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# Journal of MARINE RESEARCH

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## Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound

by Peter L. McCall<sup>1</sup>

### ABSTRACT

Nearshore communities of infaunal benthos on soft bottoms are characterized by a highly variable species composition. Some species undergo large spatial and temporal variations in local abundance; other members of the same community change only a little.

This study examines the importance of disturbances of the seafloor which result in local mortality of resident populations as a cause for spatial and temporal faunal changes commonly observed in nearshore benthic communities. The role of disturbance in ecologic succession was examined by *in situ* experiments in central Long Island Sound.

Samples of defaunated mud were placed on the bottom at two sites in central Long Island Sound on July 17, 1972, to simulate a local disaster. Samples collected 10 days later contained high numbers ( $\cong 10^7/\text{m}^2$ ) of the species *Streblospio benedicti*, *Capitella capitata*, and *Ampelisca abdita*. These small, sedentary, tube-dwelling deposit-feeders, named Group I species, are classified as opportunists and are characterized by rapid development, many reproductions per year, high recruitment, and high death rate. These Group I species produce few eggs per female ( $10^2$ - $10^3$ ), but all possess some form of brood protection. Another species group, Group III, made up of the errant polychaete *Nephtys incisa* and the razor clam *Ensis directus*, are present early in the colonization samples, but remain at low and constant abundance throughout the experiment ( $\cong 10^2/\text{m}^2$ ). These large and mobile species are classed as equilibrium species and relative to more opportunistic species exhibit slow development, few reproductions per year, low recruitment, and low death rate. They do not brood developing young; they produce large numbers of planktotrophic larvae ( $10^3$ - $10^6$  per female). Group II species, composed of *Tellina agilis* and *Nucula proxima*, are intermediate in peak abundance ( $\cong 10^3$ - $10^4/\text{m}^2$ ), death rate, and life history. The colonization sequence is based on observations made on 74 samples in four

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colonization experiments conducted in two successive years (7/72-8/73; 7/73-10/73) on 3 different bottom types.

Regional grab sample surveys were also made in central Long Island Sound for comparative purposes. Group I species are found to have highly variable sample abundances in both space and time. *Nephtys incisa* (Group III), on the other hand, is fairly constant in space and time. Opportunist-dominated stations are restricted to shallow water less than 20 meters deep. Storm waves and tidal turbulence may be especially effective in resuspending the bottom at these depths. Biological bottom disturbance due to aggregations of bottom-feeding fish and starfish, however, cannot be ruled out.

Differences in the distribution and abundance of benthic organisms in central Long Island Sound may be explained in terms of two different adaptive strategies, opportunistic or equilibrium. The relative opportunism of the Long Island Sound benthos is most closely related to mobility and living and feeding position in the substratum. Sedentary animals and those living or feeding close to the sediment-water interface are more likely to be opportunistic and less predictable in space and time. Mobile animals and those living or retreating deep into the sediment are more likely to be equilibristic, and generally tend to have populations that are more predictable in space and time.

## 1. Introduction

Nearshore soft-bottom communities have a highly variable species composition. The local abundance of certain species may vary by orders of magnitude in time and space, while at the same time the abundance of other species changes only a little. Causes for these phenomena are poorly known.

Year to year fluctuations in species composition may reflect catastrophic adult mortality brought about by climatic factors (Coe, 1956; Gunter, 1947; Brongersma-Sanders, 1957). More often the fluctuations are believed to be the result of factors affecting the success of spawning and dispersion patterns of larvae (McIntyre, 1970; Trevallion, *et al.*, 1970; Loosanoff and Davis, 1963; Segerstrale, 1960).

Benthic samples taken in close proximity are often found to be less alike in species composition than widely separated samples (Eagle, 1973; Stephenson *et al.*, 1972). Such patchiness has been explained as the result of dispersal or concentration of planktonic larvae by currents (Fager, 1964; Ayers, 1956), small scale habitat heterogeneities, inter- and intraspecific competition, and amensalistic interactions (Ford, 1925; Rhoads and Young, 1971).

Johnson (1973) envisages the bottom as a temporal mosaic; different parts of a habitat disturbed at different times contain different faunas. "The community," he says, "is conceived of as continually varying in response to a history of disturbance. In this view, the community is a collection of relics [and recoveries] of former disasters." Sutherland (1974) has likewise emphasized the role of history in determining the structure of a variety of natural communities.

Temporal mosaics may be due to the spatially heterogeneous pattern of disturbance and the differential response of organisms to disturbance. Early and late colonizers of a new environment created by a disturbance will have different adap-

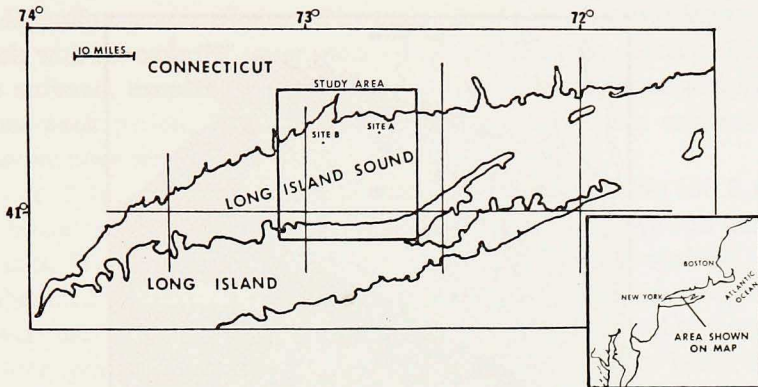


Figure 1. Location of Long Island Sound on the northeast coast of the United States.

tive strategies: r-strategies (opportunistic) or K-strategies (equilibrium) (MacArthur and Wilson, 1967; Grassle and Sanders, 1973). The temporal and spatial population fluctuations undergone by opportunistic species in response to environmental disturbance, for example, are liable to be much larger than those experienced by equilibrium species.

In view of our present knowledge of the structure and function of benthic infaunal communities, the purpose of this study has been to: (i) determine the response of Long Island Sound benthos to a simulated local disaster by means of field experiments; (ii) correlate the adaptive strategies of Long Island Sound benthos to temporal and spatial fluctuations in population size; and (iii) relate adaptive strategies to such niche parameters as trophic type, life position, and mobility.

## 2. Study area

This study was conducted in Long Island Sound, a tidal embayment on the northeast Atlantic coast of the U.S. (Fig. 1). Long Island Sound is approximately 190 kilometers long and 20 kilometers wide with a surface area of 2600 km<sup>2</sup>. Most of the Sound is less than 30 meters deep; the greatest depth recorded is 100 meters.

Riley (1956a,b) and Gordon and Pilbeam (1974) describe the hydrography of Long Island Sound. According to them, average peak tidal current velocity at the surface is about 30 cm/sec in the central Sound. Tidal turbulence may produce even higher velocities (H. Bokuniewicz, pers. comm.). There are large spatial and temporal variations in resuspension of bottom sediment by currents. Instantaneous measurements of suspended sediment may range from 1-100 mg suspended sediment/cm<sup>2</sup> of bottom. The large-scale distribution of sediment types is shown in Fig. 2. Sediment descriptions refer to the Udden-Wentworth classification (Pettijohn, 1957).

The annual temperature range of Long Island Sound surface water in 1972-1973

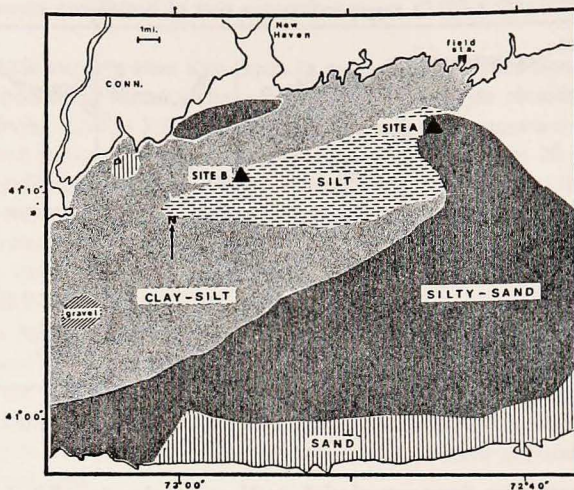


Figure 2. Gross patterns of sediment distribution in central Long Island Sound. (after Buzas, 1965).

was 20°C (3-23°C). Bottom and surface temperatures usually differ by less than 0.1°C. The seasonal salinity range in 1972-1973 was about 3‰ (25-28‰).

### 3. Methods

Four colonization experiments were carried out in 1972-1973 at two sites in Long Island Sound, referred to as site A and site B (Fig. 2). Site A is located in 14 meters of water (MLW) on a firm silty sand bottom. Site B is located in 15 meters of water (MLW) on a soft silt-clay bottom. There are no significant temperature or salinity differences between the two sites (Gordon and Pilbeam, 1974).

In 1972, two field experiments were performed at site A. The purpose of the experiments was to determine if there are repeatable patterns in recolonization of the bottom by fauna following a local disturbance. Local disturbances of the bottom were simulated by placing defaunated substratum on untreated natural bottom. Some plots of defaunated substratum and natural bottom were covered with screens to assess the affect of predation on species composition.

In order to correlate temporal patterns observed in the experiments with naturally occurring spatial patterns in species composition, grab sample surveys were made in the central region of Long Island Sound on three different occasions over a one-and-a-half year period.

In June, 1972 ten tons of high organic carbon content (5%) silt-clay sediment were removed from the harbor of the Yale Biological Field Station and placed in 700 0.1m<sup>2</sup> plastic boxes. The depth of sediment in these boxes was approximately

10 cm. Macrofauna were eliminated by letting the sample boxes remain onshore for one week with no covering water, next covering them with sheets of black plastic to raise sediment temperature, and finally covering the sediment with fresh water for a one-week period. Three sample boxes were sieved for evidence of living macrofauna; none were found.

Six large (3.1m × 3.7m × 0.15m) wooden boxes, each holding 100 0.1m<sup>2</sup> plastic sample boxes filled with mud, were constructed from 5/8" plywood and 2" × 6" pine planks. Predator exclusion screens to cover the tops of two of the large boxes were fabricated from 1/2" galvanized mesh. Two of the four remaining unscreened boxes were used to study short-term (one year) colonization, and two were used to follow long-term (greater than one year) fluctuations. Wooden boxes holding 20 and 2 samples respectively were constructed to examine the effect of box size on recolonization patterns.

A black plastic covering was placed over each plastic sample box to prevent washout of sediment during transport to the experimental site and to prevent any colonization until all boxes were placed on the bottom. The covered plastic boxes were put into the large wooden frames and wired in place. Three empty 55 gallon oil drums were attached to the sides of the wooden frames for flotation. The boxes were towed individually to experimental site A. At the start of the experiment on July 17, the individual plastic covers were removed from each of about 600 plastic boxes by divers using SCUBA.

In June, 1973 colonization experiments were repeated at site A using 1.5 meter square wooden frames containing 20 plastic boxes (0.1m<sup>2</sup>) of defaunated mud. These smaller wooden frames were easily transported on the deck of a boat and did not require flotation. Two frames, one without a predator exclusion screen and one screened with 1/2" mesh, were placed at the firm bottom site A. The same procedure was followed at site B.

Beginning July 27, 1972, divers periodically removed the 0.1m<sup>2</sup> mud samples from inside the large wooden frame boxes. Freshly defaunated mud samples were put down in their place and collected at the next sampling interval. These are called "replacement" samples. With this technique, colonization from the start of the experiment and over one sampling interval was monitored. At the same time that samples were collected from the experimental plots, samples of the surrounding natural bottom were taken with 0.147m<sup>2</sup> and 0.041m<sup>2</sup> Van Veen grab samplers.

Initially three 0.1m<sup>2</sup> samples were taken from each of the experimental plots. This yielded a total of thirteen samples per sampling interval (six samples from unscreened boxes, six from screened boxes, one replacement sample). A processing time of 50-80 hours per sample made this intensive sampling impossible, and it was eventually decided to take a total of two 0.1m<sup>2</sup> unscreened samples, and one replacement sample from inside the plots. Depending on the availability of Van Veen grabs, one 0.147m<sup>2</sup> sample or two or four .041m<sup>2</sup> samples were taken from the sur-

Table 1. Dates of biologic sampling of colonization experiments at sites A and B.

