the structuring of macrobenthic communities. These subtle regulation mechanisms cannot be adequately defined by caging experiments such as those used in this study.

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APPENDIX I

List of presence (+) or absence (0) of macrobenthic invertebrates collected inside (in) and outside (out) cages at the Haulover, Link Port and St. Lucie sampling sites, 29 August 1974 to 27 February 1975; (DF)-deposit feeder; (SF)-suspension feeder; (C)-carnivore; (0)-other (herbivore, scavenger, parasite, etc.). Feeding types for molluscs and polychaetes primarily from Abbott (1974), Santos and Simon (1974), Bloom et al. (1972), Young and Rhoads (1971), Day (1967), Hyman (1967), Dales (1963), Morton (1963), and Perry and Schwengel (1955). Taxa are listed in order of abundance under each major taxonomic heading.

anomous heading.			•				
	<u>Hau</u>	<u>Haulover</u>		Port	St. Lucie		
v. 12	In	Out	In	Out	In	Out	
Mollusca							
Gastropoda							
1. Cerithium muscarum (DF,0)	+	+	+	+	+	+	
2. Crepidula fornicata (SF)	+	+	+	+	+	+	
3. Diastoma varium (DF,0)	+	+	. +	+	+	+	
4. Marginella apicina (C,0)	+	+	+	+	0	+	
5. Turbonilla incisa (0)	+	+	+	+	0	0	
6. Marginella sp. A (C,0)	+	+	+	+	0	0	
7. Mitrella lunata (C,0)	+	÷	+	+	+	+	
8. Neritina virginea (0)	0 +	0	0	+	+	+ 0	
9. Vitrinella sp. A (0)	+	+	+ +	0 +	0		
10. Melongena corona (C)	+	0	+	+	0 0	0 0	
11. Pyrgocythara plicosa (C)	+	+	0	+	0	0	
12. Circulus suppressus (0) 13. Haminoea elegans (?C)	+	+	0	+	+	+	
14. Kurtziella atrostyla (C)	Ö	+	0	Ö	0	0	
15. Nassarius vibex (DF,0)	0	+	+	+	+	+	
16. Cerithiopsis greeni (?DF)	+	0	Ó	0	Ö	ó	
17. Bulla striata (C)	+	Õ	ō	Ö	+	+	
18. Odostomia sp. A (0)	+	+	0	Õ	0	0	
19. Acteocina candei (?C)	+	0	+	+	+	+	
20. Acteocina canaliculata (?C)	0	0	0	+	+	+	
21. Anachis avara (C)	0	0	+	+	0	0	
22. Caecum pulchellum (O)	0	+ .	0	0	0	0	
23. Bursatella leachii pleii (0)	0	0	0	0	0	+	
24. Crepidula plana (SF)	0	0	0	0	+	+	
25. Aeolidacea sp. A (C)	0	0	+	0	+	0	
26. Rissoina bryerea (0)	0	0	0	+	+	0	
27. Haminoea succinea (?C)	0	+	0	0	0	0	
28. Acteon punctostriatus (DF)	0	+	0	0	0	0	
29. Alaba incerta (?DF)	0	0	0	0	0	+	
30. Tricolia affinis (0)	0	0	0	0	0	+	
31. Melampus bidentatus (0)	0	0	0	0	+	0	
32. Epitonium rupicola (C)	0	0	0	+	0	0	
33. Cephalaspidea sp. A (C)	0	+	0	0	0	0 0	
34. Elysia sp. A (0)	0 0	+	0	0	0 0	0	
35. Granulina ovuliformis (0)	+	0	0 0	0	0	0	
36. Sayella fusca (0)	7	U	U	U	U	U	
Pelecypoda							
37. Brachidontes exustus (SF)	+	+	0	+	0	0	
38. Amygdalum papyrium (SF)	+	+	+	+	+	+ .	
39. Parastarte triquetra (SF)	0	0	+	+	0	0	
40. Tellina tampaensis (DF)	+	+	+	+	0	0	
41. Chione cancellata (SF)	+	+	0	+	+	+	
42. Lyonsia hyalina floridana (SF)	+	+	+	+	+	+	
43. Lucina pectinata (SF)	0	0	+	+	+	+	

