Animal-sediment relations and community analysis of a Florida estuary

S. A. Bloom, J. L. Simon and V. D. Hunter

Department of Biology, University of South Florida; Tampa, Florida, USA

Abstract

Five species assemblages of the intertidal infauna of Old Tampa Bay, Florida, USA are identified. Two assemblages are judged to constitute distinct communities, while a third is shown to be an interdigitation of the two communities. Dominance by one species is the prevalent pattern within the assemblages. Numbers of deposit feeders are found to be inversely correlated to that of filter feeders, and both trophic types are found to be correlated to the sediment parameters of median grain size, sorting and skewness. Three transects with three stations each were established along the south side of Courtney Campbell Causeway in Tampa Bay, Florida. A faunal sample (0.4 m²), a sediment sample, and a water sample were taken at each station in September, December, and March of 1968/1969. Sediment samples were wet-seived. Animal samples were reduced to numbers of organisms and biomass per species. Trellis diagrams and correlation tests were generated. Support is shown for the trophic group-amensalism hypothesis, however, the silt-clay fraction is apparently of lesser importance to deposit feeders in Florida sediments than in Buzzards Bay sediments. An attempt is made to relate an analysis of the optimal grain size for filter feeders to the trophic group-amensalism hypothesis. A view of communities as abstractions from continua is more realistic than communities as discrete units.

Introduction

The purpose of this study was to gather quantitative information on the shallow water estuarine infauna of Tampa Bay, Florida, USA, and to attempt to relate community structure and trophic type distribution to sediment parameters. Work of this type has been performed elsewhere in subtidal areas (Sanders, 1958, 1960; Rhoads and Young, 1970; Stephenson, et al., 1970) and in estuaries (Sanders et al., 1962; McIntyre and Eleftheriou, 1968; Moore et al., 1968; Green and Hobson, 1970). Species-occurrence lists of macro-invertebrates for the estuary have been compiled (Dragovich and Kelly, 1964) and an animal-sediment relationship study of mollusks in a nearby bay has also been carried out (Taylor et al., 1971).

Methods and materials

Three locations with distinct sediment types were selected along the south side of Courtney Campbell Causeway in Tampa Bay, Florida (Fig. 1). Transects were established at each location with three stations per transect. The criteria used in determining transect location were sediment color, texture, ability to support weight, and odor. The first station on each transect was 5 m into the intertidal zone from the spring high-tide mark. A second station was established at the spring low-water mark as determined by either the edge of the Diplanthera grassbed (Transects 1 and 2) or the edge of a sharp dropoff into the subtidal (Transect 3). A third station was established at the halfway point between the first and second station on each transect. The exact position and designation of the three stations on the three transects along with the code for the subscripted station designations are given in Fig. 1.

When samples were taken, the stations were either recently exposed or were covered with a few centimeters of water. All stations were sampled in September, December, and March 1968/1969 (hereafter referred to as fall, winter, and spring, respectively). On each occasion, 4 pooled fauna samples were taken with an 0.1 m² corer. Sediment was removed from the corer to a depth of 20 cm at Transects 1 and 3, to 40 cm at Transect 2, and seived through a 1.0 mm screen. All animals retained on the screen were removed, were sorted live to species (identified by JLS) and preserved in 10% formalin. Animals were counted, dried at 60 °C, weighed, burned in a muffle furnace at 550 °C, and reweighed, giving ash-free carbon weight (hereafter referred to as biomass).

A sediment sample of approximately 0.5 kg was taken from one core. A water sample was taken from seepage after the corer was removed. The sediment was wet-seived through a Wentworth series of seives and dried at 60 °C. Each fraction was weighed. Water samples were titrated for salinity by the Mohr method. Temperatures were not recorded.

Analysis of data were performed by a CDC 6400 computer using a Fortran IV trellis program developed by the senior author for this study, and packaged statistical programs (Dixon, 1967). The trellis program generates three indices of sample overlap: (1) common percentage overlap (Sanders, 1960); (2) Morisita's index (Morisita, 1959); (3) information theory overlap (Horn, 1966) for numbers of organisms or biomass for up to 100 species. The three resulting
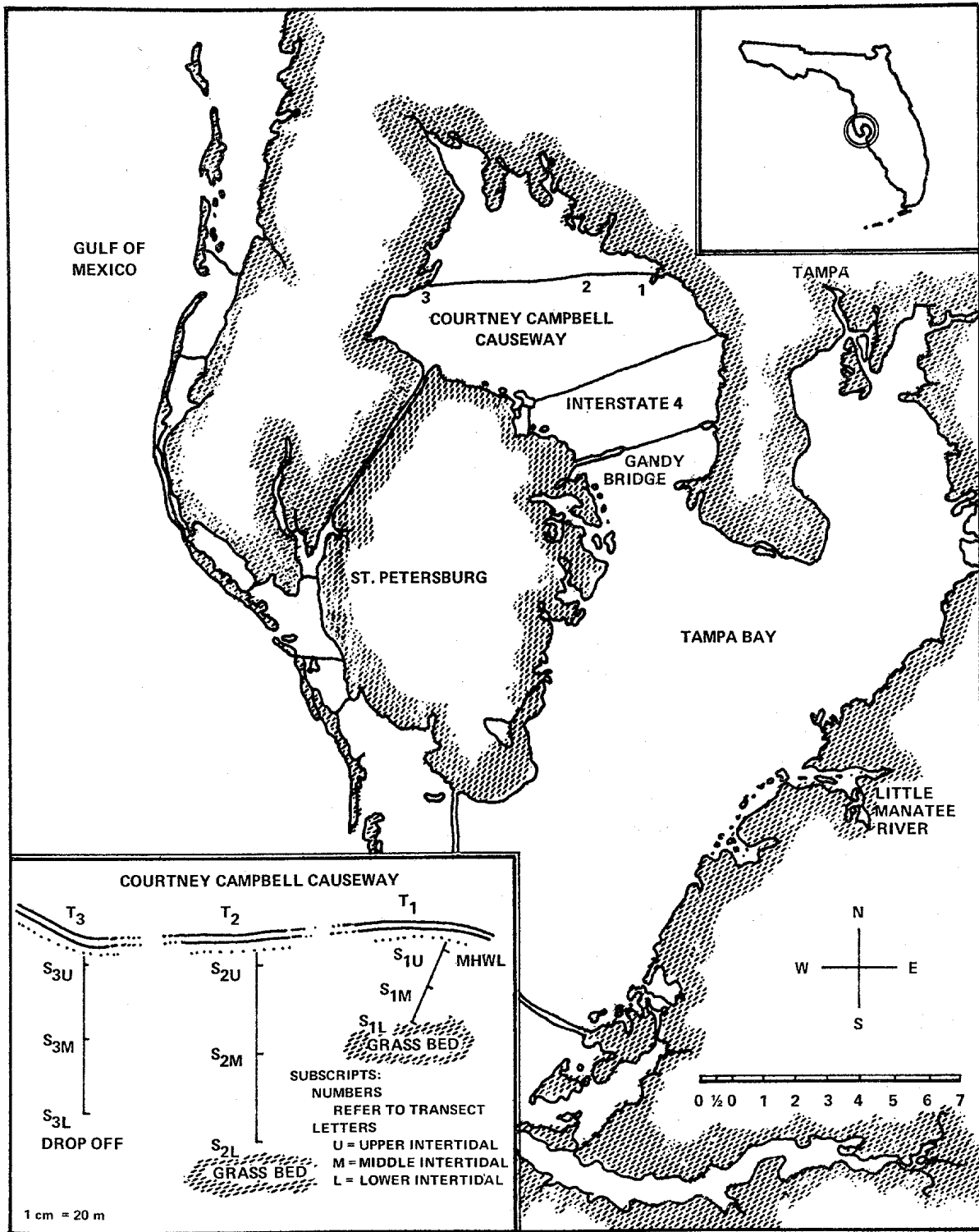
Fig. 1. Tampa Bay, Florida, USA. Study area, Courtney Campbell Causeway

