THE APPLICATION OF SYSTEMATIC SAMPLING TO A STUDY OF INFAUNA VARIATION IN A SOFT SUBSTRATE ENVIRONMENT[1]

Stephen Scherba, Jr.[2] and Vincent F. Gallucci[3]

ABSTRACT

Stratified systematic sampling was applied to an intertidal macrofauna sediment study. A stratified systematic sampling plan retains the advantages of the more common fixed level transect sample, and possesses additional advantages which recommend it for use in some intertidal studies. The field data collected in this study demonstrated the effectiveness of stratified systematic sampling for quantifying both sediment and population characteristics along a sediment gradient, and for the testing of biological hypotheses.

Intraarea, interarea, and interseason hypotheses about sediment composition were tested in terms of particle size distributions. Populations of bivalves and polychaetes were simultaneously sampled and hypotheses concerning spatial and seasonal variations in an intertidal mud flat were tested. Experimental results using stratified systematic sampling suggest that Newell's hypothesis can be extended to encompass temporal variation. Fine sediment grades (silty areas) may act to insulate infauna against the extremes of seasonal stresses.

Sediment composition, as measured by the average percentage composition by weight of various grain sizes, was not sufficient to predict macrofaunal presence.

The study of the complex relationship existing between macrofauna (e.g., bivalves and polychaetes) and their soft substrate environment is of wide interest in marine biology. Soft sediments are both a shelter from predators and a food source for deposit feeders. The particle size distribution of the sediment influences such factors as food availability, the depth of the aerobic layer, water content, pH differentials, and growth rates. Detrital content and particle size distribution of the sediment are largely determined by the hydrodynamics of currents. However, Rhoads (1967) demonstrated that macrofauna modify sediment stability, composition, and water content by activities such as building tubes, ingesting sediment and detritus (to remove bacteria from sediment particles), depositing feces, etc. The particle size distribution of the sediment is, therefore, one measure of certain types of biological activity (Newell 1965).

Studies in soft substrate environments usually involve sediment samples which contain large numbers of macrofaunal species in different densities as well as different particle size distribu-

tions. Then, it may be necessary to make comparisons between samples which may call for the use of statistical methods as found in standard textbooks (e.g., Sokal and Rolf 1969). The validity of tests of comparisons, however, must rest upon the application of valid sampling plans in the field, but most valid sampling plans do not meet the needs of the ecologist. This paper reports on the use of stratified systematic sampling which, to our knowledge, is heretofore unused in the marine literature. Stratified systematic sampling seems to meet the needs of most studies that would have used transecting methods which, generally, are statistically unacceptable. The sampling method is applied to a study of animal and sediment gradients in a basically marine embayment subject to seasonal variation in density of animals and algae. Hypotheses comparing areas of different sediment composition in the winter, spring, and summer are tested using animal-presence and sediment-particle-size data collected using a stratified systematic sampling plan. The bay is shown to contain a sediment gradient from fine silt to coarse sand, with an associated polychaete distribution expressed by both the number of animals per species and by the number of species found.

A variety of sampling methods are described in the literature. For example, the works of Skellam (1958) and Sen et al. (1974) presented different

types of transect methods, and Saila and Gaucher (1966), Russell (1972), and Loesch (1974) described subtidal stratified random sampling methods.

Transecting methods used in the soft substrate of the intertidal zone usually involve the choice of a narrow belt of one or two sampling units in width, placed perpendicular to the water line. Samples are collected at fixed and predetermined tidal levels (e.g., every 10 m) to correspond to changes in such things as algal and sediment composition (Matthiessen 1960; Vassallo 1969; Warme 1971; Bloom et al. 1972). This method will be referred to as fixed level transect sampling (FLTS). A common denominator in this type of work is that no probability model is used in selecting the location of the sampling units. An alternative to FLTS is simple or stratified random sampling where the discrete uniform probability distribution underlies the selection of sample sites. The disadvantage of random sampling is that there is no guarantee that sample sites will be in those areas where experimental interest is focused. However, without an underlying probability model, valid statistics may not be estimated (Cochran 1963) because the sample sites may not be independently located and subsequent statistical tests may be invalid. These points are often overlooked.

