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Seasonality and Structure of a Macrobenthic Seagrass Community on the Florida Gulf Coast

key words: seasonality, macrobenthos, seagrass, detritus, deposit feeders

Abstract

Macrofauna at two intertidal sites, quantitatively sampled monthly for 25 months, exhibited distinct reoccurring population fluctuations which were poorly correlated with abiotic parameters. Faunal dominants, *Laeonereis culveri* and *Onuphis simoni*, showed reciprocal fluctuations. *Laeonereis* exhibited non-synchronized reproduction and recruitment while *Onuphis* exhibited synchronized release. *Laeonereis* peaked before *Onuphis* while *Onuphis* fluctuated with the majority of other species. The faunal dominants exhibited one cycle in autumn at both sites but also exhibited a cycle at only one site in spring. Temperature is thus not indicated as causal and detrital input was suggested as the overriding factor. A hypothesis was advanced that *Laeonereis* is an opportunistic species exploiting fresh detritus, while *Onuphis* is a detritus feeder utilizing bacterial populations.

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1. Introduction

As marine benthic community studies expanded from single sampling dates to yearly or longer surveys, the existence of population fluctuations were obvious and became a subject for study, often with the same analytical techniques used to explore spatial differences in faunal assemblages. The problem of fluctuations has been noted and explored within descriptive data sets (BOESCH 1973, STEPHENSON *et al.* 1974). Documented patterns include systems where various species show population peaks at different times but with little annual repeatability (HARRIS 1972a, 1972b,

HOLLAND *et al.* 1977); systems which are highly variable from cycle to cycle but return to the same population mix within an annual cycle (SANTOS & BLOOM 1980) or over a longer period (BUCHANAN *et al.* 1974), and seasonal systems which are highly variable, but show the same pattern from year to year (COULL & FLEEGER 1977, HAEDRICH & HAEDRICH 1974, LIVINGSTON *et al.* 1975).

Seasonal population fluctuations are conceivably due to a variety of phenomena such as sedimentary changes, temperature effects or shifts in resource availability. This research sought to quantify a heretofore undocumented macrobenthic community located between the better-studied but environmentally different areas of Tampa Bay and Appalachicola Bay and to evaluate seasonal changes in population abundances in this deposit-feeding community. If seasonal fluctuations were observed, testable hypotheses of the causal mechanisms were to be advanced.

2. Methods and Materials

Two intertidal stations (0.3 meters above mean tide level) were established at Seahorse Key (83° 04' West and 29° 06' North), a small island 5 kilometers offshore from Cedar Key, Florida on the Gulf Coast (Fig. 1). One station (South Beach) was located on the south beach of the island,

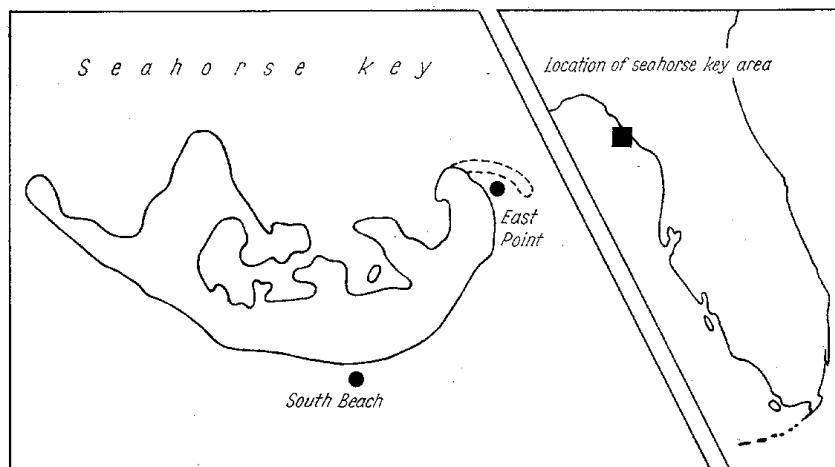


Figure 1. Map of the study sites at Seahorse Key, Florida.

an area characterized by a narrow upper beach margin of coarse white sand (approximately 3 meters wide) which grades into a 10 to 12 meter-wide muddy but firm sandflat (equivalent to CALDWELL'S (1957) open beach habitat). The sandflat supports a sparse population of enteropneusts which create the dominant topographic feature, fecal mounds. These animals generally live at sufficient depths to avoid being sampled by standard macrofaunal coring techniques. Adjoining the sandflat are extensive beds of turtle grass, *Thalassia testudinum* BANKS ex KONIG, and shoal grass, *Halodule beaudettei* (DEN HARTOG) (see DEN HARTOG (1970) and PHILLIPS (1967) for conflicting viewpoints of whether *H. beaudettei* or *H. wrightii* ASCHERSON is the appropriate taxonomic designation). South Beach station was located 2 meters into the sandflat from the edge of the *Halodule* grassbed. A second station (East Point) was located on the eastern point of the island (Fig. 1). A sandspit extends eastward from the island and curves to the south, delineating an embayment open to the south. The sandspit, at its southern tip, is approximately 30 meters from shore. The bottom of the embayment closely resembles the muddy sandflat bordering the south beach, and East Point station was established 15 meters from shore in the same depth of water as South Beach station. The major difference between the two stations is that there is no

appreciable macrophytic growth near East Point station. The patterns of macrodetrital accumulation in time and amount were different from one site to the other. South Beach is characterized by a massive accumulation of shed seagrass leaves in fall while East Point accumulates seagrass detritus in lesser quantities in the spring and the fall.

Faunal and environmental samples were taken monthly at both stations from January 1979 to January 1981 (a span of 25 months) with the exception of February 1979. Faunal samples consisted of five replicates of five pooled cores, each 3.81 cm in radius and 30 cm deep, for a total monthly sample of 0.114 m². All 25 cores taken from each station each month were taken along a line parallel to the beach to avoid the confounding effects of tidal gradients and were taken without prior examination of the substrate to avoid biasing the sample due to the presence or absence of substrate features. Preliminary species-area analysis (HOLME 1953) indicated that a representative sample could be attained with a sample size of 16 to 20 cores. Samples were sieved in the field using a 500 μ m mesh, relaxed in a solution of 0.15 % propylene phenoxymethylol (MCKAY & HARTZBAND 1970), and preserved with buffered 40 % formaldehyde treated with Rose Bengal stain (MASON & YEVITCH 1967). Samples were sorted and the specimens transferred to 70 % isopropyl alcohol. All specimens were identified to the lowest practical taxonomic level and counted. All replicates were processed separately and after identification and enumeration, were examined for major sampling discrepancies. None were found and replicate data was then pooled for subsequent analyses.

Twenty-two sediment samples were taken monthly from January 1979 to December 1979, and 14 samples were taken thereafter. Samples were taken with a core 1 cm in diameter and 10 cm long. Seven of the sediment samples were analyzed for granulometric properties using wet-sieve techniques (see RHOADS 1967 and 1974 for the rationale behind wet sieving) and standard procedures (BUCHANAN & KAIN 1971). The balance of the sediment samples were combusted at 550 °C to determine organic content (BYERS *et al.* 1978). All organic content samples were sieved through a 1000 μ m mesh prior to drying and burning to separate macrodetritus from microdetritus.

Monthly water samples were taken at each station and salinity was determined using a temperature-compensating refractometer calibrated with Standard Seawater. Monthly sediment temperature was determined at a depth of 10 cm.

Since the two dominant species in preliminary sampling were a nereid, *Laeonereis culveri* WEBSTER and an onuphid, *Onuphis simoni* SANTOS (SANTOS *et al.* 1981), these species were selected for size-frequency determinations. The width of the first setiger of all individuals of both species was measured at 50 power using an ocular micrometer. The width of the first setiger has been shown to be a good predictor of overall length (BUCHANAN & WARWICK 1974, DAUER 1974, HOBSON 1971). All specimens of each species from each monthly sample at the two stations were pooled and combusted at 550 °C to obtain ash-free dry weights. Since *Onuphis* broods its young within its tube and young were often released during the sorting or identification procedures, it was necessary to distinguish free-living, but small specimens, from brooded young. Young found in parental tubes never exceeded 260 μ m in width, while free-living individuals clearly in their own tubes were never found to be smaller. A width of 260 μ m was taken as the threshold between brooded young and free-living individuals.

Laeonereis produces a dispersing but non-planktonic 3-setiger larva which is reported to select medium sands and retain the ability to continue dispersal if the sediment becomes excessively fouled with organic material (MAZURKIEWICZ 1975). Since settlement is reported from the 3-setiger stage on, an arbitrary division of dispersing young and newly recruited individuals was necessary. By interpolation of length to setiger number (MAZURKIEWICZ 1975), a width of 260 μ m would correspond to a 14–15 setiger animal (checks of the local population support this figure). Since the "esophagus remains a plug-like mass . . . until the 12-setiger stage", larval ciliature (the nototroch) remains until the 16 to 18-setiger stage, and normal buccal morphology is not attained until the 20-setiger stage (MAZURKIEWICZ 1975), adoption of the same arbitrary division of 260 μ m seemed justified.

Granulometric parameters were calculated from sedimentary data by SEDANA (BLOOM *et al.* 1977). The program utilizes granulometric equations taken from FOLK (1966) with the exception of Inclusive Graphical Skewness which appears to have been incorrectly cited from the original formulation (FOLK & WARD 1957). The original equation is used here.