symmetrical matrices are then statistically tested for similarity of the indices using Tukey's ω-procedure. The packaged programs were BMDO5R (polynomial regression) and BMDO1V (analysis of variance for a one-way design). BMDO5R was used to test for correlations of trophic parameters to one another and to various sediment parameters, while BMDO1V was used to test for homogeneity between trophic and

($\bar{x} = 7.68$ g/m²). These values fall within the range of biomass from other benthic studies (SANDERS, 1958; SANDERS et al., 1962; McINTYRE and ELEFTHERIOU, 1968; MOORE et al., 1968).

Trellis diagrams were generated for numbers of organisms and biomass of all species that occurred more than once in all the samplings. A second series of trellis diagrams was also generated which excluded

Table 1. *Sediment characteristics (See Fig. 1 for explanation of sample codes). Parameters are computed in ϕ units according to* KRUMBEIN, 1936

Sample		Median particle diameter		Sorting coefficient (φ)	Skewness (Sk φ)	Percent weight distribution of sediment						
		(φ)	(mm)			−2 to −1	−1 to 0	0 to 1	1 to 2	2 to 3	3 to 4	4 to —
S₁U	Fall	2.408	0.188	0.947	−1.353	3.77	0.89	0.82	2.35	81.31	9.85	1.30
	Winter	2.729	0.151	1.056	−0.778	2.39	1.30	1.21	2.67	59.90	23.55	8.95
	Spring	2.695	0.154	0.893	−0.035	0.86	0.21	0.40	4.26	78.48	2.85	12.91
S₁M	Fall	3.229	0.105	1.028	−0.610	0.84	0.47	1.08	6.41	27.00	42.09	22.99
	Winter	2.504	0.176	0.952	−0.154	0.92	0.81	0.67	20.28	58.35	10.68	8.77
	Spring	2.735	0.150	0.692	−0.145	0.00	0.12	0.78	10.25	54.73	32.48	1.61
S₁L	Fall	3.509	0.087	1.063	−0.228	0.05	0.11	0.60	6.67	30.70	14.41	47.58
	Winter	3.082	0.118	1.234	0.006	0.08	0.27	0.69	4.44	50.61	22.65	21.25
	Spring	2.649	0.160	0.271	0.045	0.12	0.08	0.67	18.46	53.03	19.69	7.91
S₂U	Fall	1.656	0.317	0.701	−0.555	2.00	1.00	3.00	68.00	22.00	1.31	0.66
	Winter	2.597	0.165	1.694	−0.839	11.66	1.58	1.46	8.04	5.96	70.68	0.74
	Spring	2.069	0.239	1.314	−0.832	8.75	1.50	1.73	14.60	60.04	12.61	0.92
S₂M	Fall	2.416	0.187	0.449	−0.183	0.02	0.03	0.08	13.63	80.50	4.82	0.38
	Winter	2.414	0.188	0.439	2.720	0.33	0.05	0.12	9.58	87.60	1.32	0.71
	Spring	2.530	0.173	0.591	0.097	0.00	0.02	0.08	14.77	67.00	16.28	0.85
S₂L	Fall	2.553	0.171	0.286	1.500	0.00	0.05	0.04	0.42	94.30	4.46	0.73
	Winter	2.647	0.160	1.003	0.063	0.24	1.10	6.36	12.85	38.08	38.38	3.16
	Spring	2.569	0.169	0.725	0.097	0.00	0.02	0.11	20.53	53.73	23.47	2.10
S₃U	Fall	2.474	0.180	0.364	−0.760	0.01	0.05	0.64	5.63	89.50	4.49	0.00
	Winter	3.126	0.115	0.832	−0.843	0.07	0.38	2.42	9.00	13.97	40.46	3.66
	Spring	2.425	0.186	0.996	−0.390	0.18	1.77	8.70	10.48	54.79	21.78	2.25
S₃M	Fall	2.277	0.206	0.804	−0.255	0.13	0.80	5.19	22.79	58.86	10.64	1.56
	Winter	2.499	0.177	1.102	−0.053	0.43	1.04	5.81	20.91	46.24	13.71	11.85
	Spring	2.580	0.167	0.828	−0.858	0.71	0.77	5.30	2.38	65.62	24.70	0.69
S₃L	Fall	2.242	0.211	0.932	−0.128	0.43	0.62	5.51	25.24	57.41	7.37	3.33
	Winter	2.232	0.213	0.712	−0.873	0.01	0.08	0.31	37.35	54.26	4.57	3.44
	Spring	1.873	0.273	1.070	0.118	0.71	2.72	11.65	45.04	27.99	6.98	4.86

sediment parameters at various stations and between overlap indices for numbers of organisms and biomass.