Experiment	Interval	Sampling Date	Location	Time (days) After Start
1	1	07-27-72	site A	10
	2	08-13-72	site A	29
	3	09-09-72	site A	50
	4	10-13-72	site A	86
	5	01-10-73	site A	175
	6	03-02-73	site A	223
	7	05-03-73	site A	285
	8	06-21-73	site A	337
	9	08-10-73	site A	384
2,3	1	07-03-73	site A	19
	1	07-06-73	site B	22
	2	08-10-73	site A	57
	2	08-25-73	site B	69
	3	10-24-73	site A	132

Site A: 41° 13.3' lat., 72 43.8' long.

Site B: 41° 10.4' lat., 72 56.3' long.

rounding natural bottom. Table 1 lists the times of sampling for the recolonization experiments.

Immediately after collection, samples were preserved in 3% formalin and seawater solution and stained with rose bengal. All samples collected at sites A and B were washed through a 297 micron sieve to separate animals from sediment. Most of the 132 grab samples from the regional faunal surveys were washed through a 1mm sieve. Animals were picked by hand from the sieve residue under a binocular dissecting microscope using magnifications of 7× and 30×. Some of the colonization samples contained thousands of animals per sample. To estimate their total abundance in a sample, the mean abundance per gram of sieve residue was calculated after counting the animals in 20 one gram aliquots of well mixed sieve residue. This number multiplied by total weight of the sieve residue (usually 200-300g) estimates the number of individuals in the sample with ~ 5% error. Only molluscs, polychaetes, and amphipods were identified and counted; these animals make up >95% of the infaunal macrobenthos. Substantial numbers of oligochaetes were sometimes encountered, but taxonomic difficulties prevented their specific identification.

The effect of colonizing animals on sediment mass properties was assessed by measuring the water content of the top 1 cm of the experimental sediment (Rhoads, 1970; Young, 1971). After collection of sediment cores (PVC core tube diameter 3.8 cm) by divers, the core was rapidly frozen, extruded from the core tube, and the top 1 cm cut off. Water content was measured as weight loss after three days drying at 100°C. A measure of sediment in suspension was obtained by arranging

sediment traps (one liter glass jars) at 0.15m, 1.0m, 2.0m, and 3.0m elevations above the bottom on a rigid pole anchored to the bottom.

$H$  diversity and equitability were calculated by the methods of Pielou (1966, 1969).  $H$  diversity is calculated as

$$H = \frac{1}{N} \log_2 \frac{N!}{\prod N_i!}$$

where  $N$  is the total number of individuals in the sample and  $N_i$  is the number of individuals in the  $i$ th species. A single sample is not sufficient to characterize species number, diversity, or equitability of infauna from the experimental plots or natural bottom. Consequently, all samples taken at a particular interval on a particular bottom type were used to calculate these. Plots of index means have the same form as plots of index aggregates, and variances are small (1.73 for species number, .23 for diversity), but of course their absolute values differ. In 1973, variances were larger and so both aggregate and mean values are reported. For statistical comparisons of sample median locations, the Mann-Whitney U test was used; computation methods follow Campbell (1967).

Two sample comparisons of faunal similarity were made using a modification of Sorenson's index of affinity (Greig-Smith, 1964). Sorenson's original index is expressed as  $\frac{2c}{a+b}$  where the two compared samples contain  $a$  and  $b$  species respectively, and there are  $c$  species in common. Bray & Curtis (1957) weighted the contribution of each species to the index by its relative abundance in a sample. However, it was not thought desirable to consider similar two samples which differed by orders of magnitude in species abundance. Consequently, the contribution of each species was weighted by its absolute abundance, and  $c$  becomes then the sum of the lesser abundances of those species common to both samples. Sample similarity might be more elegantly measured using Mahalanobis' generalized distance calculation (Hughes and Lindley, 1955) or canonical variate analysis (Seal, 1964). However, they were not considered useful in this study since a small number of samples were taken at each interval during the colonization study and calculation of variance-covariance matrices for each interval is demanded by these techniques.

#### 4. Results

*Colonization experiments—1972.* The purpose of the experiments with unscreened boxes was to look for successional patterns in the colonization of a barren substratum. Ten days after the start of the first experiment in July, 1972, boxes of sediment placed at site A had been covered with a 2-3 cm thick layer of sediment resuspended by tidal currents from the surrounding silty sand bottom. Thus all animals encountered natural bottom sediment upon entering the experimental boxes. Animals gained entry as settling larvae, as juveniles or adults passively transported



Table 2. Species composition of experimental box samples and natural bottom samples from Site A at 10, 86, and 334 days after the start of the experiment. Abundances are reported as individuals/m<sup>2</sup>.

Species	July 27, 1972		October 13, 1972		June 21, 1973	
	Experimental Bottom Samples	Natural Bottom Samples	Experimental Bottom Samples	Natural Bottom Samples	Experimental Bottom Samples	Natural Bottom Samples
<i>Nucula proxima</i>	205	116	510	530	110	183
<i>Yoldia limatula</i>	—	20	—	7	—	—
<i>Mulinia lateralis</i>	5	—	10	—	—	—
<i>Pitar morrhuana</i>	—	7	—	7	—	12
<i>Tellina agilis</i>	265	170	1400	54	20	121
<i>Ensis directus</i>	10	122	0	75	—	—
<i>Petricola pholadiformis</i>	0	—	10	—	—	—
<i>Lyonsia hyalina</i>	0	0	25	—	—	—
<i>Crepidula sp</i>	—	7	—	—	—	—
<i>Polinices duplicatus</i>	10	—	—	—	—	—
<i>Mitrella lunata</i>	—	—	85	—	5	—
<i>Nassarius trivittatus</i>	15	7	100	34	—	31
<i>Heliascus bisculata</i>	—	7	—	—	—	—
<i>Retusa obtusa</i>	—	—	430	—	—	12

<i>Phyllodocidae sp.</i>	8515	7	605	347	—	—
<i>Lepidonotus squamatus</i>	—	—	10	—	—	—
<i>Glycera dibranchiata</i>	—	27	170	7	—	60
<i>Nephtys incisa</i>	—	34	35	136	150	436
<i>Podarke obscura</i>	—	—	—	—	—	—
<i>Sigambra tentaculata</i>	200	—	—	258	5	—
<i>Capitella capitata</i>	36120	1700	7385	884	6815	4283
<i>Streblospio benedicti</i>	418,315	6800	16,830	6072	5	254
<i>Spionid sp.</i>	10	—	5	—	—	—
<i>Cirratulid sp.</i>	5	1020	—	932	—	65
<i>Amphitrite johnstoni</i>	—	—	5	—	—	—
<i>Pectinaria gouldii</i>	—	—	185	—	—	—
<i>Ampharete acutifrons</i>	—	—	—	68	10	—
Maldanid A	—	20	—	82	—	—
Maldanid B	—	20	—	82	—	—
<i>Sabella crassicornis</i>	—	—	—	—	—	12
<i>Ampelisca abdita</i>	5130	3176	1000	82	—	12
<i>Unciola irrorata</i>	—	88	—	20	—	—
<i>Leptocheirus pinguis</i>	—	—	—	—	—	—
No. SPP	14	18	20	18	9	12
No. INDIV	470,115	13,348	28,765	9676	7125	5433

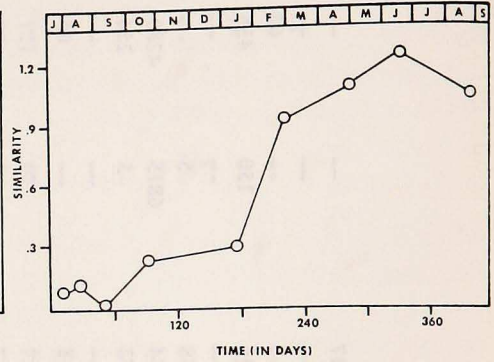
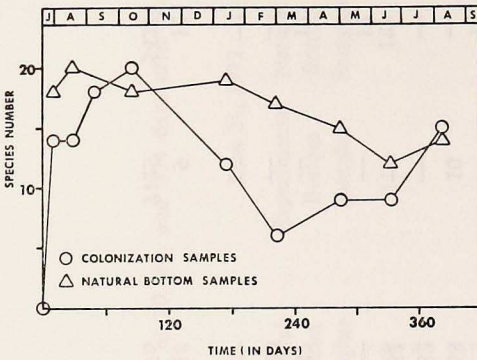


Figure 3. Number of species found at Site A 1972-1973. The total number of unique species found in all samples taken at one interval is plotted as the ordinate. Abscissa is time in days after the start of the experiment.

Figure 4. Similarity of samples taken from experimental boxes and natural bottom at Site A 1972-1973.

by tidal currents, or as active swimmers and crawlers. Larval recruitment accounted for the greatest proportion (over 90%) of all individuals, although in a few species a significant proportion of animals in the colonizing population entered as adults.

I will first describe changes in community attributes during colonization (number of species, diversity, dominance), secondly examine colonization patterns of individual species, and finally examine the variation of physical environmental factors at Site A which may initiate or affect colonization sequences.

*A. Community attributes.* Uninhabited substratum placed on the sea bottom at Site A was soon colonized by Long Island Sound infauna. Ten days after the removal of the plastic sample coverings fourteen species were found in all samples collected from the experimental plots. An equivalent area of natural bottom supported about 18 species (Fig. 3). A maximum of twenty species was found just three months after the start of the experiment.

Although by this time species number was equal to species number on the surrounding bottom, Table 2 and Fig. 4 show that the species composition of colonization samples and natural bottom samples were still dissimilar. Similarity among samples collected at the same time on natural bottom averaged over the period of study was .60; for colonization samples this value was .76. (Possible range for this index is 0-1.0.) Since .6 was about as similar as samples on natural bottom ever became, similarities between samples collected from experimental plots and natural bottom reported in Fig. 4 were restandardized by dividing the calculated index by this value. Inspection of faunal lists in Table 2 supports the observation from Fig. 4 that the species composition of colonization samples and natural bottom samples

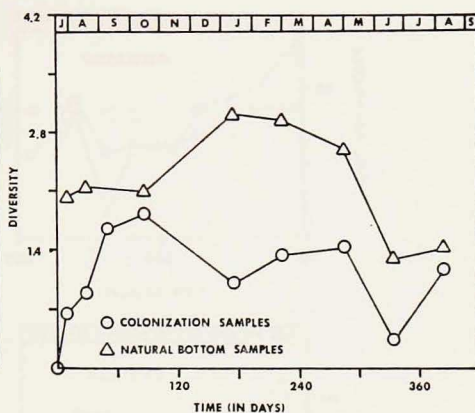
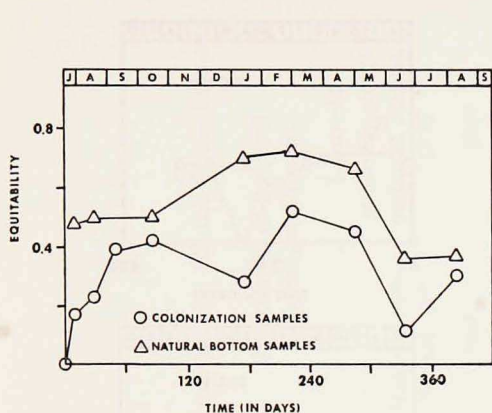


Figure 5. Aggregate equitability at Site A, first colonization experiment.

Figure 6. Diversity of Site A, July 1972-August, 1973. Ordinate is the diversity of the aggregate of all samples taken at each interval.

did not become similar until almost a year after the start of the experiment. Complete faunal lists for all samples collected in this study are in McCall (1975).

The decline in number of species found in the experimental plots and on surrounding bottom was coincident with the onset of winter. Colonizing populations suffered greater winter mortality than natural populations, reflecting the low relative ability of 0-year class individuals to withstand winter conditions. The increase in equitability in both recolonizing and natural bottom populations under winter conditions (Fig. 5) resulted from a more severe decline in numbers suffered by the most abundant species relative to rarer species. The differential effects of winter conditions on experimental and natural bottom populations led to a decrease in diversity of the experimental populations and an increase in diversity in natural bottom populations (Fig. 6).

Table 3. Colonizing potential of benthic infauna found from July, 1972-March, 1973, in samples from experimental plots. (See Table 1 for dates corresponding to sampling intervals.)

