

BULLETIN  
OF  
THE BINGHAM OCEANOGRAPHIC COLLECTION  
Volume 15  
Oceanography of Long Island Sound, 1952-1954  
*Issued February 1956*

*published by*  
Peabody Museum of Natural History  
Yale University  
New Haven, Connecticut, USA  
[www.peabody.yale.edu](http://www.peabody.yale.edu)

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YALE UNIVERSITY

VOLUME XV

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OCEANOGRAPHY OF  
LONG ISLAND SOUND, 1952-1954

By

GORDON A. RILEY  
SHIRLEY A. M. CONOVER  
GEORGIANA B. DEEVEY  
ROBERT J. CONOVER  
SARAH B. WHEATLAND  
EUGENE HARRIS  
HOWARD L. SANDERS

*Issued February, 1956*  
*New Haven, Conn., U. S. A.*

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# OCEANOGRAPHY OF LONG ISLAND SOUND, 1952-1954

## X. THE BIOLOGY OF MARINE BOTTOM COMMUNITIES

BY

HOWARD L. SANDERS\*  
*Bingham Oceanographic Laboratory*

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### ABSTRACT

The results of a bottom survey carried out from August 1953 to September 1954 revealed that Long Island Sound, in contrast to other areas, supports extremely large populations of benthic animals. The mean number at each station varied from 5,563 to 46,398, while the mean weight of animals less than 0.2 g dry weight ranged from 4.54 to 36.38 g/m<sup>2</sup>. The infauna of each station was characterized by a narrow range of biomass values which were largely dependent on sediment composition. The greatest biomasses were found when the sediment contained from 13-25% silt and clay. This appeared to be an optimal concentration, since both increases and decreases of the silt-clay fraction gave progressively smaller biomass values.

The biology of some of the dominant animals is discussed. The genus *Ampelisca* was particularly interesting in that it could be divided into two distinct groups with respect to size and distribution although the groups could not be separated on the basis of taxonomic characters. Form A was confined to coarser sediments and was 3-4 times as heavy as its counterpart, form B, which was found only in the softer sediments. In both species the females appeared to be about 15 times more abundant than the males. However, on closer examination, it was apparent that approximately half of the females were gynomorphic males.

Values for organic production were obtained for four of the dominant species. On the basis of these figures, the annual productivity (2.44 times larger than that of the mean standing crop) was determined for the infauna.

The relationship between primary feeding types and sediment composition was investigated. Suspension feeders were clearly the major feeding types in coarser sediments, while selective and nonselective deposit feeders dominated the finer sediments.

A new association of animals, the *Nephtys incisa-Yoldia limatula* community is described. This soft bottom community is limited to sediments containing more than 25% silt-clay and is found at depths of from 4 to at least 30 m.

### ACKNOWLEDGMENTS

G. A. Riley, E. F. Thompson and G. E. Hutchinson gave considerable advice on many matters relating to this study. The analyses of the sediment were carried out with the facilities of the Soil Department of the Connecticut Agricultural Experiment Station, where T. Tamura generously gave his time and supervision in this aspect of the work. Miss Olga Hartman, P. A. Morris and Willard Hartman identified or verified the identity of certain specimens. The field work was done aboard the U. S. Fish and Wildlife Vessel SHANG WHEELER with the assistance of its skipper, H. R. Glas. The facilities of the U. S. Fish and Wildlife station at Milford, Connecticut were always available and the staff, particularly the director, Victor Loosanoff, was helpful in many ways. The manuscript, read by G. A. Riley, E. F. Thompson, Daniel Merriman and G. E. Hutchinson was greatly improved by their constructive suggestions. Finally, my wife, Lillian Sanders, undertook the tedious tasks of preparing the illustrations and of typing and retyping the manuscript. To all of these persons, individually and collectively, I am indebted.

### INTRODUCTION

Since 1911 numerous quantitative bottom investigations have been undertaken in many parts of the world, particularly in northwestern Europe. However, with the exception of a single modest study in the Cape Cod region of Massachusetts (Lee, 1944), no quantitative survey of bottom communities from any region of the eastern coast of North America has been published. The present investigation, within the limited area of Long Island Sound, was undertaken in an attempt to correct this condition.

This study represents a single component of a comprehensive oceanographic and biological survey of Long Island Sound carried out by members of the Bingham Oceanographic Laboratory of Yale University. Aspects that will be considered in this paper are: (1) species composition of the benthic populations; (2) quantitative evaluation of benthic animals; (3) relation of biomass to physical factors, such as sediment composition; (4) the effect of certain physical factors on the distribution of the primary feeding types of benthic animals; (5) comparison of biomass and numerical values in Long Island Sound with those found in other regions; (6) life histories of



the more important dominant species; (7) productivity and the standing crop; and (8) a description of the benthic communities of Long Island Sound.

### METHODS

The central area of Long Island Sound (see Fig. 1) was investigated for a period extending from the summer of 1953 until the fall of 1954. Collections were made aboard the U. S. Fish and Wildlife Vessel, SHANG WHEELER, stationed at Milford, Connecticut. Eight stations were set up as shown in Table I.

TABLE I. LIST OF STATIONS

Station	Latitude, N	Longitude, W	Depth (m)	Bottom Temperature °C		Bottom Salinity ‰	
				Max.	Min.	Max.	Min.
Charles Is.	41-11.3	73-06.4	6 - 8	*	*	*	*
1	41-11.1	73-01.8	10 -12	22.10	1.55	28.67	24.77
2	41-08.0	72-53.9	19 -22	21.95	1.85	28.73	24.84
3	41-06.3	73-00.2	27 -29	21.65	2.15	28.87	25.45
4	41-04.9	73-05.2	18.5-22.5	21.95	1.85	28.69	25.35
5	41-01.4	72-58.6	28.5-31	21.60	1.25	28.76	24.78
7	41-13.6	72-50.6	10 -13	22.00	0.80	28.96	24.70
8	41-14.6	72-46.4	11.5-14	22.05	1.35	29.18	25.02

\* Not taken.

Charles Island and Sts. 1 and 3 were sampled every other month; Sts. 4, 5 and 7 every three months; Sts. 2 and 8 twice yearly.

In the present study, consideration of currents is particularly important from the standpoint of the food supply of suspension feeders. Strong currents have the double effect of rapidly renewing the water in the immediate vicinity of the bottom and of resuspending particles that have settled out while weak currents would be less effective in these respects. In addition, a weak flow permits an accumulation of silt and clay which forms a surface that tends to hamper resuspension of organic materials, as will be described later.

The general order of magnitude of maximum current speed at approximately one meter from the bottom was 20-35 cm/sec in the central area, and the average speed of the entire tidal cycle was about two-thirds of the maximum current speed (see Riley's PHYSICAL OCEANOGRAPHY in this volume). Since there are only minimal differences in the measured currents from one station to another, and since the current speeds decrease toward bottom, it is difficult to get an accurate measurement close enough to bottom to be useful for present purposes.

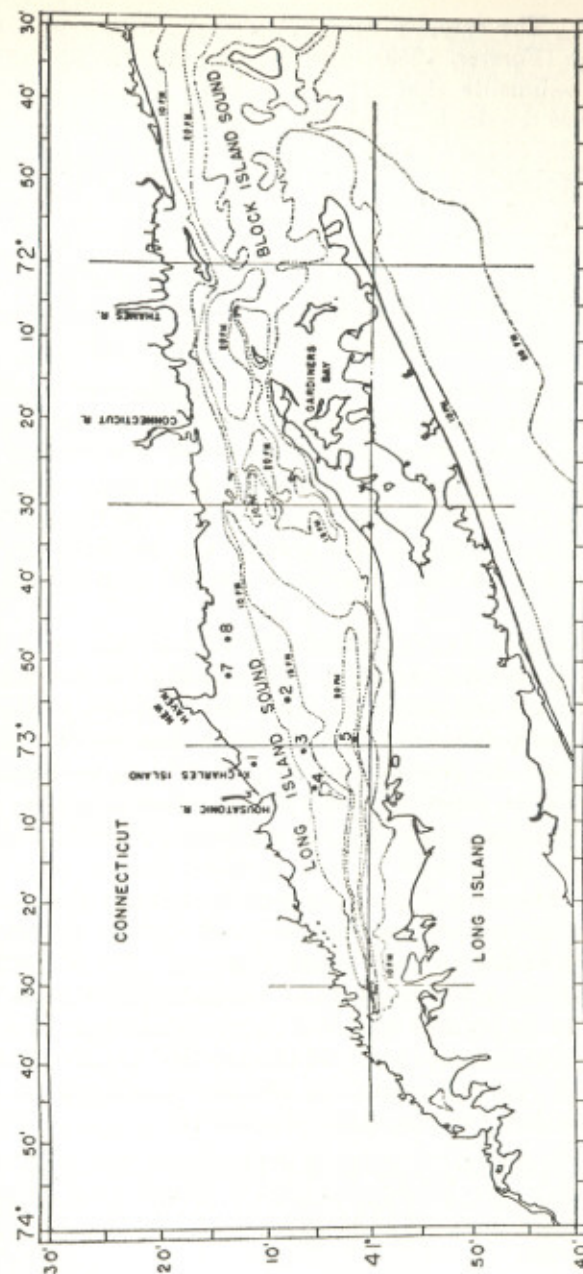


Figure 1. Map of Long Island Sound showing the location of the eight stations occupied in the survey.



*Equipment.* The samples were collected by means of a modified anchor dredge (Forster, 1953) which was designed to obtain samples from sandy sediments that are inadequately sampled by ordinary dredges. Since the dredge, loaded with sediment, was often damaged against the sides of the vessel in rough seas, it was necessary to build a protective frame around the instrument. To facilitate digging, bars of lead were placed within the frame, particularly over the digging edge, thus increasing the weight of the dredge from 25 to 85 pounds. The dredge cut to a depth of 7.6 cm in all types of sediments, and a small-meshed burlap bag attached to the frame caught and retained the sediment that passed into it.

*Treatment of Samples.* Each sediment sample was emptied into a large bucket where it was divided into three parts and then measured. Large fractions, such as those of about 13,000 cc, were washed through a No. 10 sieve; smaller fractions of about 1,500 cc were put through a No. 50 sieve to retain the smaller organisms. Since the gear dug to a depth of 7.6 cm, the area of the sample was obtained by dividing the volume by 7.6. About 500 cc were saved for mechanical analysis of the sediment.

The organisms in both large and small fractions were carefully picked out and sorted to species; each individual of a nondominant form was counted and weighed with other members of its species. Initial use of wet weight gave such unreliable data that the use of dry weight was adopted. Specimens were placed in an oven and heated at about 100° C to constant weight, after which they were weighed on a sensitive balance. The calcium carbonate of mollusc shells was removed by use of dilute hydrochloric acid.

For each of the numerically abundant (dominant) species, a series of graduated size ranges was obtained and individuals were stored in formalin according to their length category. When enough individuals of each size group had been accumulated, the total dry weight was obtained in the manner described above and this figure was divided by the number of animals used. In this manner an exact relationship between length and dry weight was obtained for the various sizes of each of the dominant species (see Appendix I).

*Mechanical Analysis.* One of the important factors in a study of benthic communities is the character of the bottom which the animals inhabit. Since particle size analysis has been extensively

studied by soil scientists, their standard procedures (Buoyoucos, 1936) were employed in this study. First the air-dried sediment was gently ground in a mortar equipped with a rubber tipped pestle and then sieved through a 2 mm round hole screen. The portion retained on the sieve was the gravel component. A portion of the residue, usually either 50 or 100 g, was placed in suspension in a mechanical agitator, and one cc of sodium oxylate and one cc of sodium hydroxide were added. Sodium oxylate is a dispersing agent in itself and sodium hydroxide has the effect of raising the pH and thus enhancing further the dispersing action. The solution, after agitation in a Waring blender for 5-10 minutes depending on the size of the sample, was placed in a Buoyoucos cylinder to which water was added to bring the water column to the desired level. The solution was again agitated for at least one minute by means of a manual agitator so as to force all of the material into suspension.

Different size particles settle out at different rates of speed, the larger the particle the more rapid the settling. In this procedure the changes in density of the medium at given intervals of time were measured and the percentages of the different size particles were determined. At the end of 40 seconds, when all sand-size particles had settled out, hydrometer and temperature readings were taken. Since temperature alters the density of the medium, it was corrected to 57° F; for every degree over 57° F, 0.2 was subtracted from the hydrometer reading, and for every degree under, 0.2 was added. Readings at the end of 15 minutes, one hour and two hours gave the concentrations by weight of coarse silt (50-20 $\mu$ ), medium silt (20-5 $\mu$ ), fine silt (5-2 $\mu$ ) and clay (< 2 $\mu$ ).

The sand fraction, which was retained and dried in an oven, was passed through a series of sieves having apertures of 1.0, 0.5, 0.25, 0.105 and 0.049 mm. The sand retained on each of these screens was weighed to obtain a measure of very coarse (1.0-2.0 mm), coarse (0.5-1.0 mm), medium (0.25-0.5 mm), fine (0.105-0.25 mm) and very fine (0.049-0.105 mm) sands.

During the preliminary dispersing treatment there was a great deal of flocculation of the finer particles due to excess salt in the marine sediments, hence it was necessary to modify the procedure. To remove this excess salt, the sample was centrifuged a number of times with distilled water and after each centrifugation the clear supernatant was decanted off. This procedure was continued until the solution







TABLE III.—Continued

Location and Date	Gravel ^ 2.0mm	Sand					Silt			Clay ^ 2μ	Type of Soil	Shell
		Very Coarse 1.0 < 2.0mm	Coarse 0.5 < 1.0mm	Medium .25 < 0.5mm	Fine .105 < 0.25mm	Very Fine .049 < .105mm	50-20μ	< 20-5μ	5-2μ			
Station 1—Continued												
8/20/54	14.56	79.887					2.392	0.769	0.256	2.136	Gravelly sand	5.65
		5Y-7/1-7/2 light gray										
Station 4												
8/23/53	9.70	10.183	25.607	28.700	17.962	0.986	1.535	0.181	1.174	3.973	Coarse sand	—
		2.5Y-5/2 gray brown										
5/20/54	27.89	5.375	17.924	10.280	32.640	0.911	0.793	0.433	0.288	3.461	Very gravelly coarse sand	0.28
		10YR-6/3-6/4 light yellowish brown										
7/2/54	12.82	16.308	30.040	17.946	17.332	0.322	1.221	1.133	0.262	2.615	Gravelly coarse sand	0.29
		2.5Y-6/2 light brown gray										
Station 5												
2/18/54	3.83	2.641	22.242	12.202	33.835	1.207	6.732	3.270	1.923	12.117	Coarse sandy loam to sandy loam	—
		5Y-6/1-6/2 light olive gray—gray										
5/20/54	0.33	1.170	27.833	26.895	35.537	0.159	1.595	0.797	1.196	4.485	Coarse sand	—
		2.5Y-6/2 light brown gray										
7/2/54	3.74	6.441	35.846	15.814	14.573	0.290	5.583	3.658	1.540	12.514	Coarse sandy loam	—
		5Y-6/1 gray										

TABLE III.—Continued

Location and Date	Gravel ^ 2.0mm	Sand					Silt			Clay ^ 2μ	Type of Soil	Shell
		Very Coarse 1.0 < 2.0mm	Coarse 0.5 < 1.0mm	Medium .25 < 0.5mm	Fine .105 < 0.25mm	Very Fine .049 < .105mm	50-20μ	< 20-5μ	5-2μ			
Station 2												
7/23/54	0.00	1.548	6.447	10.176	25.629	0.000	19.80	10.80	4.6	21.0	Loam	—
		43.800										
		5Y-7/1-7/2 light gray										
Station 7												
5/20/54	3.44	7.789	17.923	6.679	23.600	4.263	12.553	5.600	1.159	16.994	Coarse sandy loam to sandy loam	2.91
		60.254										
		5Y-7/1 (mainly) -8/1 light gray										
Station 8												
7/23/54	0.00	72.000					15.4	4.2	0.8	7.6	Coarse sandy loam	1.00
		5Y-6/2-7/2 light olive gray—light gray										
Station 3												
2/13/54	0.00	0.537	1.842	1.543	5.939	15.543	22.4	11.0	7.2	34.0	Silty clay loam	—
		25.404										
		5Y-7/1-7/2 light gray										
4/19/54	0.00	0.509	2.244	1.599	14.103	10.345	20.4	11.4	6.0	33.4	Silty clay loam	—
		28.800										
		5Y-6/1 gray										
6/29/54	0.00	0.00	0.00	1.339	10.238	13.023	9.8	13.4	6.4	45.8	Silty clay	—
		24.600										
		5Y-6/1-7/1 light gray—gray										
8/20/54	0.00	40.4					19.6	9.4	4.4	26.2	Loam to silty clay	—
		5Y-6/1 gray										



a significant fraction of shell was present it was placed in a separate column and its percentage computed.

It is somewhat difficult to compare the sediment analysis of this investigation with that of previous studies because of the variety of standards used. Beanland (1940) separated the particles into three grades: sand, with a minimum diameter of 0.04 mm; silts, with a minimum of 0.01 mm; and fine silts, with a minimum of 0.002 mm. The proportions of the three components in each sample were added and the mean-sized particle or "Representative Number" was determined. This was multiplied by a factor of 100 to give the whole number which was used to characterize the sample.

Fraser (1932), working in estuarine mud, divided his sediments into the following grades: (1) above 0.1 mm; (2) between 0.06 and 0.1 mm; (3) between 0.02-0.06 mm; (4) below 0.02 mm; and finally silt. Crawford (1937), using the procedure of Allen (1899), separated the sediment into eight grades: stones, coarse gravel, medium gravel, fine gravel, coarse sand, medium sand, fine sand, and silts; these were defined as materials which will not pass through sieves of 15, 5, 2.5, 1.5, 1.0, 0.5 mm, material which will pass through a 0.5 mm sieve but which settles out in one minute, and particles which remain in suspension at the end of one minute. Holme (1949, 1953) employed the Wentworth grade scale, using sieves of the following apertures: 2.0, 1.0, 0.5, 0.25, 0.20 and 0.125 mm; particle separation at 1/32 mm was made by repeated decantations. Aside from the large number of scales used, these works suffer from failure to separate the clay from the silt fraction.