Stratified systematic sampling (SSS) is proposed as an alternative to the FLTS method currently popular in intertidal fieldwork. The usefulness of SSS is demonstrated by applying it to a study of spatial and temporal variation in a macrofauna-sediment relationship. This field study was conducted at Garrison Bay (Figure 1), a small embayment on San Juan Island, Wash. (lat. 48°35'N, long. 128°08'W).

MATERIALS AND METHODS

Applications of systematic sampling are found in the forestry literature (Osborne 1942; Finney 1948; Matern 1960; Faber 1972). Mathematical details are found in sampling texts such as Cochran (1963), Raj (1968), or Sukhatme and Sukhatme (1970) and in many theoretical papers.[4] Systematic sampling assumes that the sampling units in the area to be studied are numbered consecutively. The attractiveness of the method is increased by the relatively sessile nature of many intertidal

[4]Scherba, S., Jr., and V. F. Gallucci. 1976. Quantification of species-presence gradients by stratified systematic sampling and the autocovariance function. Unpubl. manuscr., 15 p.
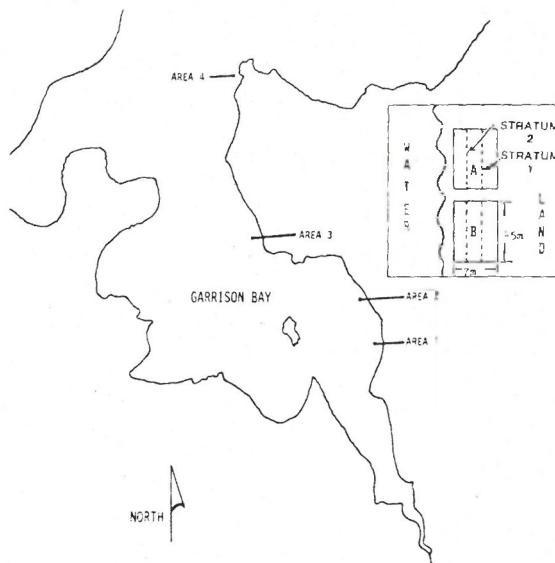
FIGURE 1.—Shoreline of Garrison Bay showing the location of the four study areas. Insert shows the representative arrangement of the subareas (A and B) and the strata (1 and 2) in these areas.

organisms. From N sampling units numbered 1, 2, ..., N; n sampling units are selected, all evenly spaced at a distance of K sampling units apart. Thus, $N = nK$. The location of the first unit to actually be sampled is randomly chosen by selecting a number between 1 and K from a table of random numbers. Hence, systematic sampling is based upon a uniform probability distribution (Raj 1968). SSS is a variation in which the region is divided into strata, e.g., at the locations of the fixed levels where samples would have been collected using FLTS. Each stratum is independently sampled in the manner described above.

Four regions with different sediment compositions were a priori defined in the intertidal area of Garrison Bay (Figure 1). Representative areas within these regions were sampled in the winter (January and February), spring (May and June), and summer (July and August) 1974. A north-south sediment gradient exists because fine sediment is deposited at the closed end of the bay where the water is less turbulent. Thus, the south (closed) end of the bay consists principally of fine grades of sediment, while the north (open) end consists mainly of coarser grades. Visual examination indicates that perpendicular to the water, there is a sediment gradient as well as a zonation of intertidal animals. However, the statistical comparisons of the data from strata, which were

placed parallel to the water, do not show the gradient. This is probably a consequence of the short distance between strata.

Field Procedures

Within each region (Figure 1), a rectangular study area was defined, measuring 95 m in length parallel to the waterline, and approximately 7 m wide, perpendicular to the waterline. Two parallel strata, approximately 2.5 m apart, were placed within each area, parallel to the waterline. The stratum at the highest tidal level was designated stratum 1 while the lower stratum was designated stratum 2. Stratum 1 within the areas was located at -1.4, -1.2, -1.1, and -1.2 feet in areas 1, 2, 3, and 4 respectively; while stratum 2 in those same areas was at -1.5, -1.7, -1.5, and -1.6 feet.[5] The study areas were numbered one (1) to four (4) (south to north) and defined by stakes marked with fluorescent tape for night identification.