	Peak Abundance	At Interval:	Final Abundance
Group I			
<i>Streblospio benedicti</i>	418,315	1	335
<i>Capitella capitata</i>	80,385	2-3	955
<i>Ampelisca abdita</i>	9,990	2-3	0
Group II			
<i>Nucula proxima</i>	3,735	3	50
<i>Tellina agilis</i>	1,400	4	0
Group III			
<i>Nephtys incisa</i>	220	5 ( $\cong$ constant)	120
<i>Ensis directus</i>	30	3-6 ( $\cong$ constant)	0

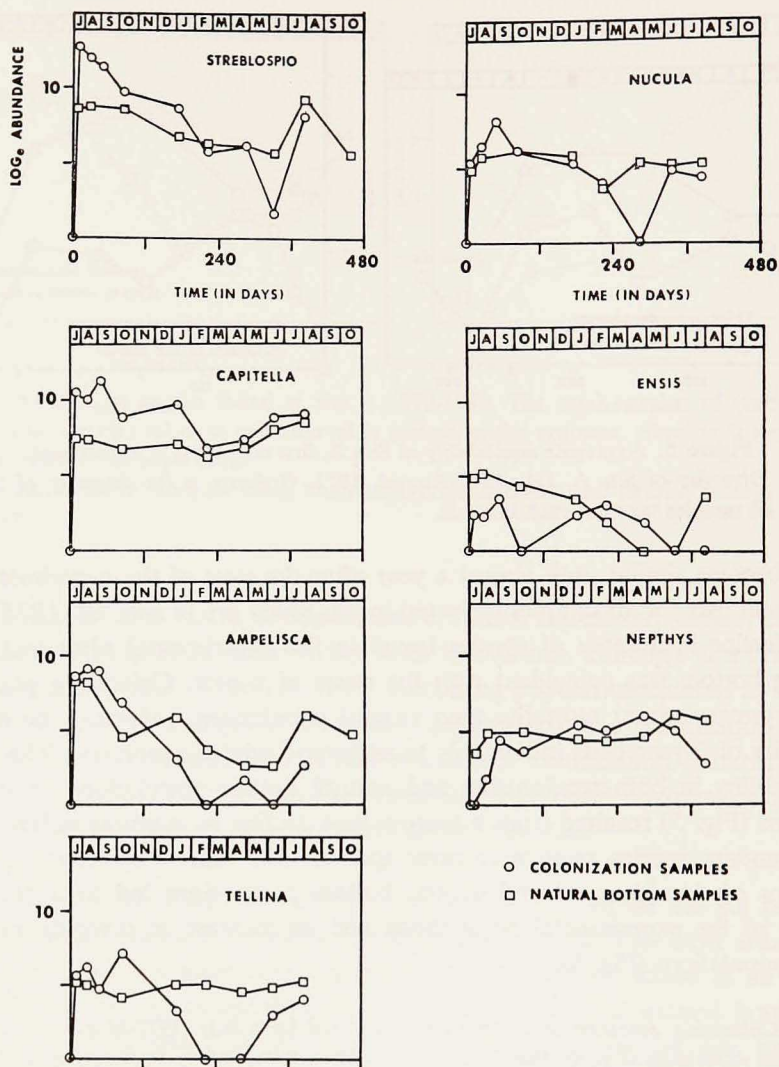


Figure 7. Log abundance (no. individuals/m<sup>2</sup>) of common species at Site A, July, 1972-October, 1973.

*B. Species abundance patterns.* Most of the colonizing species exhibited an initial rise in abundance in the defaunated areas through the summer and autumn, followed by a decline in winter. Colonization curves of species consistently present in the experimental samples are shown in Fig. 7. Species were considered "consistently present" if they were present for four or more consecutive sampling intervals. One qualifying species, a phyllodocid polychaete, was left out of this discussion since its identification was uncertain and life habits and reproductive type unknown.

Table 4. A comparison of colonization of empty sediment with colonization of sediment with animals present. For full species lists see McCall (1975). Abundances reported as number of individuals per square meter.

	Colonization of Empty Sediment		Colonization of Sediment with Animals Present	
	Colonization in August, 1972	Colonization in August, 1973 (partially empty)	Natural bottom August, 1973	1-year old previously empty sediment, August, 1973
<i>Capitella capitata</i>	36120	170585	5868	8940
<i>Streblospio benedicti</i>	418315	12575	13310	4015
<i>Owenia fusiformis</i>	0	86650	240	0
<i>Ampelisca abdita</i>	5130	45	15	472
<i>Tellina agilis</i>	275	60	206	55
<i>Nucula proxima</i>	205	35	205	75
<i>Yoldia limatula</i>	0	10	24	45
<i>Nephtys incisa</i>	0	95	266	15
<i>Ensis directus</i>	10	0	36	0
Group I totals	459,565	269,855	19,433	13,427

Table 5. Comparison of colonization of defaunated samples emplaced on 7/27/72 with replacement samples showing colonization over one sampling interval.

	Colonization Sample		Colonization Sample	
	Density Change from 7/27/72 to 8/13/72	Replacement Sample 8/12/72	Density Change from 8/13/72 to 9/9/72	Replacement Sample 9/9/72
<i>Capitella capitata</i>	-12,660	108,350	+56,925	17,620
<i>Streblospio benedicti</i>	-23,975	263,980	-72,460	94,000
<i>Ampelisca abdita</i>	+ 4,860	—	- 1,336	28,170
		Total 213,515/m <sup>2</sup>		Total 196,645/m <sup>2</sup>

Colonizing species can be placed into one of three groups based on differences in peak abundance, time of peak abundance, and death rate (Table 3).

About forty percent of the thirty-three species found during the period June-March were present ten days after the start of the experiment. Three species, however, contained over ninety-seven percent of the approximately one half-million individuals per m<sup>2</sup> found at the first sampling interval; and they were found at densities two orders of magnitude higher than those on the surrounding natural bottom. These three species are the polychaetes *Streblospio benedicti* and *Capitella capitata*, and the amphipod *Ampelisca abdita*. These Group I species are able to discover new areas quickly, in this case in less than ten days. They enter in great numbers (between 10<sup>5</sup> & 10<sup>6</sup> indiv./m<sup>2</sup>), but peak early and have very high death rates (Fig. 7). Populations of *Streblospio benedicti*, for example, suffered an average net loss of 58,856 individuals/m<sup>2</sup>/month between July, 1972 and March, 1973 in experimental plots (as compared to a loss rate of 1298 individuals/m<sup>2</sup>/month for natural bottom samples).

Even in the face of large and continuous recruitment (Table 4,5), Group I species declined rapidly after their initial peak abundance. A different pattern was shown by the Group II species *Nucula proxima* and *Tellina agilis*. Peak abundances (10<sup>3</sup> indiv./m<sup>2</sup>) were smaller than for Group I species and were not reached until the third or fourth sampling interval between fifty and ninety days after the start of the experiment. Most individuals entered the experimental areas as newly settled individuals as in Group I. The death rate of these juveniles was smaller than for Group I species, but without the continuous recruitment and rapid development of species like *Streblospio* and *Capitella* their densities inside the experimental plots sank below that of the outside population by March. Between September, 1972 and March, 1973 the population of *Nucula proxima* in the experimental boxes suffered an average net loss of 646 individuals/m<sup>2</sup>/month; over this same period natural bottom samples experienced a loss rate of 26 individuals/m<sup>2</sup>/month.

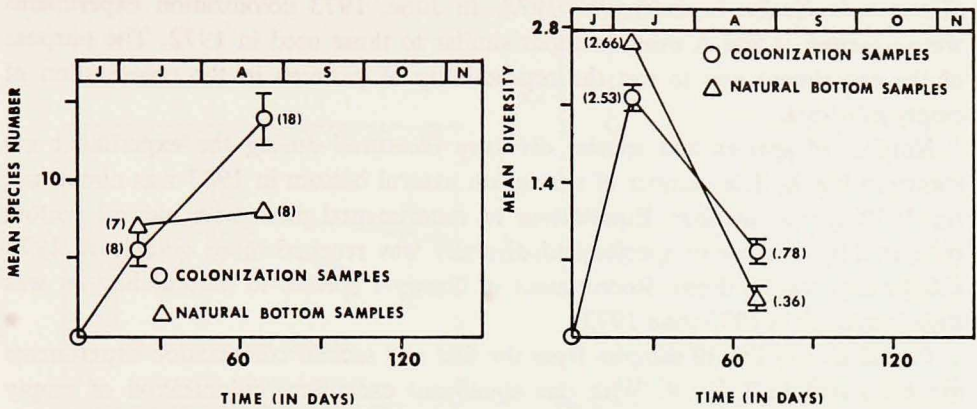


Figure 8. Mean number of species and H diversity during second colonization experiment (summer, 1973) at Site A. Vertical bars indicate range of variable values. Numbers in parenthesis are aggregate indices.

Group III species, *Nephtys incisa* and *Ensis directus*, either peaked later than ninety days after the start of the experiment or remained at low and constant levels ( $10$ - $10^2$  indiv./ $m^2$ ) throughout the period June-March. Although the presence of gravid and spent females indicated that these species underwent reproduction at the time of the experiment, few of the individuals found in the experimental plots were newly settled juveniles. Most individuals of these very mobile species gained entry either by passive dispersal or active swimming and leaping, the latter a common phenomenon among invertebrates (Thomas and Jelley, 1972; Ansell, 1968, 1969; Stanley, 1970). These were the only species whose density in the experimental areas was equal to or less than the density on the surrounding bottom. They were not particularly effective colonizers, but had low death rates once in the experimental areas.

The important differences in colonizing potential and abundance patterns over time of species consistently present in the experimental plots are shown in Table 4. Significant differences in life habits of the species groups erected on the basis of abundance patterns are discussed later.

Except for the Group III species which did not fluctuate greatly in abundance, all species underwent a decline under winter conditions. Populations increased during the summer, but did not attain the densities reached in 1972 when empty sediment was being colonized (Table 4). Species composition of the experimental samples was at this point not too different from species composition of natural bottom samples (Table 2, Fig. 4). Samples taken at this time from the two-square-meter experimental boxes were not significantly different from samples from the ten-square-meter boxes.



*Site A colonization experiments—1973.* In June, 1973 colonization experiments were repeated at Site A using methods similar to those used in 1972. The purpose of the experiment was to test the repeatability of patterns in the colonization of empty substrata.

Number of species and species diversity measured during the experiment are shown in Fig. 8. The number of species on natural bottom in 1973 was about half the 1972 species number. Equilibrium of experimental plots with natural bottom measured by number of species and diversity was reached more quickly in 1973 (20-40 days vs. 90 days). Recruitment of Group I species to natural bottom was slightly greater in 1973 than 1972.

Partial species lists of samples from the first and second colonization experiments are compared in Table 4. With one significant exception, colonization of empty sediment at site A in 1973 followed the same patterns of peak abundance as in 1972. Group I species were again present in densities several orders of magnitude above natural bottom densities. *Owenia fusiformis*, absent in 1972, was present in 1973 in densities approaching  $10^5/\text{m}^2$ . Concomitant with the large numbers of *Owenia* in 1973 was the relatively reduced density of the functionally similar species *Streblospio benedicti* and *Ampelisca abdita*.

Table 4 compares settlement of individuals on empty substrata in 1972 and 1973 with settlement on substrata already containing animals. Median abundance of Group I species colonizing empty substrate was significantly greater than abundance of Group I species entering sediment already containing other animals ( $p < .05$ , Mann Whitney U test).

*Site B colonization experiments—1973.* Site A has a hard silty sand bottom (water content 50-60%). Sediments at Site B are silt and clay size and form a soft, unstable (water content 80%) bottom from which suspension feeders and animals maintaining permanent burrows are largely excluded.

Boxes of defaunated low-water-content harbor sediment (water content 50%) were placed at Site B to assess the effect of a different sedimentary environment on the colonization sequence. When placed on the bottom they were not immediately covered by resuspended sediment as were the samples at Site A. The results of colonization at Site B are shown in Fig. 9 and in Table 6. Again, it was the animals of Groups I and II that were the most abundant early colonizers, even on this hard, low water content substratum. Peak abundances for most species were of the same order of magnitude as at Site A.

Sixty-nine days after the start of the experiment at Site B, there were almost twice as many species on the hard bottom experimental plots as on the soft surrounding natural bottom. The experiment was terminated three months after it began when a tugboat and barge overran the buoy marking the experimental plots.