Results

Sediment characteristics, species and biomass, and numbers of organisms per species are presented in Tables 1 and 2 a, b, c, respectively. Salinity ranged from 22.38 to 30.14‰ ($\bar{x} = 25.13\%$, $\sigma = 2.544$). Numbers of organisms for all samples ranged from 22/m² to 5240/m² ($\bar{x} = 510/$m²) and the biomass for the same samples ranged from 0.96 g/m² to 17.90 g/m²

the ubiquitous species *Nassarius vibex* and pooled species such as amphipods, cumaceans, insect larvae, rhynchocoels, and shrimp. The three indices of overlap within both sets of trellis diagrams were distinguishable at the 0.05 level. Biomass and numbers of organisms within a set of diagrams for any one index were not distinguishable at the 0.05 level (BMDO1V). However, the qualitative pattern of overlap was virtually identical between indices and between sets of trellis diagrams. For brevity, the trellis diagram utilizing MORISITA's index with regard to biomass for all species is presented (Fig. 2).

Table 2. Species with numbers of organisms (No.) and biomass (B) found in 0.4m² of sediment along (a) Transect 1; (b) Transect 2; (c) Transect 3; n: negligible weight, set equal to 1 mg for trellis calculations; C: carnivore; S: scavenger; SF: suspension feeder; SDF: selective deposit feeder; NSDF: non-selective deposit feeder; feeding types from SANDERS (1960), PAINE (1963), BARNES (1964), and MACGINITIE and MACGINITIE (1968). All biomass figures are in milligrams and are ash-free carbon weight. See Fig. 1 for explanation of sample codes

Table 2a

Species		S_{IV}						S_{LM}						S_{LL}					
		Fall		Winter		Spring		Fall		Winter		Spring		Fall		Winter		Spring	
		No.	B	No.	B	No.	B	No.	B	No.	B	No.	B	No.	B	No.	B	No.	B
Echinodermata																			
Ophiophragmus filograneus (LYMAN)	NSDF											5	340	12	550	7	465	8	546
Leptosynapta sp.	NSDF											10	77					2	56
Miscellaneous phyla																			
Ptychodera sp.	NSDF																	1	70
Rhynchocoel	C											3	49						
Polychaeta																			
Arabella iricolor (MONTAGU)	C					1	65							29	736	6	198	25	496
Arenicola cristata STIMPSON	NSDF			2	810	2	365											1	381
Branchiosyllis americana[a] HARTMAN	NSDF																	1	n
Clymenella mucosa (ANDREWS)	SDF					2	n					3	121	3	n	8	108		
Capitellid[a]	NSDF											2	109						
Diopatra cuprea (BOSC.)	C, S													1	92	3	n	1	62
Eteone heteropoda HARTMAN	C, NSDF									2	n					3	102		
Glycera americana LEIDY	C, NSDF					1	n					1	n	4	195	10	94	1	94
Nereis sp.	S			7	107														
Nereis succinea (FREY & LEUCKART)	C, S					17	86												
Onuphis eremita oculata HARTMAN	NSDF									1	n	82	943	5	50	65	148	6	60
Orbiniid	NSDF											2	n						
Pectinaria gouldii VERRILL	SDF					6	113			1	95	5	83			9	60		
Scoloplos rubra (WEBSTER)	NSDF											3	n						
Scoloplos sp.	NSDF																		
Arthropoda																			
Amphipoda	S											13	n			9	n	8	n
Apanthuras sp.	C											1	n						
Insect larvae	S					2	n			1	56								
Pinnixia sp.	S, C																		
Shrimp	S, C			10	96					5	78			1	n			3	94
Xanthid crab	S, C													1	106				

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S_{1L}	Fall	3.509	0.087	1.063	−0.228	0.05	0.11	0.60	6.67	30.70	14.41	47.58
	Winter	3.082	0.118	1.234	0.006	0.08	0.27	0.69	4.44	50.61	22.65	21.25
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S_{2U}	Fall	1.656	0.317	0.701	−0.555	2.00	1.00	3.00	68.00	22.00	1.31	0.66
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Mollusca (continuation of table)

Species		Fall No.	B	Winter No.	B	Spring No.	B	Fall No.	B	Winter No.	B	Spring No.	B	Fall No.	B	Winter No.	B	Spring No.	B
Bittium varium PFEIFFER	S																		
Ensis minor DALL	SF											3	739	40	n			1	313
Macoma constricta BRUGUIERE	SDF											7	n						
Mercenaria campechiensis[a] GMELIN	SF	2	417	4	552	11	1281									22	n		
Mitrella lunata SAY	S			1	n														
Nassarius vibex SAY	S, NSDF	1	n	4	124	6	n			13	276	5	148	2	n	29	644	6	227
Prunum apicinum MENKE	S, C			1	n					7	264	2	n	2	n	15	432	1	n
Tagelus divisus SPENGLER	SDF	40	453	142	3283	117	5244	37	444	87	2332	27	1092			2	n		
Tellina tampaensis CONRAD	SF							5	n	5	225								

Table 2b

Species		S_2U						S_2M						S_2L					
		Fall No.	B	Winter No.	B	Spring No.	B	Fall No.	B	Winter No.	B	Spring No.	B	Fall No.	B	Winter No.	B	Spring No.	B
Chordata																			
Branchiostoma caribaeum SUNDEVALL	SF	4	152			1	82	112	2874	63	3272	80	4468	67	2060	48	2072	136	5869
Echinodermata																			
Ophiophragmus filograneus (LYMAN)	NSDF	4	292	3	436	5	544	11	275	11	198	11	97	11	92				
Miscellaneous phyla																			
Glottidia pyramidatum (STIMPSON)	SF							4	405	4	518	3	98						
Ptychodera sp.	NSDF							1	n									3	98
Rhynchocoel	C																	1	68
Polychaeta																			
Arabella iricolor (MONTAGU)	C							3	140										
Clymenella mucosa (ANDREWS)	SDF							1	n										
Diopatra cuprea (BOSC.)	C, S					2	118	12	1009			1	145	2	173			2	144
Nephtys sp.[a]	NSDF															1	n	1	66
Nereis sp.	S																		
Onuphis eremita oculata												1	n					1	n
HARTMAN	NSDF							3	170										
Orbiniid	NSDF							1	n										
Pectinaria gouldii VERRILL	SDF					5	58									8	56	5	56
Scoloplos rubra (WEBSTER)	NSDF																		
Scoloplos robustus (VERRILL)	NSDF					3	81	12	157							6	188	6	112
Scoloplos sp.	NSDF																		
Travisia sp.	NSDF							1	n			1	n						

Table 2b (continued)

