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Benthic Studies in Buzzards Bay. I. Animal-Sediment Relationships[1]

HOWARD L. SANDERS

Woods Hole Oceanographic Institution, Woods Hole, Mass.

ABSTRACT

During October and November 1955 a bottom faunal study was undertaken at 19 localities in Buzzards Bay, Massachusetts. The number of animals ranged from 1,064 to 12,576/m² with a mean number of 4,430. In comparison with certain other areas these numbers appeared small and seemed to be due to the relatively low concentrations of chemical nutrients and modest primary production of the region. Two faunal assemblages were recognized: one, present in the muddy sediments and dominated by the lamellibranch *Nucula proxima* and the polychaete *Nephthys incisa* was essentially the same community described from Long Island Sound; the other, restricted to the sandier sediments and characterized by species of the amphipod genus *Ampelisca*. The two primary feeding types, the filter-feeders and the deposit-feeders, numerically dominated in the sand and mud sediments, respectively. The distribution of certain dominant deposit-feeders in Long Island Sound and Buzzards Bay was poorly correlated with the silt-clay fraction of the sediment. However, when clay alone was used, a much better agreement was obtained. It was suggested that clay is probably the most valid criterion for the distribution of deposit-feeders. The distribution of infaunal filter-feeders seemed related to the degree of sorting and the median grain size of the sediment, with largest populations present in well-sorted fine sand. The hydrodynamic implications of this distribution are discussed.

INTRODUCTION

A quantitative benthic survey was undertaken in Buzzards Bay, Massachusetts, during October and November of 1955. Four survey stations (Fig. 1: H, J, P, and R) were selected as being representative of different widespread sediment and faunal assemblages. They were subjected to intensive monthly sampling over a twelve-month period (February 1956–February 1957) with the purposes of measuring some of the dynamic properties of benthic communities such as growth, mortality, and organic turnover of the more important species components; of obtaining additional data on animal-sediment relationships; and of defining the niches of the numerically abundant species. This paper is concerned with animal-sediment relationships.

Buzzards Bay is a somewhat elongate body of water approximately 46 kilometers in length and about 19.5 kilometers wide at its greatest diameter. It opens to the sea at the south, and along part of the eastern boundary there is appreciable water exchange with Vineyard Sound through the channels that separate the Elizabeth Islands. There is also some water exchange with Cape Cod Bay by means of the Cape Cod Canal (not shown in Fig. 1).

The Bay, as a whole, is relatively shallow, averaging only 11 meters in depth. Bottom temperatures vary from a maximum of approximately 22°C in summer to about 2°C in winter, while salinity values range from 29.5 to 32.5‰.

The locations and depths of the nineteen stations included in this study are shown in Figure 1.

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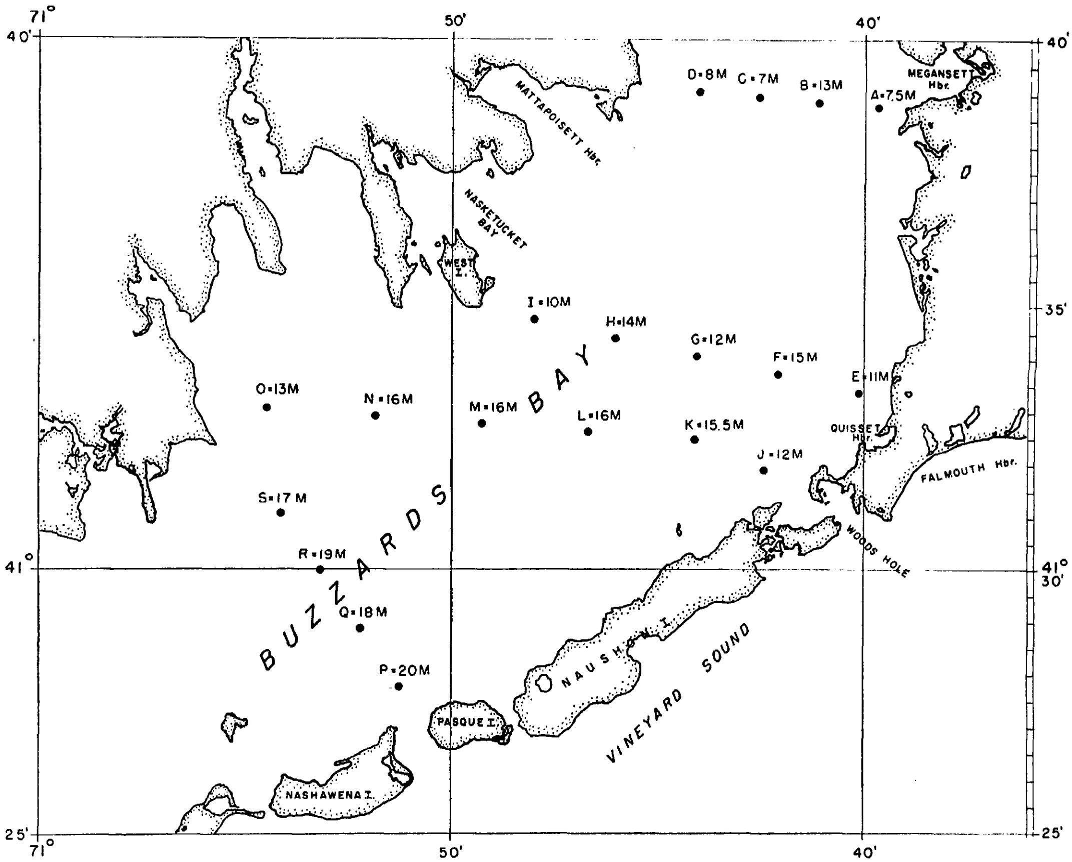

FIG. 1. Map of Buzzards Bay showing the locations and depths of the stations represented in the survey.

METHODS

Samples were obtained with a Forster anchor dredge that was modified by welding the entire frame into a single unit. The apparatus was calibrated to dig to the depth of 7.6 cm, and a small-meshed burlap bag attached to the frame retained the sediment. A small portion of the sediment was saved for sediment analysis, and the volume of the remainder was measured before washing the contents through a sieve of 0.5 mm aperture. The animals retained on the screen were carefully picked out alive in the laboratory and preserved in formalin.

A graded series of sieves was used to divide the sands and gravels into seven size categories. The five silt fractions and the clays were determined by pipetting (Soil Survey Staff 1951). The silt components consisted predominantly of feldspar and some quartz, and the absence of clay particle aggregates indicated that the dispersing agent, sodium hexametaphosphate, was effective. The clay fraction, analyzed by Dr. Ivan Milne of the Gulf Research Development Company, consisted predominantly of illite and chlorite. Montmorillonite, kaolonite, feldspar, and quartz were also detected. The results of the mechanical analyses are given in Table 1. Silt-clay percentages, median grain sizes, and sorting coefficients are given in Table 2. The sorting value was obtained by dividing the variation between the 20 and 80 percentiles by two.