Faunal data were processed into a standard data matrix by DATPUN (BLOOM *et al.* 1977) which also calculates sample characteristics such as the number of species, the density per square meter, diversity (H' calculated in bits, i. e. log base 2) and relative evenness ($(H' - H_{min}) / (H_{max} -$

H min), sometimes referred to as scaled evenness (HEIP & ENGLÉS 1974). The matrix of 48 samples (2 stations \times 24 months) and 109 species was analyzed by ORDANA (BLOOM *et al.* 1977) to generate a classification analysis. No transformations or standardizations were used so as to avoid obscuring dominance patterns. The similarity index was CZEKANOWSKI'S Quantitative Index (also known as the Bray-Curtis Index, Proportional Similarity and a host of other names—see BOESCH 1977 for a general literature review). The index takes the form:

$$S_{jk} = \left(2 \sum_{i=1}^s \min(X_{ij}, X_{ik}) \right) / \left(\sum_{i=1}^s X_{ij} + \sum_{i=1}^s X_{ik} \right)$$

where X_{ij} and X_{ik} are the densities of the i th species in the j th and k th samples respectively, S_{ij} is the similarity between samples j and k , and s is the total number of species. This index has a range from 0 to 1, approximates the calculus in estimating overlap, and has been shown not to distort similarity values (BLOOM 1981). The sorting strategy was Group-Average (also known as Unweighted Arithmetic Average) (SNEATH & SOKAL 1973).

The interpretation of the dendrogram resulting from a classification analysis is greatly aided by the identification of those biotic and abiotic parameters which can statistically separate the clusters of the dendrogram. The parameters extracted from the data set for the purpose of identifying such parameters consisted of the species which accounted for a cumulative 90 % of the counts (21 species), summary biotic parameters (number of species, density per square meter, diversity, relative evenness, and density excluding the two faunal dominants), biotic parameters for the two faunal dominants, *Laonereis* and *Onuphis*, (density per square meter, percent of dispersing and brooded young to total numbers of individuals, total biomass and mean width of the first setiger), trophic parameters (carnivores-scorpionids, selective deposit feeders, selective deposit feeders excluding the faunal dominants, non-selective deposit feeders, and suspension feeders), and abiotic parameters (mean particle size, sorting coefficient, silt-clay percent, sediment organic content, temperature and salinity) to yield a total matrix of 45 parameters by 48 samples.

The dendrogram resulting from the classification analysis was examined and clusters identified. A mean and standard deviation for each characteristic listed above within each cluster was calculated and a Kruskal-Wallis One-Way Analysis of Variance (SIEGEL 1956) was performed for each characteristic (with the clusters being regarded as treatments). Since a non-parametric multiple range test for unequal sample sizes was not available and parametric statistical assumptions were not likely to be met, all possible pairwise combinations of the dendrogram clusters for each characteristic were analyzed by a Mann-Whitney U-test (SIEGEL 1956). This analysis scheme resulted in 45 ANOVAs and 450 U-tests (assuming 5 clusters or 10 pairwise combinations). Assuming randomness and an alpha level of 0.05, rejection should have occurred for 2.3 ANOVAs and 23 U-tests even if there were no pattern. Because the data were not independent (being derived from a time-series, two stations and interdependent characteristics), the number of expected rejections under the null hypothesis needed to be estimated. The samples were randomized by linking a random number drawn from a random number table (ROHLF & SOKAL 1969) to each sample, ordering the random numbers and rearranging the 48 samples (columns of the matrix) accordingly. The rearranged data matrix was then sequentially divided into clusters equivalent to the original dendrogram (although the identity of the samples within each cluster had been randomized). The analysis using the randomized samples resulted in no rejections of the Kruskal-Wallis test and only 14 rejections of the U-test (3.1 %) while the analysis of the clusters as delineated by the classification analysis resulted in 40 and 214 rejections respectively. This result lent weight to the likelihood of there being a meaningful pattern within the data, and to this analytical approach.

To examine correlations within the data, the set of 45 biotic and abiotic parameters was reduced by exclusion of individual species (with the exception of the two dominants) and density of selective deposit feeders including the dominants, leaving 23 parameters. For each station individually and for both stations pooled, all pairwise comparisons of parameters were examined by a Spearman-Rank Correlation Analysis (a total of 759 tests). For those pairs of parameters which were statistically correlated at both sites and overall, bivariate plots were made to assess the apparent monotonicity of the relationship since nonparametric correlative analyses are based on the assumption of monotonic relationships of variables.

All computer analyses were performed at the University of Florida Northeast Regional Data Center using an Amdahl 470 V/6-II and an IBM 3033 N with OS/MVS Release 3.8 and JES 2/

NJE Release 3. Two-way analyses of variance were performed by SAS release 79.5 General Linear Models procedure (SAS Institute Inc.). All other programs were written by the author in FORTRAN IV.

3. Results

a) Abiotic Parameters

Temperature varied from 9.5 °C to 32 °C and was consistent from year to year and station to station (Fig. 2). Salinity varied from 26 to 32‰ with little overall pattern (Fig. 2). Even though the study site is situated between the Wacassassa and Suwannee river-mouths (28 and 18 km respectively), there was little appreciable estuarine influence during the observational period.

Sedimentary parameters were analyzed with a two-way analysis of variance (stations and months) and a Duncan's multiple range test (SAS GLM PROC) (Table 1). Four of the parameters are presented in Figure 3. Sediment mean grain size was found

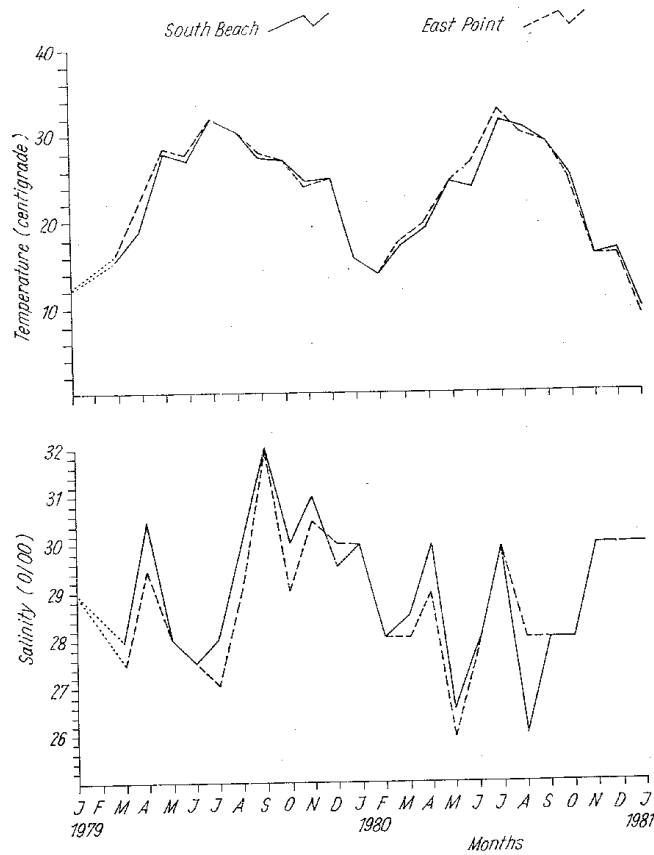


Figure 2. Temperature and salinity values from January 1979 to January 1981 at two stations at Seahorse Key, Florida. Absence of data in February 1979 is indicated by broken-line segments between January and March 1979.

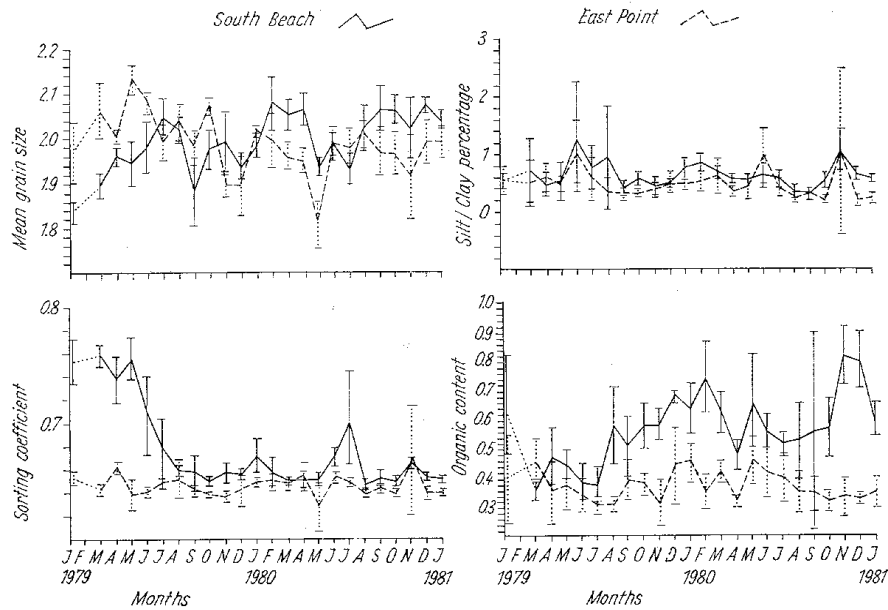


Figure 3. Granulometric parameters (mean grain size in phi units, sorting coefficient and silt-clay percentage) and organic content of sediments from January 1979 to January 1981 at two stations at Seahorse Key, Florida. Bars represent one standard error on either side of the mean. Absence of data in February 1979 is indicated by broken line segments between January and March 1979.

to be statistically indistinguishable at the 0.05 level between stations or between months. Sorting, skewness, kurtosis, and silt-clay percentages were statistically different between the stations but with the exception of sorting, no temporal pattern was evident. Sorting fell into two distinct temporal groups, a January-to-July group and an August-to-December group, with only February being in both. Organic content was significantly greater at South Beach than at East Point (as was silt-clay percentage) even though South Beach is better sorted (Table 1). The temporal pattern of organic content was complex but a pattern was evident. Three major groups are recognizable: (1) a winter (October to February) group; a spring autumn (March to May and August to September) group; and (3) a summer (June to July) group (ranked in descending order of organic content). Essentially, organic content cycled between a winter maximum and a summer minimum.

b) Biotic Parameters

Over a period of 25 months, 109 taxa consisting of 18,506 individuals were collected. As is typical of many benthic communities, relatively few species dominated, i. e. 60 species accounted for 99 %, 21 species for 90 %, and two species (*Laonereis* and *Onuphis*) for over 42 % of all individuals. A species list and overall statistics are presented in Table 2.