*Animal-sediment interactions at site A.* Data on sediment mass properties and sedi-

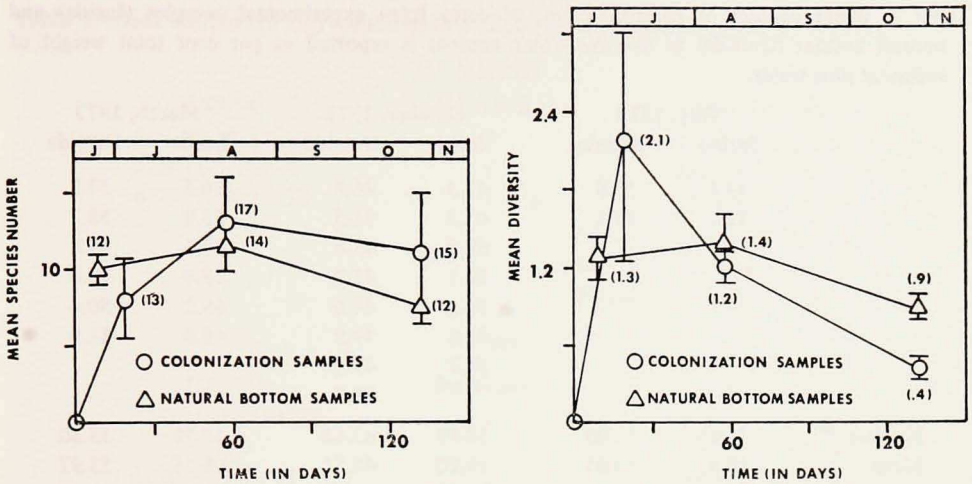


Figure 9. Number of species and H diversity during second colonization experiment at Site B (summer, 1973). Vertical bars indicate the standard deviation of variate values. Numbers in parenthesis are aggregate indices.

Table 6. Comparison of 'hard-bottom' recolonization sample and 'soft-bottom' natural surrounding bottom samples at Site B, August, 1973. Abundances reported as #/m<sup>2</sup>.

	Colonization Sample	Natural Bottom Sample
Deposit feeders		
<i>Nucula proxima</i>	35	12
<i>Yoldia limatula</i>	110	133
<i>Tellina agilis</i>	35,965	0
<i>Nassarius trivittatus</i>	20	48
<i>Glycera dibranchiata</i>	90	12
<i>Nephtys incisa</i>	66	266
<i>Capitella capitata</i>	267,850	9,560
<i>Spionid sp.</i>	80	12
<i>Owenia fusiformis</i>	13,570	593
<i>Orbiniidae sp.</i>	20	0
<i>Ampharete acutifrons</i>	35	0
<i>Ampelisca abdita</i>	5	0
Suspension feeders		
<i>Pitar morrhuana</i>	20	0
<i>Mulinia lateralis</i>	110	0
<i>Ensis directus</i>	35	12
Carnivores		
<i>Polinices duplicatus</i>	5	0
<i>Retusa obtusa</i>	5	0

Table 7. Water content of the top 1 cm. of cores from experimental samples (Inside) and natural bottom (Outside) at Site A. Water content is reported as per cent total weight of sediment plus water.

	July, 1972		October, 1972		March, 1973	
	Inside	Outside	Inside	Outside	Inside	Outside
	43.4	50.8	43.5	46.8	76.5	57.2
	53.9	55.3	65.5	58.5	53.8	58.7
			69.0	41.8	60.6	47.8
			68.7	45.7	58.4	47.8
			58.2	44.6	68.2	50.4
			53.6	39.9	48.8	61.9
			53.7	49.1		
				37.7		
Median**	48.65	53.05	58.89	45.15	59.50	53.80
Mean	48.65	53.05	58.20	45.51	59.55	53.97
S.E.	5.25	2.25	3.57	2.28	3.10	2.48
	NS		p < .01		NS	
	May, 1973		June, 1973		August, 1973	
	Inside	Outside	Inside	Outside	Inside	Outside
	50.8	36.9	56.3	43.6	62.7	43.2
	61.1	49.2	48.1	37.0	54.5	49.1
	57.1	40.0	44.9	48.4	49.0	55.4
	61.2	45.3	55.0	43.7		53.3
	60.6	52.0		43.0		
Median	60.60	45.30	51.50	43.60	54.50	51.20
Mean	58.16	44.68	51.07	43.14	55.40	50.25
S.E.	1.99	2.78	2.73	1.81	3.98	2.69
	p < .05		NS		NS	

\*\* Difference of medians tested with Mann-Whitney U statistic.

ment resuspension at Site A were taken for two purposes. The first was to see if animal activities in the experimental plots result in changed sediment properties that might affect further colonization. The second was to determine the frequency and degree of physical disturbance of the bottom so that the role of physical disturbance in initiating local successions could be assessed.

*a. Bottom stability and resuspension.* Rhoads (1970, 1973), Rhoads and Young (1970, 1971), and Young (1971) showed that sediment water content can be related to bottom stability. Unstable and easily resuspended sediment surface layers of greater than 50-60% water content produced by the activities of deposit-feeding animals are unsuitable for suspension feeders and animals maintaining temporary burrows. Water content of the bottom sediments at Site A was measured at

Table 8. Near bottom (15 cm) measurements of suspended sediment at Site A, 1972-73.

Summer		
Interval	Replicate	Resuspension
9/9/72-10/15/72	1	230.6 mg/cm <sup>2</sup> /day
5/3/73-6/21/73	1	229.2 mg/cm <sup>2</sup> /day
6/21/73-8/10/73	1	291.6 mg/cm <sup>2</sup> /day
	Mean	250.5 mg/cm <sup>2</sup> /day
	S.E.	14.5 mg/cm <sup>2</sup> /day
	Median	230.6 mg/cm <sup>2</sup> /day
Winter		
Interval	Replicate	Resuspension
10/15/72-1/10/73	1	133.5 mg/cm <sup>2</sup> /day
	2	131.0 mg/cm <sup>2</sup> /day
1/10/73-3/3/73	1	84.5 mg/cm <sup>2</sup> /day
	2	129.1 mg/cm <sup>2</sup> /day
3/3/73-5/3/73	1	117.9 mg/cm <sup>2</sup> /day
		132.5 mg/cm <sup>2</sup> /day
	Mean	121.4 mg/cm <sup>2</sup> /day
	S.E.	10.8 mg/cm <sup>2</sup> /day
	Median	130.1 mg/cm <sup>2</sup> /day

six intervals throughout the course of the experiment (Table 7). Only at the first sampling interval (ten days after the start of the experiment) was water content of cores from the experimental plots lower than water content of cores from natural bottom. The small number of measurements made at this time (two) was insufficient for testing the statistical significance of this difference, but it may be noted that this low water content coincided with the presence of  $10^5$  tubedwelling animals per m<sup>2</sup> of experimental sediment.

Table 7 shows that median differences in sediment water content of experimental and natural bottom sediment occurred throughout the experiment. In all cases, the water content of experimental plot sediment was higher than the surrounding bottom, although the difference was not always statistically significant. It is tempting to ascribe this result to differences in biogenic activities in the two populations. However since the top centimeter of sediment in the experimental plots was deposited from sediment suspended several centimeters off the bottom, the difference might well be due to a difference in the number of sand-sized particles in the two sediments. There was a statistically significant difference in median water content in summer and winter, but the difference was slight (about 1%) and probably not physically meaningful.

Suspended sediment (due primarily to resuspension of bottom sediment by tidal currents) was measured by a method similar to that of Young. Results are presented in Table 8. The grand mean of sediment suspended 15-20 cm off the bottom was

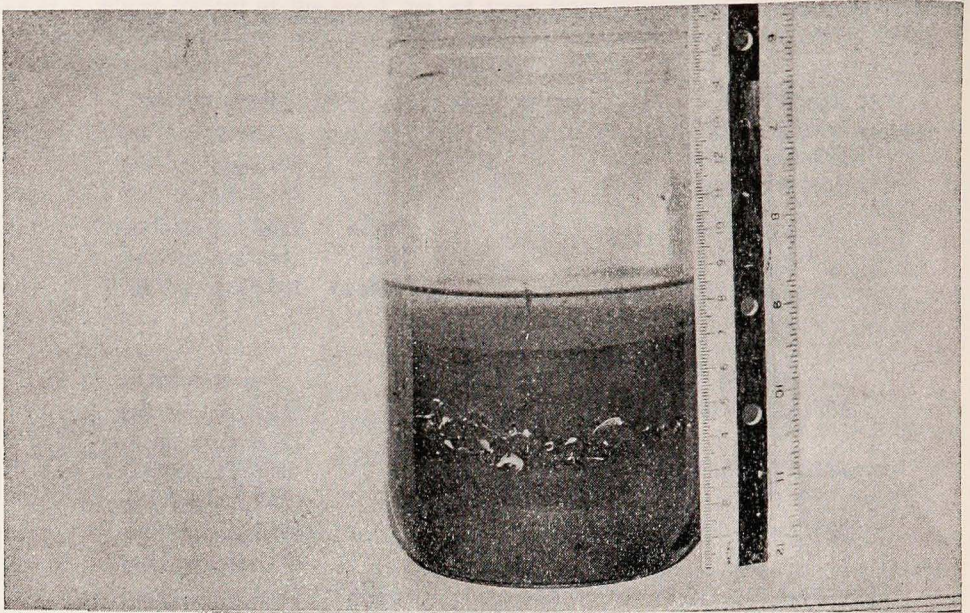


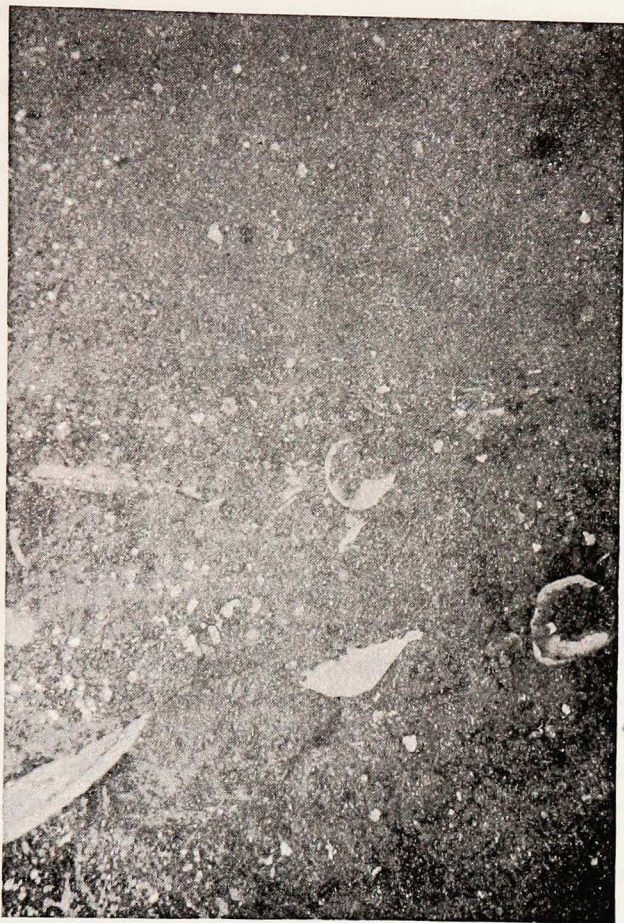
Figure 10. Sediment trap bottle and storm layer produced in late November, 1972. Bottle mouth was 15 cm off the bottom.

$153 \pm 33$  (S.E.)  $\text{mg}/\text{cm}^2/\text{day}$ , a value over seven times that found by Young in Buzzards Bay, Mass. Resuspension in summer was significantly greater than in winter ( $p < .02$ , Mann-Whitney U test).

*b. The effect of storms.* The wave forecasts of Bretschneider (1958) and the equations of small amplitude wave theory (Allen, 1970) predict that Force 6 winds (25-31 mph) blowing from the E, SE, or SW for 4-5 hours will produce at Site A, where depth at MLW is 14m and the bottom is silty sand, bottom water particle velocities of  $\sim 35$ -65 cm/sec. This is more than sufficient to entrain quartz sand particles (Allen, 1970).

Weather records show that based on the above predictions, there were three storms in the winter of 1972-1973 which were capable of resuspending bottom sediments at a water depth of 15-20m. One particular storm in late November 1972 carried winds of 25 knots into central Long Island Sound and produced a one centimeter thick storm layer in the sediment trap bottles at Site A (Fig. 10). This layer contained shell fragments 1 cm in diameter and quartz particles larger than 1mm. The failure of other storms to produce layers in the sediment traps cannot be explained at present, but production of storm layers of sediment is probably not uncommon; Aller & Cochran (1976) report a similar phenomenon at site B in Long Island Sound.