	<u>H</u> au]	lover	Link	Port	St.	Lucie
The large of the l	In	0ut	In	Out	In	Out
Pelecypoda (cont.) 44. Tagelus plebeius (DF)	0	+	+	+	+	+
45. Anomalocardia auberiana (SF)	+	+	Ó	+	+	+
46. Macoma constricta (DF)	0	0	+	+	+	+
47. Macoma sp. A (DF)	+	+	+	0	+	+
48. Parvilucina multilineata (SF)	0	0	0	0	+	+
49. Laevicardium sp. A (SF) 50. Corbula contracta (SF)	+ 0	+ 0	0 0	0	0 +	0
51. Tellina versicolor (DF)	+	0	0	0	+	ő
52. Codakia orbicularis (SF)	0	0	0	0	+	+
53. Pteria colymbus (SF)	0	0	0	0	+	+
54. Anomia simplex (SF)	0	0	+	0	0	+
55. Mulinea lateralis (SF)	0	0	0	+	+	0
56. Tellina paramera (DF) 57. Crassostrea virginica (SF)	0 0	0 0	0 +	0 0	0 0	+ 0
Annelida	U	U	Г	U	o	Ü
Polychaeta						
58. Polydora ligni (DF)	+	+	+	+	+	+
59. Clymenella mucosa (DF)	+	+	+	+	+	+
60. Exogone dispar (?C)	+	+	0	+	+	+
61. Capitella capitata capitata (DF)	+	+	+	+	+	+
62. Tharyx annulosus (DF) 63. Fabriciola sp. A (SF)	+	+	+ 0	+ 0	+ 0	+ 0
64. Prionospio heterobranchia (DF)	+	+	+	+	+	+
65. Fabricia sabella (SF)	+	+	0	+	+	+
66. Laeonereis culveri (0,?C)	+	+	+	+	+	0
67. Streblospio benedicti (DF)	+	+	+	+	+	+
68. Terebella rubra (DF)	+	+	0	0	0	0
69. Aricidea sp. A (DF)	+ +	+	+	 -	++	++
70. Melinna maculata (DF) 71. Branchioasychis americana (DF)	+	+	+	0	Ó	Ó
72. Dorvillea rudolphi (?C)	+	+	+	+	0	0
73. Podarke obscura (?C)	+	+	+	0	0	0
74. Capitella capitata ovincola (DF)	+	+	+	÷	+	+
75. Haploscoloplos foliosus	+	+	+	+	+	+
76. Potamilla sp. A (SF) 77. Microphthalmus aberrans (?C)	+	++	+ 0	+ 0	0 0	0
78. Parahesione luteola (?C)	, +	+	+	+	+	0
79. Capitomastus sp. A (DF)	+	+	0	+	+	+
80. Platynereis dumerilii (0)	+	+	0	0	0	0
81. Polydora socialis (DF)	0	0	0	+	+	+
82. Ctenodrilus serratus (?DF)	+	+	0	0	0	+
83. Capitellidae sp. A (DF)	+	+	+	+	+	+ +
84. Nereis (Neanthes) succinea (0,?C) 85. Thelepus setosus (DF)	+ 0	+ 0	0 1	+ 0	+	+
86. Sepiochaetopterus costarum oculatus (SF)	ő	ő	+	+	0	+
87. Glycinde solitaria (C)	+	+	+	+	+	÷
88. Gyptis vittata (?C)	+	+	+	+	+	0
89. Onuphis microcephala (?C)	0	0	0	0	+	+
90. Eusyllis lamelligera (?C)	+	+	+	+	0	0
91. Branchiomma nigromaculata (SF)	+	++	0 +	0 +	0	0 0
92. Diopatra cuprea (C,SF) 93. Mediomastus ambiseta (DF)	0	0	+	+	+	+
94. Cirriformia sp. A (DF)	ő	ő	o	+	+	+
95. Scolelepis texana (DF)	+	+	+	+	+	0
96. Arenicola cristata (DF)	+	+	+	. +	0	0
97. Capitella capitata tripartita (DF)	+	+	0	0	. 0	+