Compared to the works referred to above, even the coarser sediments (see Sts. 1 and 4) in the present study yielded appreciable fractions of clay particles. Certain samples, primarily from St. 3, gave larger concentrations of clay than any of those obtained by the above investigators. Although these larger concentrations may reflect high concentrations of these particles in certain deposits in the Long Island Sound area, it is probable that they are due in large measure to the technique used. More accurate procedures for mechanical analysis with pipetting techniques are published by Soil Survey Staff (1951), but such techniques are much more time consuming than the Buoyocos hydrometer method unless a laboratory is specially equipped to do mechanical analysis. The values obtained for the silt-clay content by the Buoyocos method are

probably somewhat low. At any rate, the low values reported for these fractions in previous benthic studies lead one to suspect that the techniques used have involved serious losses of these components.

#### QUANTITATIVE EVALUATION OF BENTHIC ANIMALS

*Results in Long Island Sound.* In 36 samples, taken from August 1953 to September 1954, 135 animals were found, 119 of which were identified to species (see Appendix II). Included among these was *Hutchinsoniella macracantha*, which represents a new subclass of

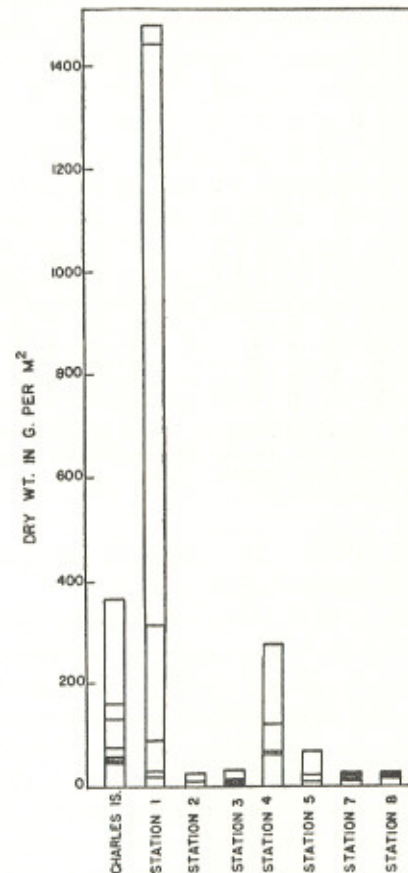


Figure 2. Total dry weight of each sample by station. The height of each horizontal line from the baseline represents the biomass of a single sample.



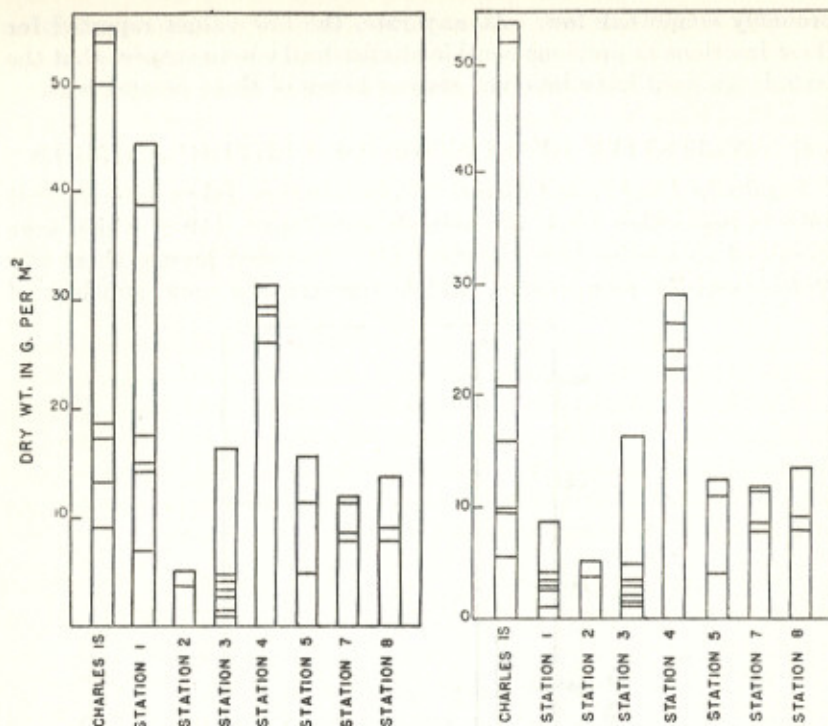
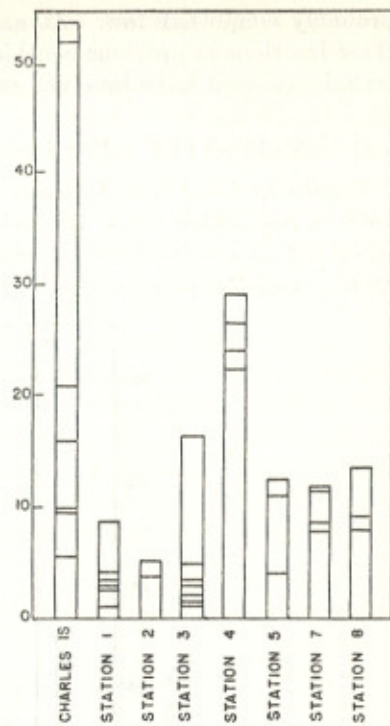


Figure 3. Dry weight of animals weighing less than 0.2 g in each sample by station. Height of each horizontal line from baseline represents the biomass of a single sample.

Figure 4. Dry weight of infauna weighing less than 0.2 g in each sample.



Crustacea (Sanders, 1955). The analyses of some representative stations are shown in Appendix III.<sup>1</sup>

In this investigation, as in others of a similar nature, the biomass frequently varied widely from sample to sample and from station to station. For instance, Holme (1953) found great variance between successive hauls at the same location and between pairs of samples from the same haul. It is apparent in the total dry weights of all samples in the present study (see Fig. 2) that the biomass varied widely in different samples from the same station, particularly those from Charles Island and from Sts. 1 and 4. Such large differences have resulted primarily from the occasional random distribution

<sup>1</sup> Complete data may be obtained from the Bingham Oceanographic Laboratory.

of certain large epifaunal animals such as *Libinia emarginata*, *Cancer irrorata*, *Ovalipes ocellatus*, *Pagurus pollicaris*, and *Asterias forbesi* whose size was sufficient to increase the weight of a sample anywhere from 200–5,000%. However, as shown in Fig. 3, if the large organisms are excluded and if only those individuals which weigh 0.2 g (dry weight) or less are included, then a greater degree of uniformity and a more workable correlation of biomass to its environment are achieved. Hereafter animals within this weight range will be referred to as "small animals." An even better homogeneity is achieved when only small animals of the infauna are considered (see Fig. 4). The infauna is defined in the manner of Petersen (1913) as "animals connected with the level sea bottom," these being forms that burrow or live in the sediment. The epifauna, on the other hand, consists of those forms which are found on the sea bottom and which may be sessile attached or motile. When only small animals of the infauna are considered, each station can be characterized by a relatively narrow range of biomass values.

Charles Island. Excluding two aberrant samples, this station supports an infauna of 5.70–20.90g/m<sup>2</sup> and its sediments contain less than 6% gravel, about 89% sands, 3.5% silts, and 4% clay. The predominant sand grain, making up 37–50% of the entire sediment by weight, is fine (0.25–0.105 mm). Shell, if included in the analysis, would comprise 4%. The sample with the highest silt-clay content (April 30, 1954) had the heaviest biomass, 20.90g/m<sup>2</sup>.

The two samples excluded from the above discussion (August 17, 1953; October 28, 1953) differed from the others in that their silt-clay content was approximately 20% greater; their recorded biomass was 53.0 g/m<sup>2</sup>. These data suggest a positive correlation between silt-clay content and biomass values at Charles Island.

Station 1. The infaunal contribution to the biomass, 1.14–8.74 g/m<sup>2</sup>, with the mode about 3.40 g, was small in that it was only one-fifth as large as the small animals in the epifauna (see Figs. 3, 5). The sediments at this station, which were very coarse, consisted of: gravel, 15–36%; sands, 60–76%; silts, about 2.5%; and clays 2.2%. A significant fraction of shell, largely from the oyster *Crassostrea virginica*, was present also: 6–17%.

Station 2. The sediment was characterized by a high fraction of silt and clay, the silts averaging 35%, the clays 21%. Sands



constituted the remaining 44%; gravel and shell were absent. The biomass of the infauna varied from 3.80–5.70 g while the epifauna contributed almost nothing to the standing crop.

Station 3. Here was found not only the highest silt-clay percentage of any station in the survey but also the lowest values for total biomass and infauna; almost no epifauna was present. Six of the seven infaunal values varied from 1.14–4.94 g/m<sup>2</sup>, and the seventh (Aug. 11, 1953), 16.49 g, was made up largely of a single species, *Nucula proxima*, which comprised more than 80% of the biomass. The sediment consisted of the following: sands, predominantly the finer grades, 24–30% by weight; gravels and shells, 0; silts, 28–40%; and clays, 26–45%. In contrast to the findings at Charles Island, the significantly larger silt-clay content at Sts. 2 and 3 is associated with low biomass values.

Station 4. Composition of the sediment at this station differed drastically from that at Sts. 2 and 3. Gravels made a major contribution with 9–28%; sands, 66–83%; silts, 1.5–2.9%; clays, 2.6–4.0%. Shell, if included, would have comprised only a fraction of one percent of the sample. When the largest animals were excluded, the infauna component was by far the most important part of the biomass, yielding relatively high values: 22.42–29.26 g/m<sup>2</sup>.

Station 5. Here two different types of sediments were found. Two of the three samples were composed of 3.8% gravel, 72–73% sand, 10.5–12% silt, and 12–12.5% clay; the biomass of the infauna was somewhat intermediate, with values varying from 11.02–12.54 g/m<sup>2</sup>. The third sample (May 20, 1954) contained a much higher fraction of sand, 91.6%, while gravel, silts, and clays comprised only 0.3, 3.6 and 4.5% respectively. The biomass value was low, 4.03 g, or about one-third of the standing crop found in the other two samples.

Station 7. Again the population was largely represented by infauna, the biomass values being intermediate, from 7.60 to 12.16 g/m<sup>2</sup>. The gravels, sands, silts and clays constituted approximately 3.5, 60.0, 19.5 and 12.0% respectively. Shell comprised less than 3% of the sample.

Station 8. This station was also characterized by intermediate biomass values, 7.60–14.0 g/m<sup>2</sup>. The sediments were made up of about 72% sands, 20.5% silts and 7.5% clays. Gravels were not present and shell made up only a minute fraction of the sample.

Although samples were taken at all seasons of the year, seasonal variations were not great enough to mask differences in biomass between stations. In fact, the biomass values were so distinctly different that it is reasonable to assume that the seasonal effect was of secondary importance. On those few occasions when one or two samples from a station departed widely from average values, it was found that such departures were associated with abnormal sediment composition (e.g., Charles Island and St. 5). Thus they represented different sediment environments rather than seasonal fluctuations.

The reason for the characteristic biomass values of each station is more difficult to explain. For example, why were the infauna of the two stations with the coarsest sediments so different? At St. 4, where no shells were present, the biomass was six times greater than that at St. 1, where shells were abundant. Since the shells at St. 1 were large and relatively flat (*Crassostrea virginica*) and since they were probably distributed for the most part on or near the surface, is it not feasible to assume that the infauna was unable to make contact with the surface sediment and was thereby excluded from the sediment when such shells were present. Thus we may postulate that the size of the infauna may be influenced in part at least by the extent to which the available bottom is covered by shells.

Also, from the data we find that there is a fairly definite relationship of infaunal values to the amount of silt and clay in the sediment. That is, assuming other factors equal, the infauna increases with increasing amounts of silt and clay up to a certain point and then decreases with further increase of silt and clay fractions. For example, at Charles Island and at St. 5, when the silt content was low, the infauna increased with increasing amounts of silt and clay. Sts. 2 and 3, with large silt-clay concentrations of 60–75%, yielded the smallest infaunal values. St. 7, with a silt-clay content of about 32%, gave appreciably higher values. It appears, then, that silt-clay concentrations which are too small or too large restrict or reduce the size of the biomass. Hence we postulate an optimal concentration of silts and clays for the development of maximal infaunal populations. The optimal range in this study is estimated to be 13–25% silt-clay, with deviations in either direction from these values yielding progressively smaller biomass values.

The mean dry weights of small infauna and epifauna at each station (Fig. 5) show that significant epifaunal values were found at stations



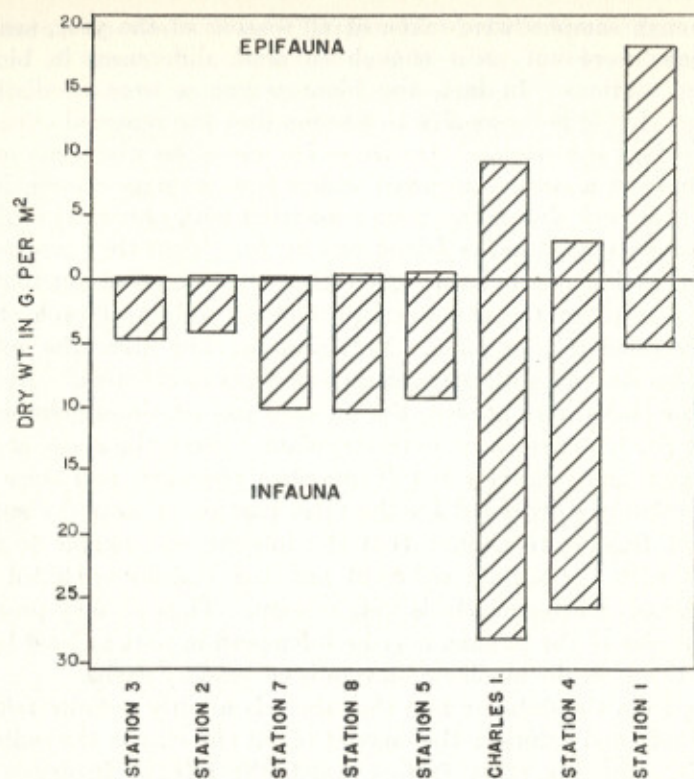


Figure 5. Mean dry weight of small infauna and epifauna at each station.

having hard sandy substrates, that is, Charles Island and Sts. 1 and 4. The remaining stations provided neither the stability nor solidity to develop such large populations.

Table IV gives the mean number of animals characteristic of each station. The large values for Charles Island, 46,398, were primarily due to high silt-clay concentrations in the two samples taken on August 17 and October 28, 1953: 173,120 and 98,507 animals/m<sup>2</sup> respectively.

Although the larger animals were numerically insignificant in comparison with the great numerical predominance of the smaller ones, they still made an important contribution to the standing crop. Table V gives the number and weight composition of the large animals for each station.

TABLE IV. MEAN NUMBER OF ANIMALS CHARACTERISTIC OF EACH STATION

Station	Animals (per m <sup>2</sup> )
Charles Is.	46,398
4	34,762
8	15,200
7	8,421
1	7,957
2	7,395
3	5,844
5	5,563
	$\bar{M} = 16,443$

TABLE V. NUMBERS AND WEIGHTS OF ANIMALS WEIGHING MORE THAN 0.2 g DRY WEIGHT

Station	Number (%)	Weight (%)
Charles Is.	00.160	49.89
1	00.163	92.19
4	00.049	29.32
5	00.228	41.42
2	00.051	51.45
3	00.018	16.58
7	absent	absent
8	absent	absent
	$\bar{M} = 00.140$	$\bar{M} = 35.11$

*Comparison with Other Areas.* It is almost impossible to compare directly the results of this study with those of previous investigations because of the varied methods and equipment. Sometimes the animals were only weighed, other times only counted; at least nine different types of sampling gear have been used, and the sieve sizes used in screening out the organisms have been almost as varied as the gear; finally, calculation of animal weight has varied widely with each individual survey. However, in spite of the diverse nature of previous work, an attempt has been made to compare the numerical results of some of these investigations by plotting mesh size against the log of the number of animals per square meter (Fig. 6).

Even with sieves of 0.5 and 1.0 mm apertures, Miyadi (1940, 1941, 1941a) obtained extremely low values (266-1,290 animals/m<sup>2</sup>) from various Japanese bays, probably due to the small size of his bottom samples, 1/37m<sup>2</sup> with the Eckman grab and 1/50m<sup>2</sup> with the Eckman-Lenz grab.



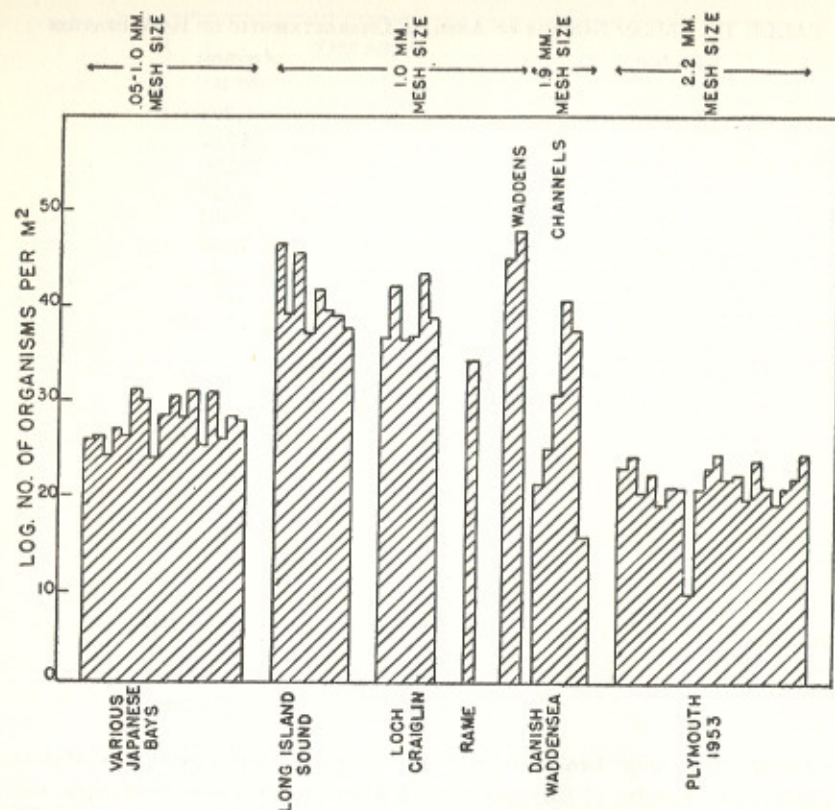


Figure 6. Numerical comparison of Long Island Sound with other regions. Each histogram consists of individual components that represent individual stations. For example, the Plymouth histogram represents 20 stations.