In addition to winter coastal storms, Long Island Sound is subject in the summer



months to the wave effects of tornadoes (1+/year in Conn.) and storms of tropical origin with winds greater than 50 knots which cause severe damage once every five years (Pouty, 1969).

For waves to disturb the silt-clay bottom of Long Island Sound and increase the amount of suspended sediment, the horizontal water particle velocity at the bottom due to waves must be greater than 5 cm/sec. (Gordon, Rhoads, and Turekian, 1972). At 20m depth, winter storms will produce predicted maximum horizontal water particle velocities at the bottom of  $\sim 10$ cm/sec. Below about 25m these storms have little effect.

*c. The effect of increased sedimentation.* The  $\frac{1}{2}$ " galvanized mesh screens placed over some experimental plots and over a 2 meter square area of natural bottom to exclude predators allowed the deposition of fine-grained, low density, high water content sediment which eventually filled the space between the old sediment surface

Table 9. Effects of increased sedimentation on natural bottom fauna. A '+' indicates presence; '-' indicates absence.

Species	Deposit Feeders		Species	Suspension Feeders	
	Natural Bottom	Under Screen		Natural Bottom	Under Screen
<i>Owenia</i>	+	+	<i>Mulinia</i>	+	-
<i>Streblospio</i>	+	+	<i>Ensis</i>	+	-
<i>Nucula</i>	+	+	<i>Pandora</i>	+	-
<i>Tellina</i>	+	+	<i>Leptocheirus</i>	+	-
<i>Nassarius</i>	+	+	<i>Sabella</i>	+	-
<i>Nephtys</i>	+	+	<i>Crepidula</i>	+	-
<i>Pectenaria</i>	-	+			
<i>Capitella</i>	-	+			
<i>Ampelisca</i>	+	-			
<i>Maldania A</i>	+	-			
<i>Glycera</i>	+	-			

and the screen (5 cm in experimental plots, 20 cm on natural bottom). Quite clearly it is not possible to test the effect of predators on soft bottoms over which any appreciable current flows by screening areas of the bottom. However, the predator exclusion experiments can be viewed as experiments to test the effect of increased sedimentation on the bottom fauna (Table 9). Five of the seven suspension feeders found on natural bottom were absent from the bottom under the screen after 57 days of sediment deposition; ten of the thirteen deposit feeders remained. *Capitella capitata*, absent from untreated natural bottom, was present under the screened natural bottom in abundances of 5000/m<sup>2</sup>. The abundance of *Tellina agilis* increased to 30,000/m<sup>2</sup>, while *Owenia fusiformis* densities remained at the same level.

*Sound-wide temporal and spatial patterns.* Grab samples from thirty-one stations in central Long Island Sound were taken in the summer and winter of 1972 and 1973 (station locations in Fig. 2) to determine if the species composition of different areas of the bottom corresponded to different stages of the recolonization sequence found in the experiments with defaunated sediment. Samples from disturbed areas should be dominated by Group I species; a station was arbitrarily defined as Group I dominated if more than seventy percent of the individuals at the station belonged to Group I species. Analysis of community patterns due to substratum differences and annual changes in standing crop due to planktonic larval mortality will be the subject of a separate study.

Six of the thirty-one stations visited in the summer of 1973 were dominated by large numbers (>70% of total fauna; >10<sup>8</sup> individuals/m<sup>3</sup>) of the Group I species *Capitella capitata*, *Streblospio benedicti*, and *Owenia fusiformis* (Table 10). Group I dominated stations occurred on sand, silty sand, and silt-clay bottoms. These sta-

Table 10. Stations dominated by Group I species in Summer 1973. S = sand; C = slit-clay. See Fig. 11 for station locations.

Group I—Dominated Stations					Remaining Stations			
Sta.	Depth (feet)	No. spp.	Diversity (H)	Species I.D.	Sta.	Depth (feet)	No. spp.	Diversity (H)
A10	40'-S	13	1.87	2	A1	25'	10	3.03
S7	43'-S	16	1.93	2,1	A2	38'	12	2.87
B1	65'-C	12	.90	2	A4	94'	12	2.51
B2	66'-C	10	2.09	3	A5	90'	10	2.31
B3	65'-C	11	2.16	2	A6	90'	10	2.74
S8	15'-C	15	2.21	2,1,4	A7	85'	10	2.46
Mean	49	12.83	1.86		A8	78'	09	2.36
Standard					A9	75'	10	2.69
Deviation	20.3	2.32	.49		C1	90'	12	3.18
					C3	120'	10	2.62
					C4	50'	15	3.32
#1: <i>Capitella capitata</i>					F1	91'	11	2.57
#2: <i>Owenia fusiformis</i>					G1	93'	10	2.80
#3: <i>Streblospio benedicti</i>					B4	64'	08	2.52
#4: <i>Ampelisca abdita</i>					B6	82'	13	3.13
					C2	100'	15	3.09
					S1	25'	19	3.23
					S4	95'	16	2.62
					S5	76'	14	3.43
					B7	86'	10	2.26
					Mean	77.32	11.8	2.79
					Standard			
					Deviation	25	2.76	.35

tions were not associated with the grade of bottom sediment but rather with depth of overlying water. The median depth of Group I dominated stations was significantly less than the median depth of stations not dominated by Group I species ( $p < .02$ , Mann-Whitney U test). All Group I dominated stations were in water less than twenty meters deep. Nevertheless, there were several shallow water stations without Group I species present in great numbers. Any phenomena invoked to explain the increase in Group I species must have a larger but sporadic effect in shallow water and a decreased effect in deeper water.

The patchy nature of the spatial distribution of Group I species relative to Group II and Group III species was measured by the variance/mean ratio of station abundances in the summer of 1973 (Table 11, Fig. 11). A high variance/mean ratio, of course, indicates a more patchy spatial distribution than a low ratio. The average variance/mean ratios of Group I and III were 208.3 and 4.4, respectively. Temporal fluctuations were measured by the mean difference in station abundance at ten stations visited in 1972 and 1973 (Table 12). The mean difference in station



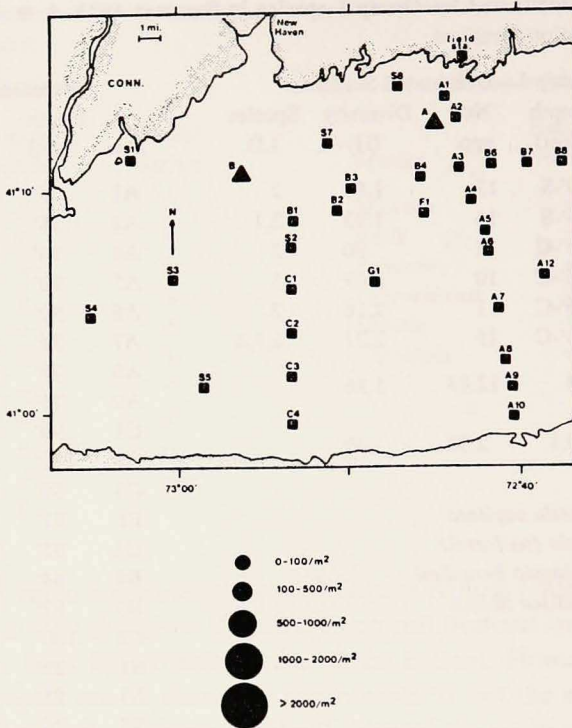


Figure 11. Map showing stations sampled and location of samples in Summer, 1973. Legend indicates abundance ranges plotted in Figures 12 & 13.

abundance was 251.8 and 83.67 individuals/m<sup>2</sup> for Groups I and III, respectively. The relatively uniform distribution of *Nephtys incisa* in space and time is illustrated in Fig. 12. Abundance of Group I species varied widely in space and time by comparison (Fig. 13).

The patchy distribution of Group I species can be demonstrated in a particular case by comparison of the summer 1973 stations B2 and B3, both situated on silt bottom one nautical mile apart (Table 13). The only species abundant at these stations in the previous winter was *Nephtys incisa*. Abundance of *Nephtys* remained fairly constant within the four samples from B2 and B3 in 1973 even though relative abundance varied. It is the Group I species *Owenia* and *Streblospio* which fluctuated in space and time at these stations.

The relative abundance of Group I species in a sample was minimized by the use of 1mm sieves to separate animals from sediment, since these species were smaller than species in Groups II and III for most of their life cycle. Only at a few stations were 297 micron sieves used (the sieve size used in all samples from the colonization experiments). At such stations where Group I species dominate, the abundance of

Table 11. Variance/mean ratios for species sampled in a summer 1973 survey of central Long Island Sound. Thirty-one separate stations were sampled.

Species	Mean (per .041m <sup>2</sup> )	Variance	Variance/ Mean ratio	Number of Station Occurrences
Group I				
<i>Owenia</i>	37.9	6251.1	164.6	25
<i>Capitella</i>	10.2	5207.1	509.1	9
<i>Streblospio</i>	3.2	79.7	24.4	6
<i>Ampelisca</i>	11.67	1577.3	135.1	16
Group II				
<i>Tellina</i>	1.6	15.8	9.8	10
<i>Nucula</i>	13.0	2578.1	195.2	19
Group III				
<i>Nephtys</i>	12.3	83.8	6.8	29
<i>Ensis</i>	.26	.51	1.99	4

Group I species compared more favorably with abundances found in the colonization experiments (Table 14).

## 5. Discussion

In discussing the results, it is first necessary to evaluate the means of entry of individuals into the experimental plots. After examining possible experimental artifacts, I will evaluate the hypothesis that the influx of organisms into the experimental boxes was the result of the presence of an initially uninhabited substratum and the substratum preferences of entering organisms. Secondly, I will examine species life histories which will suggest a discussion of colonization patterns in terms of r- and K-selection. The rapidity with which Long Island Sound benthos colonize a bottom empty of macrofauna suggests that certain species are specially adapted to maintaining populations in a frequently disturbed environment. Finally, I will speculate on factors initiating and modifying successional sequences in Long Island Sound and identify deficiencies in our knowledge of factors controlling the growth and decay of benthic populations.

*Active selection of colonization sites.* There are several lines of evidence leading to the conclusion that the colonization sequence described earlier is not the simple result of sequential reproduction and random settling of larvae. First, juveniles of many species settle from the plankton throughout the period July-October. Secondly, defaunated sediment placed on the bottom during this period (whether original or replacement samples) was first colonized by very high numbers of Group I species. Lastly, patterns of abundance of species colonizing the defaunated sediment were not duplicated on natural bottom.

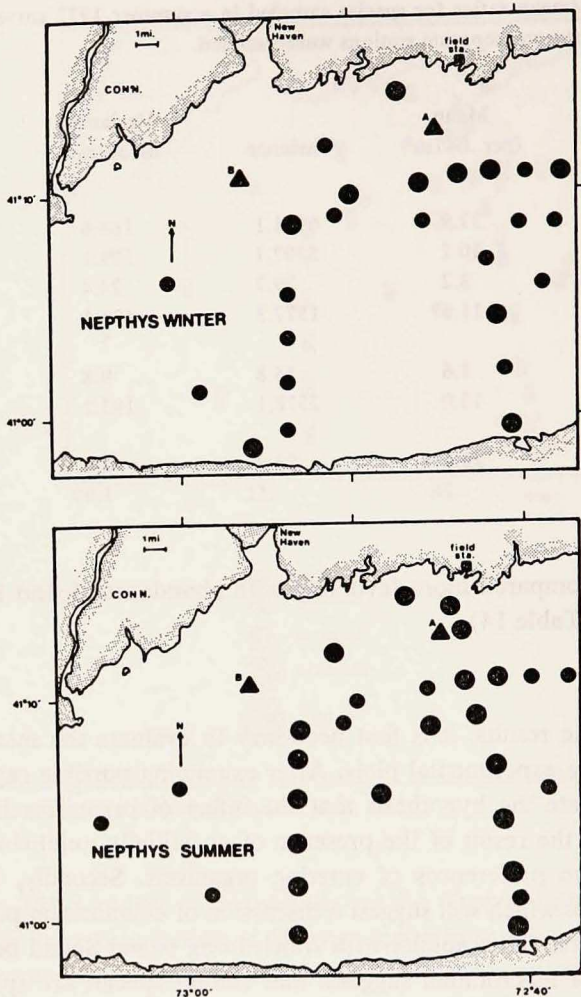


Figure 12. Spatial distribution of *Nephys incisa* in two surveys of central Long Island Sound.