Biotic parameters (number of species, density per square meter, diversity and relative evenness) for both stations are presented in Figure 4. These parameters with the exception of density exhibited a bimodal annual pattern with maxima in summer (June or July) and winter (December or January). The maximum peak occurred in winter preceded by the maximum trough in autumn (August or September). The

Table 1. Results of two-way analyses of variance contrasting the effect of time for 6 sedimentary parameters. Data from January 1979 to January 1981 were pooled by month. Temporal sequence of months (January = 1, December = 12) ranked in decreasing order from left to right. Bars underlying temporal symbols indicate no statistical difference between these months (Duncan multiple range test) ($\alpha = 0.05$ for all tests).

Granulometric Parameter	Mean Value at:		East Point	Two-way ANOVA ($\alpha = 0.05$)	Stations Distinct? ($\alpha = 0.05$)	Temporal Sequence of Months											
	South Beach	East Point				2	8	10	11	6	4	3	7	12	9	1	5
Mean Grain Size	1.994	1.991	accept	accept	accept	4	3	1	7	5	6	2	9	8	12	11	10
Sorting Coefficient	0.676	0.642	reject	reject	reject	11	12	9	5	1	7	10	3	4	8	6	2
Skewness	0.003	-0.041	reject	reject	reject	5	3	1	4	7	11	9	6	12	2	10	8
Kurtosis	0.783	0.757	reject	reject	reject	6	11	2	3	7	1	4	5	8	12	10	9
Silt/clay Percentage	0.647	0.491	reject	reject	reject	12	2	1	11	10	5	3	8	9	4	6	7
Organic Content	0.561	0.377	reject	reject	reject												

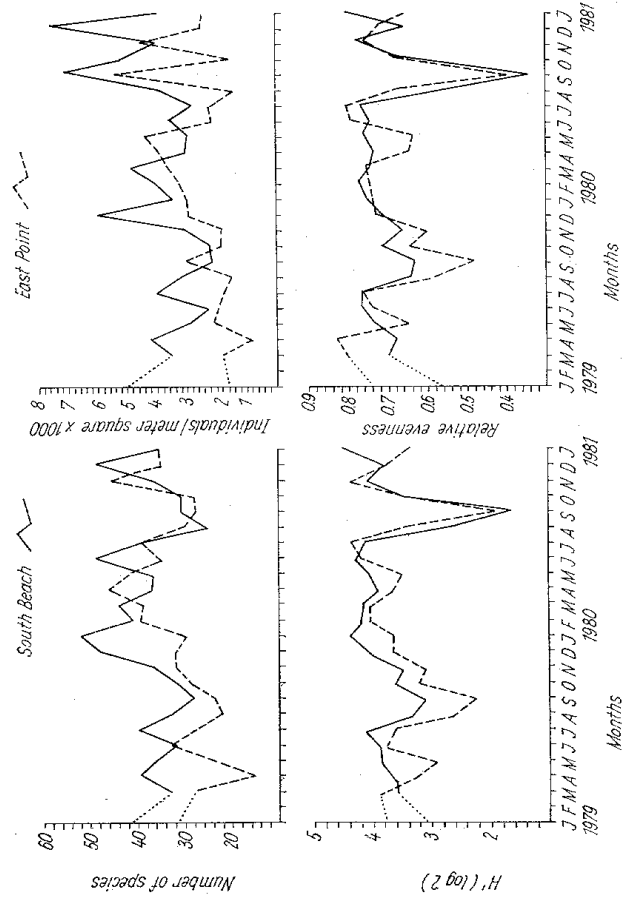


Figure 4. Summary biotic parameters (number of species, density per square meter, diversity and relative evenness) from January 1979 to January 1981 at two stations at Seahorse Key, Florida. Absence of data in February 1979 is indicated by broken line segments between January and March 1979.

Table 2. Species representing 99 % of all individuals encountered from January 1979 to January 1981 at two sites at Seahorse Key, Florida with trophic types (taken from SANDERS 1960, BLOOM *et al.* 1972, MAZURKIEWICZ 1975, FAUCHAULD & JUMARS 1979, STONER 1980), total count and number of months in which the species occurred for each site (column labeled Occurrence) and percent of all counts and rank order for both sites combined. Guild type (FAUCHAULD & JUMARS 1979), codes: S—surface deposit; B—subsurface deposit; C—carnivore; F—filter feeders which are M—motile, D—discreetly motile, S—sessile with feeding structure: J—jaws, T—tentacles, X—miscellaneous. Trophic type codes: SF—suspension feeder; SDF—selective deposit feeder; NSDF—nonselective deposit feeder; O—omnivore; C—carnivore. All counts expressed at density/m² per occurrence and summed.

Taxa	Guild Type	Trophic Type	South Beach Density	South Beach Occurrence	Density	East Point Density	East Point Occurrence	Percent Occurrence	Overall Percent	Overall Rank Order
Platyhelminthes										
Polychaeta unidentified	CMX	C	98	5	126	10	10	0.142		44
Rhynchocoela unidentified	CDX	C	1553	24	563	21	21	1.344		16
Sipunculida unidentified	SST	NSDF	160	10	45	4	4	0.130		48
Mollusca										
Gastropoda										
<i>Granulina ovuliformes</i>	SMX?	NSDF	284	15	35	2	2	0.203		38
<i>Haminoea succinea</i>	CMX	C	913	15	1204	18	18	1.344		15
<i>Nassarius vibex</i>	SMX	NSDF	397	13	283	13	13	0.432		28
<i>Olivella pusilla</i>	CMX	C	81	7	36	4	4	0.074		57
<i>Utricularia canaliculata</i>	CMX	C	472	15	54	5	5	0.334		34
Bivalvia										
<i>Anodontia alba</i>	FDP	SF	36	4	80	5	5	0.074		58
<i>Ensis minor</i>	FDP	SF	90	7	124	8	8	0.136		45
Annelida										
Polychaeta										
<i>Aricidea philbiniae</i>	SMX	SDF	7061	24	2527	23	23	6.088		4
<i>Aricidea taylora</i>	SMX	SDF	1447	21	318	16	16	1.121		19
<i>Armandia agilis</i>	BMX	NSDF	88	3	511	14	14	0.380		30
<i>Capitella capitata</i>	SMX	NSDF	3175	24	1309	21	21	2.847		7
<i>Chone duneri</i>	FST	SF	89	7	45	4	4	0.085		56
<i>Clymenella mucosa</i>	BSX	SDF	2939	23	3578	21	21	4.138		5
<i>Diopatra cuprea</i>	CDJ	C,SDF	125	9	35	2	2	0.102		53
<i>Drilonereis magna</i>	CMJ	C	223	14	90	9	9	0.199		39
<i>Eteone heteropoda</i>	CMJ	C	1194	22	599	19	19	1.138		18
<i>Glycera americana</i>	CDJ	C	318	13	196	11	11	0.326		35
<i>Glycera dibranchiata</i>	CDJ	C	90	7	143	9	9	0.148		43
<i>Glycinde solitaria</i>	CDJ	C	283	11	291	12	12	0.364		31
<i>Gyptis brevipalpa</i>	CMJ	C	152	10	53	4	4	0.130		47
<i>Heteromastus filiformis</i>	BMX	NSDF	1579	23	915	21	21	1.584		14
<i>Laenoneis culveri</i>	SMX	O,SDF	22431	24	18309	24	24	25.869		1
<i>Lumbrineris tenuis</i>	BMJ	NSDF	1564	21	167	7	7	1.099		20

<i>Magelona pettiboneae</i>	SDT				740	22	0.549	26
<i>Notomastus hemipodus</i>	BMX			142	8		0.130	46
<i>Onuphis simoni</i>	SDJ			8669	24		16.231	2
<i>Paraprionospio pinnata</i>	SDT			256	8		0.286	37
<i>Phyllodoce arenae</i>	CMS			449	16		0.487	27
<i>Polydora socialis</i>	SDT			1465	10		1.103	20
<i>Prionospio heterobranchia</i>	SDT			606	14		2.213	12
<i>Sabella microphthalma</i>	FST			106	6		0.163	41
<i>Scotolepis squamata</i>	SDT			2973	23		2.717	8
<i>Scotoplos foliosus</i>	BMX			1370	19		2.692	9
<i>Scoplos rubra</i>	BMX			152	11		0.159	42
<i>Spio</i> sp.	SDT			126	10		0.109	50
<i>Spiophanes bombyx</i>	SDT			2341	23		2.584	10
<i>Sirellospio benedicti</i>	SDT			545	11		2.229	11
Syllidae unidentified	CMJ			89	6		0.107	51
Oligochaeta (unidentified)	BMX			4157	24		6.110	3
Arthropoda								
Merostomata								
<i>Limulus polyphemus</i>	CMX			63	7		0.097	54
Amphipoda								
<i>Ampelisca homesii</i>	SMJ			1344	21		2.981	6
<i>Cyadusa compta</i>	SML			27	2		0.073	59
<i>Gammarus mucronatus</i>	SMJ			0	0		0.096	55
<i>Grandierella bonnieroides</i>	SMJ			177	7		0.728	24
<i>Monoculodes edwardsi</i>	SMJ			1142	20		0.916	23
<i>Orchestia platensis</i>	SMJ			177	8		1.188	17
Isopoda								
<i>Apanthura magnifica</i>	SMJ?			528	15		0.709	25
<i>Edotea montosa</i>	SMJ?			9	1		0.102	52
Cumacea								
<i>Ocyurostylis smithi</i>	SMJ			859	17		1.686	13
Tanaidacea								
<i>Hargeria rapax</i>	SMJ			90	8		0.421	29
Decapoda								
<i>Pagurus</i> sp.	CMJ			45	5		0.069	60
<i>Pinnixa</i> sp.	CMJ			293	16		0.361	32
Procellidae (unidentified)	SMJ?			44	3		0.112	49
Echinodermata								
<i>Leptosynapta</i> sp.	BMT			432	12		0.916	22
<i>Ophiophragmus filigraneus</i>	SDX			72	6		0.303	36
Phoronida								
<i>Phoronis</i> sp.	FST			178	10		0.344	33
Chordata								
Cephalochordata								
<i>Branchiostoma caribaeum</i>	FMP			134	8		0.170	40