Species		S_{U2} Fall		Winter		Spring		S_{2M} Fall		Winter		Spring		S_{2L} Fall		Winter		Spring	
		No.	B	No.	B	No.	B	No.	B	No.	B	No.	B	No.	B	No.	B	No.	B
Arthropoda																			
Acanthohaustorius sp.	SF	1	n					79	70	112	104	94	88	1	n	24	n	45	n
Amphipoda	S									8	n					1	n	1	n
Cumacean	SF																		
Lepidopa websteri Benedict	SF															1	94	1	70
Libinia dubia Milne Edwards	S, C	1	73											1	72				
Pagurus annulipes (Stimpson)	S	4	n					2	54	5	38	7	70			20	244		
Pinnixia sp.	S, C	2	n													1	n	11	100
Shrimp	S, C													3	n	4	n		
Xanthid crab	S, C	1	75																
Mollusca																			
Anachis avara Say	S	2	n											13	121	15	475		
Anadara transversa[a] Say	SF													50	n	4	n		
Bittium varium Pfeiffer	S																		
Brachiodontus recurvus[a] Rafinesque	SF																		
Diplodonta punctata Say	SF	1	n											1	n				
Ensis minor Dall	SF					1	n												
Macrocallista nimbosa Solander	SDF							1	n					1	4178				
Mitrella lunata Say	SF	3	n													60	n		
Laevicardium mortoni Conrad	SF	1	n																
Mulinia lateralis[a] Say	SF													1	n				
Musculus lateralis[a] Say	SF													1	n				
Nassarius vibex Say	S, NSDF	18	198	6	220	3	177	4	n	15	323	3	158	13	95	21	500	1	n
Olivella mutica Say	S, C							20	234					3	n	2	n		
Tellina sp.	SF																		

Table 2c

Species	Feeding	S_au Fall No	B	Winter No	B	Spring No	B	S_SM Fall No	B	Winter No	B	Spring No	B	S_SL Fall No	B	Winter No	B	Spring No	B
Echinodermata																			
Ophiophragmus filograneus (LYMAN)	NSDF							11	103	4	190	2	n			2	79		
Miscellaneous phyla																			
Glottidia pyramidatum (STIMPSON)	SF																		
Phychodera sp.	NSDF									1	103	1	120					2	68
Rhynchocooel	C			1	95					2	13					1	52	2	192
Polychaeta																			
Clymenella mucosa (ANDREWS)	SDF			7	n	14	92	11	124					15	1176	3	217	3	72
Diopatra cuprea (BOSC.)	C, S			1	86	6	264	6	284					4	128	1	112	5	608
Glycera americana LEIDY	C, NSDF					1	n	4	167					9	70	3	54		
Melinna cristata MOORE	SDF					1	48												
Nereis succinea (FREY & LEUCKART)	C, S	5	57																
Onuphis eremita oculata HARTMAN	NSDF			1	n	110	268	86	169					34	79	61	114	64	180
Pectinaria gouldii VERRILL	SDF					1	74							2	68	4	110	1	148
Arthropoda																			
Amphipoda	S							2	n	27	n	25	n					21	n
Apanthurus sp.	C					1	n												
Insect larvae	S			4	66														
Pinnixia sp.	S, C					3	110	4	80	3	96	2	56					4	88
Shrimp	S, C									3	n	1	n			6	n	5	n
Upogebia affinia (SAY)	SF							2	110	4	956	5	538	9	615	10	524	2	532
Mollusca																			
Bittium varium PFEIFFER	S													2000	1961			7	182
Ensis minor DALL	SF																		
Laevicardium mortoni	SF									1	n	2	n						
Macoma constricta BRUGUIERE	SDF			4	n	7	220			12	165	9	225			2	772	8	n
Mitrella lunata SAY	S									1	n							3	n
Murex sp.[a]	C																		
Nassarius vibex SAY	S, NSDF	2	n			9	165	9	216	147	1882	36	735	3	n	12	353	29	640
Tagelus divisus SPENGLER	SDF	67	2404			13	680	6	257	8	380	1	n	4	264	1	n		
Tellina alternata SAY	SF									7	n	8	108						
Tellina sp.	SF							2	n					16	185				
Tellina tampaensis CONRAD	SF			4	134														

a Excluded from trellis calculations.

Five areas of generally higher values of overlap appeared on the trellis diagram in Fig. 2[1]. The species mixtures responsible for the overlap values in these five areas will be referred to as assemblages and will be denoted by the subscripts of the station coordinates. Thus, the clustering of values of S_{2M} and S_{2L} and