Neither was the sequence due to exotic sediment composition of the experimental boxes. Harbor mud put down at silty sand Site A was very quickly covered by a 2-3 centimeter thick layer of silty sand sediment resuspended from the surrounding bottom. Thus settling larvae did not 'see' harbor sediment. The fact that larvae were not found in appreciable numbers in any of the sediment trap bottles indicates that larvae are not passively deposited along with sediment settling into the 'dead space' at the top of the 0.1m<sup>2</sup> sampling boxes. Even where milder currents and smaller amounts of sediment resuspension prevailed (at Site B), high initial densities of Group I species were found.

There is ample evidence that many benthic invertebrates actively select their

Table 12. Changes in mean abundance (given as numbers per m<sup>2</sup>) at ten stations sampled in both 1972 and 1973.

Species	Change from 1972 to 1973	Group Mean Difference (absolute value)
Group I		251.80
<i>Capitella</i>	159.59	
<i>Owenia</i>	-188.73	
<i>Streblospio</i>	524.59	
<i>Ampelisca</i>	134.31	
Group II		128.98
<i>Nucula</i>	-96.69	
<i>Tellina</i>	161.27	
Group III		83.67
<i>Ensis</i>	-105.00	
<i>Nephtys</i>	62.35	

site of settlement (Gray, 1966; Thorson, 1966; Wilson, 1952). It appears that those species that are able to discover the new "empty" habitat quickly and settle in great numbers ( $5 \times 10^5$  individuals/m<sup>2</sup>) possess the most refined powers of substratum discrimination. Gray (1971), for instance, points out that the ability to discriminate among substratum characteristics is especially well developed in polychaete larvae with sedentary adult stages (Group I species) and poorly developed in a errant polychaete species such as *Nephtys* (Group III).

In some forms, metamorphosis can be delayed from several days to several weeks until a substratum suitable for adult life is found (Wilson, 1928, 1932, 1937). The suitability of a site is determined to some extent by the grade of the deposit, but it is often more dependent on chemical and biologic properties such as microbial films and presence of other animals of the same species (Wilson, 1958; Meadows, 1964). Although the appropriate laboratory experiments have not yet been performed, differential recruitment to experimental plots and natural bottom areas suggests that the macroinvertebrate species composition of the bottom is an important factor in site selection for some species. For example, far more Group I larvae settle on empty substrata than on inhabited substrata, such as the natural bottom at Sites A and B (Table 5). A comparison of settlement on experimental boxes which have been on the bottom for some time with newly emplaced samples of uninhabited substratum demonstrates the same point (Table 5). Predator exclusion screens placed on natural bottom caused the deposition of a physically unstable 20 centimeter thick layer of sediment beneath the screens which resulted in mortality of a large part of the original fauna. This unstable and partially empty substratum was then subsequently colonized by  $3 \times 10^5$  individuals/m<sup>2</sup> belonging to Group I species (Table 6). The mechanisms by which a resident population of macroinvertebrates affects subsequent arrivals of new individuals remain obscure even twenty

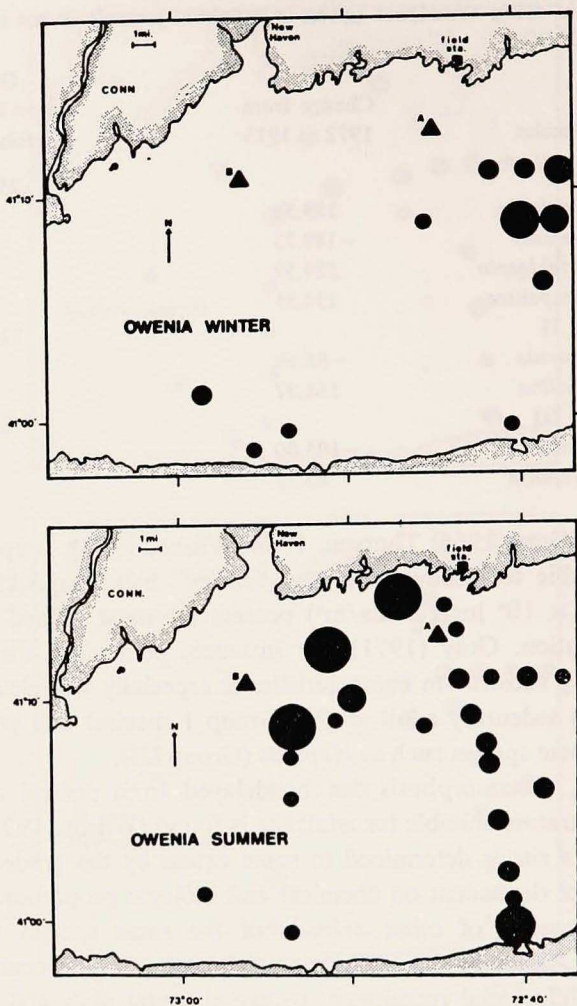


Figure 13. Spatial distribution of *Owenia fusiformis* in two surveys of central Long Island Sound.

years after Thorson (1957) postulated their probable importance. Established macroinvertebrates may affect new arrivals indirectly through alteration of sediment physical properties and sediment food content, or more directly via allelopathic affects and predation. Thorson (1957), Mileikovsky (1969), and Woodin (1976) review the literature and discuss other possible interactions.

*Life histories.* Entry of individuals into experimental boxes is apparently the result of active site selection. Results show that *Capitella*, *Streblospio*, and *Owenia* colonize the experimental boxes early and in large numbers, then suffer high mortality.

Table 13. Most abundant species at Stations B2 and B3, separated by one nautical mile. See Figure 11 for station locations.

## Station B2

Sample B2a	Sample B2b
7 species, 630 indiv./m <sup>2</sup>	6 species, 1350 indiv./m <sup>2</sup>
<i>Sigambra tentaculata</i> — 58%	<i>Streblospio benedicti</i> — 79%
<i>Nephtys incisa</i> — 12%	<i>Nephtys incisa</i> — 7%
<i>Owenia fusiformis</i> — 12%	<i>Sigambra tentaculata</i> — 5%
<i>Streblospio benedicti</i> — 0%	<i>Owenia fusiformis</i> — 0%

## Station B3

Sample B3a	Sample B3b
7 species, 1480 indiv./m <sup>2</sup>	8 species, 995 indiv./m <sup>2</sup>
<i>Owenia fusiformis</i> — 77%	Maldanid A — 34%
Maldanid A — 7%	Maldanid B — 22%
Maldanid B — 2%	<i>Owenia fusiformis</i> — 15%
<i>Nephtys incisa</i> — 2%	<i>Nephtys incisa</i> — 7%

Species like *Nephtys* and *Ensis* are comparatively slow but constant colonizers (Fig. 7). Why do not all species arrive at once, in numbers proportional to their relative abundance on the surrounding bottom? The answers to these questions are related to the life histories, habits, and trophic types of the colonizing species.

When one considers that Long Island Sound infauna have been studied for over a century (Verrill and Smith, 1873; Verrill, 1879), it is remarkable how little is known about species life histories. To cite but two examples: we know almost nothing about the life history of perhaps the most common and abundant (in terms of biomass) polychaete species on muddy bottoms along the northeast coast of the U.S., *Nephtys incisa*. Another common species, *Capitella capitata*, which appears in a variety of habitats, apparently has a worldwide distribution, and is an oft-cited

Table 14. The effect of sieve size on absolute and relative abundance. Data from station S8, summer, 1973.

Species	Abundance in sample sieved to 1 mm (#/m <sup>2</sup> )	Abundance in same sample sieved to 297 microns (#/m <sup>2</sup> )
<i>Capitella capitata</i>	5,145	43,275
<i>Ampelisca abdita</i>	2,263	4,203
<i>Owenia fusiformis</i>	2,114	Same
<i>Nucula proxima</i>	194	9,425
<i>Tellina agilis</i>	218	554
<i>Nephtys incisa</i>	398	Same
<i>Ensis directus</i>	156	Same

Table 15. Summary of life habits of species found in experimental plots at Site A. Unless

	Maximum* linear size	Biomass* dry Wt.	Relative mobility	Feeding type	Larval feeding type	Development type
<b>Group I</b>						
<i>Streblospio benedicti</i>	20X1mm	.15-.5mg	sedentary	SDF**	P	Short pelagic
<i>Capitella capitata***</i>	20X1mm	.15-.5mg	sedentary	NSDF	L,P	S. pelagic, L. pelagic & direct
<i>Ampelisca abdita</i>	5-7mm	.5-1mg	sedentary	SDF,SF	L	direct
<i>Owenia fusiformis</i>	20X3mm	.5-1mg	sedentary	SDF,SF	P	short pelagic
<b>Group II</b>						
<i>Nucula proxima</i>	5-7mm	1-5mg	sporadic	DF	L	short pelagic
<i>Tellina agilis</i>	10mm	1-5mg	mobile	SDF	P	long pelagic?
<b>Group III</b>						
<i>Nephtys incisa</i>	50X5mm	30-70mg	very mobile	NSDF	P	long pelagic?
<i>Ensis directus</i>	50X10mm	100-300mg	very mobile	SF	P	long pelagic

indicator of pollution, has only recently been discovered to be not even a single species but a complex of at least six sibling species each with a different life history (Grassle and Grassle, 1976). These lacunae in our knowledge are reflected in Table 15 in which life habits and demographic parameters of species consistently present in the experimental plots are gathered from the literature.

Despite difficulties in determining life histories of these species, it can be seen that there are significant differences in life habits and reproductive strategies among the species groups erected on the basis of temporal abundance patterns. Group I species are small, sedentary, tube dwelling deposit feeders with rapid development and many reproductions per year. During reproduction few eggs per female ( $10-10^3$ ) are produced, but all species have some form of brood protection. Group II species are intermediate between Groups I and III in size, mobility and several reproductive characteristics such as number of eggs per female ( $10^3$ ) and length of pelagic larval phase. Group III species are large and mobile and relative to Group I species exhibit slow development and few reproductions per year. They do not brood developing young, but rather produce large numbers of planktotrophic larvae ( $10^3-10^6$  per female). More complete elaborations of these species life histories can be found in McCall (1975).

*Adaptive strategies in a chronically disturbed habitat.* The natural division of species colonizing defaunated sediment into two end member groups on the basis of abun-

otherwise noted, data are from the literature.

Egg Protection	# Eggs per female	Time to maturity (days)	Relative* death rate	Source
brood chamber	30-400	30	high	Hartman (1945, 1969), Sanders <i>et al.</i> (1962) Reish & Winter (1954) Hannerz (1956), Dean (1965), Grassle & Grassle (1974)
egg cases in tube	6-600	30-40	high	Grassle & Grassle (1974, 1976), Rasmussen (1956), Franzen (1956)
brood chamber	20-40	40-80	high	Mills (1963, 1967a, 1967b)
gelatinous string	U	U	high	Watson (1901), Wilson (1932), Dales (1957), Stanley (1970)
none	4100	U	medium	Hampson (1971), Drew (1899), Chanley (1968), Scheltema (1972), Carey (1962), Blake & Jeffries (1971)
none	U	U	medium	Sanders, <i>et al.</i> (1962), Stanley (1970), Boss (1966), Sullivan (1948)
none	U	U	low	Carey (1962), Pettibone (1963), Clark (1961, 1962), Sanders (1956), Thorson (1946)
none	12-20×10 <sup>6</sup>	U	low	Stanley (1970), Ansell (1969), Turner (1953, 1955), Sullivan (1948), Loosanoff & Davis (1963)

\* data from this study

\*\* U = unknown

Feeding types: DF = deposit feeder; SDF = surface deposit feeder; NSDF = non-selective deposit feeder; SF = suspension feeder.

Larval feeding types: L = lecithotrophic; P = planktotrophic

\*\*\* Individuals assigned to *Capitella capitata* may belong to more than one species (Grassle & Grassle, 1976)

dance patterns and life habits suggests that there are at least two kinds of adaptive response by the benthic infauna to environmental fluctuations in Long Island Sound.