magnitude of variation of the spring-summer cycle for diversity and evenness is quite small relative to the autumn-winter cycle. The major differences between the two stations are (1) East Point is generally lower for all parameters than is South Beach; (2) there is an apparent time-lag of one to two months for East Point relative to South Beach for number of species and density which is not evident for diversity and evenness; and (3) East Point exhibits a distinct minimum in spring relative to South Beach for diversity and evenness. Density does correspond to the bimodal pattern when *Laeonereis* and *Onuphis* densities are excluded.

Much of the variation in species numbers is due to the inclusion of species with few individuals as can be seen by a lack of a corresponding change in diversity. The April 1979 and February 1980 South Beach samples clearly demonstrate this effect.

Among the multiplicity of peaks in numbers of individuals, only a few could not be attributed to either *Laeonereis culveri* or *Onuphis simoni*, the faunal dominants. Peaks in April, July and December 1979 at South Beach and May 1980 at East Point were due to varying mixtures of co-occurring population maxima, i. e. *Ampelisca homesii* and *Aricidea philbiniae* in April 1979, *A. homesii*, *Scoloplus foliosus* and oligochaetes in July 1979, *Cymenella mucosa*, *Haminocoe succinea*, *Oxyurostylis smithii* and *A. philbiniae* in December 1979 and *C. mucosa* and *A. philbiniae* in May 1980.

c) Faunal Dominants

Laeonereis culveri and *Onuphis simoni* were the dominant species at Seahorse Key and their population dynamics greatly influenced the changing patterns of community structure. The population densities of these two species were in inverse relationship to one another (Figure 5) and repeated from year to year. The populations cycled once a year at South Beach (*Laeonereis* reaching a sharp peak in autumn with a sub-

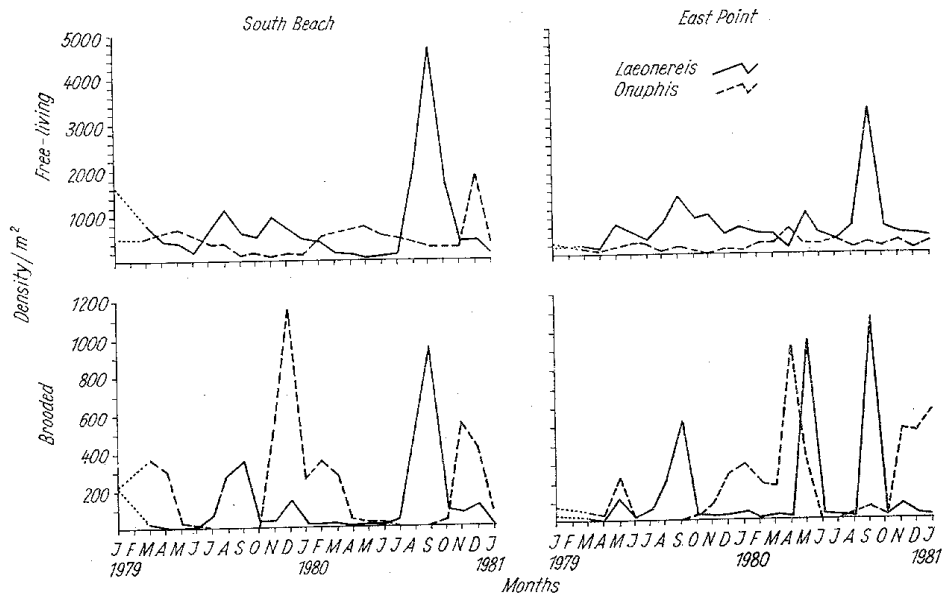


Figure 5. Monthly densities per meter square of free-living and brooded (or dispersing) young of *Laeonereis culveri* (WEBSTER) and *Onuphis simoni* SANTOS from January 1979 to January 1981 at two stations at Seahorse Key, Florida. Absence of data in February 1979 is indicated by broken line segments between January and March 1979.

sidiary peak in winter, while *Onuphis* reached a sharp peak following the winter 1980 peak of *Laeonereis* and attained a gradual maximum in spring of all years). On East Point, the pattern was similar except that the cyclical pattern of these species also occurred in late spring (May). These cycles are also apparent in trends in mean setiger width and in ash-free dry weight for these two species (Figure 6).

Juvenile *Laeonereis* and the brooded young of *Onuphis* also showed distinct seasonal trends which were inversely related and clearly demonstrated the presence of the additional cycle in the late spring at East Point (Fig. 5). Juveniles of *Laeonereis* tracked the adult population peaks at both stations. The proportion of juvenile to adult *Laeonereis* ranged from 50% (May 1980) to 0% (April 1979), with a mean of 10.88% (S.D. 9.58; N=48). Since the proportion of juveniles was small and their density closely tracked the peaks of the adult population, reproduction appeared to be nonsynchronized. The general pattern was the presence of relatively few but large adults (compare Figures 5 and 6) followed by a rapid increase in both adults and juveniles (the later representing 20 to 50% of the total population), followed by a rapid decline in juveniles and a slower decline in adults. This pattern occurred in

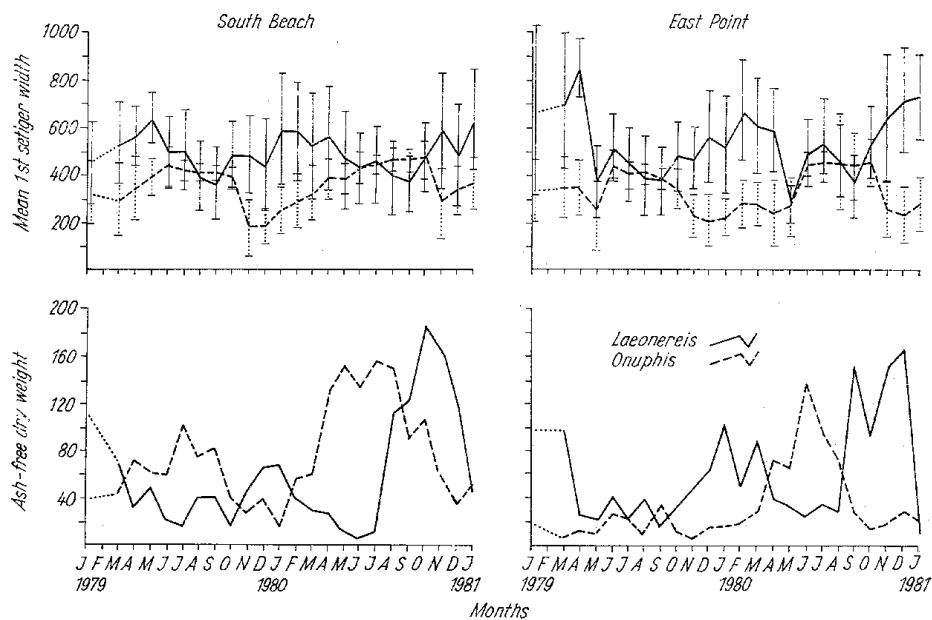


Figure 6. Monthly mean first setiger widths and ash-free dry weights (in 0.114 m²) for *Laeonereis culveri* (WEBSTER) and *Onuphis simoni* SANTOS from January 1979 to January 1981 at two stations at Seahorse Key, Florida. Absence of data in February 1979 is indicated by broken line segments between January and March 1979.

autumn (September) in both years at South Beach and East Point but also consistently occurred in late spring (May) only at East Point. It should be noted that (1) the sedimentary parameters were extremely similar at these two sites in spring; (2) the direction of temperature change was reversed in autumn and spring; and (3) the actual temperatures during May 1979 and September 1979 were very different from the temperatures of May and September 1980.

The brooded young of *Onuphis* were inversely related to adult densities or at least peaked before adult densities peaked (with the exception of May 1980 at East Point)

(Fig. 5). The general pattern for *Onuphis* was a slow decline in adult densities paralleling a slow rise in mean size (Fig. 6), followed by a rapid influx of brooded young and a rapid decline in population biomass. There was also a distinct decline in mean width which could occur either by the addition of many small individuals to a persisting population of adults or by the replacement of the adults. The decline in population biomass indicated the latter. The density of juveniles then declined rapidly and adult densities reached their peak. This pattern is consistent with synchronized semelparous reproduction with primary reproduction occurring in the winter months but with reproduction also occurring in late spring on East Point. Brooded young represented 29.20 % (S. D. 16.38; N = 48) of the population of *Onuphis* with a range from 88 % to 0 %.