FAUNAL ANALYSES

The numbers present at each station are given in Table 2. The mean number of organisms at all the stations is 4,430/m^2,

TABLE 1. *The particle size analysis by per cent weight of the 19 stations included in the Buzzards Bay survey*

Station	Gravel		Sand					Silt					Clay
	(8.0–4.0 (mm)	(3.9–2.0 mm)	(1.9–1.0 mm)	(0.9–0.5 mm)	(0.49–0.25 mm)	(0.24–0.125 mm)	(0.124–0.062 mm)	(61–31 μ)	(30–16 μ)	(15–8 μ)	(7–4 μ)	(3–2 μ)	(>2μ)
A	2.04	4.76	14.63	53.74	20.48	2.58	0.74	←——	——	0.99	——	——	——→
B	0.29	0.46	4.98	23.14	44.20	17.16	3.76	←——	——	5.82	——	——	——→
C	1.41	1.62	5.46	31.30	48.32	8.85	0.35	←——	——	3.00	——	——	——→
D	0.14	0.20	1.86	14.52	43.40	33.70	2.06	←——	——	4.02	——	——	——→
E	—	0.27	5.16	35.06	49.30	7.62	0.28	←——	——	2.20	——	——	——→
F	—	—	0.06	0.30	1.43	2.62	4.37	10.66	18.38	20.35	12.57	9.85	19.55
G	—	0.07	1.73	13.66	34.19	32.96	2.13	1.05	3.18	3.00	2.47	1.12	4.19
H	—	0.21	3.49	26.70	46.05	13.40	2.33	0.92	0.78	1.05	1.86	0.97	2.42
I	3.34	3.58	8.99	19.92	30.16	21.85	4.48	2.09	0.93	0.93	1.07	0.42	2.20
J	—	0.06	0.43	3.47	7.39	7.11	15.65	14.35	11.53	8.69	10.33	6.41	14.28
K	—	—	—	—	0.10	0.21	1.78	10.75	16.93	22.23	22.23	8.00	17.47
L	—	—	0.05	0.12	0.27	1.67	4.21	23.50	14.13	13.52	13.73	10.05	19.10
M	—	—	—	0.04	0.23	0.93	5.45	11.96	18.63	17.67	16.51	9.52	18.70
N	—	0.06	1.24	9.18	40.48	42.18	2.30	0.89	0.18	0.53	—	0.71	2.21
O	1.09	1.16	1.25	1.29	2.24	3.37	15.99	16.45	15.17	14.26	10.79	4.20	12.57
P	—	0.06	0.04	0.32	12.50	78.05	4.04	0.79	0.54	1.58	1.20	0.52	0.38
Q	—	—	0.06	0.45	0.68	5.96	20.87	13.62	14.53	13.05	12.72	6.62	11.40
R	—	0.20	0.12	0.28	0.84	1.36	5.27	17.23	20.09	16.87	7.19	12.22	18.18
S	1.24	0.19	1.23	4.27	12.57	19.43	10.04	9.87	11.72	6.47	8.51	2.90	11.59

TABLE 2. *The values of certain geological and ecological factors measured in the survey*

Station	Silt-clay percentage	Clay percentage	Sorting coefficient (mm)	Median grain size (mm)	No. Animals $/m^2$	Epifauna		Filter-feeding infauna				Deposit-feeding infauna			
						No./m^2	% of total	No./m^2	% of total	No. dominant spp. $/m^2$*	% of total filter-feeders	No./m^2	% of total	No. dominant spp. $/m^2$**	% of total deposit-feeders
A	0.99		0.67	0.68	1629	745	45.73	295	33.27	124	42.03	233	26.35	0	0.00
E	1.79		0.48	0.45	2259	115	5.09	980	45.71	837	85.41	227	10.59	213	93.84
C	3.00		0.50	0.44	3305	450	13.62	1841	64.48	1765	95.87	363	12.71	0	0.00
D	3.81		0.31	0.31	3283	191	5.82	2371	76.68	2007	84.65	321	10.38	136	42.37
N	4.40		0.30	0.26	5859	125	2.13	4648	81.06	3945	84.22	687	11.97	30	4.37
P	5.00		0.10	0.18	12576	5290	42.06	5185	62.91	3114	60.06	3084	34.72	941	30.51
B	5.32		0.45	0.37	2619	179	6.83	1761	72.17	1452	82.45	258	10.57	189	73.26
I	6.68		0.70	0.38	4379	437	9.98	2575	65.32	2186	84.79	426	10.81	315	73.94
H	6.90		0.45	0.37	5519	179	3.24	3227	60.43	2855	88.49	1539	28.82	448	29.10
G	13.29	4.19	0.34	0.26	3061	33	0.11	1497	49.44	739	49.37	1423	46.99	1004	73.37
					44489			24380	$\bar{x}=64.87$	19024	$\bar{x}=78.03$	8561	$\bar{x}=22.79$	3316	$\bar{x}=38.73$
S	43.64	11.59	0.26	0.04	4319	267	6.18	1362	33.61	1002	73.51	1845	45.53	1578	85.58
J	59.42	12.35	0.089	0.03	5455	447	8.19	2072	41.29	1238	59.75	2836	56.52	2272	80.11
Q	63.00	11.40	0.080	0.023	3211	57	1.78	620	19.31	55	8.87	2391	74.46	1955	81.76
O	67.14	12.52	0.079	0.023	4462	0	0.00	405	9.08	0	0.00	3892	87.23	3758	96.56
R	81.19	18.18	0.038	0.013	6068	126	2.08	125	2.10	0	0.00	5545	93.32	4527	81.61
M	83.95	18.70	0.029	0.010	5934	146	2.46	104	1.80	62	59.62	5632	97.30	5173	91.85
F	85.47	19.45	0.029	0.010	1187	0	0.00	41	3.45	8	19.51	1049	88.37	737	70.26
L	86.23	19.10	0.042	0.012	7982	182	2.30	377	4.87	109	28.91	7089	91.52	6114	86.25
K	93.36	17.45	0.020	0.015	1064	18	1.69	215	20.55	106	49.30	742	70.94	673	90.70
					39628			5321	$\bar{x}=13.81$	2580	$\bar{x}=48.49$	26787	$\bar{x}=78.35$	26787	$\bar{x}=86.35$

* *Ampelisca spinipes*, *A. macrocephala*, *Byblis serrata*, *Cerastoderma pinnulatum*.

** *Tellina tenera*, *Nephthys incisa*, *Nucula proxima*, *Turbonilla* sp., *Retusa caniculata*, *Cylichna orzya*, *Nerinides* sp.

with a range of from 1,064 at Station K to 12,516 at Station P.

Buzzards Bay has numerically smaller benthic populations than some other areas. This is shown in the following table.

Location	No. of stations	Range	Mean	Screen mesh size
Buzzards Bay (present study)	19	1,064–12,576	4,430	0.5
Loch Craiglin, Scotland (Raymont 1949)	5	5,409–19,065	14,275	1.0
English Channel (Mare 1942)	1		2,356	1.0
Long Island Sound (Sanders 1956)	8	5,566–46,404	16,446	1.0

The Buzzards Bay-Woods Hole environment can be compared with Long Island Sound (Riley 1955, Sanders 1956) in regard to at least a limited number of factors. Chlorophyll readings (Yentsch, unpublished) and phosphorus concentrations (Crowin, unpublished) have been collected from the dock of the Woods Hole Oceanographic Institution. From the nature of the local current system it is apparent that such samples are fairly typical of the water present in the surrounding regions, and the values measured, therefore, can be applied directly to Buzzards Bay. The mean depth of Long Island Sound is 20 meters and of Buzzards Bay 11 meters. Yet Long Island Sound exceeds Buzzards Bay in winter maximum phosphorus, average chlorophyll/m^3, and mean benthic population by factors of 2.5, 3.5, and 3.6, respectively. It seems obvious that since the depth is not markedly different in these two areas, the very much larger bottom population present in Long Island Sound is the result of the larger phytoplankton population, its major source of food.