Group I species such as *Capitella capitata* and *Streblospio benedicti* are able to discover recently created empty habitats quickly and colonize them in great abundance, only to suffer high subsequent mortality. Their populations are large but patchily distributed in time and space across central Long Island Sound. Densely populated patches are associated unpredictably with the shallow and more frequently disturbed parts of the habitat. Hutchinson (1951) has applied the descriptive term "fugitive" to such species. Grassle and Grassle (1974) use "opportunist" to mean the same thing.

Many researchers have pointed out that life history strategies which optimize fitness result from the differential allocation of the finite resources of organisms to reproductive and nonreproductive activities (Fisher, 1930, quoted in Pianka, 1970; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972). Populations subject



to frequent catastrophic mortality (failure of individual behavioral and physiologic adaptations) will devote a greater part of their energies to rapid reproduction under favorable conditions (Slobodkin, 1964, 1972) and have been called r-strategists (MacArthur and Wilson, 1967). Thus Group I species in Long Island Sound have an early sexual maturity, many reproductions per year, and a large effort put into the production of young (although no one has yet measured this effort on a caloric basis).

Gadgil and Solbrig (1972) and Rabinovich (1975) are careful to distinguish between r-strategist and opportunist species. Both adaptive types arise in environments where organisms suffer high density-independent mortality, but fugitive species are additionally characterized by possession of features assuring rapid and widespread dispersal in habitats that are short-lived in space and time. All opportunist species are r-strategists, but not all r-strategists are opportunist species.

Complementing the opportunistic life strategy is the concept of K-strategy (MacArthur and Wilson, 1967) or equilibrium strategy (MacArthur, 1960). Relative to the r-strategist, the K-strategist meets environmental stress by devoting a larger portion of its resources to nonreproductive activities such as growth, predator avoidance, and competition (Cody, 1966; Gadgil and Bossert, 1970) and in Long Island Sound promotes contribution of offspring to the next generation by increased postlarval survival, slow growth rate and delayed reproduction, and high fecundity of larger adults (Table 15).

Group III species are both large and mobile. Increased size usually implies increased physiological tolerance (Pianka, 1970; Jackson, 1972; Wolvekamp, 1958), but this is not a necessary relationship (Rao and Bullock, 1954; Vernberg, 1967; Newell and Roy, 1973). Experiments on the tolerance of Group III species *Ensis directus* and *Nephtys incisa* have not been done, but there some evidence that *Nephtys*, with its unspecialized adaptations to a wide variety of habitats, is highly tolerant of some environmental stresses (Jones, 1955; Weber, 1971) and is physiologically equipped for infrequent feeding and long periods of starvation (Clark, 1964). Mobility and size also aid these species in both escape from predators and migration to more favorable micronvironments. Association of two end member adaptive types with life history characteristics for Long Island Sound infauna is summarized in Table 16.

It should be remembered that there are no absolute criteria for classifying species as r-strategists or K-strategists: the terms have meaning only as they form a basis of comparison of individual life histories. No claims are made that Group III species are the most K-selected species in L.I. Sound (it is unlikely that they are), only that their adult life stages are more K-selected and less opportunistic than those of Group I species.

Finally, Wilbur, *et. al.* (1974) have pointed out that the use of the r-K dichotomy in its strictest sense and as originally defined by its authors, MacArthur and Wilson

Table 16. Summary of Group I and Group III adaptive types.

Group I	Group III
1. Opportunistic Species	1. Equilibrium Species
a. Many reproductions per year	a. Few reproductions per year
b. High recruitment	b. Low recruitment
c. Rapid development	c. Slow development
d. Early colonizers	d. Late colonizers
e. High death rate	e. Low death rate
2. Small	2. Large
3. Sedentary	3. Mobile
4. Deposit Feeders (mostly surface feeders)	4. Deposit and Suspension Feeders
5. Brood Protection; Lecithotrophic Larvae	5. No Brood Protection; Planktotrophic Larvae

(1967), is inadequate to explain observed life history phenomena of many plants and animals. They recommend instead that ecologists attempt to identify casual mechanisms in the evolution of species life histories on a more individual basis. While retaining the useful connotations of the descriptive opportunist—equilibrium species dichotomy, it is also possible to suggest such a causal explanation for central Long Island Sound infauna.

*Relation of life histories to infaunal niches.* As mentioned above opportunism is favored where a population is subjected to frequent catastrophic mortality where individual physiologic adaptations fail. It is suggested that mortality of infaunal organisms is related to life position relative to the sediment-water interface and mobility perpendicular to the interface. There are major differences between Groups I and III in mobility and body size (Table 15).

For the mobile infaunal animal, increased size offers two significant advantages: ability to burrow deeply into the sediment, where environment disturbances arising at the sediment-water interface are damped out (Jackson, 1972; Levinton, 1973); and freedom from smaller and slower predators. It is likely that adult mortality of mobile Group III species is significantly reduced in high stress environments by selection for increased body size. It is interesting to note in this regard that intertidal populations of both *Nephtys* and *Ensis* may be two to three times larger than the subtidal populations.

Group I species are relatively immobile tube-dwellers and in all but one case are surface deposit-feeders. Deep burrowing is energetically expensive for an animal committed to sedentary life in a tube for the reason that there is a larger volume of harder sediment to be removed, greater tube surface area to be constructed, and a larger tube volume to be irrigated. The response of Group I species subject not only to high adult mortality from the greater physical disturbance and predation

at the sediment-water interface but also to a fluctuating food supply is adaptation for rapid reproduction, rapid use of a limited feeding area, and dispersal. Larger sedentary tube dwellers (e.g. ceriantharian anemones, maldanid and flabelligerid polychaetes) are generally more abundant in the deeper parts of Long Island Sound. Group II species are intermediate in the sense that although they gain some freedom from disturbance by possession of a shell, they are relatively immobile and still restricted to the stressful near surface microhabitat through dependence on near surface food supplies.

Thus we may conclude that, within a chronically disturbed habitat, infaunal animals capable of greater isolation from environmental stress, either by possession of a shell or by retreating to the lower stress microhabitat deep below the sediment-water interface, are more likely to pursue equilibrium than opportunist strategies, and sedimentary infaunal animals dependent on near-surface food resources are more likely to be opportunists than mobile species.

Adult size is probably an important factor determining the larval type of opportunistic and equilibrium species. Large animals capable of producing many eggs are likely to possess planktotrophic larvae. Planktotrophic larvae acquire their food from the plankton and require no food provided by the parent. They are thus cheap to produce and in addition possess many desirable dispersal characteristics (Strathmann, 1974). They suffer high mortality during their long planktonic life, however, so that it is necessary to produce many of them.

Small species are perhaps not able to produce sufficient numbers of planktotrophic larvae to offset larval mortality. Small species instead produce a smaller number of more costly lecithotrophic larvae that are more likely to survive, or else incubate eggs in a brood chamber for a major portion of the development period. Swedmark (1958) believes this is the reason for the low number of species possessing planktotrophic larvae in the interstitial fauna of marine sands. Lecithotrophy or brood protection also frees a species from a total dependence on seasonal planktonic food sources and permits year-round reproduction and instant response to environmental disturbances.

This analysis makes fairly good sense for Long Island Sound species, but this should not be taken to mean that all species possessing Group I reproductive characteristics are likely to be opportunists. Many deep sea invertebrates, for instance, are brooders or at least produce lecithotrophic larvae (Scheltema, 1972). A lack of a planktonic food source for developing larvae in the deep sea, however, is a more likely explanation for the development of this life history phenomenon there.

*Dynamics of colonization.* In unpredictable chronically disturbed environments, the creation of new microhabitats will be followed by an influx of species exhibiting various degrees of opportunism. Colonization sequences can be initiated by storms,

increased sedimentation, and destabilization of the substratum; in other words, any disturbance which results in a decrease in local species abundance. Thus large differences in predation may also be effective in initiating the colonization sequence.

Predator aggregations are probably important in clearing small areas of the bottom of macrofauna. Unfortunately, the effects of biologic and physical disturbances are difficult to separate in Long Island Sound. Opportunist-dominated stations are restricted to depths less than 20 meters, which suggests that storm-generated currents are the major disturbing factor. However, there is some evidence that the principal predators of the benthic fauna, the starfish *Asterias forbesi* and the winter flounder *Pseudopleuronectes americanus*, are also much more abundant in these shallower areas and show aggregated feeding behavior (Richards and Riley, 1967). Determination of the relative roles of storm and predator-induced disturbance awaits an effective method of excluding predators from areas of the bottom.

Sediment reworking activities of the macrofauna can change the susceptibility of the bottom to physical disturbance. Erodibility of the bottom changes significantly from summer to winter. The decrease in sediment reworking activities by the macrofauna in winter may allow sediment to be bound more effectively by the mucus-secreting activities of the macrofauna and microfauna (Rhoads, et al., in press). This would explain why winter near-bottom suspended sediment as measured by sediment traps was half what it was in summer (Table 8), even though there was no large seasonal difference in tidal current velocities. With a greater threshold of erodibility, the bottom may become more patchy under the influence of unpredictable tidal turbulence and winter storms. Diver observations at Site A indicated much more small scale relief on the bottom in winter.

In addition to ripple markings, fist-size clumps of substratum were eroded out of the bottom and deposited on the surface. Using a sediment-water interface camera (Rhoads and Cande, 1971), D.C. Rhoads (pers. comm.) has obtained photographic evidence of the incipient stages of this "plucking" erosion. Such disturbances can result in significant mortality, especially if animals are less active and in physiologically poorer condition in winter. Micro-relief features produced by winter storms and tidal turbulence remain until they are destroyed by the reworking activities of the benthic macrofauna the following summer. Emery (1953) reported a similar phenomenon at 190 foot depths on Osborn Bank.

Initial substratum conditions determine in large part the diversity and abundance of subsequent colonizers. Substratum is colonized by Group I opportunists to the extent that it is initially empty of organisms of the same and other species. The highest number of opportunists are found on the most "empty" substrata (Table 4). Complete catastrophic mortality is not a requirement for the influx of opportunists, as Levin (1974) has pointed out. Also, initially stable substrata support a higher diversity of colonizers than unstable substrata, as results from the second colonization experiment show.

Horn (1974) defines secondary succession as:

“the process of reestablishment of a reasonable facsimile of the original community after a temporary disturbance. Secondary succession is usually a result of interspecific competition, with pioneer species often beating later species to openings and perhaps outcompeting them in openings as well, but themselves producing an environment in which later species are superior.”

The lack of synchronicity in the abundance patterns of populations in the experimental plots and natural bottom areas subjected to the same climatic regime from July-October, 1972 at least suggests some biologically mediated cause for many of the changes in species compositions and abundance in the experimental plots. At very high densities (greater than  $10^4/\text{m}^2$ ), the feeding activities of some spionid polychaetes can cause the biodeposition of layers of physically unstable sediment as much as 20 cm thick, which eliminate other fauna (Daro and Polk, 1973). Mills (1969) speculated that high numbers of *Ampelisca* tubes in an intertidal sand initially promote the settlement of other species, but eventually result in the wash-out of large clumps of bound sediment. Rhoads (1974) and Driscoll (1975), among others, examined the possibility that the activities of deposit feeders significantly alter not only physical properties of surface sediment but also their food content.

The cause for the decline of opportunist populations in the experimental plots is poorly known. Both interference and resource competition and amensalistic interactions are known to occur among the benthic infauna (Levinton, 1971; Rhoads and Young, 1970; Woodin, 1974), but could not be directly examined in this study. Increased abundance of opportunists is directly related to the decreased total abundance of other species in both the colonization experiments and the sample surveys. This may indicate that opportunists are poor competitors in undisturbed situations, although the basis for competition is unknown.

On the other hand, in disturbed local situations interspecific competition for food or space may be small, and so it is possible that the decline of opportunists is facilitated by intraspecific competition. Table 5 shows that boxes of fresh sediment put down at each sampling interval were able to support large numbers of *Streblospio* and *Capitella* even as their numbers in the original experimental samples were declining. Grassle and Grassle (1974) obtained the same results with *Capitella capitata* in Buzzards Bay, Mass., and in addition showed a decline in adult size and egg number per female at high densities. They speculated that intraspecific competition for the most labile food components of the sediment that are needed for rapid growth resulted in slower maturation and density-dependent survival. Gage and Geekie (1973) found *Capitella* patchily disturbed in Scottish lochs, with large numbers restricted to small discrete patches of land-derived organic debris. The fact that both individual species abundances and species composition of experimental plots converge with those of natural bottom samples could be taken as

further evidence of population regulation, with the equilibrium level for each species population changing from year to year.