In summary, reproduction (defined as the appearance of juveniles or brooded young) by *Laeonereis* tended to precede reproduction by *Onuphis* at both sites, the adult populations were inversely related to one another, populations of *Laeonereis* exhibited greater variance in density but less in reproductive output than populations of *Onuphis* and both species exhibited an annual cycle at South Beach and a biannual cycle at East Point.

d) Community Structure

Faunistic similarity (without transformation) ranged from 83 % to 43 %. Five clusters were readily recognizable in Figure 7 but the reason for which samples made up each cluster were not obvious. While Cluster C is composed of only South Beach samples, and Cluster E is composed of only East Point samples, the stations are intermixed within the other clusters. With the exception of Cluster D (November to January), there is little seasonal pattern evident. Cluster A spans January to October, Cluster B and Cluster C span January to November, and Cluster E spans January to December.

The statistical analysis of abiotic parameters (see Methods for details) (Fig. 8) failed to reveal any single factor which completely separated the clusters recognized in the classification. There was insufficient variation in salinity and sediment mean particle size to reject the null hypothesis of the difference between clusters. Temperature, while being sufficiently variable to generate a rejection of the Kruskal-Wallis test, was found to be statistically indistinguishable between pairs of clusters. Sediment sorting coefficients were indistinguishable between Clusters A, B, D and E and clearly separated Cluster C from the others. Silt/clay percentages of sediments failed to link the clusters along a gradient. Clusters A, C and D were linked together by higher organic content and separated from clusters B and E (the last two clusters had on the average only 70 % of the organic content of the first three).

As might be expected, biotic parameters were more useful than abiotic parameters in defining the clusters (Fig. 8). Cluster A is unified primarily by large numbers of small *Laeonereis*, relatively few but large *Onuphis* (with few brooded young), and a low overall diversity. Cluster B is composed of samples which are generally depauperate (few species and few individuals) and Cluster C contained samples with minimal biomass of *Laeonereis* and maximal biomass of *Onuphis*. High numbers of species, of individuals, of *Onuphis* and large biomass of *Laeonereis* characterize samples in Cluster D. Cluster E is characterized by relatively low numbers of individuals, few but large *Laeonereis* with few juveniles present and moderate numbers of *Onuphis* with a large proportion of brooded young (also reflected in a small first setiger width).

A careful simultaneous examination of Figures 7 and 8 while keeping in mind the basic fluctuation patterns of the two dominant species clarified these patterns.

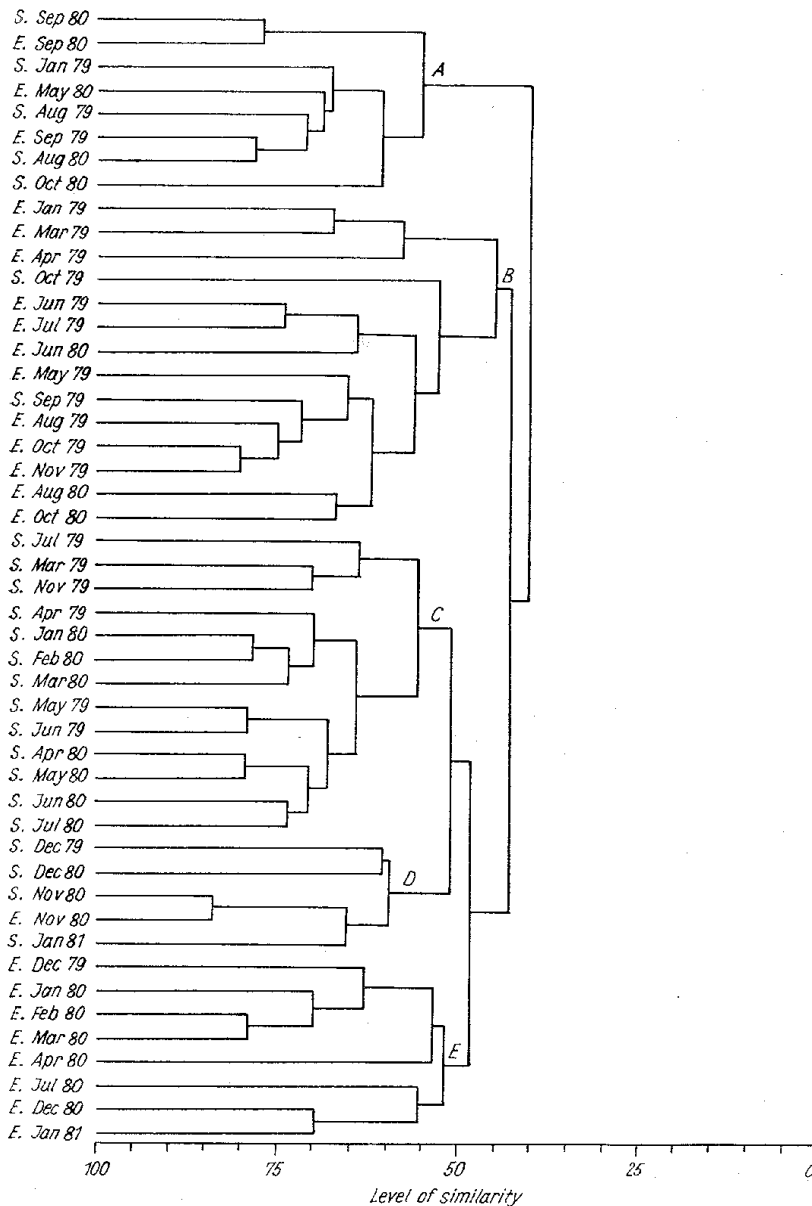


Figure 7. Classification analysis (see text for details of analytical procedures) from two stations (S. = South Beach; E. = East Point) from January 1979 to January 1981 at Seahorse Key, Florida.

Cluster A represented the peak of *Laeonereis* at both stations. When populations of *Laeonereis* reached their zenith in terms of numbers and biomass, populations of *Onuphis* were in a holding or 'residual' phase with few but large adults present. As the peak of *Laeonereis* subsided, Cluster D (South Beach) or Cluster E (East Point) became expressed. *Laeonereis* declined while populations of *Onuphis* increased. Cluster C (South Beach) and Cluster B (East Point) represented the period between the cyclical population increases. Thus, the community cycled from Cluster A to D

Abiotic	<i>Temperature</i>	<i>Salinity</i>	<i>Mean Grain size</i>	<i>Sorting</i>
	<u>D E C B A</u>	<u>A B C E D</u>	<u>E A C B D</u>	<u>B E D A C</u>
	— —	<i>Silt / Clay %</i>	<i>Organic Content</i>	
		<u>E A B C D</u>	<u>E B A C D</u>	
		— —		
Summary Biotic	<i>Number of Species</i>	<i>Total Density</i>	<i>Density w/o Dominants</i>	<i>Diversity (H')</i>
	<u>B A E C D</u>	<u>B E C A D</u>	<u>B A E C D</u>	<u>A B E C D</u>
Dominants	<i>Laeonereis culveri</i>			
	<i>Density</i>	<i>Juvenile %</i>	<i>Mean Width</i>	<i>Biomass</i>
	<u>E C D B A</u>	<u>E C B D A</u>	<u>A B C D E</u>	<u>C B E A D</u>
	<i>Onuphis sp.</i>			
	<i>Density</i>	<i>Juvenile %</i>	<i>Mean Width</i>	<i>Biomass</i>
	<u>B A E C D</u>	<u>A B C D E</u>	<u>E D C B A</u>	<u>B E D A C</u>
Trophic Groups	<i>Garnivores & Scavengers</i>	<i>Selective Deposit Feeders (w/o Dominants)</i>	<i>Nonselective Deposit Feeders</i>	<i>Suspension Feeders</i>
	<u>B A C E D</u>	<u>B A C E D</u>	<u>B A E C D</u>	<u>B A C E D</u>

Figure 8. Statistical linkage pattern of biotic and abiotic parameters delineated by the classification analysis. Bars connecting symbols indicate that the clusters so linked were statistically indistinguishable from one another (Mann-Whitney U-test, $\alpha=0.05$). Clusters are ranked from right to left in increasing value of the indicated parameter.

to C and back to A at South Beach and Cluster A to E to B and back to A at East Point. The essential pattern was identical at both sites but the sites were separated by the existence of a spring peak at East Point, lower organic content during periods of low densities of *Laeonereis* at East Point, and greater amplitude of cycles at South Beach.

e) Correlation Analyses

The results of the correlation analyses are presented in Figure 9. If there were a strong direct causal relationship, the resultant correlation should be demonstrable at each station and for both stations pooled. Of the 109 rejections (out of 253 possible) for pooled data, only 41 of the rejections were also rejected at the stations individually. While acceptance of the null hypothesis at a station may have been due to fewer degrees of freedom than for the pooled data (22 instead of 46), the biological importance of the correlation of the pooled data was suspect. The 41 bivariate comparisons were plotted and no deviation from monotonicity was apparent in any of the plots.

There was little discernable pattern of correlations of abiotic to biotic parameters. Of the possible 102 correlations, only 7 were rejected at each station and overall, and 5 of these involved temperature. In general, low temperature tended to be correlated with the characteristics of the more diverse and denser winter assemblage.