In other surveys, including the present study, sieves with 1 mm apertures were also used. Raymont (1949), in his studies of the effect of fertilizers on an enclosed Scottish loch, obtained values over a period of five years that varied from 4,554 to 23,014 animals/m<sup>2</sup>; however, if we exclude the two peaks which appear to result directly from addition of fertilizers, then the upper limit of the range would be 7,451 organisms/m<sup>2</sup>. In a single sample of macrofauna, Mare (1942) obtained a numerical value of 2,356 animals/m<sup>2</sup> during her investigation of various trophic levels in a bottom community of the open shallow coast near Plymouth. In Long Island Sound the mean values for the eight stations varied from 5,566 at St. 5 to 46,404

animals/m<sup>2</sup> at Charles Island, with the average of the means being 16,446.

Although Smidt (1951) studied intertidal flats or "waddens" rather than permanently submerged areas, his investigation was the only one of those considered that showed populations which were as large or larger than those of the Sound (31,000/m<sup>2</sup> during July-August 1941 in the southern area; 63,600/m<sup>2</sup> at Skallingen, August 1942). Since most of his values consisted of 0-group or newly settled lamellibranchs, samplings at other times of the year, particularly during winter and spring, might reveal sharply reduced numbers. Smidt also took samples from the shallow channels in the waddens (2-8m), and in these permanently submerged areas he found greatly reduced numbers, about 40-11,100, with a mean value of 3,073 animals/m<sup>2</sup>. Only a partial explanation for this wide difference in subtidal areas can be found in the fact that he used a screen with 1.9 mm mesh.

Holme (1953), in an extensive survey of the English Channel, sampled a grid of 20 stations and passed the sediment contents through a 2.2 mm sieve. The number of animals per sample ranged from 10-292, with a mean of 160/m<sup>2</sup>. He then passed the residue from one of these samples through a 1.2 mm sieve; 28 animals were retained on the larger screen and 70 additional specimens were retained on the smaller screen. Although Holme's samples were taken close to the same general locality investigated by Mare, he found a whole order of magnitude less than that reported by Mare. The great discrepancy was probably due to sampling error, although differences in mesh size may have been a contributing factor.

From this brief listing of results, it is apparent that Long Island Sound, in contrast to other regions, supports significant numbers of benthic animals. Even when one considers the varying methods and techniques of other investigators it is probable that the number of animals in a unit area of bottom in Long Island Sound is as high as that found in any other extensive, permanently submerged area.

Comparison of biomasses from the various areas investigated is even more difficult than a comparison of numbers. Frequently the larger and less abundant animals are not adequately represented in small samples and their inclusion then leads to distortion in the biomass calculations. In view of the fact that it is impossible to separate out this component in many of the investigations, such data are excluded from the comparison in Fig. 7.



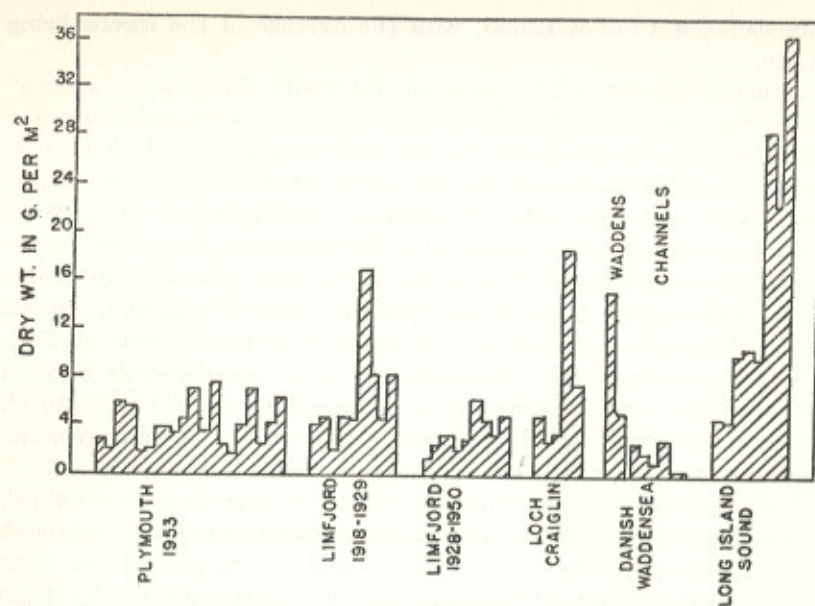


Figure 7. Comparison of the weight of the biomass of Long Island Sound with other regions. See explanation in Fig. 6.

In the present study the animals are separated after the manner of Holme (1953) into those that weigh more (large animals) than 0.2 g dry weight and those that weigh less (small animals), excluding molluscan shells. Keeping in mind the different mesh sizes used, the results of this study are directly comparable to those of the Plymouth studies; in Fig. 7 the components smaller than 0.2 g from both surveys are illustrated. Also included in Fig. 7 are the dry weights obtained from the Loch Craiglin fertilization experiment (Raymont, 1949), since all of the bottom samples consisted of small animals, with few if any larger organisms.

Other results used in Fig. 7 are obtained indirectly. The biomass figures for the long range investigation at Limfjord (Blegvad, 1928, 1951) were given in "rough weight," which is defined by Blegvad as "the weight of animals somewhat free of water and molluscs where the shell was opened to drain off excess water." This term, then, is equivalent to wet or live weight. Since Petersen and Jensen (1911) worked out the relationship between wet and dry (decalcified in the case of molluscs) weight for a number of the more common

animals found in Limfjord, we have used these ratios to change Blegvad's values to dry weights. When there was no equivalent dry weight percentage given, as in the case of some molluscs or polychaetes, an average of the range of values found in that group was used. For example, Petersen's (1918) dry weight range for small bivalves was 5-8%, for polychaetes 16-20%; thus the means of these groups, 6.5% and 18%, were used. Furthermore, the Danish workers included in their biomass values only those animals which were eaten by the plaice; this so-called "plaice food" consists of most of the smaller macrofauna found in Limfjord. Here it is assumed that plaice food is equivalent to that component of the biomass that weighs less than 0.2 g dry weight in the Plymouth and Long Island Sound surveys. While this is approximately true, a few forms like the gastropod *Nassarius*, which are included in the values for the Long Island Sound investigation, would be excluded from the plaice food determinations.

Since the populations found in the Danish intertidal areas (Smidt, 1951) were essentially the same as those in Limfjord, the same corrections were applied.

All of these localities, in common with Long Island Sound, are situated in shallow water, and some, as in the case of Limfjord and Loch Craiglin, are enclosed environs. It is apparent from Fig. 7 that, among the benthic macrofauna which were small enough to be adequately sampled, the biomass in Long Island Sound was much greater than that in the other localities, even when the peak value in Loch Craiglin, due to fertilization, is considered.

Reference to Fig. 6 shows that the numerical values for the waddens at Skallingen were higher than any of those from Long Island Sound, whereas the biomasses from Skallingen were much smaller, due primarily to the fact that the newly-settled spat at Skallingen contributed significantly to the numerical value but added little to the biomass.

*Environmental and Biological Conditions.* Spärek (1935) has reviewed the available results of bottom studies and has tried to relate them to various climatic and hydrographic factors. With other factors equal, he found that the shallower the water the greater the benthic biomass. Much higher values were obtained at Limfjord than in deeper waters in the same general locality. The smallest values were obtained in nutrient-poor waters, such as the Mediterranean, White Sea and East Greenland fjord, while maximal values



were found in areas of considerable water renewal surrounded by regions of high precipitation.

Long Island Sound is shallow, averages only about 20 m in depth, and has a maximum depth of about 100 m at the eastern end. This somewhat enclosed body of water is about 90 miles long and 15 miles wide. The drainage area is approximately 11 times greater than the Sound itself, and the annual volume of nutrient-rich freshwater drainage is approximately 35% of the volume of the Sound (see Riley's PHYSICAL OCEANOGRAPHY in this volume). The most important feature of the nontidal circulation in the Sound is a two-layer exchange; the lighter surface water, which has become somewhat deficient in nutrients as a result of phytoplankton growth, moves eastward out of the Sound while a more saline bottom current, whose nutrient-rich water is readily made available for photosynthesis, flows westward. Thus two mechanisms are responsible for the high concentrations of nutrients, the extensive freshwater drainage and the two-layer transport exchange just described.

During the midwinter nutrient maximum, the total nutrients under a unit column of water in the Sound are about the same as those in the English Channel despite the fact that the mean depth in the English Channel is 70 m compared with only 20 m in the Sound; thus the nutrients/m<sup>3</sup> in the Sound are about 3.5 times greater than those in the Channel; furthermore, the longer the water column the less efficient the vertical transport of nutrients to the euphotic zone. It is not surprising, then, that the average standing crop of phytoplankton in the Sound is four times that in the Channel. However, the zooplankton populations in the Channel appear to be only slightly smaller (ratio of 3:4) than those in the Sound. Assuming all other things equal, this implies that the zooplankton in the Channel utilize a much larger fraction of the available phytoplankton than do those of the Sound. The portion of phytoplankton not consumed by zooplankton is available to other groups such as the bacteria in the water column and the macro-, meio- and microfauna and flora found on the bottom. Since the water column in the Sound is much shallower on an average than that of the Channel, the bacteria in the water column of the Sound would have less time to exploit the sinking phytoplankton cells. Thus, relatively huge quantities of plankton are probably available to the bottom dwelling organisms of Long Island Sound in contrast to those in the English Channel.

This hypothesis finds support in the results of the present investigation and in the studies of Mare (1942) and Holme (1953). Mare, using a 1.0 mm sieve, obtained 2,356 animals/m<sup>2</sup> in the Channel while the average of the means for eight stations in the Sound, using the same sieve size, was 16,446/m<sup>2</sup>; thus we have a ratio of 7 : 1. The mean total dry weight given by Holme for the Channel was 11.2 g/m<sup>2</sup> while the figure obtained for the Sound was 54.627 g/m<sup>2</sup>. If one considers only the smaller more abundant animals, then the value for the Channel would be 4.0 g and that for the Sound 15.88 g/m<sup>2</sup>. Therefore the bottom macrofauna values for the Sound appear to be about 4-5 times larger than those for the English Channel.

#### LIFE HISTORIES

*Nephtys incisa*. Of the samples taken in this study, this polychaete constituted a large fraction of the biomass in the softer sediments, where it made up 27.6, 31.7, 33.7, 34.6 and 39.1% of the small animals at Sts. 2, 7, 5, 3 and 8. On the harder sediments, where it was an insignificant member of the population, it comprised only 2.0, 0.8 and 0.9% of the biomass at Charles Island and at Sts. 4 and 1.

The dry weights of this animal have been plotted against the silt-clay content of the sediment, and, as shown in Fig. 8, *N. incisa* was either absent or gave quite low values. At higher concentrations of silt and clay the values rose rapidly to a maximum at about 26%. Thereafter the values dropped but remained relatively high until the sediment contained about 70% of silt and clay. Beyond this point the values diminished sharply but never reached the low found in the hardest sediments.

Apparently *Nephtys incisa* feeds indiscriminately in much the same manner as an earthworm. In many samples its entire gut was full, and the alimentary canal contained the sediment in which the animal lives. The interdigitating processes at the end of its everted proboscis are better adapted for taking in large portions of sediment (much as an earth-remover) than for seizing prey, and the proboscis, when inverted, brings the sediment to the beginning of the alimentary canal. As the sediment is carried backward through the gut, the organic matter is probably removed and utilized. In view of these observations, together with the fact that it comprises a third of the biomass in soft, highly organic sediments, it is difficult to accept the opinions that this species is a carnivore (Smith, 1932; Mare, 1942;



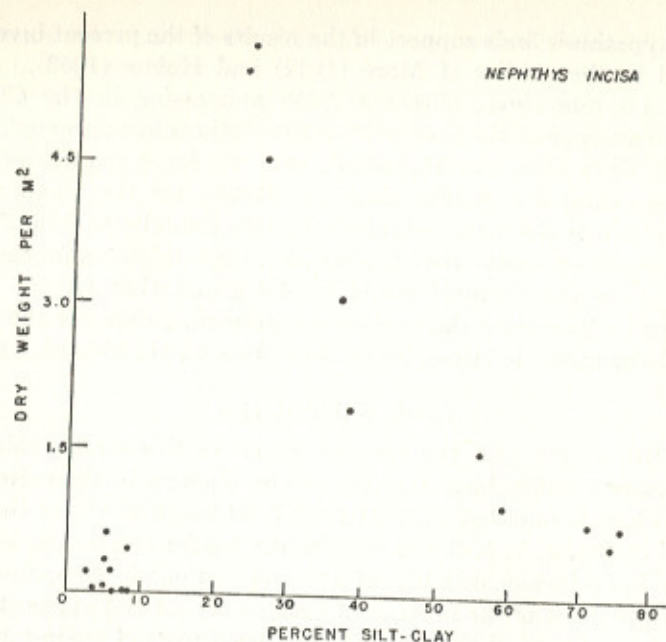


Figure 8. Relationship of biomass to sediment composition of *Nephthys incisa* (weight in grams).

Blegvad, 1914). It is much more reasonable to suppose that it is an ooze feeder.

Presumably the low values found in hard sediments (Fig. 8) are due to the low organic content characteristic of such substrates and to the compactness of the soil which offers significant resistance to burrowing animals. With an increase in the silt-clay component, conditions become more favorable for a nonselective deposit feeder until an optimal silt-clay is reached. Then beyond this point the larger content of organic matter reduces the mud to make conditions less favorable for aerobic animals.

Growth rates for *N. incisa* have been difficult to determine, since the large spread in the size dimension of the year-classes gave a high degree of overlap. In the first sample, taken on 11 August 1953, two year-classes appear to be adequately represented, the newly metamorphosed animals and the one-year-olds; the average animal<sup>2</sup>

<sup>2</sup> Weight of the animal of mean length among animals in sample of a given year-class.

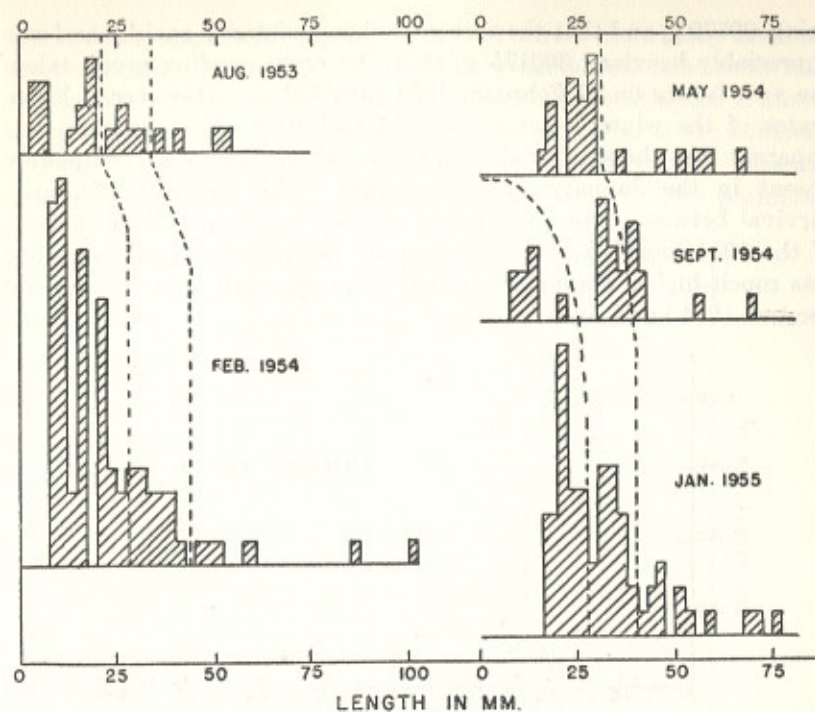


Figure 9. Histograms showing size distribution of *Nephthys incisa*. Interpretation of the limits of the year-classes is indicated by dotted lines.

in this group weighed .000230 g. The sample of 9 September 1953 gave adequate numbers of only the zero year-class, with the average animal weighing .000350 g; thus there were new recruits added to the zero year-class after the 11 August sampling. The February 1954 histogram (Fig. 9), a composite of four samples, shows that the zero year-class at this time weighed .000533 g and that the one-year-olds weighed .00803 g. By 20 May 1954 the zero year-class had grown rapidly to .00240 g, and by 23 July 1954 representatives of the newly spawned year-class were present, the average animal in this latter group weighing .00032 g, the one-year-olds .00350 g. By 19 September 1954, the one-year-old class doubled its weight to .00710 g while the weight of the zero year-group remained essentially the same as that in the 23 July sample, probably due to increased recruitment. The final sample, taken on 13 January 1955, showed that the rate of increase in the one-year-old group was somewhat reduced, its weight



being .00770 g, and that the zero year-class had grown rapidly and was appreciably heavier (.000175 g) than the corresponding group taken the year before on 10 February 1954 (.000533 g). However, if histograms of the winter samples of 1954 and 1955 are compared, it is apparent that the smaller sizes of the zero year-class were completely absent in the January 1955 histogram. This implies differential survival between animals spawned at the beginning and at the end of the 1954 breeding season; it is quite probable that the mortality was much higher among those that were spawned later, because of the two 1954 hurricanes.

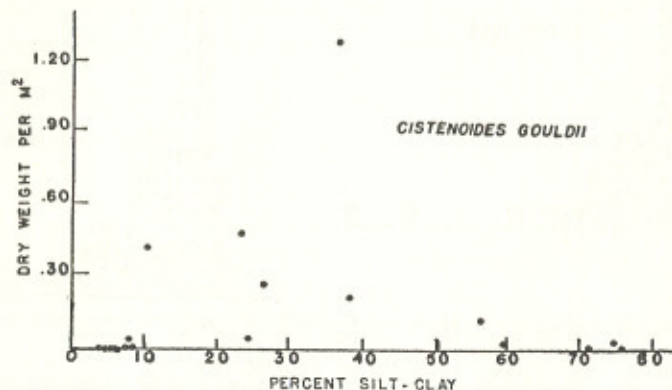


Figure 10. Relationship of biomass to sediment composition of *Cistenoides gouldii* (weight in grams).