values within each assemblage, revealed three categories: (1) strong ($A_{2(M+L)} = 0.942$, $A_{1(U+M)} = 0.780$), (2) moderate ($A_{2U} = 0.823$, $A_{1L} = 0.661$), and (3) weak ($A_{3(M+L)} = 0.473$). The moderate category assemblages were characterized by only three samples, and the means of animal numbers for these two assemblages
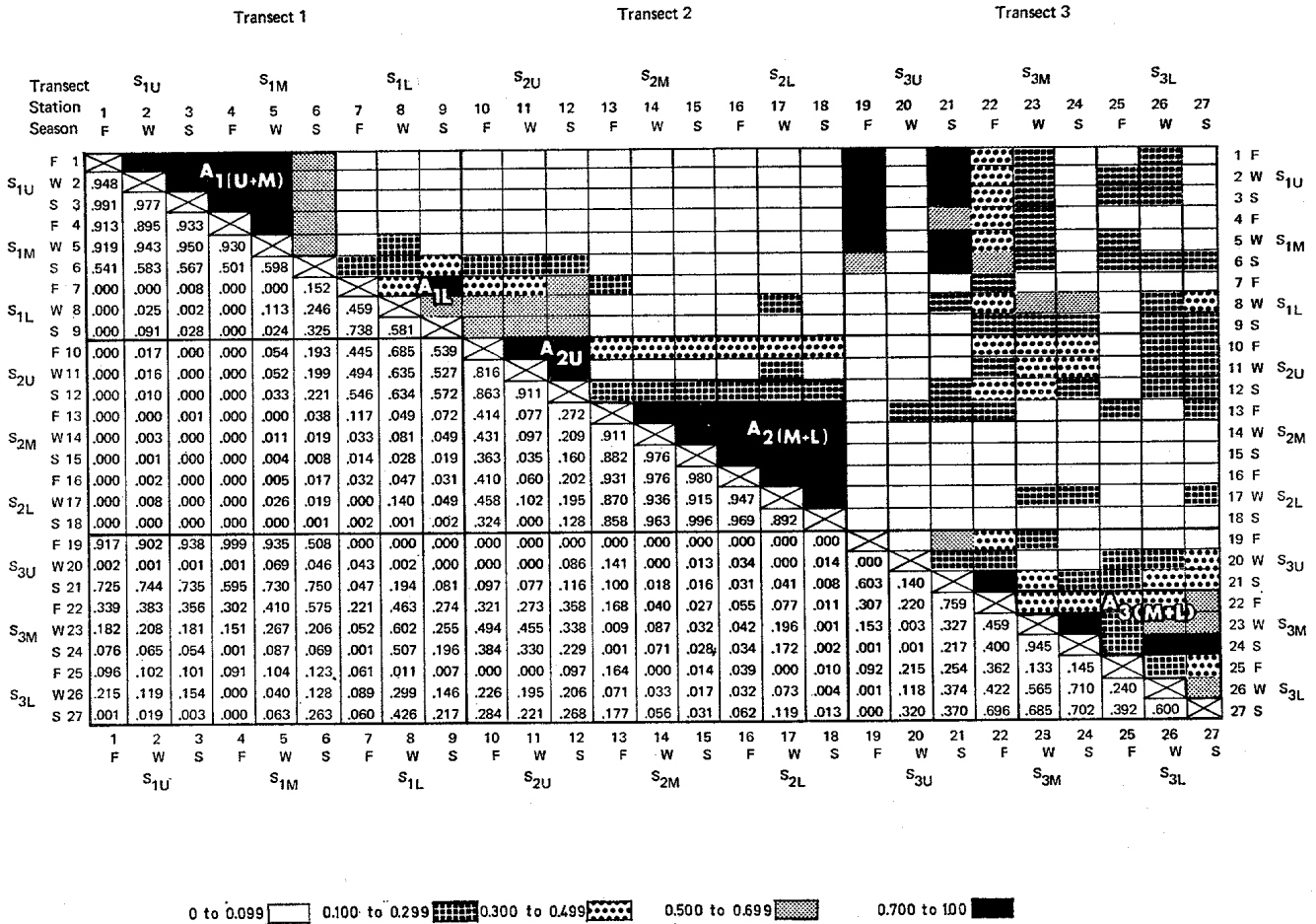
Fig. 2. Trellis diagram (MORISITA's index) for all stations and all species which appeared more than once (station code from Fig. 1). Overlap values vary from 0 (nothing in common) to 1.0 (identical). *F*: fall; *W*: winter; *S*: spring

their interrelations will be referred to as $A_{2(M+L)}$. Similarly, the other assemblages are $A_{1(U+M)}$, A_{1L}, A_{2U}, and $A_{3(M+L)}$ (Fig. 2). An examination of these assemblages with regard to sample size and magnitude of overlap as estimated by the mean of the overlap

were low, $67/m^2$ and $210/m^2$ for A_{2U} and A_{1L}, respectively. Species-area curves for $A_{2(M+L)}$ and $A_{3(M+L)}$ reach a plateau, while curves for the other three assemblages do not.

Examination of the overlap values showed that species composition at a station was generally consistent throughout the sampling period, thus allowing the collapse of the time dimension. The overlap of a station with itself, i.e., through time, had a mean for the eight stations within the five assemblages of

[1] It should be noted that the position of the rows and columns of the trellis matrix reflect spatial location and temporal sequence and have not been rearranged to cluster high values. Thus, a cluster of high values represents a cluster of similar organisms in space and time.

Table 3. *Species components for the various assemblages indicated by the trellis diagram. Major components are any species with 10 % numbers of organisms (No.) and/or biomass (B) or more in an assemblage; minor components are species with 1 to 10 % numbers or biomass in an assemblage. Figures in parentheses next to subheadings: percentages of species in that assemblage within the indicated category*

Sample code	Major components	No. (%)	B (%)	Total major components No. (%)	B (%)	Minor components	No. (%)	B (%)	Total minor components No. (%)	B (%)	Overall total No. (%)	B (%)	Overlap mean (Morisita) No. B	Overlap mean (Common %) No.	B
A₁(U+M)	(3.7%) Tagelus divisus	71.9	69.0	71.9	69.0	(7.4%) Macoma constricta	3.1	9.3	7.2	11.9	(11.1%) 79.1	80.9	0.780	59.41	60.59
						Nassarius vibex	4.1	2.6							
A₁L	(21.7%) Arabella iricolor	30.8	25.5	88.5	76.0	(4.4%) Diopatra cuprea	1.1	2.8	1.1	2.8	(26.1%) 89.6	78.8	0.661	35.20	44.66
	Nassarius vibex	10.6	13.2												
	Onuphis eremita oculata	20.1	4.2												
	Ophiophragmus filograneus	12.4	26.5												
	Prunum apicinum	14.6	6.6												
A₂U	(14.3%) Ophiophragmus filograneus	25.3	54.2	70.0	80.6	(7.2%) Branchiostoma caribbaeum	5.7	9.8	5.7	9.8	(21.5%) 75.7	90.4	0.823	42.22	63.58
	Nassarius vibex	44.7	26.4												
A₂(M+L)	(8.0%) Branchiostoma caribbaeum	40.4	71.9	62.2	72.8	(16.0%) Diopatra cuprea	1.3	5.3	10.8	13.2	(24.0%) 73.0	86.0	0.942	46.84	70.43
	Acanthohaustorius sp.	21.8	0.9			Nassarius vibex	4.8	4.6							
						Ophiophragmus filograneus	2.6	2.5							
						Pinnixia sp.	2.1	0.8							
A₃(M+L)	(21.0%) Diopatra cuprea	4.9	16.6	69.1	66.8	(15.8%) Macoma constricta	3.8	8.2	7.7	18.6	(36.8%) 76.8	85.4	0.473	28.60	41.19
	Nassarius vibex	24.6	24.1			Pinnixia sp.	1.4	2.4							
	Onuphis eremita oculata	34.5	4.4			Tagelus divisus	2.5	8.0							
	Upogebia affinis	5.1	21.7												

7*

0.747^2. The overlap mean between assemblages and stations within a transect was only 0.160^3.

Two major patterns of superdominance and trophic-type segregation were shown. When the species complex of each assemblage was arbitrarily divided into major and minor components (Table 3), the assemblages were shown to result predominantly from one or two species.