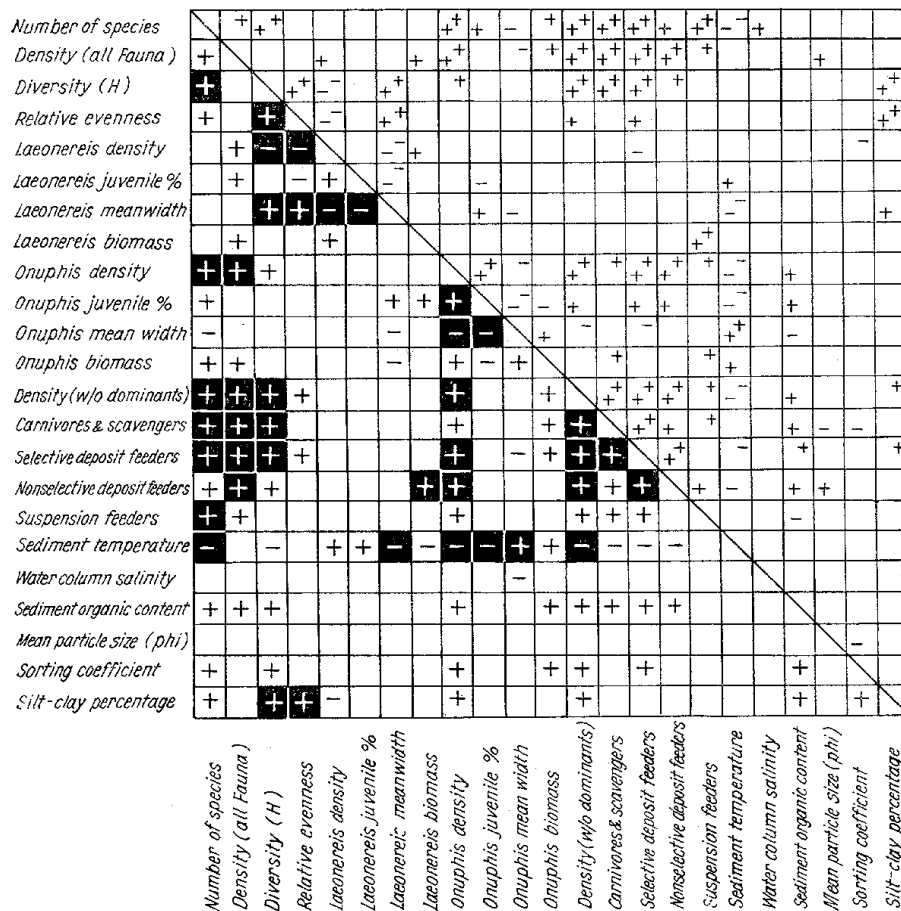


Figure 9. Correlation matrix of 23 biotic and abiotic parameters for two stations and pooled stations from January 1979 to January 1981 at Seahorse Key, Florida. The lower left hemi-matrix represents pooled data while the upper right hemi-matrix represents individual stations (in each cell of the upper hemi-matrix, a symbol in the lower left represents South Beach while a symbol in the upper right represents East Point). The presence of a symbol represents a statistically significant correlation (alpha = 0.05) between two parameters (row and column which define the cell in which the symbol appears). A blackened cell with a symbol occurs when the same correlation occurred for both stations and the pooled data.

However, since such a 'winter' assemblage occurred at East Point in the spring under a different temperature regime, the causal significance of these correlations is debatable.

Comparisons of biotic parameters tended to fall into a cohesive pattern. The various trophic categories and densities of *Onuphis* were positively intercorrelated and as a result, were also positively correlated to the summary biotic parameters. *Onuphis* thus appears to be an interrelated component of the community and to be responding to general controlling factors. In that the community was dominated by deposit feeders (65 % of the species and 93 % of the individuals), positive correlations to organic content would be expected. Such correlations did occur for pooled data (but not at stations individually). Conceivably, had organic content of the upper sediment layers (0 to 1 cm) been determined rather than the average content (the first

10 cm), the correlations might have been strengthened. Determination of an organic content vertical profile was performed in September 1981 as part of a separate study of the vertical distribution of fauna and abiotic factors at South Beach. The organic content of the first 10 centimeters was 0.64 % while that of the first centimeter was 0.97 %, an increase of over 58 % from the mean organic content.

Laeonereis, on the other hand, showed little correlation to *Onuphis* or to other trophic categories. Due to its relative dominance numerically (Table 2), a positive correlation to total density would be expected but was not found. Moreover, *Laeonereis* was negatively correlated to diversity (and therefore to relative evenness), thus indicating that when *Laeonereis* was found in large numbers, relatively few species with relatively low densities were also found. In general, *Laeonereis* appeared to be responding to different controlling factors than the rest of the community.

4. Discussion

Theoretical formulations have been proposed for seasonal effects in suspension- and deposit-feeding communities (LEVINTON 1972). The general prediction was that communities dominated by suspension feeders would show greater fluctuations than communities dominated by deposit feeders. Suspension-feeding communities were pictured as reflecting the inherent variability of plankton densities while deposit-feeding communities would be buffered from changes in food availability by recycling organic material through bacterial pathways and through coprophagy. The suggestion has also been made that species possessing planktonic larvae should be more likely to have high seasonal populational variations than would be expected in species which brood young (HOLLAND & POLGAR 1976).

This view of deposit-feeding community stability is predicated on the assumption that periodic organic input becomes available to the macrofaunal community only through bacterial pathways and hence the appreciable time-lags would smooth out temporal variations in food availability. A physical analog to this concept is a funnel with a narrow spout. The actual level of material in the funnel (food resources entering the system) can change greatly through time while the outflow (food actually available to deposit feeders) remains reasonably constant. However, since seasonality, i. e. consistent population fluctuation, does occur in some deposit-feeding communities (see examples in Introduction), this paradigm is obviously not universal. Consistent population fluctuations could be conceivably generated by habitat alterations such as cyclical changes in sediment structure or in temperature regimes or by changes in resource availability (if the paradigm above is not totally correct). Since granulometric properties of sediments are known to be important in structuring benthic communities along spatial dimensions (RHOADS & YOUNG 1970, BLOOM *et al.* 1972 among many others; see GRAY 1974 and RHOADS 1974 for general reviews), a reasonable first approach to examining the causes of seasonality in infaunal communities or changes along temporal dimensions would be to examine correlations of granulometric changes to faunistic changes. However, the more that is learned of the autecology of the infauna and their influence on the sediment, the more naive this approach appears (see WOODIN 1974). As an example, *Diopatra cuprea* (BOSC.), a common component of many deposit-feeding communities, has been shown to be controlled by currents rather than by granulometric properties of the sediment (MANGUM *et al.* 1968) and their tubes have been shown to influence the populations near them (WOODIN 1978) by acting as refuges from predation (WOODIN 1981). Nevertheless, sediment alterations must be evaluated when exploring the causes of seasonality in deposit-feeding communities. While population fluctuations of infaunal species can be linked

to temperature effects (GUNTER 1957, HARRIS 1972a), often the direct causal role of temperature is questionable. Temperature may act as a reproductive synchronization cue and thus may greatly affect the composition of the plankton and hence the availability of species for settlement. Additionally, temperature may be important in generating organic input, i. e. massive blade-shedding of seagrasses (PHILLIPS 1960, McMAHAN 1968, REID 1954). Thus the role of temperature is likely to be complex and indirect.

Changes in food resources are another potential source of seasonality. If a deposit-feeding community were periodically exposed to massive influxes of organic material, paralleling influxes due to organic pollution (PEARSON & ROSENBERG 1978), opportunistic species (GRASSLE & GRASSLE 1974) utilizing fresh detritus should exhibit populational peaks immediately after the introduction of the organic material. The utilization of the fresh detritus by these species would fragment and pelletize the detritus, thus increasing bacterial decomposition (FENCHEL 1970). These actions would enhance the introduction of the organic material into bacterial pathways and hence increase the availability of the material to the rest of the deposit-feeding community (see WELSH 1975 for an example). Returning to the analogy of a funnel, these species would act to dilate the spout and to increase the flow rate from the body of the funnel. Variations in input to the funnel would then begin to appear in the outflow. In a biological sense, available resources as well as potential resources would fluctuate and population responses would occur. Responses to organic influx coupled with potential interactive mechanisms between members of the infauna, i. e. consumption of settling larvae (DAYTON & HESSLER 1972, EAGLE 1975), potential refuges created by tubicolous species (WOODIN 1981), and altered sediment turnover rates due to population and size-class changes (NICHOLS 1974), could result in large and consistent variations in the densities and sizes of individuals of infaunal species. Within this scenario, the reproductive strategies of earlier consumers which consume less-predictable resources (fresh detritus) would be predicted to be more dispersal-oriented than species employing coprophagy and utilizing the decomposition products of bacterial pathways (see VANCE 1973a, b for a general discussion). Thus large quantities of fresh detritus added to a community, the utilization of that material by opportunists, and the subsequent ramifications of that use to other members of the infauna could be a source of seasonal change.

Seasonality, e. g. consistent annual population fluctuations, are an observable fact in the community described here in which over 93 % of the individuals are classed as deposit-feeders and in which distinct, major and consistent population fluctuations occur. Of the abiotic factors such as changes in granulometric properties of the sediment and changes in temperature, which are known to be responsible for alterations in macrofaunal community structure, there is no evidence that population fluctuations documented here are correlated to or caused by alterations in the sediment.

Temperature has been assumed to be the causal factor of annual cycles of *Laonereis* in Massachusetts (MAZURKIEWICZ 1975) and biannual cycles in Texas (KLESH 1970; cited in MAZURKIEWICZ 1975). This conclusion is challenged by the results presented here. One coordinated cyclical pattern of changes in adult and larval densities of the co-dominants, *Laonereis culveri* and *Onuphis simoni* occurred at similar temperatures each autumn at both stations. However, a second complete cycle also occurred at the East Point station each spring and not at the South Beach station. The temperature regimes at both stations in both springs were virtually identical and were very different between spring and autumn of 1979 and spring and autumn of 1980 at the East Point station. Thus, temperature does not appear to play a direct or clear role in driving the seasonality.