A fair sample of the two-year-old class was also found in the January 1955 sample, the average animal weighing .0385 g (not shown in Fig. 9).

*Cistenoides gouldii*. The trumpet worm, a minor form at Charles Island, comprised only 0.7% of the population, while at Sts. 8, 5, 3, 2 and 7 it formed 2.1, 2.7, 3.3, 4.3 and 11.1% of the small animals. It was never encountered at St. 4, and at St. 1 it was present only as a trace of the biomass, constituting less than 0.1% of the population.

When the dry weight in a given square meter was plotted against the silt-clay content (see Fig. 10), it was evident that this polychaete was most abundant in intermediate sediments, since all of the higher values were confined to the 10-60% range of silts and clays.

The distribution pattern can best be understood in terms of its mode of life, which is probably quite similar to that of the closely related

European amphictenid, *Pectinaria koreni*, whose life history has been worked out by Watson (1927). The polychaete lives head downward in a conical sand tube which is open at both ends and which is almost completely buried, only the smaller end projecting out of the sediment. Through this opening, sand and faeces are discharged by muscular contraction and water is taken in for respiration. The prominent

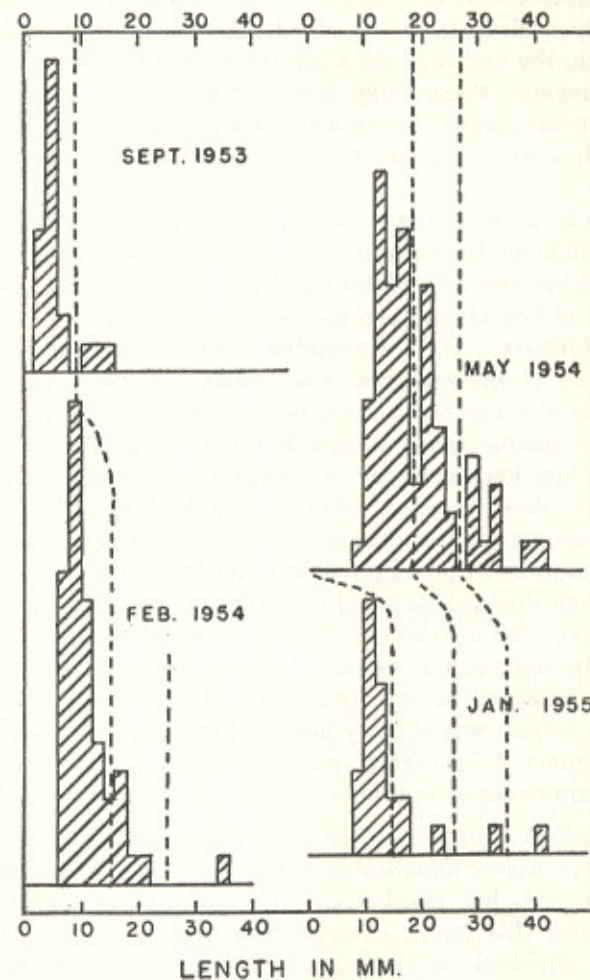


Figure 11. Histograms showing size distribution of *Cistenoides gouldii*. Interpretation of the limits of the year-classes is indicated by dotted lines.



large golden combs at the anterior end are used for digging, and the tentacles about the head have prehensile tips which bring sediment from above the head to the mouth; in time the cavity created by the digging causes a cave-in of additional nutrient-rich surface sediments. After extracting the organic matter, the animal either discharges the residual sediment at the surface or uses the sand for tube building. Thus the amphictenids are deposit feeders, and their absence from the sterile sandy sediments is explained. When the silt-clay content becomes high, the nature of the sediment is such that the soil becomes sticky or clayey. Presumably fresh sediments do not drain down from the surface, since the animal excavates from below. At any rate, in such a sticky substrate this mode of feeding becomes highly inefficient.

The growth of the trumpet worm, as in the case of certain other forms, was difficult to evaluate. Since a number of samples had to be discarded because a fair fraction of the smaller forms was missed, the division of the histograms into year-classes (Fig. 11) must once again be subjective. On 9 September 1953 a sample was composed predominantly of the zero year-class which had been spawned that summer, and the average animal of this group weighed .000125 g. A composite sample taken during February 1954 showed that the mean individual had increased in weight to .00041 g, the one year-group at that date weighing .0045 g. By 20 May 1954 both year-classes had grown rapidly during the intervening three months; the zero year-group had tripled its weight to .0014 g and the one year-class had more than doubled its weight to .0094 g; representatives of the two year-class, with a weight of .0223 g, were taken at this time also. No adequate sample was obtained again until 13 January 1955; this sample consisted almost exclusively of the new year-class, and the average animal was slightly heavier (.00072 g) than its counterpart of February 1954 (.00045 g). The similarity in form of both winter histograms seems to support the above interpretation of growth.

**The *Ampelisca* Complex.** The most important amphipods found in this survey were undoubtedly members of the genus *Ampelisca*. Reid (1951), who has pointed out the difficult taxonomic problem in dealing with this genus, observed that it is almost impossible to assign an individual to species within certain species complexes. No single animal has all the given characteristics of the species and individuals differ among populations regardless of whether the col-

lections are from widely scattered areas, from different habitats in the same area, or from a single locality.

Similar difficulties to those of Reid were encountered in trying to determine the specific identity of amphipods of this genus from the Sound. The two *Ampelisca* forms most frequently encountered fall within the *diadema-spinipes-tenuicornis* complex and are probably what Holmes (1903) and Kunkel (1918) have referred to as *Ampelisca spinipes*, but due to the confusion within the group, it was decided to leave both forms undescribed temporarily. For present purposes they are separated on the basis of size difference and habitat preference and are tentatively called *Ampelisca* A and *Ampelisca* B, hereafter referred to as merely A and B.

A, which was found in the harder sediments of the Sound, particularly at Charles Island and at Sts. 1 and 4, constituted 9.6, 5.2 and 2.5% of the small animals and 15.0, 29.1 and 2.8% of the infauna respectively at these same stations. When the sediment contained 30% or more silt and clay, A was replaced by B, a morphologically identical though significantly smaller form. At Sts. 8, 7, 3 and 2, B made up 4.1, 2.6, 0.5 and 0.8% of the small animals and only slightly greater percentages of the infauna: 4.6, 2.6, 0.6 and 0.1%. The fact that there is no significant difference in size within the range of either A or B indicates that this difference is probably due to genetic rather than environmental causes.

Both types, with essentially the same life cycle, produce two generations a year—a short summer and a long overwintering generation; the winter population of both forms first appeared during September and October 1953.

In the case of A (Fig. 12) the young were 2.0 mm long upon becoming free living, and at this time the average individual weighed .000035 g. By 8 November 1953 the average animal was .00015 g; by 20 December 1953, .0005 g; by 19 April 1954, .0013 g; by 30 April 1954, .0014 g; and finally, by 17 May 1954, .00162 g. On this last date the overwintering generation was ready to spawn. During June, few large individuals were found, but towards the end of that month great numbers of the new generation were evident. These grew rapidly, and by 20 August 1954 they were mature and weighed .00055g. Thus the reproducing adult of the summer population was only about one-third as heavy as the adult of the winter stock.

The cycle in B was less clear. During October 1954 the average



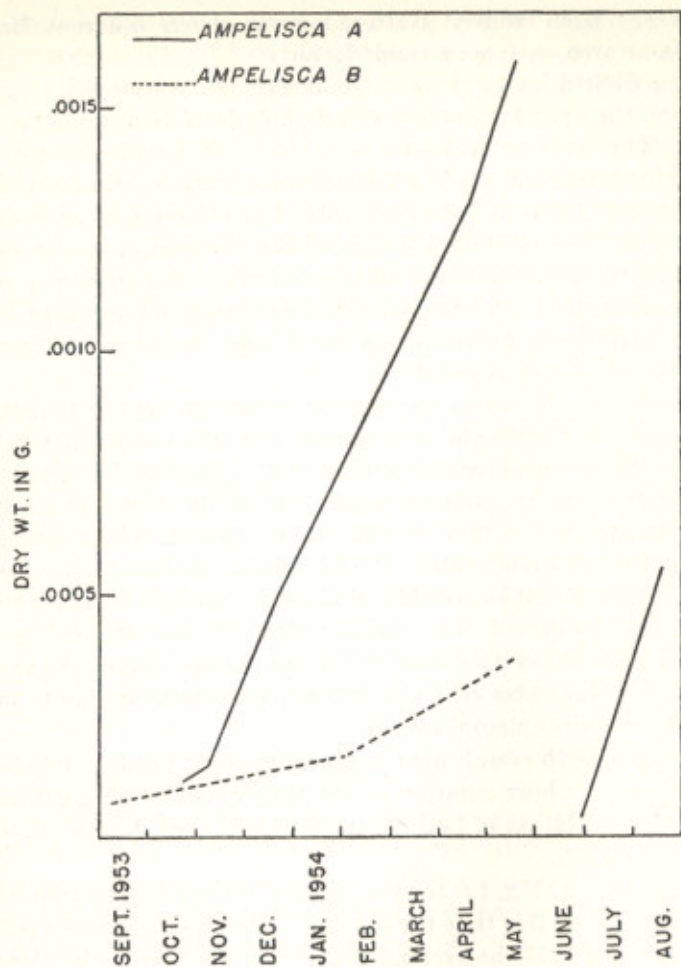


Figure 12. Growth (in grams) of *Ampelisca A* and *Ampelisca B*.

individual weighed slightly less than its counterpart in A, and on 3 February 1954 it was .000163 g, or less than a quarter the weight of A at that time (Fig. 12). This slower growth rate continued so that by 20 May 1954 the animal was mature and weighed .000362 g, its weight still being less than a quarter of the weight of A on the corresponding date. The other generation of B (summer generation) was much more difficult to follow than that of the overwintering

generation. The summer adult was much smaller than the winter adult and its breeding period was somewhat extended; hence it was difficult at times to separate the two generations of B.

While both forms have a fairly wide though nonoverlapping distribution in regard to sediment type, large concentrations of these animals were found in a narrow sediment range. In Fig. 13 the dry weight of A per square meter is plotted against the silt-clay content; location and time have been omitted. In this figure it is evident that the points fall into two groups: a cluster of low values where

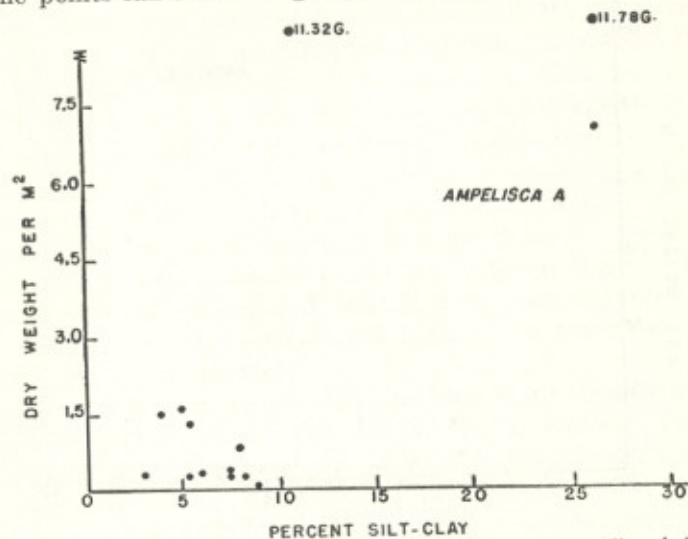


Figure 13. Relationship of biomass to sediment composition of *Ampelisca A* (weight in grams).

the silt-clay percentage was low (< 9%) and another cluster of values which were much higher and which increased with increasing percentages of silt and clay. But no A individuals were found in sediments containing more than 30% of silt and clay.

These observations are interpreted in the following manner. Since members of the genus *Ampelisca* are filter-feeders and since food is taken out of the water immediately over the bottom, the food that is available to the animal is directly related to the amount of water that passes over the animal. Since the coarser sediment reflects more pronounced current activity than the silt-clay sediment, primarily because few of the finer particles (silts and clays) have



settled out, it is not surprising that the species with the larger total biomass, *Ampelisca* A, was found in coarser sediments. However, extremely coarse sediments are unfavorable because the extreme compactness of the sediment makes burrowing by this animal difficult.

For B, the silt-clay content is plotted against dry weight in Fig. 14, but here the results are not as evident as they were for A. However, it is clear that at high silt-clay concentrations the biomass of this amphipod is small; since currents over such sediments are probably

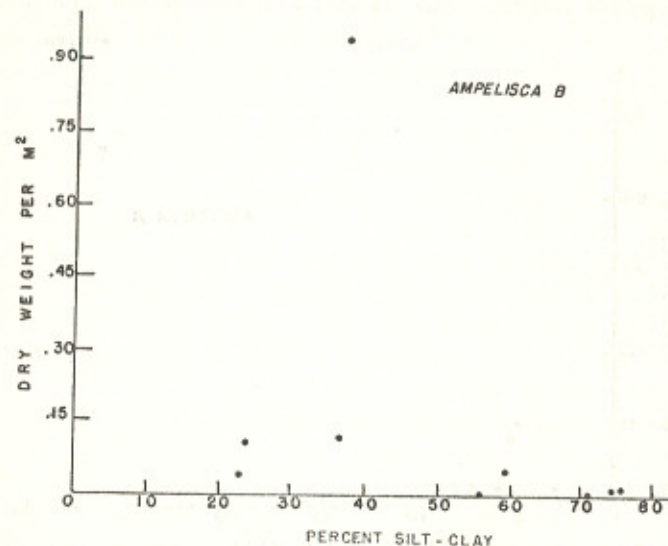


Figure 14. Relationship of biomass to sediment composition of *Ampelisca* B (weight in grams).

weak, an unfavorable environment is afforded filter-feeders. In addition, these sediments, being highly flocculent, may readily clog the filtering apparatus, and finally, in highly organic sediments the oxygen content below the surface of the soil can be severely reduced, making conditions unfavorable for aerobic organisms. At lower concentrations of silt and clay the biomass increased, presumably because of the less flocculent, less reduced nature of the sediment and the greater velocity of the bottom current.

During this study, none of the smaller B forms were found in sediments containing less than 35% silt and clay, and none of the larger A forms were found in sediments containing more than 30%. The

lack of overlap between A and B indicates a high degree of competition between these similar forms, and the larger dry weight measurements for A reflect the more favorable conditions for a filter-feeder on coarser rather than on finer sediments. Thus, exclusion of the larger A form from the finer sediments may indicate that the smaller B form is more efficient in filtering the smaller food particles.

In every sample that contained either A or B, females always predominated; usually there were at least 15 times more females than males, and frequently there was not even a single male. Recently Barnard (1954) reported that he seldom found the adult male of species of *Ampelisca* in abundant material from the eastern Pacific.<sup>3</sup> Somewhat earlier Reid (1951) had pointed out that many of the females, particularly in the *diadema-spinipes-tenuicornis* complex, are in reality intersexes. According to him, they resemble the female morphologically but lack the brood plates or oostegites and possess two slight protuberances, the copulatory hooks characteristic of the male, near the midline immediately in front of leg 7. Undoubtedly earlier workers were completely unaware of the widespread intersex phenomenon in this group and, since various workers probably used gynomorphic males to describe the female, the taxonomic picture was complicated still further.

So far as is known, no attempt has been made to determine the relative proportion of intersex to female in nature. Therefore, the pertinent characters necessary for an appraisal of such a relationship were observed on 100 adults of the A group, taken from the Charles Island sample of 30 April 1954. Results regarding the presence or absence of setal tufts on the antennae were variable, although in most cases they were either female or were approaching the female condition. The character of the third uropod was in every case female. Precisely 50% of the animals possessed oostegites, and in every case these same animals lacked copulatory hooks; conversely, precisely 50% possessed copulatory hooks but lacked oostegites. Thus it appears that females and gynomorphic males occur in about equal numbers, while andromorphic males constitute only a mere trace of the population. The genetic basis for this peculiar ratio is difficult to postulate.

<sup>3</sup> A male can be readily distinguished from the female by the longer first antenna, the presence of setal tufts on both the lower surfaces of the peduncle of the second antenna, and by the larger spines on the third uropod.



*Yoldia limatula*. This species was commonly found in certain sediments, primarily at Sts. 3, 2, 8 and 7 where it constituted 4.7, 5.5, 9.7 and 19.3% of the biomass of small animals; at Charles Island and at Sts. 4 and 5 it was entirely absent, and at St. 1 it comprised only 1.1% of the biomass.

In Fig. 15 the dry weight values are plotted against silt-clay content of the sediment; here again location and time are omitted. *Y. limatula* is either excluded from the coarser sediments altogether or is present in only small numbers, and dry-weight values remain insignificant until the silt-clay content exceeds 30%, after which abundance increases markedly, with maximal values being reached at about 40% silt-clay. At still higher percentages the values drop off signifi-

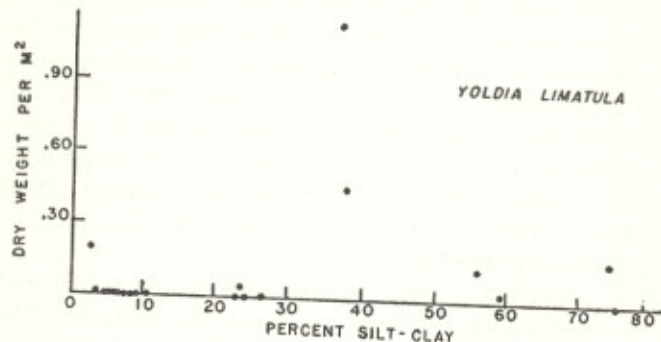


Figure 15. Relationship of biomass to sediment composition of *Yoldia limatula* (weight in grams).

cantly, though small populations are found in sediments with an extremely high fraction of silts and clays (> 70%).

Drew (1899) has shown that this species, in common with other protobranchiate molluscs, feeds by means of palp proboscides. The animal, when feeding, raises the posterior third of its body above the sediment in an almost perpendicular position and then extrudes the palp proboscides so that at least one is inserted into the substrate. Thus *Y. limatula* is a deposit-feeder which derives its food from the organic-rich soil beneath the surface of the sediment.