BENTHIC COMMUNITIES IN BUZZARDS BAY

One of the main objectives of this paper is to delimit the level-bottom animal communities present in Buzzards Bay. To facilitate this end, the distribution by num-

TABLE 3. *The numbers and proportion of 8 species of animals commonly associated with sandy sediments in Buzzards Bay*

Station	1		2		3		4		5		6		7		8	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
A	124	7.61	—	—	—	—	—	—	—	—	62	3.81	15	0.92	78	4.79
E	14	0.62	57	2.52	28	1.24	738	32.67	14	0.62	419	18.55	85	3.76	114	5.05
C	1715	51.89	50	1.51	—	—	—	—	—	—	275	8.32	75	2.27	25	0.76
D	1628	49.59	322	9.81	57	1.74	—	—	136	4.14	336	10.23	64	1.95	14	0.43
N	98	1.67	833	14.22	2720	46.42	294	5.02	6	0.10	74	1.26	270	4.61	25	0.48
P	566	7.77*	849	11.65	1520	20.89	179	2.41	92	1.26	238	3.27	209	2.87	—	—
		4.50**		6.75		12.09		1.42		0.73		1.89		1.66		
B	1306	49.87	129	4.93	17	0.65	—	—	189	7.22	258	9.85	266	10.16	34	1.30
I	928	21.20	91	2.08	22	0.50	1145	26.14	229	5.23	22	0.50	480	10.96	437	9.98
H	471	8.53	90	1.63	—	—	1394	25.26	362	6.56	36	0.65	615	11.14	326	5.91
G	439	14.34	54	1.76	11	0.30	—	—	268	8.76	32	1.05	64	2.09	—	—
	7289	x̄=18.59	2475	x̄=6.31	4375	x̄=11.16	3750	x̄=9.39	1296	x̄=3.29	1752	x̄=4.47	2143	x̄=5.47	1053	x̄=2.69
S	639	14.80	303	7.02	60	1.39	—	—	218	5.05	36	0.83	36	0.83	72	1.67
J	455	8.34	—	—	—	—	789	14.46	—	—	—	—	—	—	55	1.01
Q	—	—	—	—	—	—	55	1.71	—	—	—	—	11	0.34	11	0.34
O	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	204	3.36
M	10	0.17	—	—	—	—	52	0.87	—	—	—	—	—	—	42	0.71
F	8	0.63	—	—	—	—	—	—	—	—	—	—	—	—	—	—
L	36	0.45	—	—	—	—	73	0.92	—	—	—	—	—	—	182	2.30
K	9	0.85	—	—	—	—	97	9.12	—	—	—	—	—	—	36	3.38
	1157	x̄= 2.92	303		60		1066	x̄=2.69	218		36		47		602	x̄=1.52

1. *Ampelisca spinipes*
2. *Ampelisca macrocephala*
3. *Byblis serrata*
4. *Cerastoderma pinnulatum*
5. *Tellina tenera*
6. *Nephthys bucera*
7. *Glycera americana*
8. *Lumbrinereis tenuis*

* Percent of infauna.
** Percent of total fauna.

ber of the abundant species is arranged according to the increasing silt and clay content of the sediment (see Tables 3 and 4. Since Station P alone carried a numerically significant epifaunal population, it was necessary to designate for that station in Table 3 both an infaunal and total faunal column.) Certain of these dominant species are wholly or largely limited to sediments with small amounts of silts and clays (*Ampelisca spinipes*, *A. macrocephala*, *Byblis serrata*, *Tellina tenera*, *Nephthys bucera*, and *Glycera* sp.), while others (*Nucula proxima*, *Nephthys incisa*, *Nerinides* sp., *Retusa caniculata*, and *Cylichna orzya*) are largely confined to soils with large concentrations of silts and clays. Other animals such as *Ninöe nigripes*, *Lumbrinereis* sp., and, less strikingly, *Unciola irrorata*, are more widely distributed.

It seems possible from this distribution that two faunal assemblages can be recognized, one found in sediments with low concentrations of fine particles and represented in the survey by Stations A, E, C, D, N, P, B, I, H, and G, the other in sediments with large concentrations of silts and clays and represented by Stations S, J, Q, O, R, M, F, L, and K. Certain stations in the middle of the soil spectrum show transitions from one assemblage to the other; for example, Station G contained appreciable numbers of *Nephthys incisa*, while *Tellina tenera* and *Ampelisca macrocephala* were abundant at Stations S and J.

It is usual to describe benthic communities after the manner of Petersen (1913) by combining the names of two of the characteristic species. Such dominant species should both be numerous and belong to different taxonomic units.

The soft-bottom association is essentially the same as the *Nephthys incisa-Yoldia limatula* community described from Long Island Sound (Sanders 1956). The common representatives in Buzzards Bay are listed below. The percentage composition is given only

TABLE 4. *The numbers and proportion of 8 species of animals commonly associated with muddy sediments in Buzzards Bay*

Station	1		2		3		4		5		6		7		8	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
A	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	1.09
E	—	—	—	—	—	—	—	—	—	—	—	—	24	1.06	—	—
C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	138	4.18
D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	1.52
N	—	—	24	0.41	—	—	—	—	—	—	—	—	25	0.43	123	2.10
P	—	—	—	—	—	—	—	—	—	—	15	0.21	641	*5.10	224	3.35
														**8.80		1.78
B	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	0.31
I	10	0.23	—	—	—	—	—	—	—	—	44	1.00	32	0.73	33	0.75
H	16	0.29	16	0.29	—	—	—	—	54	0.98	—	—	326	5.91	18	0.33
G	755	24.67	10	0.33	—	—	—	—	11	0.36	—	—	117	3.82	21	0.69
	781	x̄=1.99	50						65		59		1165	x̄=2.97	647	x̄=1.65
S	603	13.96	121	2.80	—	—	579	13.41	169	3.91	96	2.22	591	13.68	169	3.91
J	418	7.66	73	1.34	1218	22.33	36	0.66	218	4.00	91	1.67	127	2.33	273	5.00
Q	739	23.01	320	9.97	254	7.91	56	1.74	255	5.71	387	12.05	88	2.74	55	1.71
O	349	7.82	70	1.57	2162	48.45	28	0.63	698	15.64	251	5.63	147	3.29	237	5.31
R	869	14.32	3306	54.48	—	—	374	6.16	159	2.62	193	3.18	68	1.12	—	—
M	1385	23.34	2040	34.38	—	—	1145	19.30	312	5.26	291	4.90	52	0.88	—	—
F	445	35.88	49	3.86	16	1.26	65	5.13	146	10.51	16	1.26	—	—	—	—
L	1642	20.71	3378	42.61	—	—	389	4.91	304	3.83	401	5.06	97	1.22	—	—
K	340	31.95	88	8.27	—	—	45	4.23	116	10.90	80	7.52	27	2.54	—	—
	6790	x̄=17.13	9445	x̄=23.83	3650	x̄=9.21	2717	x̄=6.85	2377	x̄=6.00	1806	x̄=4.56	1197	x̄=3.01	734	x̄=1.85

1. *Nephthys incisa*
2. *Nucula proxima*
3. *Turbonilla* sp.
4. *Nerinides* sp.
5. *Retusa caniculata*
6. *Cylichna orzya*
7. *Ninöe nigripes*
8. *Unciola irrorata*

* Percent of infauna.
** Percent of total fauna.

for those species comprising more than one per cent of the population.