These results are not unique. In one intensive study of seasonality, SUBRAHMANYAM

and COULTAS (1980) found few convincing links between abiotic parameters and seasonal shifts in fish and macroinvertebrate populations. They concluded that "breeding patterns, recruitment, seasonal succession of dominants had more profound influence than physical factors on the seasonal changes in community composition." A similar conclusion was reached for amphipods in seagrass meadows (STONER 1980).

The only measured parameter which was partially correlated to the overall set of seasonal patterns was sediment organic content. Deposit-feeding communities are known to be correlated to high organic content (PEARSON 1970, POORE & RANIER 1974 and see PEARSON & ROSENBERG 1978 for a general review) and the principle that organic material actually becomes available to the macrofauna only after bacterial processing is well established (FENCHEL 1970, 1972, 1977, GIERE 1975, LEVINTON 1977, NEWELL 1965, and see SEIBURTH 1976 and FENCHEL 1969 for general reviews). Sediment organic content was correlated to the number of species, the density of all fauna, diversity, density and biomass of *Onuphis*, and all trophic groups except suspension feeders. Organic content was also correlated to silt/clay percentage which in turn was correlated to many of the parameters just listed. Silt/clay percentage has been shown to be correlated to deposit-feeder abundances (SANDERS 1958) but this is most likely a simple reflection of the same physical factors which allow the accumulation of organic material. Unfortunately, determination of organic content by combustion (BYERS *et al.* 1978) cannot distinguish between available organic and refractory organic material nor does the mean organic content in a 10 cm core reflect asymmetries in organic content distributions due to biogenic grading (RHOADS & STANLEY 1965, HUGHES & THOMAS 1971, JOHNSON 1974) or consumption (MARSHALL 1970).

Even when these potential confounding factors concerning the measurement of organic content are appreciated, organic content *per se* still does not appear to be the driving force of the observed seasonal patterns. *Laeonereis culveri*, the dominant species (with over 25 % of all individuals) was extremely variable. Maximum numbers of individuals were 57 and 28 times greater than minimum numbers, and percent of *Laeonereis* to total fauna monthly ranged from 3.2 % to 76.7 % and 3.7 % to 74.0 % at South Beach and East Point respectively. Biotic parameters of *Laeonereis* did not correlate to any sediment characteristic (with the exception of a negative correlation between density and silt/clay percentage which was only generated by pooling data from both stations) or to sediment organic content. If *Laeonereis* populations were controlled by food abundance and if that resource was proportional to total sediment organic content, either increases in populational biomass of *Laeonereis* should be accompanied by a decrease in organic content (food limiting) or should be accompanied by an increase in organic content (food superabundant). Given an average organic content of 0.6 %, a sediment density of 1.5 g/cm³, and the determination that the majority of the *Laeonereis* occur within the upper 5 cm of the sediment (BLOOM, unpubl.), a square meter of sediment would contain 450 grams ash-free dry weight of organic material. The populational biomass of *Laeonereis* attained a maximum of 1.67 g/m², 0.37 % of the total organic material present. Organic content would superficially seem to be superabundant, yet no correlations were found. This is in contrast to the result of YOUNG & YOUNG (1978) who found that artificially enriching experimental plots with nitrogen-rich detritus increased the density of *Laeonereis*.

The overall conclusion that can be reached is that there were distinct and reoccurring population fluctuations in a deposit-feeding community. The community exists in an intertidal habitat which is subjected to severe and frequent perturbations (JOHNSON 1970, HOLLAND & POLGAR 1976) and thus should be a physically controlled rather than a biologically accommodated community (SANDERS 1968, but see LEVINTON 1972, 1977 and ABELE & WALTERS 1979 for counter-arguments). Standard abiotic parameters (salinity, temperature, sediment granulometry and sedi-

ment organic content), however, failed to correlate to the cyclical patterns and are thus unlikely causal factors of the seasonality.

While it might be tempting to involve arguments of population interactions which exhibit cyclical behavior similar to that documented here (SMITH 1974), especially given the theoretical foundation available (see PIANKA 1974), too little is known of the autecology of these organisms to justify such an extension (see WEINSTEIN 1977 for an example of the dangers of extrapolating observed cycles to causal hypotheses for the lynx-snowshoe hare interactions).

Seasonal faunal population changes and trophic shifts have been tied to seasonal fluctuations in seagrass beds (KIKUCHI 1970). One obvious seasonal change which occurred at Seahorse Key and which was not adequately reflected in the abiotic parameters measured was the defoliation of the seagrass beds (REID 1954). *Thalassia* is reported to shed its blades when water temperatures exceed 30 °C or fall below 20 °C (PHILLIPS 1960, TAYLOR *et al.* 1973, cited in GREENWAY 1974) and *Halodule* has also been reported to shed blades (PHILLIPS 1960) or reduce its standing crop (MCMAHAN 1968) at low temperatures. Given that the estimates of defoliation temperatures are inexact and that changes in water temperature precede changes in sediment temperature, the defoliations would be predicted to occur approximately in late spring (with floating *Thalassia* blades as a major component) and in late autumn (with both grasses represented) at both stations. *Syringodium filiforme* KUTZING is a third seagrass occurring in the Seahorse Key area. *Syringodium* occurs in deeper waters (STRAWN 1961), has not been found rooted within 150 meters of the beach, and makes up a minor component of the total detritus pool (BLOOM unpubl.). Defoliation became obvious with the appearance of floating rafts of *Thalassia* and *Syringodium* leaves in the late spring. Since *Halodule* is less susceptible to damage at elevated temperatures (PHILLIPS 1960), there was relatively little contribution to the defoliation pool from *Halodule*. Due to hydrological features, floating material tended to collect within the embayment formed by the sandspit around East Point while little material collected along South Beach due to long-shore drift. During the late fall, low temperature defoliation occurred and massive quantities of floating *Thalassia* and *Syringodium* blades and bottom-drifting *Halodule* blades were released from the grassbeds. This material was deposited on or near both sites. There was, therefore, a major food resource provided to East Point biannually and to South Beach annually, though South Beach received more overall material due to its proximity to the grassbeds. This input pattern can be seen in organic content at the two stations (Fig. 3) but it is certainly not as striking as changes in the amount of accumulated plant material on the beach (from virtually absent to a band a meter wide and half a meter high running for kilometers along South Beach).

Seagrass detritus is known to lose rapidly its soluble organic content (HARRISON & MANN 1975), which for *Thalassia* can include up to 22 % protein (annual mean of 13 %) and up to 13 % soluble carbohydrates and lipids (annual mean of 9.7 %) (DAWES & LAWRENCE 1980). These levels are equivalent to cereal grains of 8 to 14 % protein (LAPPE 1975, p. 24). Since *Laeonereis* can be maintained in the laboratory on fresh dried algae (MAZURKIEWICZ 1975) and will readily accept fresh dried grass detritus (*Thalassia* and lawngrass) (HICKS unpubl.), *Laeonereis* may well be exploiting the temporally unpredictable resource of freshly shed seagrass leaves. Although FENCHEL (1977) strongly supports a view that all detritus feeders feed on bacteria or else require that bacterial decomposition has occurred, the existence of opportunistic species utilizing fresh detritus is not inconceivable (see KRAEUTER & WOLF 1974 for examples of salt marsh fauna which exploit both detritus and living plant tissue, and TENORE & GOPALAN 1974 for an experimental example of a polychaete which successfully utilized clam tissue as well as detritus). If *Laeonereis* were such an

opportunistic species, this would account for the match between defoliation peaks and population peaks of *Laeonereis*. Benthonic dispersing larvae and a rapid generation time (MAZURKIEWICZ 1975) combined with the ability to establish temporary mucus burrows and to forage away from these burrows (BLOOM, unpubl.), all characteristics of *Laeonereis*, are expected evolutionary correlates to exploiting a temporally unpredictable prey (see MENGE 1975 for an example of this reasoning in a hard-substrate system). The marked increase in densities of *Laeonereis* (24-fold in the autumn of 1980 at South beach) must have some impact on other species. Such impacts might be negative due to consumption of larvae (DAYTON & HESSLER 1972, EAGLE 1975) (though preliminary experiments failed to support this possibility) or due to bioturbation (NICHOLS 1974). The impact may be positive due to fragmentation and pelletization of macrodetritus into a resource more rapidly decomposed by bacteria (FENCHEL 1970, HARRISON & MANN 1975, WELSH 1975). The decline of *Laeonereis* may be due to several factors, but predation does not appear to be a major factor (see THORP & BERGEY 1981 for a similar conclusion from a fresh-water benthic system). Infaunal predation is not severe (carnivore and scavenger populations rise and fall with densities of *Laeonereis* and thus track but do not appear to control the prey population) although hemichordate, fish and avian predation have not yet been evaluated. The most likely reason for the decline in populations of *Laeonereis* is die-off after spawning and failure to recruit due to increased organic loads in the upper sediment layers (MAZURKIEWICZ 1975), although consumption of larvae of *Laeonereis* by increasing deposit-feeding populations may play a role. *Laeonereis* may thus play a role to facilitate passage of refractory organic material into available food resources for deposit feeders, or, within the analogy of the funnel, it may act as a 'dilator' species. Such a role may also occur among grassbed amphipods (ZIMMERMANN *et al.* 1979).

As densities of *Laeonereis* declined, populations of *Onuphis* could then be rapidly and simultaneously established from the residual adult population which persisted during the peak population of *Laeonereis* (equivalent to the transition of Cluster A to Cluster D or E of Fig. 7). In that this species would exploit a predictable resource (bacterially decomposed detritus and fecal pellets), brooding and a permanent tube would be expected. The formation of a multiplicity of vertically-oriented sand tubes might play a role, on a smaller scale, similar to that of *Diopatra* tubes on a larger scale, i. e. they may act as biogenic refuges (WOODEN 1981).