Its feeding habits explain in large measure the distribution pattern shown in Fig. 15. Its absence from the coarse sediments is due to its inability to thrust the proboscides into the hard substrate, and furthermore, the organic content of such sediments is low. Also, in its exposed feeding position the animal must be able to burrow rapidly

into the bottom to escape its enemies, a feat which is difficult to perform in the coarser substrates.

Fig. 16 shows the size composition of *Y. limatula* at different dates. There appears to be no sharp separation between year-classes, hence interpretations must be subjective, but not to the same degree as in some other species. The dotted lines indicate how the year-classes are separated. The first sample, taken in early August 1953, indicated two modes: the one year-group with an average individual weight of .0104 g and the recently spawned zero year-class with a weight of .0010 g. By 9 September 1953 the one year-group had increased to .0151 g, the zero year-group to .00165 g. A composite sample taken in February 1954 showed weights of .00438 g and .0230 g for the zero and one year-classes respectively, and the 20 May 1954 sample showed that the animals had grown rapidly enough so that the zero year-class now weighed .0098 g, the one year-group .0342 g. This was the last date on which adequate numbers of the one year-class were obtained. On 23 July 1954 a new generation with an average individual weight of .00085 g was present, and the mean animal of the recent zero year-class, now the one year-group, weighed .01272 g. By 10 September 1954 the new generation was .00277 g, while individuals of the one year-group were found in so few members that no analysis could be made. Finally, on 13 January 1955 a large sample that gave adequate representation of both classes showed that the new generation weighed .0059 g and the older class .0255 g.

Independent evidence from growth ring measurements tends to support this growth interpretation. The size of the first winter ring,<sup>4</sup> measured in five animals from the 9 September 1954 sample, varied in length from 9.2 to 12.0 mm, with a mean of 10.48 mm. This agrees well with the mean winter values, 9.40 and 10.59 mm, found for February 1954 and January 1955. Six other specimens with two winter rings, from the January 1955 sample, were also observed; the length range of the first ring was 6.5–11.0 mm, with a mean of 9.25 mm, while the variation in the size of the second ring was 16.0–20.5 mm, with a mean of 18.58 mm. This latter mean was higher than those found in the February 1954 sample (15.5 mm) and in the January 1955 sample (16.9 mm). However, the winter ring in those later samples had not been laid down; probably there was still a small increment in growth before this occurred.

<sup>4</sup>It can be shown from the size distribution data that the ring is laid down early in the spring.



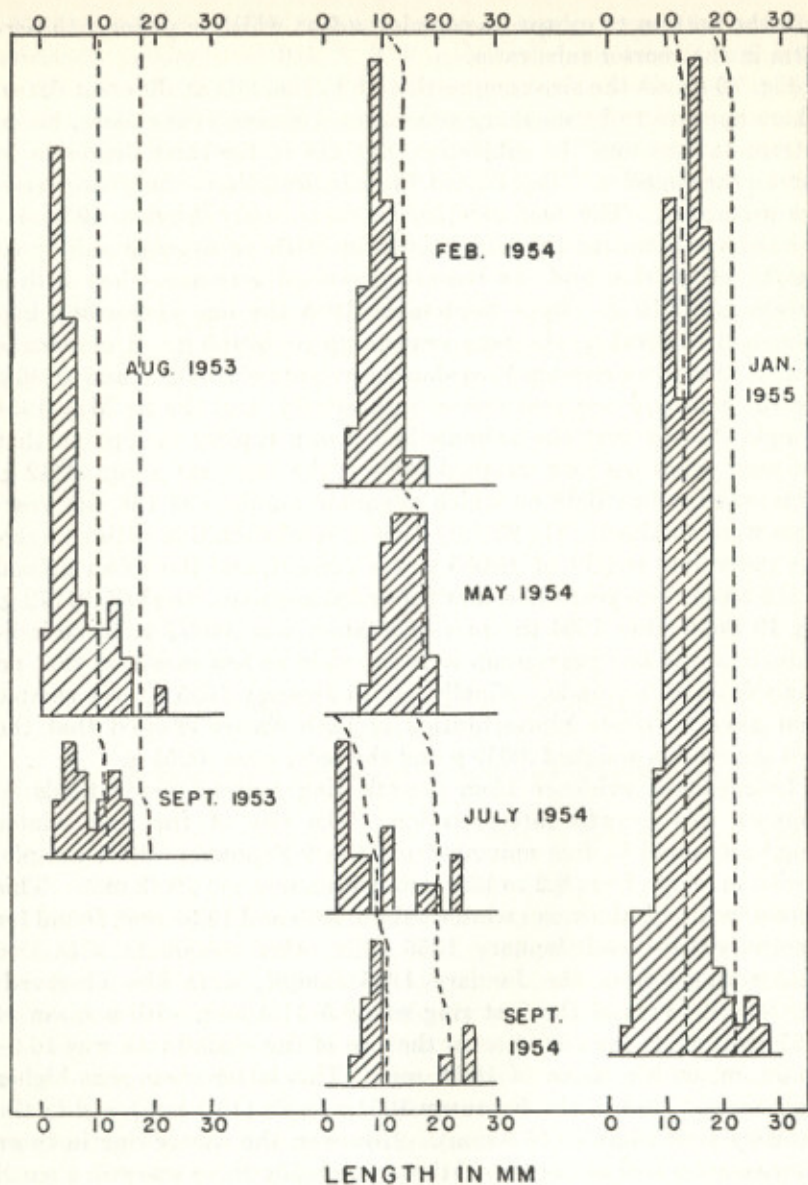


Figure 16. Histograms showing size distribution of *Yoldia limatula*. Interpretation of the limits of the year-classes is indicated by dotted lines.

If the two winter histograms (February 1954 and January 1955) in Fig. 16 are compared, those portions that represent animals less than 14 mm in length are essentially similar. This implies that those portions represent the zero year-class at about the same stage of growth in 1954 and in 1955. However, in these same histograms the proportion of zero- to one-year-olds is much more varied. Since the zero year-class was only slightly larger than the one year-group in January 1955, it seems probable that there was a poor set of *Y. limatula* in 1954.

*Nucula proxima*. This is a ubiquitous lamellibranch of the softer sediments. At Sts. 7, 8, 3, and 2 it formed 12.5, 19.1, 23.4 and 42.9%

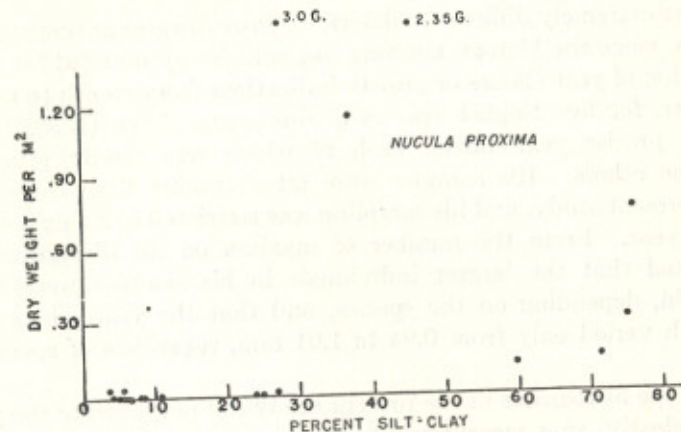


Figure 17. Relationship of biomass to sediment composition of *Nucula proxima* (weight in grams).

of the biomass of small animals, whereas at Charles Island and at Sts. 4 and 5 it constituted a mere trace with less than 0.1%. Its restriction to the softer sediments is clearly illustrated in Fig. 17, where a sharp break is apparent at a silt-clay content of about 33%. At lower silt-clay concentrations the dry weight values are extremely small, while at higher concentrations the values are appreciably higher.

This species, like other protobranchs such as *Y. limatula*, possesses a large foot which is specialized for burrowing into the softer sediments (Yonge, 1939). Normally this small lamellibranch, which lies just beneath the surface, makes a small opening to the surface at its



posterior end for the discharge of faecal pellets. This animal, in common with *Y. limatula*, utilizes palp proboscides in feeding, the tips of which collect sediments which are then carried by means of a ciliated groove to the base of the proboscis. Moore (1931) has pointed out that *N. proxima* can resist anaerobic conditions for a certain period of time, hence the somewhat reduced soils of high organic content which characterize high concentrations of silt and clay form a satisfactory source of food that can be exploited by such a deposit feeder. Conversely, hard substrates offer meagre nutrients and constitute an unfavorable medium for burrowing. The distribution of *N. proxima*, as shown in Fig. 17, is approximately what could be postulated from its life history.

It was extremely difficult to determine growth rates in these minute animals, since the histograms were not sufficiently detailed for either separation of year-classes or growth indications from month to month. However, for five English species of this genus, Allen (1953; 1954a) showed precise year-classes, each of which was clearly separated from the others. His samples were often smaller than those used in the present study, and his sampling was restricted to a single season of the year. From the number of maxima on his histograms, he postulated that the largest individuals in his samples were 12-20 years old, depending on the species, and that the yearly increment in length varied only from 0.94 to 1.01 mm, regardless of species or age.

Since the histograms in the present study did not indicate the year-classes clearly, ring measurements were used as an alternative. In a sample taken at St. 2 on 23 July 1954, 10 animals possessing two rings had a mean length of 2.37 mm and a weight of .00027 g, 47 with three rings had a mean length of 2.94 mm and a weight of .00069 g, and 8 individuals with four rings had a mean length of 3.51 mm and a weight of .00106 g. A sample from St. 7, taken on January 13, 1955, gave a mean length of 2.4 mm for 14 animals with two rings and of 2.98 mm for 43 animals having three rings, this last length being equivalent to .00071 g. It is doubtful whether the above measurements give a precise picture of growth in *N. proxima*. Nonetheless, this information may be utilized in gaining some concept of the general order of growth in this animal.

*Pandora gouldiana*. This lamellibranch was found during the survey at one time or another at all eight stations. At seven stations

it formed only a minor part of the population, ranging from less than 0.1 to 2.1% of the biomass of small animals, but at Charles Island it comprised 14.0% of the population. If the samples of 17 August and 23 October 1953 at Charles Island are disregarded, since the samples on those dates contained a much higher percentage of silt and clay, then *P. gouldiana* would make up 19.0% of that station's biomass.

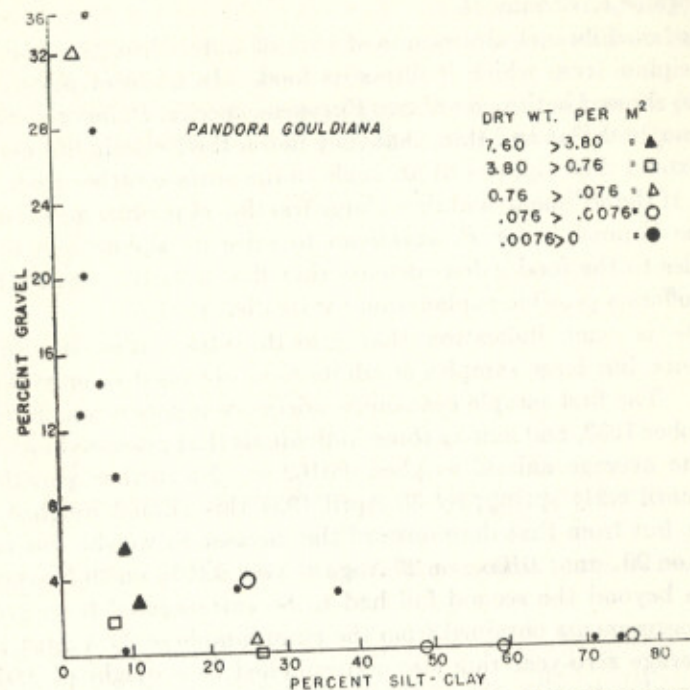


Figure 18. Relationship of biomass to sediment composition of *Pandora gouldiana* (weight in grams).

In Fig. 18 the dry weights are plotted against silt-clay as well as gravel content, and it is seen that all of the high values are crowded into that corner of the graph where percentages for both of these fractions are low. Charles Island was the only station in the survey that contained such a sediment composition.

The fact that this lamellibranch is a suspension feeder may help to explain its distribution pattern. Like the *Ampelisca* forms, the food available to the animal is directly related to the amount of water that passes over it in a given period of time, and since coarser sedi-



ments reflect greater current activity, it is not surprising that the silty sediments appear unfavorable for *P. gouldiana*. Its exclusion from the gravelly sediments, however, is more difficult to explain. If we note the sudden sharp break from high to low values along the ordinate axis, we discover that a small increase in the percentage of gravelly sand can convert the sediment from a favorable to a highly unfavorable environment.

This lamellibranch draws in a stream of water through a relatively short siphon from which it filters its food. In a recent paper, Allen (1954b) showed in the case of two European species, *P. inaequalis* and *P. pinna*, both flat and thin, that they lie on their side in life and that they extend their siphons at an angle to the surface rather than vertically. If the sediment contains a large fraction of pebbles and stones, it may be impossible for *P. gouldiana* to raise its siphon above these obstacles to the food-laden currents that flow over it. Such a hypothesis offers a possible explanation for its distribution.

There is some indication that growth rates varied in different sediments, but large samples of adults were obtained at only Charles Island. The first sample containing adequate numbers was taken on 23 October 1953, and among those individuals that possessed no winter ring, the average animal weighed .00162 g. No further growth was noted until early spring; by 30 April 1954 this animal weighed only .0020 g, but from that date onward the increase in weight was rapid: .0045 g on 20 June; .0106 g on 20 August; and .0210 g on 30 November. Growth beyond the second fall had to be extrapolated from growth ring measurements obtained from the large sample of 20 August 1954. The average zero-year ring size corresponded to a weight of .0030 g, which implies that the so-called winter ring was actually laid down in early spring. The mean-length first-year ring corresponded to a weight of .0240 g, and a year later (20 August 1955) the weight had doubled and the average-length animal weighed .0487 g. Too few older animals were found to give valid results.

Apparently there was a poor set of this species during the summer of 1954, since few zero-year animals were found. In this it agrees with *Y. limatula* and *N. incisa*. Perhaps all invertebrates having planktotrophic larval stages during the late summer and early fall suffered similarly from hurricanes "Carol" and "Edna" which hit New England on August 31 and September 11.

*Macoma tenta*. Extensive sampling reveals that this species has a somewhat uneven distribution in the Sound; even at the locations where this lamellibranch was present, quantitative values fluctuated widely from sample to sample. Unfortunately, Fig. 19, with only a single significant value shown (Charles Island, 23 October 1953), does not give a clear picture of the distribution of *M. tenta*. At Charles Island and at Sts. 1, 8, 7 and 4, it averaged on a yearly basis 12.7, 1.2, 0.8, 0.5 and 0.1% of the small infauna, and at Sts. 2, 3 and 5 it was absent from all samples.

This species is a deposit-feeder, but unlike *Y. limatula* or *N. proxima*, it feeds on the surface. The siphons, long and extremely mobile,

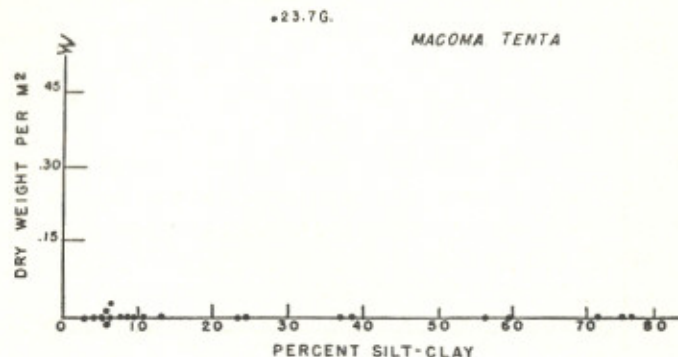


Figure 19. Relationship of biomass to sediment composition of *Macoma tenta* (weight in grams).

are separate, and the inhalent siphon moves over the surface to draw in food. As a result of its narrow lumen, the inflow current is small but powerful (Yonge, 1949). By this suction device it can actually tear bottom diatoms from the substrate.

In Long Island Sound this lamellibranch feeds on settled detritus, and the availability of this food probably determines its distribution. In sediments of low silt-clay content where there is little net deposition of food and in those of high silt-clay content where there is reduced oxygen and flocculence, *M. tenta* probably finds the environment unfavorable. From the limited data that are available, it appears that this species is found primarily in sediments having a silt-clay content of 15-35%. Since few samples were taken from substrates of this type, more adequate sampling will be necessary to determine



whether or not this species is an important constituent of the populations that inhabit these sediments.

*Lyonsia hyalina*. This is a moderately common lamellibranch in some of the sediments. At Charles Island and at Sts. 5, 1, 4, 8 and 7 it comprised 10.4, 3.2, 2.8, 1.6, 1.3 and 0.4% of the biomass of the small animals. At St. 2 it was absent and at St. 3 it comprised less than 0.1% of the population. From Fig. 20 it is obvious that this species was found primarily in the harder substrata and that it was

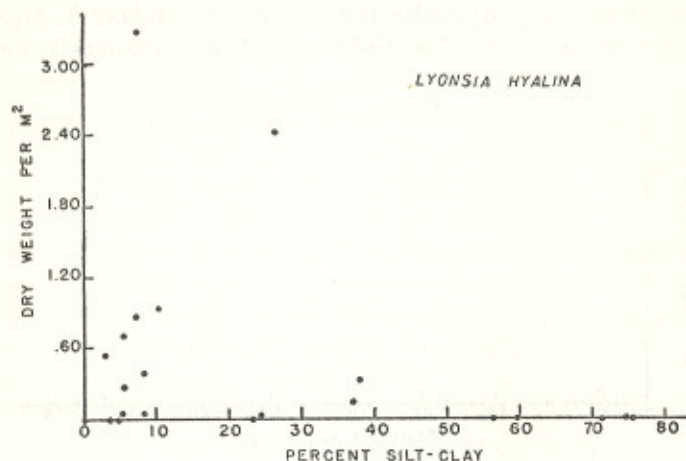


Figure 20. Relationship of biomass to sediment composition of *Lyonsia hyalina* (weight in grams).

largely absent from those sediments having a silt-clay content greater than 50%. The distribution pattern is in essential agreement with the suspension feeding habit of this animal. *L. hyalina's* thin and extremely delicate shell is an unexpected feature in a lamellibranch that inhabits a hard substrate, but, once buried, it is probably sedentary (Yonge, 1952)—a fact which largely eliminates the abrasive action of sand granules on the shell. In addition, further protection is afforded by the sand particles which adhere to the periostracum.