$A_{2(M+L)}$ was dominated by *Branchiostoma carib-baeum*. *B. caribbaeum* represented a range of 23.8 to 63.8% of numbers of organisms ($\bar{x} = 40.4\%$) and a range of 59.3 to 87.7% of biomass ($\bar{x} = 71.8\%$). The second most common species was *Acanthohaustorius* sp. which was a constant component only in samples from S_{2M}.

The minor components were responsible for the overlap between assemblages. If the ubiquitous *Nassarius vibex* is ignored, *Ophiophragmus filograneus* is the primary source of overlap between A_{2U} and A_{1L}. $A_{2(M+L)}$ and $A_{3(M+L)}$ are related by *Diopatra cuprea*, *Pinnixia* sp., and *Onuphis eremita oculata*. The large overlap of $A_{1(U+M)}$ and $A_{3(M+L)}$ is due to *Macoma constricta* and *Tagelus divisus*. The percentage of biomass and numbers of organisms for these species within the various assemblages are presented in Table 3.

Trophic types of infaunal species are generally poorly known. However, if the trophic types represented by the infauna are simplistically reduced to three categories, filter feeders, deposit feeders and others (herbivores, carnivores, and/or scavengers),

Table 4. *Results of statistical testing for correlations between trophic parameters. Data form: form of data used in computation*

Correlations between:		Data form	Significant? ($\alpha = 0.05$)	$F_{(1,25)}$	Correlation coefficient
Numbers of filter feeders	Biomass of filter feeders	Raw data	Yes	34.553	0.762
		Percentage	Yes	59.746[a]	0.840
	Numbers of deposit feeders	Raw data	Yes	5.060	−0.410
		Percentage	Yes	53.150	−0.825
Biomass of deposit feeders	Biomass of filter feeders	Raw data	No	2.826	−0.317
		Percentage	Yes	69.128[a]	−0.857
	Numbers of deposit feeders	Raw data	Yes	23.550	0.696
		Percentage	Yes	62.192	0.845

[a] Of doubtful validity, since percentages of the two correlated parameters are not independent.

$A_{1(U+M)}$ was dominated by *Tagelus divisus* with a range from 16.7 to 93.0% of numbers of organisms ($\bar{x} = 71.9\%$) and a range from 30.8 to 99.8% of biomass ($\bar{x} = 69.0\%$). *T. divisus* ranked first in biomass in all samples and in all samples but one (S_{3M}-spring) with regard to numbers of organisms. *Macoma constricta*, the second most dominant species, was not a constant component in all the samples of the assemblage.

$A_{3(M+L)}$ had only one non-ubiquitous species, *Upogebia affinis*. This species did not dominate the assemblage. Within this assemblage, species that occurred in other assemblages totaled 71.7% of numbers of organisms and 63.7% of biomass.

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[2] If Fig. 2 is regarded as a matrix, $M = m_{ij}$ where $i = 1,2,\ldots,$ 27 and $j = 1,2,\ldots,27$, then the mean of the temporal overlap for the assemblages is (regarding the numerical matrix below the main diagonal and i as rows): $1/24\ \Sigma(m_{xy} + m_{xz} + m_{zy})$ where $x = 2 + 3n$, $y = 1 + 3n$, $z = 3 + 3n$, and $n = 0,1,2,3,4,5,$ 7,8.
[3] Similarly, the mean of the nonassemblage, intratransect overlaps is: $1/54\ (\Sigma m_{ij} + \Sigma m_{kl} + \Sigma m_{pq})$ where $i = 7 \ldots 9$, $k = 13 \ldots 18$, $p = 22 \ldots 27$, $j = 1 \ldots 6$, $l = 10 \ldots 12$, $q = 19 \ldots 21$.

the biomass or numbers of organisms for the first two trophic types were found to be inversely correlated (Table 4). Correlations were also computed between the three calculated sediment parameters (median particle-size, sorting, and skewness) and the four trophic parameters (numbers of deposit feeders, biomass of deposit feeders, numbers of filter feeders, and biomass of filter feeders). Significant correlations were found between 50% of all trophic-sediment comparisons (Table 5).

In tests for homogeneity (BMD01V), all four trophic parameters and two of the three sediment parameters (median particle-size and skewness), were found to be heterogeneous between the assemblages ($\alpha = 0.05$). The only sediment parameter for which the null hypothesis of homogeneity was not rejected, i.e., sorting, was sufficiently diverse so that the null hypothesis would have been rejected if $\alpha = 0.10$ (Table 4). McNULTY et al., (1962) also found that there was no significant correlation between trophic distributions and sorting. The mean percentages of biomass and numbers of organisms for filter and deposit feeders

and the means of the three sediment parameters for the various assemblages are given in Table 4.

The heterogeneity of the measured sediment parameters was reflected in their qualitative appear-

to the exclusion of other organisms. The severity of environmental conditions, i.e., desiccation and lack of water cover due to being high on a sand beach, would account for the lack of filter feeders.

Table 5. *Results of statistical testing for correlations between trophic parameters (expressed as raw data and as percentages of total biomass or numbers/sample) and sediment parameters. Only significant tests ($\alpha = 0.05$) are shown. F: F value of the test; C: correlation coefficient*

Sediment parameters		Deposit feeders				Filter feeders			
		Raw data		Percentages		Raw data		Percentages	
		Biomass	Numbers	Biomass	Numbers	Biomass	Numbers	Biomass	Numbers
Sorting	F	5.1486		7.7582	6.6481		5.0649		7.1941
	C	0.0453		0.4866	—0.4583		—0.4104		—0.4727
Mean particle size	F			6.5095		9.3440			
	C			—0.0161		—0.0610			
Skewness	F		9.6043	7.3378		16.0913	10.7028	9.4220	9.9785
	C		—0.0618	—2.48 · X + 0.19 · X²		0.6258	0.5475	0.0019	—0.0631

Table 6. *Means of trophic and sediment parameters for 5 assemblages, 3 transects, and all samples. Homogeneity: one-way analysis of variance F-value > $F_{0.05}$ (19,4) = 2.90 implies heterogeneity, data tested was raw data, mg biomass and numerical counts, and not percentages for trophic parameters. See Fig. 1 for explanation of sample codes*