While purely descriptive information (faunistic and abiotic data) has been used to "yield most of our information on any structural and causal relationships within benthic ecosystems" (HUGHES & THOMAS 1971), such data does not prove causation (FIELD 1971, LIE 1974). The value of description data lies in providing a catalog of species present and their fluctuations through time and space which can serve as a description of a community or a quantitative baseline against which perturbations can be measured, and as a generator of hypotheses (see LEVINTON 1977 for such an example.) However, as DAYTON (1973, 1975) has strongly asserted, assuming the validity of hypotheses from descriptive and correlative data can be highly misleading and experimental verification is required. The seasonal patterns of the macrofauna of Seahorse Key are demonstrable, clear and intriguing and if the role of 'dilator' species can be substantiated, alterations in the paradigms of trophic organization in soft-bottom communities would be required. Experiments aimed at settlement preferences, community responses to fertilization (with a variety of enrichment media) and autecological examinations of foraging and burrowing behaviour are required to clarify the patterns and test whether the hypotheses advanced above are supportable.

5. Summary

1. The macrofaunal community was monitored monthly for 25 months at two intertidal sites at Seahorse Key, Florida.

2. While the community and the faunal dominants, *Laeonereis culveri* and *Onuphis simoni*, exhibited distinct seasonal patterns, the changes were only poorly correlated to changes in sedimentary parameters, salinity or temperature.

3. Populations of *Laeonereis* rose and declined to be immediately followed by a rise and fall in *Onuphis* populations. The complete cycle of both species occurred at both sites in the autumn (corresponding to major defoliation of seagrass beds) but only at one site in spring (corresponding to drift grass accumulating at that site).

4. Classification and correlation analyses supported the concepts of coordinated faunal cycles which were not linked to changes in abiotic factors.

5. Recruitment of *Laeonereis* via benthonic dispersing larvae tracked adult densities while the release of brooded young of *Onuphis* preceded increases in adult densities, suggesting non-synchronized and synchronized reproduction and the exploitation of unpredictable and predictable resources respectively.

6. The suggestion was made that *Laeonereis* facilitates the conversion of macroseagrass detritus into microdetritus and fecal pellets and by doing so, transmit variations in potential food resources into variations in available food resources. Such rapid conversion would contribute to increasing seasonal variation among the rest of the deposit-feeding community.

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8. Appendix. Species List

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| Phylum Cnidaria | <i>Capitella capitata</i> (FABRICIUS 1780) |
| Class Anthozoa | <i>Chone duneri</i> MALMGREN, 1867 |
| <i>Cerianthus</i> sp. | <i>Cirratulus</i> sp. |
| Unidentified anemone | <i>Cistenides gouldi</i> (VERRILL, 1873) |
| Phylum Platyhelminthes | <i>Clymenella mucosa</i> (ANDREWS, 1891) |
| Class Turbellaria | <i>Diopatra cuprea</i> (BOSC, 1802) |
| Unidentified polyclad | <i>Drilonereis magna</i> WEBSTER & BENEDICT, 1887 |
| Phylum Rhynchocoela | <i>Eteone heteropoda</i> HARTMAN, 1951 |
| Unidentified rhynchocoel | <i>Eumidia sanguinea</i> (ORSTED, 1843) |
| Phylum Sipunculida | <i>Glycera americana</i> LEIDY, 1855 |
| Unidentified sipunculid | <i>Gylcera dibranchiata</i> EHLERS, 1868 |
| Phylum Mollusca | <i>Gyclinde solitaria</i> (WEBSTER, 1879) |
| Class Gastropoda | <i>Gyptis brevipalpa</i> (HARTMAN & SCHRÖDER, 1959) |
| <i>Acteon punctostriatus</i> C. B. ADAMS, 1849 | <i>Heteromastus filiiformis</i> (CLAPARÈDE, 1864) |
| <i>Granulina ovuliformes</i> (ORBIGNY, 1841) | <i>Hydroides dianthus</i> (VERRILL, 1873) |
| <i>Haminoca succinea</i> (CONRAD, 1846) | <i>Laonereis culveri</i> (WEBSTER, 1879) |
| <i>Nassarius vibex</i> SAY, 1822 | <i>Lepidonotis variabilis</i> WEBSTER, 1879 |
| <i>Olivella pusilla</i> (MARRAT, 1871) | <i>Lumbrineris tenuis</i> (VERRILL, 1873) |
| <i>Polynices duplicatus</i> SAY, 1822 | <i>Lysidice ninetta</i> AUDOIN & MILNE EDWARDS, 1833 |
| <i>Prunum apicinum</i> MENKE, 1828 | <i>Magelona pettiboneae</i> JONES, 1963 |
| <i>Pyramidella</i> sp. | <i>Nainereis setosa</i> (VERRILL, 1900) |
| <i>Stellatoma stellata</i> (STEARNS, 1872) | <i>Notomastus hemipodus</i> HARTMAN, 1947 |
| <i>Utriculastra canaliculata</i> (SAY, 1822) | <i>Onuphis simoni</i> SANTOS, 1981* |
| Class Bivalvia | <i>Paraonis fulgens</i> (LEVINSEN, 1884) |
| <i>Anodontia alba</i> LINK, 1807 | <i>Paraprionospio pinnata</i> (EHLERS, 1901) |
| <i>Brachiodontes exustus</i> LINNEAUS, 1758 | <i>Phyllodoce arenae</i> (WEBSTER, 1879) |
| <i>Ensis minor</i> DALL, 1900 | <i>Polycirrus examinus</i> (LEIDY, 1855) |
| <i>Parastarte triquetra</i> CONRAD, 1846 | <i>Polydora socialis</i> (SCHMARDA, 1861) |
| <i>Solemya occidentalis</i> DESHAYES, 1857 | <i>Prionospio heterobranchia</i> MOORE, 1907 |
| <i>Strigilla mirabilis</i> PHILIPPI, 1841 | <i>Sabella microphthalmia</i> VERRILL, 1873 |
| <i>Tellina</i> sp. | <i>Scololepis squamata</i> (MÜLLER, 1806) |
| Unidentified bivalve B | <i>Scoloplos foliosus</i> (HARTMAN, 1951) |
| Unidentified bivalve C | <i>Scoloplos rubra</i> (WEBSTER, 1879) |
| Phylum Annelida | <i>Spio pettiboneae</i> FOSTER, 1971 |
| Class Polychaeta | <i>Spio</i> sp. |
| <i>Arabella iricolor</i> (MONTAGU, 1804) | <i>Spiophanes bombyx</i> (CLAPARÈDE, 1870) |
| <i>Aglaphamus verrilli</i> (MCINTOSH, 1885) | <i>Streblospio benedicti</i> WEBSTER, 1879 |
| <i>Aricidea fragilis</i> WEBSTER, 1879 | <i>Terebella rubra</i> LINNAEUS, 1788 |
| <i>Aricidea philbiniae</i> BROWN, 1976 | |
| <i>Aricidea taylora</i> PETTIBONE, 1965 | |
| <i>Armandia agilis</i> (ANDREWS, 1891) | |

- Tharyx* sp.
Travisia hobsonae SANTOS, 1976
 Unidentified syllid
 Class Oligochaeta
 Unidentified oligochaetes
 Phylum Arthropoda
 Class Insecta
 dipteran larvae
 Class Merostomata
Limulus polyphemus (LINNAEUS, 1758)
 Class Crustacea
 Order Copepoda
 Unidentified calgoid
 Order Amphipoda
Acanthohaustorius sp.
Ampelisca homesii PEARSE, 1908
Amphithoe longimana SMITH, 1873
Atylus urocarinatus MCKINNEY, 1980
Cymadusa compta (SMITH, 1873)
Gammarus mucronatus SAY 1818
Grandidierella bonnieroides STEPHENSON,
 1949
Monoculodes edwardsi HOLMES, 1905
Orchestia platensis KROYER, 1845
Polycheria sp.
Pontogeneia sp.
 Unidentified gammarid
 Order Isopoda
Apanthura magnifica MENZIES & FRAN-
 KENBURG, 1966
Edotea montosa (STIMPSON, 1853)
Erichsonella attenuata (HARGER, 1873)
Exosphaeroma diminutum MENZIES & FRAN-
 KENBERG, 1966
 Unidentified isopod
 Order Mysidacea
Mysidopsis robustispina BRATTEGARD, 1969
 Mysid sp. B
 Order Cumacea
Oxyurostylis smithi CALMAN, 1912
 Order Tanaidacea
Hargeria rapax (HARGER, 1879)
 Unidentified Kalliapseudid
 Order Decapoda
Ambidexter sp.
Libinia dubia MILNE EDWARDS 1834
Pagurus sp.
Pinnica sp.
 Unidentified penaid shrimp
 Phylum Echinodermata
Leptosynapta sp.
Ophiophragmus filigraneous (LYMAN, 1875)
 Phylum Phoronida
Phoronis sp.
 Phylum Brachiopoda
Glottidium pyramidata MORSE, 1873
 Phylum Hemichordata
 Unidentified enteropneust
 Phylum Chordata
 Subphylum Cephalochordata
Branchiostoma caribaeum SUNDEVALL,
 1853
 Subphylum Vertebrata
 Class Pisces
Symphurus sp.

* revised to *Kinbergonuphis simoni* by FAUCHALD 1982. Revision of *Onuphis*, *Nothria* and *Paradiopatra* (Polychaeta: Onuphidae) based on type material. Smithsonian Contr. to Zool. 356: 32-34.