	<u>Haul</u>	Lover	Link	Port	St.	Lucie
	In	Out	In	Out	In	Out
Polychaeta (cont.)		_				
98. Marphysa sanguinea (DF)	+	+	+	+	0	++
99. Parapionosyllis longicirrata (?C)	+	0	+	0 0	0 +	+
100. Minuspio cirrobranchiata (DF) 101. Heterocirrus alatus (DF)	0	0	0	0	+	+
101. Neteroctivas autus (Br) 102. Pectinaria gouldii (DF)	+	+	0	Ö	+	Ö
103. Glycera tesselata (?C)	0	0	0	0	+	+
104. Polydora attenata (DF)	0	0	0	0	0	+
105. Cirratulus sp. A (DF)	0	0	0.	+	+	0
106. Brania elavata (?C)	0	+	0	0	0	0
107. Pista sp. A (DF)	+	0	+	0	+	0
108. Chone duneri (SF)	0 0	0 0	+	+ 0	0 0	0 +
109. Heteromastus sp. A (DF) 110. Armandia agilis (?)(DF)	0	0	0	0 '	+	o O
111. Spionidae sp. ? (DF)	ŏ	Ö	Ö	Ö	+	ō
112. Terebellides stromeii (DF)	. 0	0	0	0	+	0
113. Armandia maculata (?)(DF)	0	0	0	0	+	+
114. Aricidea fragilis (DF)	0	+	0	0	. 0	+
115. Sabellidae sp. ? (SF)	0	0	0	+	0	0
116. Trypanosyllis zebra (?C)	+	+	0	0	0	0 0
117. Lysidice ninetta ninetta (0)	+	0 0	0 0	0 0	0 0 ·	0
118. Stenoninereis martini (0,?C) 119. Malacoceros vanderhorsti (DF)	Ö	0	0	0	Ö	+
120. Websterinereis sp. A (0,?C)	ŏ	ő	Ö	Ö	Õ	+
121. Cabira incerta (?C)	0	0	0	0	+	0
122. Eteone heteropoda (?C)	0	0	0	0	+	0
123. Lumbrineris tetraura (?C)	0	0	0	0	+	0
124. Paraprionospio pinnata (DF)	0	0	0	0	+	0
125. Isolda pulchella (DF)	0 0	0	0 +	+	0 0	0 0
126. Amphicteis gunneri floridus (DF) 127. Potamilla sp. C (SF)	0	+	0	0	0	0
128. Glycera americana (?C)	ő	+	Ö	ő	Ö	Ö
129. Polycirrus sp. A (DF)	0	+	0	0	0	0
130. Sphaerosyllis pirifera (?C)	0	+	0	0	0	0
131. Amphitrite ornata (DF)	+	0	0	0	0	0
132. Eteone longa (?C)	+	0	0	0	0	0
133. Etcone trilineata (?C)	++	0 0	0	0 0	0	0 0
134. Dasybranchus lunulatus (DF)	+	0	0 0	0	0	0
135. Harmothoe aculeata (?C) 136. Ophryotrocha puerilis (0)	+	0	0	ő	0	0
137. Serpulidae (SF)	+	+	+	+	+	+
138. Hydroides dianthus (SF)	+	+	0	0	0	0
139. Spirorbis (Janua) corrugatus (SF)	+	+	0	0	0	0
140. Serpula vermicularis (SF)	+	0	0	0	0	0
141.01igochaeta	+	+	+	+	+	+
Sipuncula						
142. Phascolion sp.	+	+	+	+	+	+
143.Nemertinea	+	+	+	+	+	+
144. Phoronida	0	+	0	0	+	0
145.Nematoda	+	+	0	0	0	0
Arthropoda						
Crustacea						
. Decapoda						
146. Pagurus sp.	0	0	+	+	+	+
147. Alpheus normanni	0	0	0	0	+	+