*Mulinia lateralis*. Although this diminutive lamellibranch has a wide distribution in the Sound, over much of its range it makes only an insignificant contribution to the biomass. Even at those stations where it was common, its abundance varied widely from date to date.

At Charles Island and at Sts. 8, 7, 1, 5 and 3 it constituted 10.6, 2.4, 1.2, 0.7, 0.4 and 0.2% of the small animals, and at Sts. 2 and 4 it formed hardly a trace of the population, comprising less than 0.1%. However, it was occasionally encountered in great quantity, as at Charles Island on 17 August 1953, when it had a value of 36.10 g/m<sup>2</sup>.

In Fig. 21, dry weight values of this animal are plotted against silt-clay content; at low silt-clay percentages these values are variable though generally low, whereas at silt-clay concentrations of about 20% the values rise sharply. Note that all major dry weight values

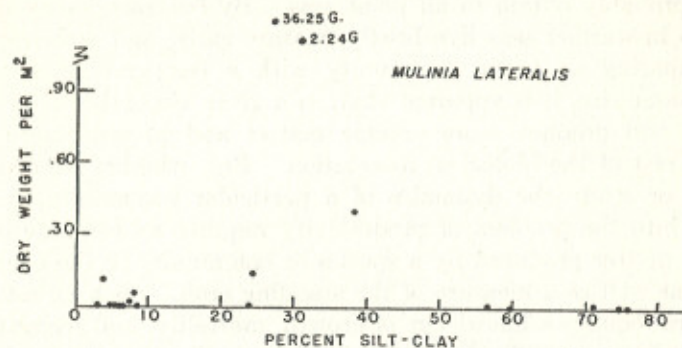


Figure 21. Relationship of biomass to sediment composition of *Mulinia lateralis* (weight in grams).

are confined within the 20–40% range. At concentrations greater than 40%, it is either absent or its biomass is extremely low.

Like many other lamellibranchs, *M. lateralis* is a filter-feeder. In gravelly sediments, as at Sts. 1 and 4, this minute clam would encounter difficulty in raising its siphon above large particles to the unobstructed current, and in sediments with high silt-clay concentrations the velocity of the current flowing over it would be much reduced. In addition, the high organic content of such soils absorbs oxygen and thus creates an even more unfavorable environment. It seems logical, then, to assume that optimal conditions for *M. lateralis* would be found in sediments with intermediate concentrations of silt and clay, an assumption which is in agreement with the picture given in Fig. 21.



PRODUCTIVITY<sup>5</sup>

Thus far in this paper, terms with static connotations, such as "standing crop" or "biomass," have been employed while the word "productivity" has been avoided purposely. However, use of the term standing crop as a basis for comparing the productivity of various regions can be quite misleading, hence it is essential to appraise briefly the connotation of productivity. Thorson (1936) has shown for northeast Greenland seas that the bottom fauna is characterized by animals that live long, grow slowly and mature late, features which probably obtain in all polar seas. By contrast, many of the animals in warmer seas live briefly, mature early, and grow rapidly. In comparing an arctic community with a temperate community of the same size, it is apparent that, in a given time, the latter community will produce more organic matter and provide more food for the rest of the biological association. But, whether we compare regions or study the dynamics of a particular community, a clear insight into the problem of productivity requires an estimate of the organic matter produced by a species or community in the course of a year as well as a measure of the standing crop. Such an estimate therefore requires a knowledge of growth, mortality, and recruitment, hence it is more difficult to obtain than a simple measure of the standing crop. Such estimates will be developed for the present survey insofar as data permit, and it is to this aspect of the work that the term "productivity" is restricted.

To date, Jensen (1919) is the only investigator who has attempted to study benthic community from the point of view just discussed. Jensen, with data gathered each spring and fall from 1909-1917 in Thisted Bredning, one of the shallow enclosed bays of the Limfjord, developed his work on the basis of the following definitions:

Stock: quantity of individual species, expressed in wet weight/m<sup>2</sup>.

Rest stock: amount of stock left in the following spring.

Consumption: quantity of individual species eaten during the year, calculated from one series of spring samples to the next.

Growth increment: increment of the stock (in wet weight) during one year to the death of the individual specimens

<sup>5</sup> Although there is considerable literature on the productivity theory (Lindeman, 1942; Riley, *et al.*, 1949; Park, *et al.*, 1946), none of these has a practical bearing on the present investigation.

$$\left( \text{i.e., growth increment} = \frac{\text{consumption} + \text{rest stock}}{\text{stock}} \right).$$

Uppgrowth: weight of 0-group/m<sup>2</sup> (i.e., upgrowth = recruitment).  
Animal production = sum of growth increment + upgrowth.

If Jensen found that a given species had more than one year-class, then each year-class was treated separately. For 1910-1915, Jensen obtained yearly productivity values that ranged from 1.00-3.23 times the values of the standing crop.

The primary difficulty with his procedure lies in the manner of computing consumption, which, by Jensen's definition, indicates that the mean mortality of an individual species during the time interval of one year would occur precisely at the end of six months; furthermore, this mean mortality would have both the mean length and mean weight of all animals that die during this interval of time. If we assume that predation is occurring at a constant rate, then a constant fraction of a continuously diminishing population is dying so that the mean mortality must occur well before the end of the six-month period. Since in most organisms the weight is proportional to the cube of the length, the mortality of mean weight must occur somewhat later than the mortality of mean length. If a long interval of time is measured, as in Jensen's work, then large errors are introduced and the results obtained are obviously too high.

In the present study a different approach has been attempted. All samples of a given species at a given station were divided into year-classes on the basis of growth histograms shown in the previous section. In the case of certain molluscs, growth rings were also used. For each year-class, the mean individual weight was determined by dividing the total weight of the year-class by the number of individuals in it.

Fig. 22 shows two separate curves, one being the log of the mean individual weight, the other that of the mean number plotted against age, the ages having been determined from year-classes. At three-month intervals the mean weight of the individual and the number of individuals at that weight were determined. The number of animals present at a given interval ( $N_{a+1}$ ) were subtracted from the number present at the previous interval ( $N_a$ ) to obtain the number that had died in the intervening time ( $N_a - N_{a+1}$ ). The average weight of the individual during the intervening period of time was



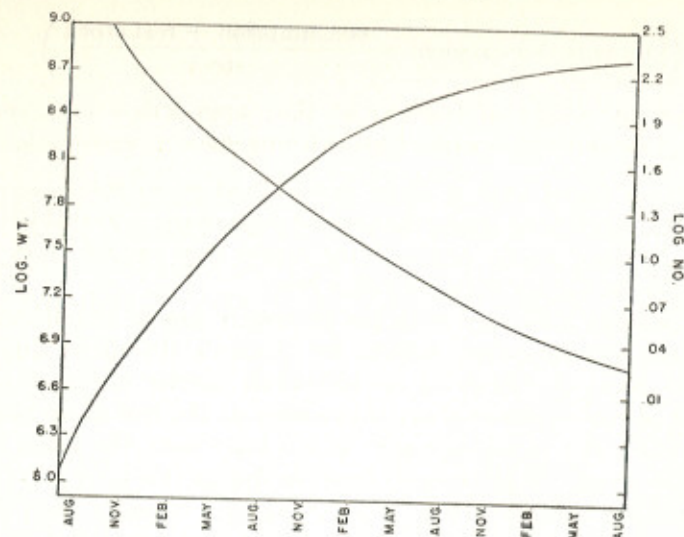


Figure 22. Relationship of numbers and weight to age in *Nephthys incisa*.

obtained by adding the mean individual weight at the beginning ( $W_a$ ) and at the end of the interval ( $W_{a+1}$ ) and dividing by two  $\frac{W_a + W_{a+1}}{2}$ . This value was then multiplied by the number of animals that had died during the interval. The resultant figure represents the mortality by weight that had occurred during the intervening period  $\left[ (N_a - N_{a+1}) \cdot \frac{(W_a + W_{a+1})}{2} \right]$ . The same procedure was used for all of the three-month intervals. Summation of these figures gave the mortality by weight that occurred during the year.

The amount of organic matter produced by a species in the course of the year was obtained by adding the figures for mortality to those of the terminal population weight  $[(W_n) \cdot (N_n)]$ . This latter value actually contributes to the total mortality figure of the following year, but under steady-state conditions this may be assumed equal to that received under similar conditions from the previous year. The sum of both of these figures is the productivity of the species.

Calculations for the polychaete *Nephthys incisa*, given in Table VI, show productivity to be 2.16 times more than the standing crop.

TABLE VI. PRODUCTIVITY DETERMINATION IN *Nephthys incisa*

Date	0 year-class		1 year-class		2 year-class	
	Wt.	No.	Wt.	No.	Wt.	No.
8/1/53	.3119	1254.53	.1267	33.29	.7344	19.99
2/3/54	.7210	1159.38	1.5892	171.84	.4333	12.31
5/20/54	2.0166	666.29	4.0950	143.03	2.9413	47.65
	3.0495	3080.20	5.8109	348.16	4.1090	79.95
$\bar{M}$ sample wt. =	1.0165		1.9369		1.3697	
$\bar{M}$ No./sample =	1026.73		116.05		26.65	
$\bar{M}$ wt./individual =	.00099		.01669		.05135	
$\bar{M}$ standing crop =	4.3231 g/m <sup>2</sup>					

Year-class	Month	Wt./indiv. (W)	No. (N)	$N_a - N_{a+1}$	$\frac{W_a + W_{a+1}}{2}$	Mortal.
0	Aug.	.0001326	2348.4	828.40	.0002700	.2237
	Nov.	.0004074	1516.2	581.40	.0008597	.4998
	Feb.	.001312	934.8	387.98	.002281	.8850
	May	.003250	546.82	229.22	.004921	1.1280
1	Aug.	.006592	317.60	123.96	.009226	1.1436
	Nov.	.01186	193.65	73.19	.01486	1.0876
	Feb.	.01787	120.46	44.84	.02109	.9457
	May	.02432	75.62	28.65	.02797	.8014
2	Aug.	.03162	50.01	15.66	.03618	.5664
	Nov.	.04074	34.35	9.04	.04590	.4149
	Feb.	.05105	25.31	5.24	.05551	.2909
	May	.05997	20.06	4.33	.06426	.2782
	Aug.	.06855	15.73	—	—	—

Total = 8.2652

Mortality (wt.)/yr. = 8.2652 g/m<sup>2</sup>.

Terminal population wt. = 1.0783 g/m<sup>2</sup>.

Total productivity/yr. = 9.345 g/m<sup>2</sup>.

Total productivity  
standing crop = 2.16.

Adequate data for similar computations were available for only a few species that live more than a single year, and results of those computations are given in Table VII.

Similar calculations were attempted for the short-lived amphipod, *Ampelesca* A. In this case the ratio of productivity to standing crop was 9.2 for the summer generation and 3.0 for the winter generation,



but little confidence can be placed in these results, for the sampling intervals were not adequate for valid mortality and growth determinations. Added to this was the difficulty of delineating the summer population, since this group was hatched over a period of a few weeks. Therefore it seemed preferable to obtain an approximation for short-lived species rather than use the above questionable values. Since *Ampelisca* produces two generations a year, and since no individual lives more than a year, it is expected that the relationship of productivity to standing crop is at least twice that obtained for species with annual year-classes. A reasonable estimate of the productivity-standing crop ratio might be about 5, possibly more.

Only the most important species provided sufficient data for analysis, but their dominance accounted for a fairly large percentage of the total biomass of bottom fauna. Of the small infauna, *Nephtys*,

TABLE VII. COMPUTATION RESULTS FOR FOUR LONG-LIVED SPECIES

Species	$\bar{M}$ stand. crop	Term. pop. wt in g	Mortal./year in g	Product. in g	Product. Av. stand. crop
<i>Nephtys incisa</i>	4.3231	1.0783	8.2652	9.3435	2.16
<i>Cistenoides gouldii</i>	0.8763	.0308	1.6697	1.7005	1.94
<i>Pandora gouldiana</i>	3.0803	.0866	6.0466	6.1332	1.99
<i>Yoldia limatula</i>	1.4067	.2022	3.0073	3.2095	2.28

*Yoldia* and *Cistenoides* constituted 32.0, 6.6, and 6.7% at St. 2; 37.6, 4.7, and 3.3% at St. 3; 32.6, 0.0, and 2.4% at St. 5; 31.8, 19.3, and 11.3% at St. 7; and 39.4, 10.0, and 2.0% at St. 8. At Charles Island, *Pandora* made up 21.5% of the biomass. Together these four species comprised 25.0% of the standing crop at Charles Island, 9.8% at St. 1, 1.0% at St. 4, 35.1% at St. 5, 45.3% at St. 2, 45.7% at St. 3, 51.8% at St. 8, and 62.8% at St. 7. In all of these long-lived species, the productivity value was about 2.1 times that of the standing crop, hence it would seem that application of the same ratio to the remaining long-lived fraction of the biomass would introduce no serious error. This is particularly true of Sts. 2, 3, 7 and 8.

Since the ratio of productivity to standing crop in the short-lived *Ampelisca* was approximately 5, this ratio can be applied similarly to other short-lived infaunal species which produced two generations a year. Species that fall in this category are the amphipods, *Leptocheirus pinguis*, *Unciola irrorata*, *Siphonacetes smithianus*, and various species of *Corophium*. At Charles Island and at Sts. 1, 4, 5, 7, 8, 2 and

3, this short-lived component of the standing crop constitutes 17.2, 34.5, 17.0, 12.7, 3.2, 4.8, 2.6 and 1.9% respectively. The long-lived forms comprise the remaining percentages.

Productivity of the infauna has been determined by using the values 2.1 for long-lived and 5 for short-lived animals, and these results are tabulated in Table VIII. Total productivity varied from 71.64 g/m<sup>2</sup> at Charles Island to 8.84 g at St. 2, and the average of the means of all eight stations was 29.60 g. The ratio by weight of total productivity to standing crop ranged from 2.17-3.10, with a mean

TABLE VIII. TOTAL PRODUCTIVITY OF INFAUNA OF LESS THAN 0.2 g

Station	$\bar{M}$ stand. crop	-Long-lived component-		-Short-lived component-		Total product.	Product. Stand. crop
		Stand. crop	Product.	Stand. crop	Product.		
Charles Is.	27.576	22.84	2.1 47.966	4.735	5.0 23.675	71.641	2.60
1	3.930	2.576	5.410	1.354	6.770	12.180	3.10
4	25.637	21.289	44.707	4.348	21.740	66.447	2.59
5	9.172	8.006	16.813	1.166	5.830	22.643	2.47
8	10.188	9.695	20.360	0.493	2.465	22.825	2.24
7	10.043	9.690	20.349	0.353	1.765	22.114	2.20
2	4.064	3.959	8.314	0.105	0.525	8.839	2.17
3	4.694	4.605	9.671	0.089	0.445	10.116	2.17
						$\bar{M} = 29.601$	2.44

value of 2.44 (see Table VIII). Although no survey of the sediment composition of Long Island Sound has been undertaken, most of the substrate appears to be made up of fine particles. If we assume that 80% is fine sediment and 20% coarse, the total productivity of the small infauna in the Sound is:

$63.894 [(\bar{M} \text{ of Sts. 2, 3, 7, 8}) \times 4] + 43.228 [(\bar{M} \text{ of Chas. I., Sts. 1, 4, 5}) \times 1] \div 5 = 21.424 \text{ g/m}^2$ .

The inadequacy of the basic data does not warrant an estimation of productivity values for the epifauna and total population. However, the mere fact that these animals make up the larger, slower growing forms makes the difference between productivity and standing crop less important.

## THE COMMUNITY

*Level-Bottom Animal Communities of Long Island Sound.* In studying an entirely new area, an investigator with limited time and facilities is faced with the choice of extending his investigation over a wide range of stations or confining his attention to a relatively



few stations. The second alternative, which permitted intensive study of a limited area, seemed to offer a more fruitful approach in this instance. However, since so few localities were sampled, it was difficult to describe and name the level-bottom communities after the manner of Petersen (1913). Although Petersen's nomenclature is not the only source for defining a community, it was adopted nonetheless because of its wide use in marine benthic studies.

At St. 4, where the depth of water is greater than that at most stations, the hard-bottom association showed such characteristic animals as the lamellibranchs, *Astarte undulata* and *Cerastoderma pinnulatum*, and the amphipods, *Leptocheirus pinguis* and *Ampelisca* A. On the other hand, most of the Charles Island samples indicated a shallow water association characterized by the bivalve *Pandora gouldiana* and *Ampelisca* A. Although these may represent communities, it is not feasible to describe them on evidence from only an isolated locality.

Nonetheless, one community did appear to be represented adequately enough to be described. This was the association of animals in the softer sediments which can be characterized by the infauna found at Sts. 2, 3, 7 and 8; possibly St. 5 can be included also, since it may be a transitional area. In this association, which probably represents the typical soft bottom community of the Sound, the biomass was completely dominated by four species which together comprised slightly over 75% of the standing crop. The most important species by weight was the polychaete *Nephtys incisa*, which made up 35.2% of the population and was present in 95% of the samples taken at Sts. 2, 3, 7 and 8. *Nucula proxima*, the next most important member, was represented in every sample and composed 24.4% of the community by weight. Another lamellibranch, *Yoldia limatula*, constituted 10.2% of the biomass and was found in 87.5% of the samples, and *Cistenoides gouldii* was present 87.5% of the time and made up 5.8% of the standing crop. Some of the animals that comprised the remaining 25% of the biomass were: the sea anemone *Cerianthus americanus*; the nemertian *Cerebratulus luridus*; the polychaetes *Melinna cristata*, *Ninoë nigripes*, *Lumbrinereis tenuis* and *Praxillella praetermissa*; the amphipods *Leptocheirus pinguis* and *Siphonacetes smithianus*; the lamellibranchs *Lyonsia hyalina*, *Macoma tenta*, *Mulinia lateralis* and *Pitar morrhuana*; and the gastropod *Lunatia triseriata*, *Retusa caniculatum* and *Cylichna alba*.