	% composition		% composition
Polychaeta		Lamellibranchia	
Nephthys incisa	17.13	*Nucula proxima*	23.83
Nerinides sp.	6.85	*Cerastoderma pinnulatum*	2.69
Ninöe nigripes	3.01	*Pitar morrhuana*	2.55
Lumbrinereis tenuis	1.52	*Yoldia limatula*	
Tharyx acutus	1.08	Gastropoda	
Exogone dispar		*Turbonilla* sp.	9.21
Lumbrinereis hebes		*Retusa caniculata*	6.00
Aricidea sp.		*Cylichna orzya*	4.56
Scolelipedes sp.		*Nassarius triviattatus*	
Maldanopsis elongata		*Bela turricola*	
		Enteropneusta	
Melinna cristata		*Dolichoglossus kowalevskii*	
Crustacea			
Ampelisca spinipes	2.92	Tunicata	
Unciola irrorata	1.85	*Molgula complanata?*	
Hutchinsoniella macracantha			
Edotea montosa			

The two most common forms are *Nephthys incisa* and *Nucula proxima*, comprising 17.13 and 23.83 % of the population by number. Since *Yoldia limatula* makes a much less significant numerical contribution in Buzzards Bay, it is proposed that *Nucula proxima* replace it as a characterizing dominant. The upper salinity associated with this community in Long Island Sound was 29.2, in Buzzards Bay 32‰. The other environmental conditions associated with this community have been described elsewhere (Sanders 1956)

The predominantly sand assemblage is clearly characterized by three closely related species of amphipods, *Ampelisca spinipes*, *A. macrocephala*, and *Byblis serrata* which together constitute over 36 % of the community. The remaining really abundant species in this association is the lamellibranch, *Cerastoderma pinnulatum*, which comprised more than 10 % of the population at the time of sampling. However, because this organism is an annual, being present in markedly reduced numbers or even absent during a significant fraction of the year, it is a poor characterizing species. It therefore seems reasonable to designate this sand bottom association as the *Ampelisca* spp. community, which in Buzzards Bay is found in sediments containing less than 35-45 % silt-clay. The common representatives are listed below. The per cent composition is given only for those species comprising more than one per cent of the population.

	% composition		% composition
Polychaeta		*Leptocheirus pingius*	
Glycera americana	5.47	*Cerapus tubularis*	
Nephthys bucera	4.47	*Corophium* spp.	
Ninöe nigripes	2.97	*Ptilanthura tenuis*	
Lumbrinereis tenuis	2.69	*Edotea montosa*	
Nephthys incisa	1.99	*Stenothöe* sp.	
Sthenelais boa		*Batea secunda* (epifauna)	
Pholöe minuta		*Erichthonius brasiliensis* (epifauna)	
Eteone lacta		*Aeginella longicornis* (epifauna)	
Phyllodoce arenae		*Crago septemspinosus* (epifauna)	
Paraspionosyllis longicirrata		*Pagurus annulipes* (epifauna)	
Podarke obscura		*Neopanope texana* (epifauna)	
Nereis zonata		Lamellibranchia	
Diopatra cuprea		*Cerastoderma pinnulatum*	10.17
Haploscolopos fragilis		*Tellina tenera*	3.29
Pista sp.		*Nucula delphinodonta*	
Polycirrus eximus		*Pandora gouldiana*	
Ampharete arctica		*Lyonsia hyalina*	
Scalibregma inflatum		*Laevocardium mortoni*	
Crustacea		*Ensis directus*	
Ampelisca spinipes	18.59	Gastropoda	
Byblis serrata	11.31	*Natica pusilla*	
Ampelisca macrocephala	6.31	*Nassarius triviattatus*	
Unciola irrorata	1.65	*Crepidula plana* (epifauna)	
Oxyurostylis smithi		*Mitrella lunata* (epifauna)	
Paraphoxus spinosus		*Anachis avara* (epifauna)	
Phoxocephalus holbölli		Tunicata	
		Molgula complanata?	1.85

The same community with most of the same species represented also occurs in the sandy sediments of Long Island Sound where the *Ampelisca* species comprised about 32 % of the fauna. Since too few stations of this type were present in the survey (Stations 1, 4, and Charles Island), the writer did not feel justified in naming the association in Long Island Sound. In view of the faunal analyses in Buzzards Bay, however, it seems apparent that the infauna of the sandy sediments of Long Island Sound also belongs to the *Ampelisca* spp. community. Evidence for the presence of similar communities elsewhere can be found in the studies of Miyadi (1940), who observed that an *Ampelisca* species was a common organism in the sandy sediments of Tanabe-wan and Osaka-wan, two somewhat enclosed Japanese Bays.

Certain differences exist in the species composition of the ampeliscids in the Long Island Sound and Buzzards Bay regions. *Ampelisca macrocephala* and *Byblis serrata* are largely absent from the region investigated in the central Long Island Sound area. Instead, two sibling species, designated tentatively by the writer as *Ampelisca A* and *B*, comprise the dominant ampeliscid species of the region. Both forms appear identical morphologically, differing only in size, the former being approximately three times as heavy as the latter. There is little overlap in the distribution of the species, with *Ampelisca A* present in sediments with relatively less silt and clay. Probably both forms have been lumped together and included in the species *Ampelisca spinipes*. (Taxonomic difficulties involved in the genus *Ampelisca* have been discussed in detail by Reid 1951.)

There is some indication that *Ampelisca spinipes* in Buzzards Bay may be composed of the same two components, although there appears to be more overlap in the distributions which tend to blur size differences. To test this contention, size-frequency distributions of the *Ampelisca spinipes* representatives were constructed for the nine samples having adequate numbers of this form. The mean length of the largest 20% in each of the four stations having the least silt-clay content was appreciably larger than any of the remaining five stations. Converting length to dry weight (Sanders 1956) the average dry weight equivalent of the largest 20% of the population at the four stations with less silt-clay was approximately 2.8 times as large as the mean dry weight equivalent of the other five stations. These data at least imply that both