		Haulover		Link Port		St. Lucie	
		In	Out	In	Out	In	Out
	Decapoda (cont.)						
148.	Alpheus heterochaelis	+	+	+	+	+	+
149.	Xanthidae	0	0	0	0	+	+
150.	Hippolytidae	0	0	+	+	+	+
151.	Palaemonetes intermedius	+	+	0	0	0	+
152.	Decapoda larva	+	+	0	+	+	+
153.	Palaemonetes pugio	+	+	+	+	+	+
154.	Panopeus sp. (?)	0	0	+	0	+	+
155. 156.	Alpheus sp. Libînia dubia	+ 0	0 0	+	0 +	0 +	+ 0
157.	Panopeus occidentalis	0	0	+	0	+	+
158.	Alpheus armillatus	0	Ö	o O	0	+	+
159.	Pinnixa sp.	o 0	ő	ŏ	+	+	+
160.	Decapoda juvenile	0	0	0	0	+	+
161.	Penaeus sp.	0	0	0	+	0	+
162.	Pinnixa retinens	0	+	0	0	+	0
163.	Palaemonetes juvenile	0	0	0	+	+	+
164.	Caridea larva	0	0	0	0	+	+
165.	Palaemonidae juvenile	+	+	0	0	0	0
166.	Eurypanopeus deprescus	+	0	0	0	0	0
167.	Callinectes ornatus (?)	0	0 0	0 +	+ 0	0	+
168. 169.	Micropanope sp. Pinnixa chaetopterana	0	0	0	0	+	0
170.	Portunus sp.	0	Ö	0	0	· +	0
171.	Latreutes fucorum	+	0	ő	0	+	ő
172.	Palaemonetes sp.	0	0	+	0	+	0
173.	•	0	0	0	+	0	0
174.	Callinectes similis (?)	0	0	0	+	0	0
175.	Hexopanopeus sp.	0	0	+	0	0	0
176.	Panopeus herbstii	0	0	+	0	0	0
177.	Palaemonidae	0	0	0	0	0	+
178.	Sergestidae	0	0	0 0	0 0	0 0	+
179. 180.	Majidae juvenile Pinnixa floridana	0	0	0	0	0	+
181.	Caridea juvenile	0	ő	0	Õ	+	Ö
182.	Palaemonetes vulgaris	ő	0	ŏ	Õ	+	0
183.	Portunidae juvenile	0	0	Ó	0	0	+
184.	Upogebia sp.	0	0	0	0	+	0
185.	Neopanope sayi	+	0	0	0	0	0
	Amphipoda						
186.	Cymadusa sp. A	+	+	+	+	+	+
187.	Grandidierella sp. A	+	+	+	+	+	+-
188.	Melita nitida	+	+	+	+	+	+
189.	Corophium sp. A.	0 .	+	+	+	+	0
190.	Ampelisca sp. A	0	+	+	+	0	+
191.	Gammarus mucronatus	0	0	+	0	0	0
	Isopoda			•			
192.	Erichsonella filiformis isabelensis	+	+	+	+	+	+
193.	Cymodoce faxoni	+	+	+	+	+	+
194.	Apanthura magnifica	0	0	0	0	+	+
195.	Edotea montosa	0	0	+	+	0	0
196.	Bopyridae	0	+	0	0	0	0
	Tanaidacea						
197.	Paratanaidae A	+	+	+ 1	÷	+	+
198.	Paratanaidae B	+	+	0	0	+	+

		Hau	Haulover		Link Port		Lucie
		In	Out	Ιn	Out	In	Out
199.	Cumacea	+	+	+	+	+	0
200.	Mysidacea	+	+	+	0	0	0
	Copepoda						
201.	Copepoda	+	+	0	+	+	0
202.	• •	+	0	0	0	0	0
203. 204.	•	+ 0	+ 0	. 0	0	0 +	0 0
204,	Calanoida	· ·	U	O	Ü	•	U
	Ostracoda						
205.	Sarsiella disparalis	0	+	0	0	0	0
206.Pyc	enogonida	+	0	+	+	+	0
Ara	nchnida						
207.	Halacaridae	0	+	0	0	. 0	0
Mer	rostomata						
208.	Limulus polyphemus	0	+	0	0	0	0
Ech	uinodermata						
	Ophiuroidea						
209.	Amphioplus thrombodes	+	+	+	+	+	+
210. 211.		++	+	+	+ +	+	0 0
211.	Amphiuridae juvenile	•		-		'	U
017	Holothuroidea	,		0	0	0	0
212. 213.	Synaptula hydriformis Thyone sp.	+	+	0 +	0 +	0 0	0 0
214.		+	0	0	0	0	0
215.	Holothuria sp.	0	0	0	0	+	0
Ect	coprocta						
216.	Conopeum tenuissimum	+	+	+	+	+	+
217.	· ·	0 +	0 +	0 +	+	+ 0	+ 0
218. 219.		0	0	+	+	+	+
220.		ő	+	0	Ö	+	+
	Bugula stolonifera	0	0	0	0	+	0
222.		0	0	+	0	0	0
223.	Bugula sp.	0	0	0	0	+	0
224.	Zoobotryon verticillatum	0	0	0	0	+	0
225. Asc	eidiacea	+	+	+	-t-	+	+
226.Cni	daria	0	0	0	0	+	0
227.H	lydrozoa	+	+	+	+	+	+
228.A	anthozoa	0	0	0	+	0	0
229.Por	rifera	+ .	+	+	+	0	0
Pro	etozoa						
230.	Folliculina sp.	0	0	+	+	0	+