It is convenient to classify communities by combining the names of two of the characteristic species, in which case these species should be numerous and should belong to different major groups. In the community under discussion, this limited the characterizing species to the four dominants and hence confined the choice to one of the two polychaetes (*N. incisa* or *C. gouldii*) and to one of the lamellibranchs (*N. proxima* or *Y. limatula*). Since the characterizing species should also be conspicuous, *N. proxima* was eliminated because the vast majority of these lamellibranchs are less than 3 mm in length. *Y. limatula* therefore remained the only choice. *N. incisa* is probably the better polychaete representative, since it was approximately six times more abundant than *C. gouldii* and since, except for St. 2, it made the largest single contribution to the biomass at every station which included this community. Inasmuch as the use of a predatory species should be avoided, this choice may be criticized. However, as shown earlier in this paper, *N. incisa*, at least in the Sound, is a nonselective deposit-feeder.

The concept of parallel communities advanced by Petersen, largely verified since then (see Spärck, 1935), states that two or more geographically separate communities living under similar physical and hydrographic conditions will have essentially similar animal populations, and that the characteristic species will belong to the same genera or, at most, to closely related genera.

Only four of the communities described previously by other investigators might be compared with the soft bottom community of Long Island Sound, the most similar one with regard to environmental factors being the *Syndosmya alba* community originally described from Danish waters (Petersen, 1913); this community, found in shallow and sheltered situations or in estuarine regions of the eastern Atlantic Ocean, Mediterranean and Black Sea, exists on muddy bottoms under conditions of reduced salinity. As implied, the characterizing species is the lamellibranch *Syndosmya alba*. Other common genera in this community are: the lamellibranchs *Cultellus*, *Corbula*, and *Nucula* (two species); the polychaetes *Nephtys* and *Pectinaria* (closely related to *Cistenoides*); and sometimes the echinoderms *Echinocardium* and *Ophiura*.

At somewhat greater depths (20-100 m) of the same geographical areas is the *Amphiura* community. In addition to the echinoderm *Amphiura*, the common genera are: the polychaetes *Nephtys*, *Lum-*



*briconereis* and *Terebellides*; the scaphopod *Dentalium*; the gastropod *Turritella*; the lamellibranch *Nucula*; and the echinoderms *Brissopsis*, *Echinocardium* and *Schizaster*.

Miyadi (1940) described a *Maldane* community from the muddy sediments of Tanabe-wan, a small Japanese Bay. Here the common genera are the polychaetes *Maldane* and *Telepsavus* and the amphipod *Ampelisca*; the somewhat less common genera are the polychaetes *Magelona*, *Praxillella* and *Glycera*; the lamellibranch *Tellina*; the gastropods *Philine* and *Cylichna*; and the scaphopod *Dentalium*.

Finally, the *Yoldia-hyperborea* community is found in the soft sediments of Icelandic waters at about 10–70 m (Spärck, 1937). The common genera are the polychaetes *Pectinaria*, *Sternaspis*, *Scalibregma*, *Amphicteis*, *Clymenella* and *Maldane*; and the lamellibranchs *Yoldia*, *Nucula* and *Leda*.

While all of these communities have characteristic genera in common with the Long Island Sound community, there are certain notable differences, particularly in regard to the most common genera. In the *Maldane* community, *Nucula* is absent and no other closely related genus is present to replace it. Although *Cistenoides* is replaced by the closely related genus *Pectinaria* in the *Syndosmya*, *Maldane* and *Yoldia-hyperborea* communities, there is no corresponding form in the *Amphiura* community. In the *Maldane* and *Yoldia-hyperborea* communities, *Nephtys* is absent, and only in the *Yoldia-hyperborea* community is the genus *Yoldia* present. Thus, of the four quantitatively dominant genera of the soft bottom community of Long Island Sound, at least one member, or a closely related form, is absent in the four communities discussed. In addition, there is no equivalent in the Sound for *Syndosmya* and *Amphiura*, the characterizing genera of two of these communities, and a third characterizing genus, *Maldane*, is only an insignificant member of the Sound community.

Obviously, then, it is extremely difficult to equate the Long Island Sound community to any of the four communities discussed. It is proposed, therefore, that this association of animals in Long Island Sound be called the *Nephtys incisa*-*Yoldia limatula* community, which is confined to sediments containing more than 25% silt and clay at depths of from 4 to at least 30 m with bottom temperatures of 0.5–22° C and salinities of at least 24.7–29.2‰.<sup>6</sup>

<sup>6</sup> On July 26, 1955 the author found this community entirely intact in Buzzards Bay near Woods Hole, Mass. (Lat. 41° 32.4' N, Long. 70° 43.9' W) in about 15 m of water; but the maximum salinity in this area is about 32‰.

*The Relationship of Primary Feeding Types to Sediment Composition.* In the remaining pages of this section an attempt will be made to see whether or not the primary feeding types (herbivores and detritus feeders) have any quantitative relationships to the character of the sediment. Information on feeding has been obtained largely from Blegvad (1914), Hunt (1926), Remane (1933), Thamdrup (1935) and Mare (1942), and, somewhat after the manner of Hunt (1926), these animals have been divided into three broad categories.

1. *Suspension feeders*, which live on organic matter suspended in the water, include: lamellibranchs with short separate siphons, namely *Pandora*, *Mulinia*, *Astarte*, *Lyonsia*, *Anadara*, *Cerastoderma*, *Pitar*, *Mercenaria* and *Ensis*; certain gastropods of the genus *Crepidula*; the filter-feeding amphipods *Ampelisca*, *Leptocheirus* and *Corophium*; the serpulid polychaete *Hydroides*; and the dendrochirote holothurian *Thyone*.

2. *Selective deposit-feeders*, which feed discriminantly either on or in the sediment, include both detritus feeders and herbivores; in this group are: lamellibranchs with long free siphons such as *Macoma*; lamellibranchs with prehensile labial palps, *Nucula* and *Yoldia*; polychaetes of the families Ampharetidae (*Ampharete* and *Melinna*), Terebellidae (*Pista* and *Trichobranchius*), Amphictenidae (*Cistenoides*), Chlorhaemidae (*Flabelligera*), and Cirratulidae (*Cirratulus* and *Polycirrus*); such amphipods as *Unciola*, *Siphonacetes*, *Stenothoë*, *Amphithoë* and *Erichthonius*; the cumaceans *Diastylis* and *Oxyurostylis*; the tanaid *Leptognathia*; the isopods *Edotea* and *Chiridotea*; and possibly the tectibranch molluscs *Retusa*, *Cylichna* and *Acteon* (Berrill, 1931).

3. *Nonselective deposit-feeders*, which indiscriminantly ingest the sediment, include: the polychaete families Ophelidae (*Ophelia*), Maldanidae (*Maldane*, *Clymenella*, *Praxillella* and *Rhodine*), Ariciidae (*Aricidia*), Scalibraemidae (*Scalibregma*) and, as shown earlier, the species *Nephtys incisa*.

Within two of the feeding types, the mechanisms vary widely. For example, among the suspension feeders, the gills act as a selective filter in the lamellibranchs while the mouthparts or certain leg appendages perform this function in the amphipods. Among selective deposit-feeders, the protobranchiate lamellibranchs use prehensile labial palps to obtain their food, other lamellibranchs probe over the bottom with long separate siphons (Yonge, 1939; 1949), and the poly-



chaetes feed by means of prehensile tentacles. In the following discussion of the general relationship of feeding types to sediment, it should be borne in mind that, in view of the different feeding habits of different animals, this relationship will be less precise than that determined for an individual species.

The dry weights of the three feeding types are shown in Fig. 23, where the stations are arranged in the order of increasing silt-clay content of their sediments. What is plotted, then, is the relationship between feeding type and sediment composition, and it is clear from Fig. 23 that such a relationship does exist. This is particularly evident in regard to suspension feeders. At stations characterized by little silt and clay, the suspension feeders completely dominated, while at stations with sediments of high silt-clay concentrations they constituted an insignificant standing crop. These results, then, support the contention made earlier in this paper that coarser sediments indicate favorable environmental conditions for suspension feeders. Since there is little net deposit of fine sediment in such environments, there are probably more pronounced bottom currents; hence more water and more food are made available to these organisms in a unit period of time. In this connection, Smith (1932) found in the typical gravel bottom of the Eddystone grounds near Plymouth that the largest number of species were suspension feeders, but he attempted no quantitative evaluation.

Results of an analysis of the nonselective deposit-feeders indicate that three different situations exist. At high concentrations of silt and clay (> 50%), as typified by Sts. 2 and 3, there were low biomass values. Between concentrations of approximately 25-50% silt-clay (Sts. 5, 8 and 7), high values were obtained. At somewhat lower concentrations (Charles Island and Sts. 1 and 4), nonselective deposit-feeders were poorly represented, particularly at Sts. 1 and 4, where the coarsest sediments were found. This distribution pattern can be interpreted to mean that coarse sediments with low concentrations of silt and clay are unfavorable because the hard substrate is not only unsatisfactory for burrowing but contains only a relatively small amount of organic matter which in turn can support only a small biomass of nonselective deposit-feeders. At the other extreme, when there are extremely high concentrations of silt and clay, the large quantity of organic matter provides a high food potential, but in this instance conditions become unfavorable due to lack of oxygen.

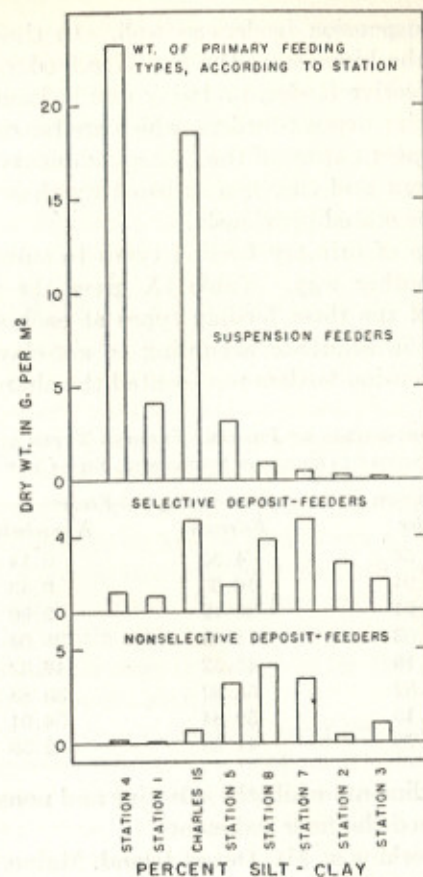


Figure 23. Weight of primary feeding types by station.

The histogram patterns for both selective and nonselective deposit-feeders are essentially similar at all stations except for that of Charles Island, where the higher biomass for the selective deposit-feeder was almost entirely due to the sample of October 23, 1953, which contained an abnormally high silt-clay concentration for that station. The poor representation of both selective and nonselective feeding types on the coarser sediments was directly related to low concentrations of settled detritus and to the small quantity of organic matter in the sediment; at high silt-clay concentrations it was the low oxygen content which created the unfavorable environment for these two



groups, and for suspension feeders as well. In these same environments, however, the biomass of the selective feeder was higher than that of the nonselective feeder, probably due in large measure to the fact that nonselective deposit-feeders, which are burrowers exclusively, find the hard compact nature of the coarse sediments and the reduced sediment of high silt and clay less satisfactory than selective feeders for obvious reasons stated previously.

The relationship of primary feeding types to substrates is demonstrable in still another way. Table IX gives the percentage composition of each of the three feeding types at each station, with the stations arranged in sequence according to silt-clay content. It is seen that the suspension feeders represented the characteristic feeding

TABLE IX. COMPOSITION OF PRIMARY FEEDING TYPES AT EACH STATION. STATIONS ARRANGED IN ORDER OF INCREASING SILT-CLAY PERCENTAGE.

Station	Suspension feeder	Deposit-Feeder		% silt-clay
		Selective	Nonselective	
4	95.56%	4.30	0.14	5.4
1	82.94	16.63	0.43	4.7
Charles Is.	76.91	20.19	2.90	11.0
5	43.03	18.93	38.04	18.5
8	10.16	43.52	46.32	28.0
7	5.82	55.82	38.88	31.5
2	6.15	59.84	34.01	56.0
3	5.78	41.68	52.39	65.0

type on coarser sediments while the selective and nonselective deposit-feeders characterized the finer sediments.

Bader (1954), working at Mt. Desert Island, Maine, found a positive correlation between the density of the lamellibranch population and the organic content of the sediment, with population density falling off sharply at concentrations of organic matter above 3%. He stated:

The pelecypod population, as used in this discussion, refers to the total density of pelecypods, including all species. This procedure was followed because the species of pelecypods which are abundant enough to consider individually show the same general trends as the total pelecypod population. The investigation did not show any major ecological hiatus to the exclusion of one or more species.

Actually, nine of the 16 species of lamellibranchs examined by Bader are suspension feeders, and for these Bader has assumed that

organic matter in the sediment is the prime source of food. This assumption seems extremely doubtful, since the correlation between suspension feeders and sediment type results from the relation between water circulation immediately over the bottom (of paramount importance to suspension feeders) and the type of sediment found. Hence the sediment content is of importance to suspension feeders, not *per se* but as an indication of other physical conditions.

## SUMMARY AND CONCLUSIONS

(1) A bottom survey of a limited area of Long Island Sound was carried out from August 1953 to September 1954, but in some instances additional data, obtained subsequently, have also been used. Most of the eight stations were worked at frequent intervals.

(2) The dry weight of each species in each sample was obtained separately. Individuals of the numerically abundant species were divided into size categories by length, and, when an adequate number of individuals of a given size category had accumulated, the dry weight was determined. From this figure the mean weight of the individual animals within this size range was computed. Tables relating length to weight were constructed for the dominant species on the basis of these computations.

(3) Modification of the techniques used by soil scientists was adopted for sediment analysis. In contrast to data given in other bottom investigations, significantly higher concentrations of silt and clay were obtained from all types of sediments. Results indicate that large fractions of these components are lost when the more commonly employed procedures are used. Since the clay component is closely associated with organic matter in sediments, the desirability of its precise determination is evident.

(4) Within a single station there were significant variations among different samples when the total biomass was considered, but when the larger, less abundant animals were excluded, the variability was significantly reduced. Still further uniformity was achieved when only the infaunal component of each sample was compared.

(5) It was possible to characterize the infauna of each sediment by a narrow range of biomass values. This was true not only between stations but even when samples from the same stations came from different sediment types.



(6) Results of the present investigation have shown that a close relationship exists between the silt-clay concentrations of the sediment and the size of the infaunal population. The largest populations were found in sediments containing 13-25% silt and clay. Deviation from this range either towards higher or lower concentrations gave progressively smaller biomass values.

(7) The animals under a square meter of bottom varied from 5,563 at St. 5 to 46,398 at Charles Island.

(8) The weight of all small organisms (those less than 0.2 g dry weight) varied from 4.54 g at St. 2 to 36.38 g/m<sup>2</sup> at Charles Island. Considering only the infauna, the values ranged from 3.93 g at St. 1 to 27.57 g at Charles Island.

(9) Long Island Sound supported a larger benthic population in both numbers and weight than that found in other areas by previous workers.

(10) Two mechanisms, the extensive freshwater drainage and the two-layer transport exchange, maintain high concentrations of nutrients in the Sound. These in turn allow dense concentrations of phytoplankton to develop, so that the ratio of phytoplankton to zooplankton is larger than that found for certain other inshore waters. This implies that the zooplankton is utilizing a smaller fraction of the available phytoplankton, leaving a larger proportion for other utilization. Since bacterial decomposition in this shallow water column must be limited, large quantities of phytoplankton are made available to benthic animals. This large supply of organic matter is the most obvious explanation for the high benthic biomass in the Sound.

(11) Detailed examination of the ecological relationships of the most dominant species was made:

a) The polychaete *Nephtys incisa* comprised approximately one-third of the biomass of smaller animals at stations with softer sediments and with maximal values within the 25 to 37% silt-clay range. Despite statements in the literature, *Nephtys incisa*, at least in Long Island Sound, must be considered a nonselective deposit-feeder rather than a carnivore. Trophic considerations and stomach analyses support this view.

b) The trumpet worm, *Cistenoides gouldii*, constituted almost 6% of the smaller animals at stations with finer sediments. The animal is a selective deposit-feeder and is found in largest numbers in sedi-

ments containing 20 to 40% silt and clay. Its mode of feeding prevents this organism from being abundant in sediments with either low or high concentrations of silt and clay.

c) The two most abundant forms of the amphipod genus *Ampelisca* are so similar that it was deemed unwise to attempt to separate them taxonomically. *Ampelisca* A, confined at all times of the year to the coarser sediments and comprising 14% of the infaunal populations, was 3-4 times heavier than its counterpart, *Ampelisca* B, which occurred only in the finer sediments and which made up 2% of their populations. The absence of overlap in their ranges suggests intense competition between them. Within the range of each form, no significant difference in size occurred, which indicates that this difference is of genetic rather than environmental origin. Each of these filter-feeding forms has a short summer and a long overwintering generation. Females were 15 times more common than males in both *Ampelisca* A and B; on closer examination, however, half of the females proved to be gonomorphic males.

d) The lamellibranch, *Yoldia limatula*, comprised almost 10% of the infauna of the softer sediments with maximal values in 30 to 45% silt-clay.

e) The lamellibranch *Nucula proxima*, despite its small size, constituted 24% of the infaunal biomass of the finer sediments. Substantial populations were found in sediments containing 35 to 75% silt-clay, thus indicating that this animal can tolerate somewhat reduced concentrations of oxygen. Like *Y. limatula*, *N. proxima* feeds by means of palp proboscides and is considered a selective deposit-feeder.

f) *Pandora gouldiana*, though found at all eight stations, made up a large fraction of the biomass at only Charles Island, where it comprised 14% of the infauna. Apparently this suspension-feeding lamellibranch is largely limited to sediments low in silt-clay and gravel.