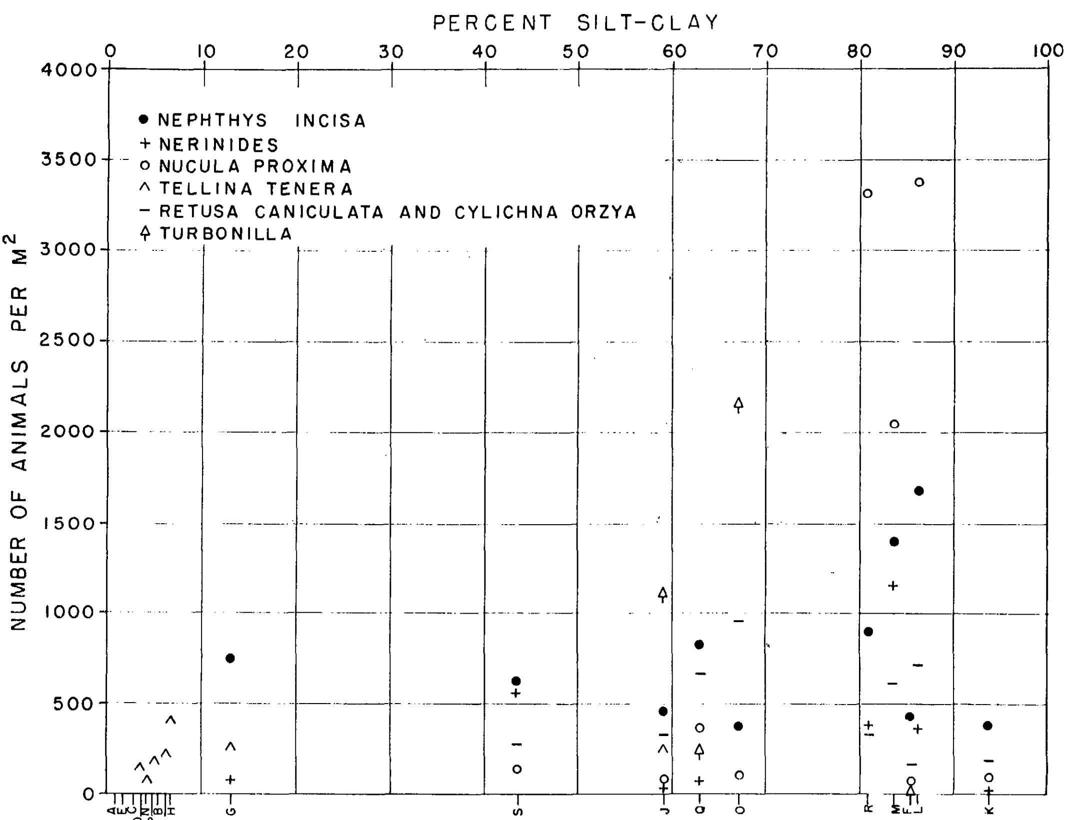

FIG. 2. Relationship of number to sediment composition for seven common deposit-feeders in Buzzards Bay.

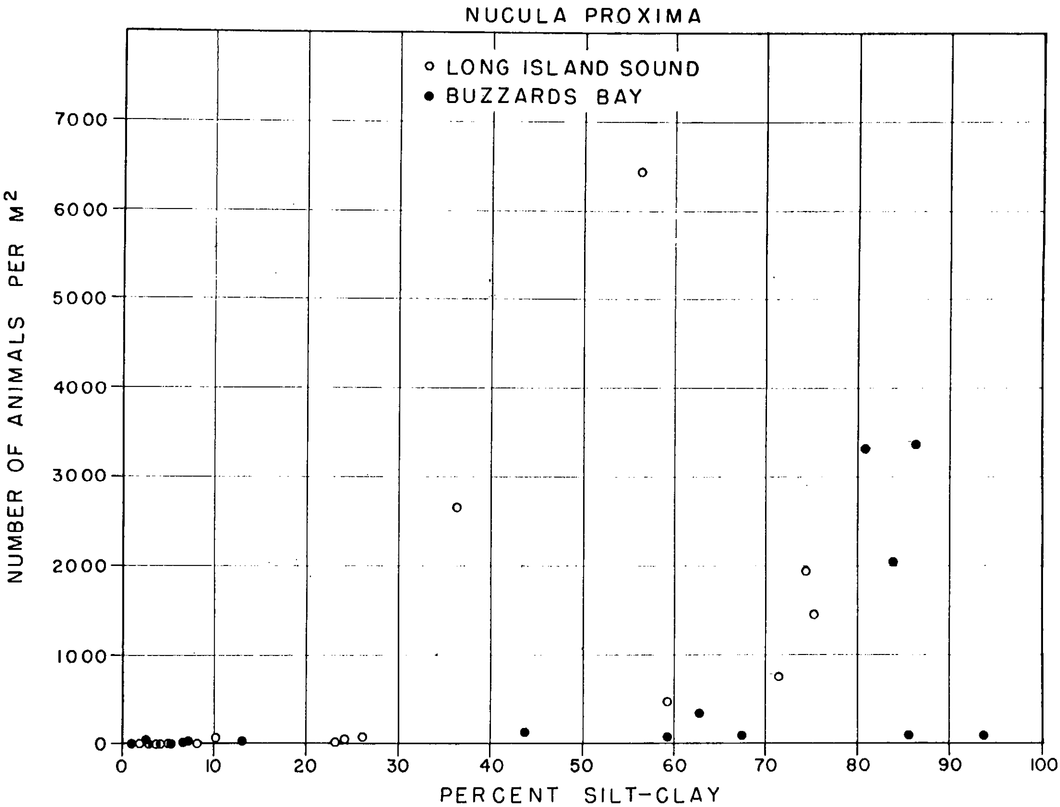

FIG. 3a. Relationship of the number of *Nucula proxima* to the silt-clay component of the sediment in Long Island Sound and Buzzards Bay.

Ampelisca A and *B* may be present in Buzzards Bay.

Stickney and Stringer (1957) describe an *Ampelisca* community in Greenwich Bay, Rhode Island. Their association is present in mud or mud and some sand, with a number of stations carrying more than 10,000 individuals of *Ampelisca spinipes* to the square meter. In contrast, *Ampelisca spinipes* appears to be restricted to the sandy sediments in Buzzards Bay (see Table 3) and Long Island Sound. Other components of Stickney and Stringer's community, *i.e.*, *Nucula proxima*, *Retusa* (Tornatina) *caniculata*, and *Pitar morrhuana* are important constituents of the *Nephthys incisa-Nucula proxima* community in Buzzards Bay (Table 4).

From observations in the laboratory Enequist (1949) defines the ampeliscid type of feeding in which the animals "do not ingest their food chiefly during burrowing but by sucking together tripton with the aid of the current set up by the pleopods and by scraping off or whirling up the surface detritus with the antennae." Since the ampeliscids in Long Island Sound and Buzzards Bay are largely limited to the sandy sediments, it is obvious that they must obtain their food predominantly from suspended matter in the water. *Ampelisca macrocephala* in Greenwich Bay inhabits a similar environment and thus probably feeds in the same manner. However, regarding the extremely abundant *Ampelisca spinipes*, Stickney and Stringer (1957) state, "The digestive tracts of *Ampelisca spinipes* were found to contain large amounts of both mineral and organic detritus suggesting that these species feed upon bottom deposits." This observation, together with the fact that the animal is most abundant in the softer deposits, indicates that in Greenwich Bay, *Ampelisca spinipes* obtains its food largely from settled detritus secondarily suspended by the animal's activity. Conceivably, *Ampelisca spinipes* of Greenwich Bay may be the same animal as *Ampelisca B* in Long Island Sound, since the latter form is found in finer sediments than *Ampelisca A*. Finally, it should be noted that the *Ampelisca* community of Greenwich Bay is replaced in Long Island Sound and Buzzards Bay by the *Nephthys incisa-Nucula proxima* community, which has an extremely small ampeliscid component.