*Infaunal successions in other nearshore benthic environments.* Field experiments in Long Island Sound have shown the existence of a characteristic colonization sequence of adaptive and functional types rather than simply a sequence of particular species. Recall for instance the substitution of *Owenia fusiformis* for the ecologically similar *Streblospio benedicti* and *Ampelisca abdita* in the 1973 experiments. It is not surprising to find similar types of faunal sequences in recoveries from disturbance in a whole range of nearshore bottom communities where physical and biologic disturbances are frequent and easily detected.

Mills (1969) documented community changes on an intertidal sand flat in Barnstable Harbor, Massachusetts. Mechanical disturbance of the bottom and reduction of food resources by large numbers of *Nassarius obsoletus* greatly reduced the number of fauna. Large numbers of *Ampelisca* juveniles were able to colonize the flat due to the low density of infauna. The high density of *Ampelisca* tubes increased available surface area for growth of diatoms and flagellates three-fold. Mills believed that increased topographic complexity and improved food resources accounted for a rise in the number of species and individuals inhabiting the area. Eventually the binding action of *Ampelisca* tubes was insufficient to counteract the instability arising from the decrease in median grain size due to the feeding activities of the animal. Relatively minor breaks in the bound mat of tubes were enough to cause washout of large patches of bottom, especially on windy days when the flat was covered with water.

Fager (1964) invoked temporal changes in a complex of nearshore currents to explain the establishment of a large bed of the polychaete *Owenia fusiformis* on a sandy bottom along the California coast (depth 6-7 meters). The presence of dense aggregations of tubes (1000/m<sup>2</sup>) stabilized the substratum and diminished the effect of wave surge. An extensive diatom layer and various macrofauna became associated with the patch of *Owenia*. However, several species of rays were also attracted to the area; these animals dug holes and buried themselves in the sand and may have fed on *Owenia*. The burrowing activities of the rays altered the bed of *Owenia* tubes into separate hummocks that rose 10cm above the surrounding sand, and the entire bed was eventually destroyed. The abundance of fish-produced markings at shallow, shelf, and slope depths (Stanley, 1971) suggests that this form of biologic disturbance is common and widespread.

Grassle and Grassle (1974) and Sanders et al. (1972) described the recovery of the benthic infauna from an oil spill in Buzzards Bay, Massachusetts. As in the present study the response of opportunistic species to the spill at a particular site was related to the extent of reduction of diversity there. Sedentary tube-dwelling polychaetes were the first organisms to recolonize the area. Spionids (including

*Streblospio*) and *Capitella capitata* were present in densities greater than  $10^5/m^2$  and were most abundant in the most severely affected areas. Opportunist populations suffered severe mortality subsequent to recolonization. Grassle and Grassle (1974) cite other pollution studies where similar patterns are found.

Other secondary successions or spatial patterns similar to those in Long Island Sound involving capitellids, spionids, large errant polychaetes and deep burrowing bivalves have been described by Rosenberg (1972, 1973), Bagge (1969), and Reish and Winter (1954).

## 6. Conclusion

In a marine environment subject to continual local disturbances, it may be possible to explain many spatial differences in species composition and abundance as different stages of recovery from a past local disaster. In such an environment there will always be some species whose population sizes change drastically in space and time, and there will be other species whose population sizes remain fairly constant.

These differences in distribution and abundance are the result of the adoption by the infaunal benthos of two different adaptive strategies, one opportunistic and the other a comparative equilibrium strategy. The relative opportunism of the Long Island Sound benthos is most closely related to the degree of mobility and living and feeding depth of species inhabiting the substratum. Sedentary animals and those living and feeding close to the sediment-water interface are more likely to be opportunistic in a chronically disturbed environment, while in the same environment mobile animals and those living or retreating deep in the sediment are more likely to pursue an equilibrium strategy.

This study raises several interesting but unsolved problems and points to some directions that further research should take. Physical disturbance of the bottom may contribute to mortality of benthic populations either directly or by exposing benthos to predators or by altering deposited food resources. We have almost no data about the velocity of bottom currents necessary to cause significant mortality, nor the frequency of occurrence. Bottom sediment type and faunal composition and density significantly modify the effect of currents on the bottom: these effects have not been quantitatively assessed. Laboratory studies of the effects of turbulent current flows of varying strength over a series of different bottom types would provide much useful information. Biologic disturbance in the form of predation is probably a significant source of mortality in shallow water soft bottom communities, but its importance could not be tested by the usual method of predator exclusion.

The mechanism of species replacement during the course of a succession will remain unknown until extensive studies have been done not only on resistance adaptations and predation, but also on amensalistic interactions among members of

the community, and intra- and interspecific resource competition. This will require fine scale *in situ* studies and laboratory feeding studies (perhaps using isotopic or immunologic methods) to determine potential competitors and food resources and utilization. No realistic conceptual or quantitative successional model for the infaunal benthos can be constructed until the importance of these factors has been assessed.

Lastly, although our present lack of precise knowledge of life history characteristics, demographic parameters, and trophic positions for most of the benthos severely limits the precision with which we can understand these organisms' distribution and abundance, results of this study indicate that there is a characteristic sequence of species that follows a disturbance of the bottom. This sequence may be determined by means of *in situ* colonization experiments. With some modification, this methodology may find immediate application in predicting the sequence and rate of recovery of the bottom fauna from such human activities as dredging and dumping of dredge spoils (McCall and Rhoads, in prep.).

## 7. Summary

1) Local disturbances of the bottom which result in catastrophic mortality are proposed to be the cause of many spatial and temporal faunal changes encountered in Long Island Sound and in nearshore benthic communities in general. This phenomenon was studied by placing samples of defaunated mud on the bottom of two sites in central Long Island Sound to simulate a local disaster.

2) Ten days after the start of the experiment, 14 of the 33 total species found in the colonization samples were present. Diversity rose to a maximum three months after the start of the experiment, followed by a 36% decline with the onset of winter. Colonizing species, mostly 0- year class individuals, suffered a more severe winter decline than natural bottom species.

3) Seven species commonly found in 1972 colonization samples have been placed into one of three groups based on difference in peak abundance, time of peak abundance, and death rate. Group I is comprised of *Streblospio benedicti*, *Capitella capitata*, and *Ampelisca* sp.; Group II is comprised of *Nucula proxima* and *Tellina agilis*; Group III is comprised of *Nephtys incisa* and *Ensis directus*. Groups separated on these bases also have characteristic life habits and reproductive strategies.

4) The number of species found on natural bottom and colonization samples in 1973 was about half the number found in 1972. Similar patterns of colonization obtain; a significant exception was the substitution of *Owenia fusiformis* for the ecologically similar *Streblospio benedicti*.

5) At Site B, boxes of low water content defaunated sediment placed on a high



water content bottom contained twice as many species two weeks into the experiment as on the natural bottom.

6) Lowest sediment water content of recolonization samples at Site A was found at the first sampling interval when  $>5 \times 10^5$  Group I individuals/m<sup>2</sup> were present. No seasonal differences in water content of colonization samples of natural bottom sediment were found.

7) Mean resuspension of natural bottom sediment in winter was 121.4 mg/cm<sup>2</sup>/day. Mean resuspension in summer was 250.5 mg sediment/cm<sup>2</sup>/day.

8) Three storms in the winter of 1972-73 produced waves capable of disturbing the bottom in water depths of 15-20 meters. One storm in late November, 1972 (25 knot winds) produced a 1 cm thick layer of coarse grained sediment in one of the sediment trap bottles suspended 15 cm off the bottom.

9) Predator exclusion screens placed over the bottom trapped a 20 cm thick layer of unstable high water content sediment under the screens. Suspension feeding animals were killed off, and high numbers ( $\cong 10^4$ /m<sup>2</sup>) of the deposit-feeders *Capitella capitata* and *Tellina agilis* entered.

10) In a regional faunal survey of central Long Island Sound benthos made in the summer of 1973, six of the thirty-one stations sampled were dominated by large numbers (>70% of total station abundance;  $> 10^3$ /m<sup>2</sup>) of the polychaetes *Capitella*, *Streblospio*, *Owenia* and the amphipod *Ampelisca*. These stations occurred on all sediment types but were restricted to water depths of less than 20 meters. Group I species were patchily distributed throughout the central Sound. The polychaete *Nephtys incisa* was more evenly distributed in both space and time than any of the Group I species.

11) Larvae colonizing new substrata at Sites A and B actively selected their settling site. Group I species may be more sensitive to many kinds of substratum differences than Group III species.

12) Group I species are opportunists. Survival in unpredictable environments may be attained by the ability to discover new habitats quickly, to develop rapidly and to reproduce many times per year. Group III species are equilibrium strategists. Survival in unpredictable environments may be attained by growth to large size and by high mobility. This allows escape from stresses at the sediment-water interface by favoring deep burrowing below this interface. Group II contains relatively opportunistic bivalves, and polychaetes with strategies intermediate between Groups I and III.

13) Infaunal species restricted by morphology or physiology to a feeding or life position near the sediment-water interface are more likely to undergo selection resulting in small size and opportunistic life history. Infaunal species capable of escaping from the sediment-water interface are more likely to undergo selection resulting in large size and equilibrium life history. Size differences probably influence larval type and development.

14) A disturbance (real or simulated) which results in mortality of bottom fauna is followed by an influx of opportunistic species. Densities depend on how "empty" the substratum is of organisms. Replacement of opportunists during recolonization may be accounted for by a number of interactions; intraspecific competition for labile food components and resulting density dependent mortality has been suggested as an important factor.

15) Secondary successional changes are probably common in nearshore environments such as intertidal, shallow subtidal, and polluted habitats—all environments subject to frequent physical and biological disturbances.

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**RALPH GORDON JOHNSON**  
**1927-1976**

THE UNIVERSITY OF CHICAGO

1971

## A Perspective on His Last Research Paper

"Vertical variation in particulate matter in the upper 20 cm of marine sediment" was in review at the time of Ralph Gordon Johnson's untimely passing.

One of Ralph's interests in the past five years concerned a long-standing yet unresolved problem in marine ecology; what do detritivores eat? Most marine invertebrates living on, or within, the seafloor feed on sediment, yet little is known about utilizable food fractions of detritus or how they are distributed in space and time. This is the third paper reporting results of his research (Johnson, 1974, and Whitlatch and Johnson, 1974).

Ralph's approach to the detritus problem was straightforward, involving very difficult work making detailed particle inventories of potential food items in near surface sediment in a variety of marine habitats. This research exemplifies Ralph's approach to field work; careful collection of data, astute observation and measurement, analysis and interpretation followed by hypothesis testing in subsequent sampling programs. I never knew him to take short-cuts in pursuit of a difficult or elusive problem.

The detritus work was done with one of his recent graduate students, Dr. Robert Whitlatch, who kindly saw the manuscript through the review process. Results of this research will stimulate and direct future research into the role of detritus in the marine food chain.

As one can see from the appended bibliography, Ralph's interests and contributions encompassed a broad area; herpetology, paleobiology, paleoecology, and marine ecology. An interesting and perceptive account of his paleontologic contributions is given by Schopf (1977).<sup>1</sup> I wish to thank Tom Schopf for providing me with materials for this article.

Because of Ralph's unusually broad view of geology and biology, many students, including myself, elected to do graduate study with him in paleozoology at the University of Chicago. Interdisciplinary graduate programs are now popular at many universities but few graduate programs permitted or actively encouraged such intellectual latitude in the late 1950's and early 1960's. Interdisciplinary work in geology-biology was nurtured in this period within the Interdivisional Committee on Paleozoology of the University of Chicago. The Committee evolved into the Committee on Evolutionary Biology, and Ralph maintained the interdisciplinary flavor of this early and innovative program up to the time of his passing.

1. Schopf, T. J. M. 1977. Ralph Gordon Johnson (1927-1976), Paleontologic contributions, *Paleobiology*, 2, 388-371.

Although the following paper is to be his last publication, it assuredly will not be Ralph's final contribution. He leaves a legacy of pioneering work on which his students and others will build. It is difficult to judge an individual's life-time contributions to a field of study beyond enumerating a list of papers and his academic progeny. I believe that the contribution should also be evaluated by the level of creativity and innovation found in the work; the way he went about thinking and doing science and his enthusiasm for the work. Using these criteria, Ralph Gordon Johnson indeed left a substantial contribution.

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of

*Ralph Gordon Johnson (1927-1976)*

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