(12) For present purposes, the productivity of a species or community, defined as the amount of organic matter produced in the course of a year, is estimated indirectly from calculations on growth, mortality and recruitment. Productivity values were obtained for four long-lived species: *Nephtys incisa*, *Cistenoides gouldii*, *Yoldia limatula* and *Pandora gouldiana*. Since the ratio of annual productivity to biomass for these species varied from 1.94-2.28, with a mean



value of 2.1, and since this value was based on forms that constituted more than 50% of the infauna of softer sediments, it seemed reasonable to use the same factor (2.1) to determine the productivity of the remaining long-lived animals in the population. A larger ratio of productivity to standing crop was indicated for short-lived animals; 5.0 appeared to be the most reasonable figure.

Using the determined amounts of long-lived and short-lived animals together with the above ratios, the factor obtained for the infauna ranged from 2.17 at Sts. 2 and 3 to 3.10 at St. 1; for all stations the ratio was 2.44.

(13) Consideration of the relationship between primary feeding types and sediment composition showed clearly that suspension feeders represented the characteristic feeding type on coarser sediments, where they comprised more than 80% of the total for the three feeding groups; in fine sediments they constituted only 6%. Conversely, in the finer substrates the selective and nonselective deposit-feeders were the dominant forms whereas in coarser sediments they represented only minor constituents of the population.

(14) Finally, an attempt was made to classify the level bottom communities, only one of which was represented adequately at the stations sampled. This was the population that inhabited the softer sediments at Sts. 2, 3, 7 and 8. Since significant differences were found between the composition of the dominant species of this community and that of similar ones from other regions of the world, it is proposed that this association of animals be called the *Nephtys incisa-Yoldia limatula* community of Long Island Sound, which is confined to sediments containing more than 25% silt and clay and which exists at depths of 4-30 m at temperatures of 0.5-22° C and at salinities of at least 24.7-29.2‰.

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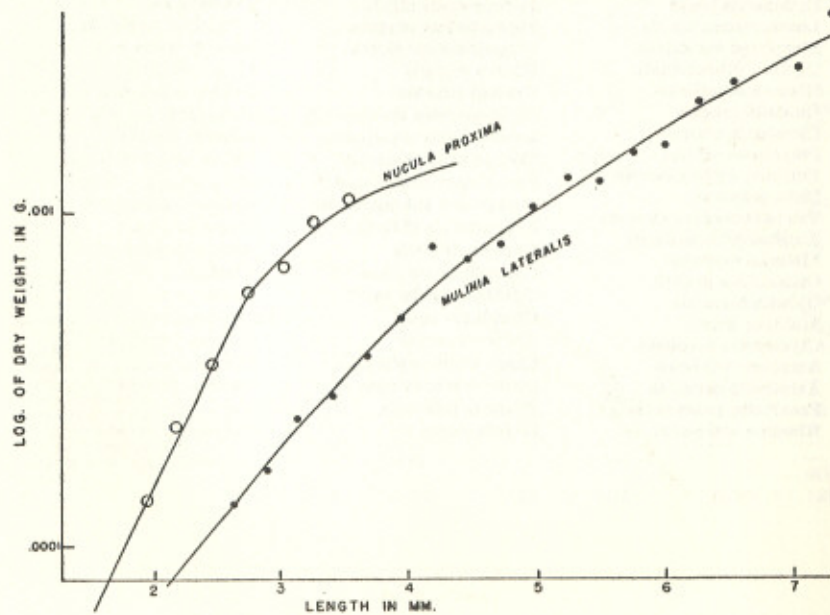
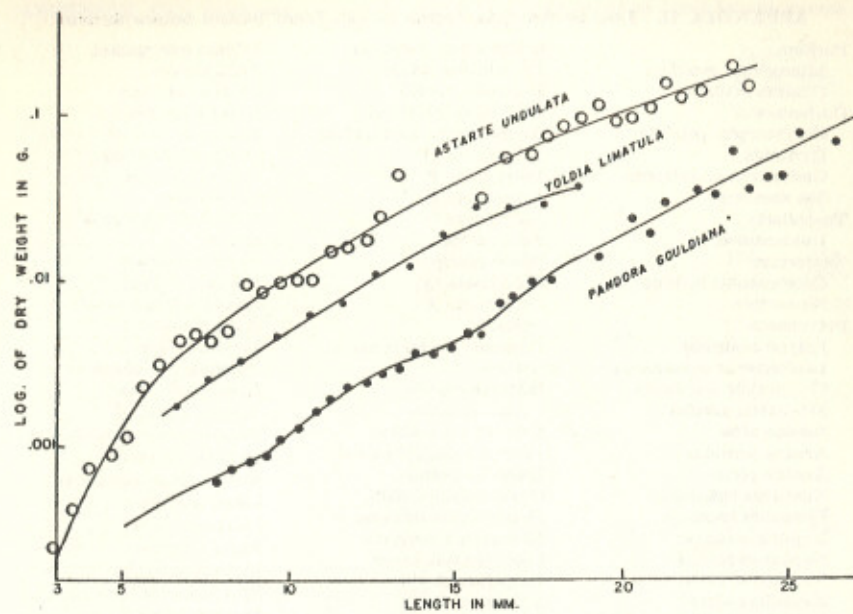
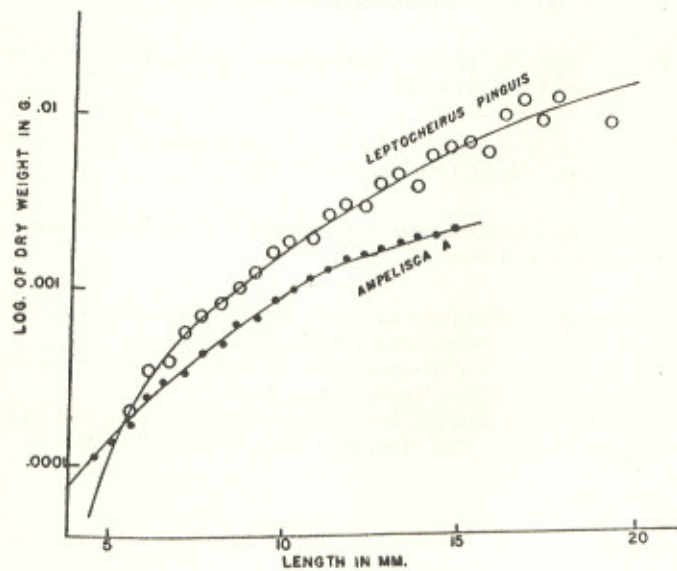
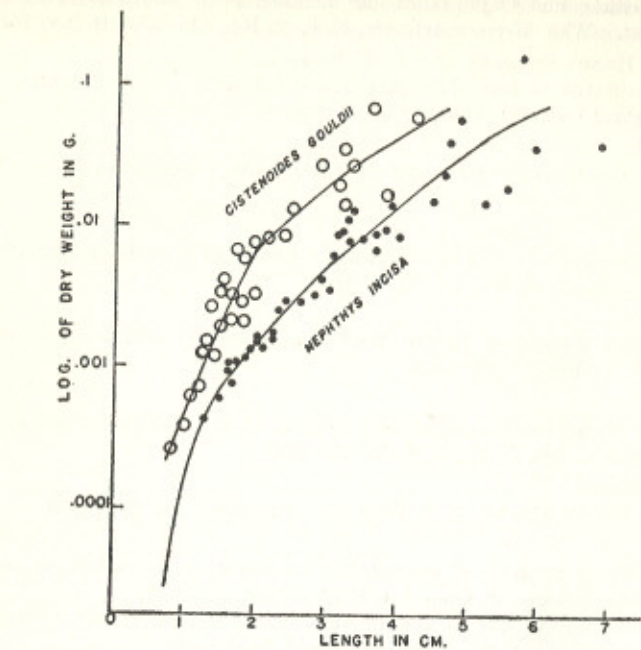


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## APPENDIX I. LENGTH-WEIGHT RELATIONSHIPS OF SOME DOMINANT SPECIES IN LONG ISLAND SOUND.





## APPENDIX II. LIST OF ANIMALS FOUND IN THE LONG ISLAND SOUND SURVEY

Porifera	Scalibregma infiatum	Libinia emarginata
Microciona prolifera	Flabelligera affinis	Pelia mutica
Chalina oculata	Potamilla torelli	Pinnixia sayana
Coelenterata	Hydroides dianthus	Neopanope texana
Corymorpha pendula	Ancistrosyllis tentaculata	Panopeus herbstii
Hydroids	Polychaete D	Ovalipes ocellatus
Cerianthus americanus	Polychaete E	Cancer irrorata
Sea anemone	Polychaete F	Pycnogonida
Turbellaria	Polychaete G	Nymphon grossipes
Unidentified sp.	Aricidia sp.	Mollusca
Nemertina	Ninoë nigripes	Nucula proxima
Cerebratulus luridus	Polychaete Q	Yoldia limatula
Nemertine	Polychaete X	Anadara transversa
Polychaeta	Splonid	Anomia simplex
Polyoë acanellae	Unidentified polychaete	Mytilus edulis
Lepidonotus squamatus	Crustacea	Pandora gouldiana
Harmothoe imbricata	Hutchinsoniella	Lyonsia hyalina
Sthenelais gracilis	macracantha	Astarte undulata
Eteone alba	Balanus balanoides	Cerastoderma pinnatum
Anaitis formosa	Diastylis quadrispinosa	Pitar morrhuana
Anaitis picta	Diastylis polita	Mercenaria mercenaria
Anaitides catenula	Oxyurostylis smithi	Gemma gemma
Neanthes succinea	Heteromysis formosa	Macoma tenta
Nephtys incisa	Neomysis americana	Ensis directus
Nephtys ingens	Leptognathia caeca	Mulinia lateralis
Nephtys caeca	Ampelisca A	Mya arenaria
Nephtys picta	Ampelisca B	Lunatia heros
Arabella iricolor	Stenothoe cypris	Lunatia triseriata
Diopatra cuprea	Elasmopus levis	Polinices duplicatus
Drilonereis longa	Podoceropepsis nitida	Leptocheirus pinguis
Lumbrineris tenuis	Leptocheirus pinguis	Crepidula convexa
Marphysa sanguinea	Amphithoe rubricata	Crepidula plana
Glycera dibranchiata	Grubia compta	Eupleura caudata
Glycera americana	Unciola irrorata	Urosalpinx cinerea
Goniada gracilis	Siphonacetes smithianus	Mitrella lunata
Cirratulus grandis	Erichthonius brasiliensis	Nassarius trivittatus
Polycirrus eximus	Corophium acherusicum	Busycon canaliculatum
Polycirrus phosphoreus	Corophium crassicornae	Retusa canaliculatum
Pista palmata	Corophium tuberculatum	Cylichna alba
Trichobranchius glacialis	Aeginella longicornis	Acteon punctostriatus
Ampharete acutifrons	Caprella linearis	Turridae
Melinna oristata	Caprella geometrica	Elysia catula
Cistenoides gouldii	Cyathura carinata	Echinodermata
Ophelia limacina	Chiridotea tuftii	Thyone briareus
Maldane sarsi	Edotea montosa	Holothurian
Clymenella torquata	Crago septemspinus	Asterias forbesi
Amphicora fabricii	Pagurus longicarpus	Pisces
Axiothella catenata	Pagurus pollicaris	Gobius sp.
Praxillella praetermissa	Libinia dubia	
Rhodine attenuata		

APPENDIX III. ANALYSES OF SOME REPRESENTATIVE STATIONS IN LONG ISLAND SOUND. NUMBERS AND WEIGHTS PER M<sup>2</sup>

Species	W. of Charles I.		Station 1		Station 4	
	Dec. 23, 1953		April 19, 1954		Feb. 19, 1954	
	No.	Wt.	No.	Wt.	No.	Wt.
Hydroids	+	1.31	+	12.89	+	.64
Polyoë acanellae	—	.24	—	—	—	—
Lepidonotus squamatus	—	.068	68	.38	—	—
Sthenelais gracilis	1558	.062	—	—	—	—
Eteone alba	—	.0015	—	.25	—	—
Neanthes succinea	—	.0015	281	.25	—	—
Nephtys incisa	—	.028	91	.037	15	.046
Nephtys ingens	—	.028	—	.033	106	.016
Nephtys caeca	—	.096	—	—	8	.0046
Nephtys picta	15	.096	—	—	—	—
Diopatra cuprea	—	.12	—	—	8	.0023
Lumbrineris tenuis	23	.12	—	—	—	—
Glycera dibranchiata	—	.0053	30	.068	—	—
Glycera americana	8	.029	—	—	—	—
Goniada gracilis	8	.011	—	—	—	—
Trichobranchius glacialis	8	.011	236	.22	106	.14
Ampharetes acutifrons	15	.14	—	—	8	.0015
Cistenoides gouldii	8	.013	—	—	—	—
Flabelligera affinis	—	.079	61	.44	—	—
Hydroides dianthus	61	.079	—	—	—	—
Unidentified polychaete	8	.0023	—	—	—	—
Oxyurostylis smithi	—	.190	190	.13	—	—
Neomysis americana	—	.32	—	—	20284	.32
Leptognathia caeca	616	.32	1307	1.50	1885	.96
Ampelisca A	—	.699	699	.052	684	.052
Stenothoe cypris	—	.46	—	.0091	—	—
Podoceropepsis nitida	—	.012	—	—	312	.95
Leptocheirus pinguis	23	.012	—	—	—	—
Leptocheirus rubricata	122	.062	—	—	—	—
Grubia compta	61	.21	91	.31	84	.13
Unciola irrorata	122	.0061	471	.047	213	.026
Erichthonius brasiliensis	935	.050	1543	.089	—	—
Corophium acherusicum	—	.23	—	.0038	471	.10
Corophium crassicornae	—	.17	23	.0084	—	—
Aeginella longicornis	433	.17	—	—	—	—
Edotea montosa	38	1.28	23	4.98	—	—
Crago septemspinus	15	.057	84	2.37	160	3.61
Pagurus longicarpus	8	13.79	53	124.79	—	—
Pagurus pollicaris	8	.050	—	—	15	2.32
Libinia emarginata	—	.061	8	.061	8	.036
Pelia mutica	—	.19	—	—	53	.52
Pinnixia sayana	84	1.19	68	1.77	—	—
Neopanope texana	—	.144	144	5.78	—	—
Panopeus herbstii	8	.0023	8	.0053	—	—
Nucula proxima	15	.078	—	—	106	.19
Anadara transversa	502	2.19	—	—	53	.031
Pandora gouldiana	15	.20	—	—	76	.25
Lyonsia hyalina	—	.3590	—	—	3590	18.64
Astarte undulata	—	.84	—	—	84	.67
Cerastoderma pinnatum	46	.036	—	—	—	—
Mercenaria mercenaria	122	.012	—	—	—	—
Gemma gemma	3177	3.43	—	—	53	.089
Macoma tenta	8	.23	—	—	53	.59
Ensis directus	1041	.41	471	.12	8	.0046
Mulinia lateralis	—	.334	—	—	8	.19
Lunatia triseriata	23	.028	334	.29	—	—
Crepidula plana	8	.0053	46	.95	—	—
Eupleura caudata	—	.8	8	.0023	—	—
Mitrella lunata	38	1.21	23	.28	23	.59
Nassarius trivittatus	8	.40	—	—	—	—
Busycon canaliculatum	3238	.70	—	—	—	—
Retusa canaliculatum	745	.050	8	.0008	—	—
Acteon punctostriatus	—	.8	—	—	8	.0068
Turridae	—	—	—	—	—	—
Totals	13203	28.3838	6742	157.8667	28472	31.1258



## APPENDIX III—Continued

Species	Station 5		Station 8		Station 3	
	Feb. 19, 1954		Feb. 3, 1954		Feb. 19, 1954	
	No.	Wt.	No.	Wt.	No.	Wt.
<i>Corymorpha pendula</i>	46	.45	—	—	—	—
Hydroids	+	.41	—	—	—	—
<i>Cerianthus americanus</i>	61	.64	—	—	—	—
<i>Eteone alba</i>	—	—	—	—	30	.14
<i>Anatides catenula</i>	8	.0030	46	.0046	—	—
<i>Nephtys incisa</i>	996	5.69	1429	3.99	106	.54
<i>Nephtys caeca</i>	—	—	137	.022	—	—
<i>Diopatra cuprea</i>	53	.20	—	—	—	—
<i>Lumbrineris tenuis</i>	15	.012	—	—	23	.028
<i>Glycera dibranchiata</i>	—	—	8	.052	—	—
<i>Trichobranchius glacialis</i>	—	—	46	.022	—	—
<i>Melinna cristata</i>	53	.052	357	.18	—	—
<i>Cistenoides gouldii</i>	213	.074	182	.13	15	.014
<i>Maldane sarsi</i>	15	.059	8	.055	—	—
<i>Flabelligera affinis</i>	23	.35	—	—	—	—
Spinoid	—	—	8	.0015	—	—
Unidentified polychaete	frag.	.086	182	.0091	213	.021
<i>Ampelisca B</i>	1360	.11	—	—	46	.0046
<i>Stenothoe cypris</i>	524	.042	—	—	—	—
<i>Leptocheirus pinguis</i>	38	.14	46	.054	—	—
<i>Unciola irrorata</i>	365	.17	—	—	—	—
<i>Siphonacetes smithianus</i>	160	.026	—	—	—	—
<i>Panopeus herbstii</i>	15	.76	—	—	—	—
<i>Nymphon grossipes</i>	8	.0008	—	—	—	—
<i>Nucula proxima</i>	8	.0023	8003	1.27	1984	.31
<i>Yoldia limatula</i>	—	—	137	.67	61	.32
<i>Anadara transversa</i>	8	.072	—	—	—	—
<i>Pandora gouldiana</i>	53	.011	23	.081	8	.0076
<i>Lyonsia hyalina</i>	258	.85	—	—	—	—
<i>Pitar morrhuaana</i>	160	.47	15	.0030	8	.0015
<i>Macoma tenta</i>	—	—	8	.0038	—	—
<i>Mulinia lateralis</i>	524	.14	8	.0015	8	.0023
<i>Lunatia triseriata</i>	—	—	15	.58	—	—
<i>Polinices duplicatus</i>	8	.60	—	—	—	—
<i>Urosalpinx cinerea</i>	—	—	8	.023	—	—
<i>Retusa canaliculatum</i>	—	—	2098	.42	167	.030
<i>Cylichna alba</i>	106	.021	1026	.21	—	—
<i>Acteon punctostriatus</i>	8	.0084	8	.0008	—	—
Turridae	312	.043	91	.031	—	—
Totals	5398	11.4925	13889	7.8143	2669	1.4190