ANIMAL-SEDIMENT RELATIONSHIPS

The primary consumers, *i.e.*, herbivores and detritus feeders, usually comprise 80–99% by number of the benthic faunal in Buzzards Bay. The filter-feeders or animals that obtain their food from suspended matter make up the majority of the fauna in the sandy sediments, while the deposit-feeders living on organic matter in or on the bottom dominate the fauna in the finer sediments. In the *Ampelisca* spp. community the filter-feeders comprise almost two-thirds of the population by number, while over 80% of the fauna of the *Nephthys incisa-Nucula proxima* community are deposit-feeders. The sand sediment, where the *Ampelisca* spp. community is found, reflects the more pronounced current activity in such environments which in turn brings more potential food to the filter-feeding organisms than would weaker currents. Conversely, over mud bottoms, the feeble currents allow organic matter to settle out, thus providing an adequate source of nutrition for large numbers of deposit-feeders.

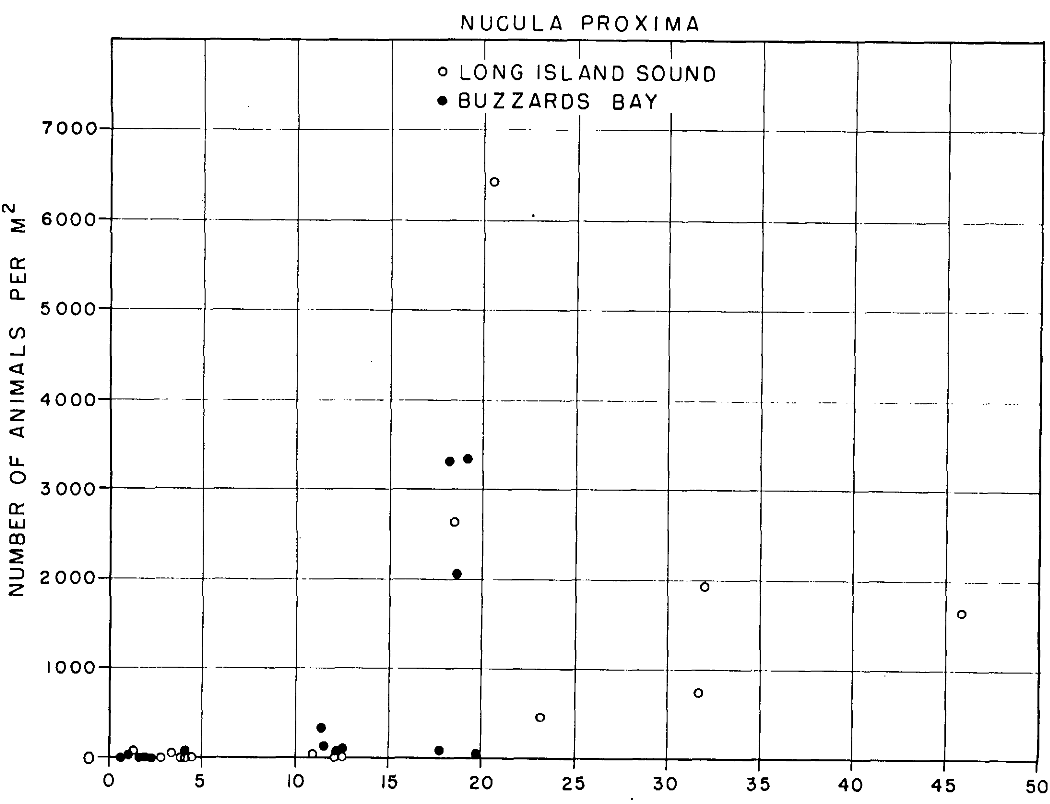

FIG. 3b. Relationship of the number of *Nucula proxima* to the clay component of the sediment in Long Island Sound and Buzzards Bay.

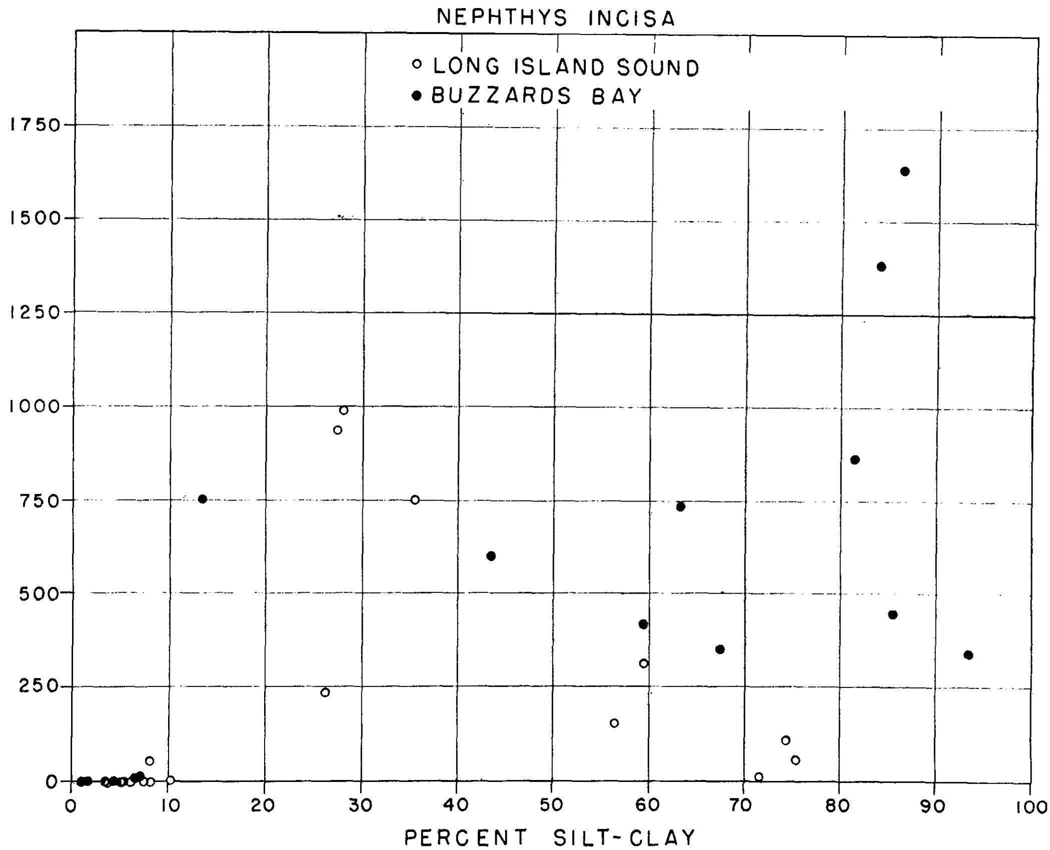

FIG. 4a. Relationship of the number of *Nephthys incisa* to the silt-clay component of the sediment in Long Island Sound and Buzzards Bay.

Within each feeding type a few species are numerically dominant. In the *Ampelisca* spp. community four species comprise 78% of the filter-feeders, and in the *Nephthys incisa-Nucula proxima* community seven forms constitute over 86% of the deposit-feeding fauna (see Table 2). Figure 2 shows the distribution of seven of these deposit-feeders plotted against the silt-clay content of the sediment. A summation of the percentages of filter-feeders and deposit-feeders gives the total for the primary consumers.