Parameters			$A_{1(U+M)}$	A_{1L}	T_1	A_{2U}	$A_{2(M+L)}$	T_2	$A_{3(M+L)}$	T_3	Total sample mean	Homo-geneity
Trophic parameters												
Filter feeders	Biomass	(%)	5.8	4.7	5.3	9.8	75.0	42.4	32.9	15.7	21.1	16.8700
	Numbers	(%)	3.0	1.0	2.0	5.7	63.2	34.5	8.6	11.3	15.9	38.5742
Deposit feeders	Biomass	(%)	91.3	59.0	75.2	82.6	11.9	47.3	55.9	60.1	60.9	3.3514
	Numbers	(%)	91.4	53.1	72.3	80.3	11.3	45.8	75.2	66.1	61.4	4.9590
Sediment parameters												
Sorting (σ $\varnothing$)			0.919	0.856	0.887	1.236	0.582	0.909	0.908	0.819	0.872	2.8013
Skewness (Sk $\varnothing$)			—0.513	—0.079	—0.296	—0.742	0.716	—0.013	—0.341	—0.503	—0.271	3.4954
Median particle size		$\varnothing$	2.716	3.080	2.898	2.107	2.522	2.314	2.284	2.458	2.557	6.1097
		(mm)	0.152	0.118	0.135	0.232	0.174	0.203	0.208	0.182	0.170	

ance. It will be remembered that the original criteria used in determining transect locations were sediment color, texture, ability to support weight, and odor. These qualities all contributed to a qualitative ranking of increasing organic content and decreasing coarseness from Transects 2 to 3 to 1. This trend, judged *a priori* to sampling, paralleled the shift of trophic types from filter to deposit feeders and the decrease in median particle-size on the transect level (Table 6).

A striking anomaly is that, in A_{2U}, deposit feeders predominated in the sediment with the coarsest Mø. A_{2U} is dominated by *Ophiophragmus filograneus* almost

Discussion and conclusions

The major areas of emphasis in this study are the factors related to trophic group-sediment type relationships and the faunal assemblages indicated by the trellis diagrams. Before these areas can be explored, certain limitations of the study should be clarified. The mesh size used, while common to benthic studies, has been judged by REISH (1959) to be too coarse to adequately determine faunal diversity. This judgement is somewhat supported in that only two of the five assemblages ($A_{2(M+L)}$ and $A_{3(M+L)}$) were shown to be adequately characterized based on species-area curves.

The degree of confidence in biomass figures is higher. The mesh size used should have been fine enough to collect over 93% of the biomass (Reish, 1959). The sample area, 0.4m², was four times the area recommended by Thorson (1957) for intertidal areas. Comparisons of biomass and numbers of organisms on a per square meter basis to other benthic studies suggest that biomass and numbers of organisms per unit area found in this study were not abnormal, and that statements based on biomass figures should be reasonably valid.

A common concept in benthic animal-sediment relations is that the feeding type of the infauna is in some way correlated to the sediment. The actual correlation between the animal's feeding type and the sediment has been suggested to be due to a direct causal relationship of the sediment controlling trophic distribution (Sanders, 1958), a coincidence of water movement factors controlling trophic distribution (Sanders, 1958; McNulty et al., 1962), and an amensalistic effect of one trophic type on another mediated by the sediment (Rhoads and Young, 1970).

The first two suggestions, direct causality and coincidental correlation, have been suggested for deposit and filter feeders, respectively (Sanders, 1958). Sediment parameters can be divided according to both of these correlation hypotheses. Direct causality would be related to static factors such as the percentage of a certain size fraction, while coincidental correlation would be related to dynamic factors such as settling velocities, turbulence, and transport of particles.

Sanders (1958), by theoretical consideration of the dynamic factors, derived the value for the optimal median grain-size for filter feeders as 0.18 mm and was able to obtain confirmation of this prediction from empirical data from Buzzards Bay. Sanders (1958) also found that, at stations where deposit feeders predominated, the silt-clay fraction showed relatively uniform high values (50 to 90%). McNulty et al., (1962) found that the median grain-size in sediments which supported the highest biomass of filter feeders was 0.4 mm, and concluded that the fine fraction of the sediment did not play the same role in Biscayne Bay as it did in Buzzards Bay. This conclusion was based on the fact that the two stations most dominated by deposit feeders in Biscayne Bay were characterized by 1.5 and 51.3% silt-clay.

The data from this study supports Sander's (1958) optimal median grain-size prediction as well as the statement by McNulty et al., (1962) concerning the importance of the silt-clay fraction in Florida sediments. Examination of Table 6 shows that the assemblage most dominated by filter feeders, $A_{2(M+L)}$, had a median grain size of 0.174 mm. Comparison of Tables 1 and 6 shows that the assemblage most dominated by deposit feeders, $A_{1(U+M)}$, has a high variance in the silt-clay fraction (1.30 to 22.09%), the highest value of which is still below Sanders' (1958) values.

The third correlation hypothesis, that the infaunal trophic type-sediment correlation takes the form of trophic group amensalism, has been proposed by Rhoads and Young (1970). The generalization that suspension feeders are largely confined to sandy or firm mud-bottoms, while deposit feeders attain high densities on soft, muddy substrata is borne out by this study. This contention is supported by the moderate filter-feeder biomass of $A_{3(M+L)}$ and the qualitative judgement of the sediment along Transect 3 as being firm mud as well as the distinct sediment and trophic segregation shown by $A_{1(U+M)}$ and $A_{2(M+L)}$.

Sanders (1958) has suggested that filter feeders are controlled by dynamic water-sediment interactions such that if the sediment were too coarse (median grain size > 0.18 mm), substratum motility would hinder filter feeders, and if the sediment were too fine, this substratum condition would indicate insufficient organic suspension in the area. Deposit feeders were suggested to be controlled by the organic content which, in turn, was highly correlated with the clay fraction. Rhoads and Young (1970) have suggested that a prime determinant of filter-feeder distribution is the occurrence of deposit feeders which rework bottom sediments. The latter hypothesis would help to explain sediment-trophic anomalies such as the relatively high biomass of filter feeders in muddy sediments ($A_{3(M+L)}$) and the occurrence of assemblages dominated by deposit feeders in sediments with low silt-clay percentages (conceivably resulting from the exclusion of filter feeders). The former hypothesis does not encompass these anomalies.

Sanders' (1958) analysis of the optimal median grain-size for filter feeders can still hold, since the analysis implies that the dynamic factors resulting in the optimal grain size would also result in the best sorted sediment. The best sorted sediment would be expected to be free of the amensalistic effects of deposit feeders. This suggestion is substantiated by $A_{2(M+L)}$, which had the best sorted sediment, a median grain size of 0.174 mm, and was the assemblage most heavily dominated by filter feeders. Filter feeders were positively correlated to sorting (or more precisely, negatively correlated to sorting coefficients) and positively correlated to skewness (Table 5).