It should be noted that one of the included dominant deposit-feeders is a species of the pyramidellid genus *Turbonilla*. All pyramidellid gastropods are believed to be highly specific ectoparasites whose hosts are usually sedentary polychaetes, molluscs, and coelenterates (Fretter and Graham 1949). Yet it is impossible to conceive that the particular species under consideration could possibly have a parasitic mode of life because of its great abundance relative to the animals that might serve as hosts.

Turbonilla is the numerically dominant species of Stations J and O, comprising 22.3 and 48.5%, respectively, of the total population. At Station Q it constitutes 7.9% of the fauna. The only associated animals that might conceivably be abundant enough to serve as possible hosts in this environment are *Nephthys* and *Nucula*. One should expect excellent agreement in a host-parasite relationship, and yet there exists a poor correlation between the distribution patterns of *Turbonilla* and the postulated hosts (Fig. 2). Furthermore, many thousands of living *Nephthys* and *Nucula* have been observed by this writer without finding any indication of a pyramidellid parasite. The actively burrowing habit of *Nephthys* makes that animal an unlikely host, and it is unreasonable to suppose that the diminutive *Nucula* could serve as a suitable host for the larger and often more numerous *Turbonilla.* It is much more likely that this particular species of *Turbonilla* is not an ectoparasite but a deposit-feeder, using its buccal pump to draw in the extremely soft, organically-rich superficial sediment.

The distribution of deposit-feeders in Buzzards Bay and Long Island Sound

Realizing that the distribution of any species in nature is the result of a complex of environmental factors, a unifactorial analysis gives, at best, only a moderately good correlation. For example, the relationship between the distribution of certain deposit-feeding species and the fine fractions of the sediment can be modified in sediments of very high concentrations of these con- constituents by the reduction of oxygen.

The numerically abundant species of deposit-feeders are essentially the same in both of these regions, yet the greatest concentration in Buzzards Bay occurs in sediments with an appreciably higher fraction of silts and clays than in Long Island Sound, although the points are too few to demonstrate this statistically. Figure 3a shows the relationship between the silt-clay composition of the sediments and the numbers of *Nucula proxima,* the most abundant deposit-feeder in both regions. The Long Island Sound samples reveal high numerical values at from 35 to 60% silt-clay, while in Buzzards Bay the highest values are found between 80 to 87%, with low numbers in the region of Long Island Sound maximum.

The differences in distribution between the two areas are much more pronounced than that indicated in Figure 3a. Sediment

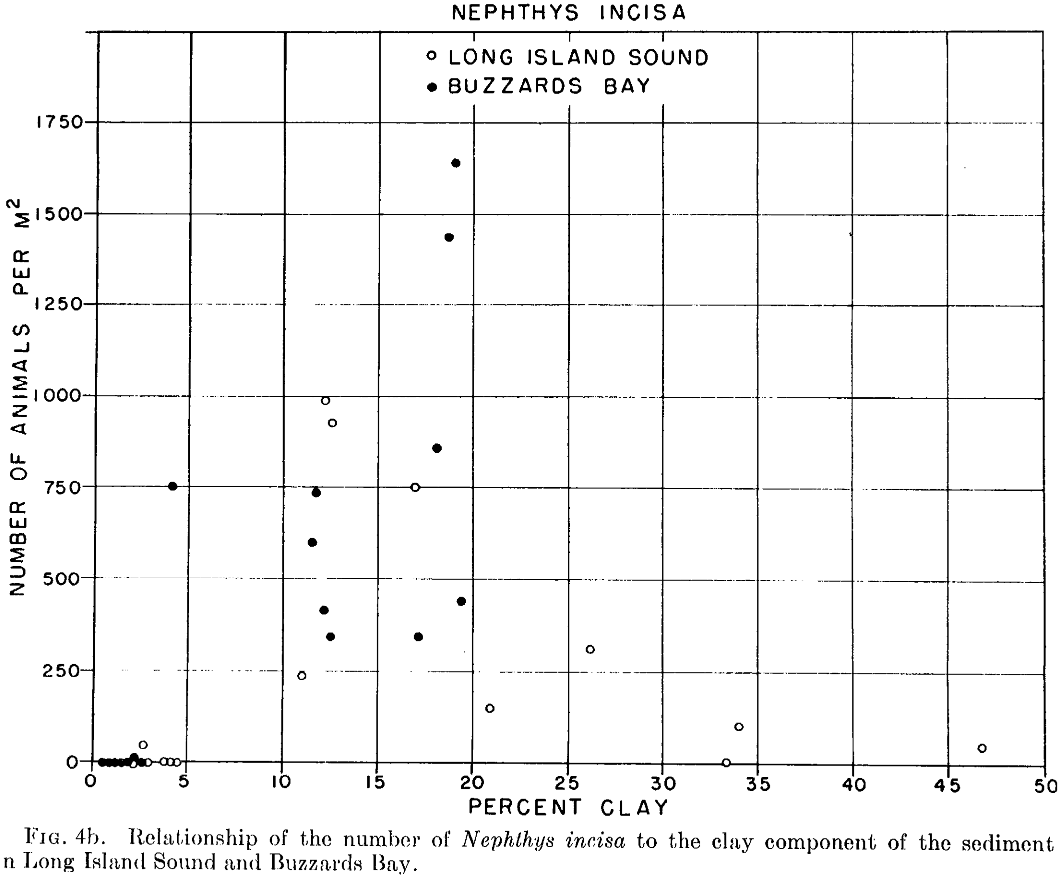

FIG. 4b. Relationship of the number of *Nephthys incisa* to the clay component of the sediment in Long Island Sound and Buzzards Bay.

analyses were not performed on all samples taken in the Long Island Sound study, particularly in regard to a number of samples from Stations 2, 7, and 8. However, the sediments that were analyzed (Sanders 1956) indicate that probably all samples from these stations had a silt-clay content that varied between 25 and 60 %. The number of *Nucula*/m² that were present in the samples not included in Figure 3a are given below. These help to confirm the existence of maximum populations in intermediate silt-clay percentages.

Station 7	September 9, 1953	9,050
	February 3, 1954	4,600
	September 10, 1954	1,200
Station 8	August 1, 1953	4,100
	February 3, 1954	8,000
	July 23, 1954	10,000
Station 2	February 5, 1954	5,450

Essentially the same distributional pattern can be demonstrated for the next most abundant deposit-feeder, *Nephthys incisa* (Fig. 4a) except that the degree of difference in distribution is even more marked. Like *Nucula*, *Nephthys* in Buzzards Bay is found in largest numbers in 80 to 87 % silt-clay, although the polychaete is abundant over a wider sediment range than *Nucula*. By contrast, in Long Island Sound the largest populations of *Nephthys* are encountered in sediments of from 22 to 40 % silt-clay, while in sediments of more than 70 % silt-clay only small numbers are present.

Why should there be an apparent regional difference in the distribution patterns of *Nephthys* and *Nucula*? A closer scrutiny of the silt-clay fraction of the sediment in these two areas gives a clue. What is immediately evident is that the clay component of this fraction is much larger in the Long Island Sound samples, averaging 48.3 % with a range of from 37.8 to 61.2 %. On the other hand, in Buzzards Bay the clays average only 21.4 % of the silt-clay fraction with a minimum of 18.1 and a maximum of 26.9 %.

Much better agreement is obtained regarding the distribution of *Nucula* and *Nephthys* in Long Island Sound and Buzzards Bay if the number of animals is plotted against only the clay percentage (Figs. 3b and 4b). The Long Island Sound data show that the largest populations of *Nucula* are found between 16 and 22 % clay, and that appreciable numbers are present in sediments with greater clay concentrations. In Buzzards Bay almost the same sediment range, 16 to 19 % clay, representing some of the stations with the largest clay fractions, support the biggest populations of *Nucula*.

There is also excellent agreement in the distribution of *Nephthys* in Long Island Sound and Buzzards Bay (Fig. 4b). With the single exception of Station G with about 4 % clay, the largest populations seem to be confined to sediments with 10 to 20 % clay in both areas. At higher and particularly lower concentrations of clay the numbers of *Nephthys* rapidly diminish.

The data strongly suggest that clay is the most valid sediment correlate for the distribution of deposit-feeding organisms. Clays are much smaller than the silt particles and therefore have a relatively much larger surface area to bind organic matter, the source of food for deposit-feeders. Larger detrital components also tend to accumulate here due to the feeble currents. On the other hand, large concentrations of organic matter may reduce the oxygen content in the sediments and can ultimately limit the environment for deposit-feeders. It is no wonder that the clay fraction seems well correlated with the distribution of deposit-feeding animals.

The distribution of filter-feeding animals in Long Island Sound and Buzzards Bay

The analyses of the samples in both regions demonstrate that the filter-feeders are the dominant feeding type in the sandy sediments, yet it is not entirely evident that the silt-clay concentration alone can explain their distribution pattern (see Table 2). The distribution of filter-feeders may be controlled by the hydrodynamic processes which determine the sediment character rather than directly by the sediment. In the following theoretical speculations three processes need to be considered: the turbulence of water flow, the settling velocities of particles, and the transport of particles. The current necessary to convert the laminar flow over the bottom into turbulent flow is dependent on two factors which are inversely related, the size of the grain protruding into the flow and the velocity of the current. This is shown as the roughness velocity in Figure 5 (Inman 1949). The larger the sediment particles the smaller the velocity necessary to convert a hydrodynamically smooth bottom to one that is hydrodynamically rough. The settling velocity of sediment particles is given by Stokes' Law for grains less than 0.18 mm diameter, and the relationship between particle size and velocity is linear. Particles larger than 0.18 mm fall more slowly than Stokes' Law might predict, because the turbulence created by the falling object becomes a factor (see Fig. 5). The velocity necessary to cause a particle to move along the bottom (threshold velocity, Fig. 5) is minimal for grain sizes of 0.18 mm. Smaller sizes act as a hydrodynamically smooth bottom, and the drag becomes distributed

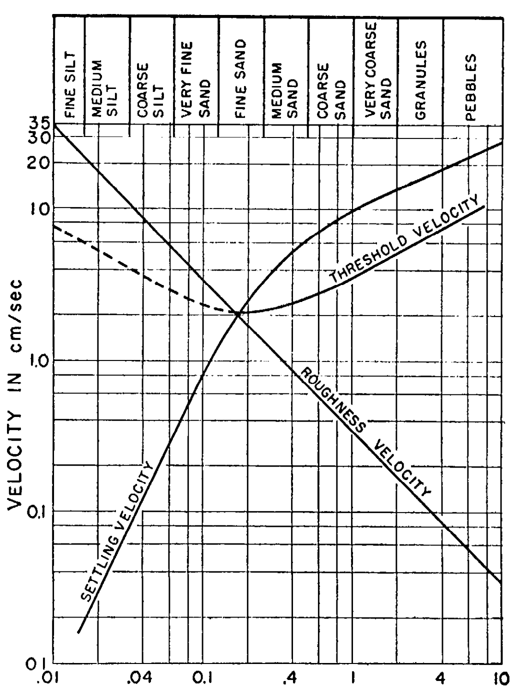

FIG. 5. Relation of grain diameter to settling velocity, threshold velocity, and roughness velocity. Modified from Inman (1949).

equally rather than on exposed individual particles. It is a point of some interest that the roughness velocity, settling velocity, and threshold velocity are the same for grains of 0.18. Thus sand grains of this size are most easily moved.

Since both finer and coarser sediments are more difficult to move, bottom sediments in the act of transport become better sorted as the diameter approaches 0.18 mm. This has been observed in the sediment studies for Cape Cod Bay (Hough 1942), Barataria Bay (Krumbein and Aberdeen 1937), and the Red Sea (Shakri and Higazy 1944).

The sediment analyses in Buzzards Bay agree with the above findings. By far the best sorted sample, Station P, had a median grain size that was precisely 0.18 mm (see Table 2). This station supports the largest total population and the largest number of filter-feeders. The probability is small that this is mere chance. This observation finds further support in the fact that the next largest number of filter-feeders were present at Station N where the sediment was relatively well sorted and median grain size of 0.26 deviated less from 0.18 mm than at any of the other stations. It therefore appears that two sediment criteria, a median grain size in the fine sands and a well-sorted sample, may be correlated with large populations of infaunal filter-feeders.

The Long Island Sound sediment data were reinterpreted from this point of view. These samples as a rule were much more poorly sorted than the Buzzards Bay series. The Charles Island sample of October 23, 1953, had a much larger population of filter-feeders than any of the other stations from which complete sediment analyses could be obtained. Within Long Island Sound the sediment at this station was the best sorted and had a median grain size of 0.15 mm. Thus the Long Island Sound data confirm the Buzzards Bay observations.

Since these results indicate a possible relationship between infaunal filter-feeders and a well-sorted, fine grain, it is pertinent to define the characteristics of such an environment. Because these sediment particles are precisely the sizes most easily moved, their presence in large concentrations is indicative of little active sediment transport. Such an environment is stable, which is an obvious advantage to organisms that live on and in the sediments.

As particle sizes become larger than 0.18 mm, the material will slide or roll over the bottom rather than go into suspension, because the roughness velocity is less than the threshold and settling velocities (see Fig. 5). Infaunal filter-feeders must maintain connection with the sediment surface in order to feed, and the shifting of the sand particles tend to make the maintenance of this connection precarious. The stations that best typify these conditions in Buzzards Bay (A and E) support very modest populations of infaunal filter-feeders.

Sediments that predominantly consist of silts and clays support meager numbers of filter-feeders for an entirely different reason. These sediments reflect the feeble currents present which allow the fine particles, including the organic matter, to settle out. There is therefore a smaller amount of organic matter in suspension to supply food for the filter-feeders. Most of the stations with fine sediments (Q, O, R, M, F, L and K) support small populations of filter-feeders.

What can be deduced about the well-sorted fine sands? For reasons previously stated, it must be a stable environment. Furthermore, the extremely good sorting indicates that the intensity of the current over the bottom during a tidal cycle must be remarkably constant, probably deviating only slightly from a velocity of two centimeters per second. Finally, currents of this intensity must be adequate to support the large populations of filter-feeders found in such sediments.

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