The second major area of emphasis in this study is the delineation and description of communities. Five assemblages (areas of high overlap) are shown in the trellis diagram (Fig. 2). Two of the five assemblages, A_{2U} and A_{1L}, consisted of only one spatial location and derived their overlap by temporal consistency. These two assemblages will not be considered further due to paucity of data and, for A_{2U}, due to paucity of organisms (presumably related to severe environmental stress associated with the station's position).

Analysis of the indices of affinity for a population of benthic studies (Sanders, 1960) yielded a mean of 42.7 and a standard deviation of 11.45. If the similarly

computed means of the indices of affinity for the three remaining assemblages are compared to these values, $A_{2(M+L)}$ and $A_{1(U+M)}$ lie above the mean by 0.36 and 1.46 standard deviations, respectively, while $A_{3(M+L)}$ lies below the mean by 1.67 units. Although the indices of affinity for all three assemblages fall within the range of published values (SANDERS, 1960), more confidence can be placed in the characterization of $A_{1(U+M)}$ and $A_{2(M+L)}$ as communities than can be placed in a similar characterization for $A_{3(M+L)}$.

The THORSON definition of a community, derived from PETERSEN's benthic studies, is that "benthic communities are not just abstractions from species lists, but are concrete, biologically organized, ecological entities" (from: MILLS, 1969). A PETERSEN-type community is characterized by, and is given the name(s) of one or several dominant, non-predaceous, non-seasonal, non-ubiquitous, and visually conspicuous species (THORSON, 1957). Since the trellis diagram was originally employed within a similar conceptual frame (MACFADYEN, 1963) and has been used to identify PETERSEN-type communities within the benthos (SANDERS, 1960), an attempt could be made to characterize the three remaining assemblages in the study area according to THORSON's criteria.

The pattern of superdominance within the three remaining assemblages casts doubt upon the usefulness of the PETERSEN concept. With the exception of the superdominant species, in $A_{1(U+M)}$ and $A_{2(M+L)}$, there was not a consistent pattern of species occurrence or dominance within the assemblages. In general, the occurrence of any particular species except the superdominant, varied through time and space.

The third assemblage, $A_{3(M+L)}$, although sufficiently coherent to appear as an assemblage on the trellis diagram, showed substantial overlap with the other two assemblages. The interrelationship between $A_{1(U+M)}$ and $A_{2(M+L)}$ was negligible (overlap $\bar{x} = 0.005^4$), while the overlap between $A_{3(M+L)}$ and $A_{1(U+M)}$ and $A_{2(M+L)}$ was more substantial ($\bar{x} = 0.154^5$ and $\bar{x} = 0.055^6$, respectively).

This pattern of overlap between the three assemblages resulted from a lack of shared elements between $A_{1(U+M)}$ and $A_{2(M+L)}$ and the presence of shared elements between these two assemblages and $A_{3(M+L)}$. Of the seven species with 1% or better of numbers of organisms or biomass within $A_{3(M+L)}$, two of the species were shared with $A_{1(U+M)}$, two were shared with $A_{2(M+L)}$, and one was shared with both of the other assemblages (Table 3). Only 10% of numbers of organisms and 23.4% of biomass was represented by all the non-shared species of $A_{3(M+L)}$ and one species, *Upogebia affinis*, accounted for 51% of non-shared numbers of organisms and 92.7% of non-shared biomass. Thus, $A_{3(M+L)}$ appears to have been an inter-

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[4] $x = 1/36 \; \Sigma m_{ij}$ where $i = 13 \ldots 18$ and $j = 1 \ldots 6$.

[5] $x = 1/36 \; \Sigma m_{ij}$ where $i = 22 \ldots 27$ and $j = 1 \ldots 6$.

[6] $x = 1/36 \; \Sigma m_{ij}$ where $i = 22 \ldots 27$ and $j = 13 \ldots 18$.

digitation of $A_{1(U+M)}$ and $A_{2(M+L)}$. This assemblage was then a functional, although not a spatial, ecotone.

Overall, the PETERSEN community concept does not appear to easily encompass the assemblages delineated by the sampling. STEPHENSON et al. (1970) also arrived at the same conclusion, but for different reasons. In Moreton Bay, there were no dominant species associated with any community other than the superdominant pattern found in the assemblages under consideration. The conclusion reached by STEPHENSON et al. (1970) that PETERSEN-type communities could be not recognized, would also seem to apply to this study.

The alternative is to espouse a view of communities as abstractions from continua of distributions of member organisms (MILLS, 1969). A general justification for this view has been expressed by JOHNSON (1970). Support for this view is shown in this study. The lack of a consistent multi-species dominance pattern combined with superdominance by one species tends to invalidate the use of the PETERSEN community concept in this study. The existence of a clear example of a functional ecotone "community" serves to support the community-as-an-abstraction view. Thus, with respect to this study, a view of communities as abstractions from continua of distributions rather than the PETERSEN-type communities would seem to be more justified.

Summary

1. Five assemblages were identified by utilization of a trellis diagram. Filter feeders were found to be inversely correlated to deposit feeders, 4 trophic parameters (numbers of organisms and biomass of filter feeders and numbers of organisms and biomass of deposit feeders) and 3 sediment parameters (sorting, median particle size, and skewness) were tested for correlations, and significant correlations were found in 50% of the cases. All 4 trophic parameters and median particle size and skewness were found to be heterogeneous between the assemblages.

2. A prediction of the optimal grain-size for filter feeders (0.18 mm) was supported, the variance in the importance of silt-clay fractions to deposit feeders between Florida sediments and Buzzards Bay sediments was reaffirmed, support for the trophic group-amensalism hypothesis was shown and an attempt was made to relate the optimal grain-size analysis to the trophic group-amensalism hypothesis.

3. Of the five assemblages which were identified, two were dismissed due to lack of data, two were judged to be reasonably valid communities based on a comparison of indices of affinity to other recognized communities, and the last assemblage was judged to have questionable status as a community due to a low index of affinity. Superdominance was found within the two valid communities. The questionable community was shown to be an interdigitation of the two

valid communities and was judged to be a functional, although not a spatial, ecotone. Based on the demonstration of an ecotone "community" and the lack of a consistent multi-species dominance pattern, a view of communities as abstractions from continua of distributions was supported over a PETERSEN-type community concept.

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First author's address: Mr. S. A. BLOOM
Department of Zoology
University of Washington
Seattle, Washington 98105
USA