It is necessary to test the homogeneity of sediment composition within a region if the areas are to be considered representative. This test was accomplished by dividing each area into two subareas,[6] separated by 5 m, and denoted as A (for the northmost subarea) and B (for the southmost). Each subarea contained about 448 sampling units. Two samples were then collected on each stratum, from each subarea, using a systematic sampling plan.

Each subarea was considered to contain separate populations, and the two population Kolmogorov-Smirnov procedure with $n = 4$ (Conover 1971) was applied to the data collected. This use of both subareas was carried out only for the winter sampling. Winter sampling of the subareas was done on: 8 January 1974 (1A, 1B), 9 January 1974 (3A, 3B), 2 February 1975 (2A, 2B), and 3 February 1974 (4A, 4B).

Spring and summer sampling was conducted only in subareas 1B, 2A, 3A, and 4A as follows: 24 May 1974 (1B, 3A), 21 June 1974 (2A, 4A), 19 July 1974 (1B, 4A), and 16 August 1974 (2A, 3A). Each stratum in these four subareas was independently sampled during these two seasons with $n = 4$ on each stratum.

All samples were collected using a thick-walled, cylindrical corer made of polyvinyl chloride pipe,

10 cm inside diameter and 18 cm long. The corer was pressed into the sediment to 18 cm, and its contents removed by hand, placed in a labeled plastic bag, and taken to the laboratory. Each sample was passed through a 1-mm sieve, and the contents retained by the sieve were sorted twice by eye to remove all bivalves and polychaetes (the only members of the macrofauna identified). These organisms were placed in 80% ethanol and 8% formaldehyde, respectively, for later identification. Only the common bivalves and polychaetes were identified to genus and species. The sediment portion of each sample was dried at 100°C for approximately 4 h. The method used to quantify the particulate properties of the sediment was the percentage composition by weight of selected sediment grain sizes. A mechanical shaker was used to pass the sediment portion of each sample through a series of Wentworth sieves (1.981, 0.495, 0.246, 0.124, 0.063 mm). The contents of each sieve were weighed and recorded as percentage of the total weight of that sample.

Statistical Procedures

Estimates of the variances of the sample means, obtained from SSS were approximated by the estimate of the variance of the sample mean from a simple random sample (see Cochran 1963), i.e., by using

$$\text{var}\,(\bar{y}) = \left(\frac{N-n}{N}\right)\!\left(\Big(\sum_{j=1}^{n}(y_j - \bar{y})^2\Big)/n(n-1)\right)$$

where $\bar{y} = \left(\sum_{j=1}^{n} y_j\right)/n.$

The rational for this approximation is discussed later.

Two statistical tests were used to quantify the sampling results. The K sample Kolmogorov-Smirnov (K-S) test with $\alpha = 0.10$, using the T_3 test statistic (Birnbaum and Hall 1960; Conover 1971), was used to test hypotheses about variation in sediment composition. The chi-square test for several multinomials with $\alpha = 0.05$ (Conover 1971) was used to test hypotheses about variation in bivalve and polychaete community structure.

In the within-area sediment homogeneity test empirical distribution functions were constructed for each subarea. The K-S test ($\alpha = 0.10$) was then used to test the null hypothesis (H_0) of equality of

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[5]Tidal heights are reported in feet to conform with U.S. Coast and Geodetic Survey Tide Tables.
[6]We thank A. R. Sen for this suggestion.

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these distribution functions. Using winter samples only, the test failed to reject H_0; thus, the data from each A and B subarea pair were combined and considered to be one subarea for comparison to the subareas sampled in the spring and summer. Hence, all data were analyzed as if they had been collected from four equal sized subareas, of dimensions 45 m by 7 m, during each season, using a sample of size four on each stratum.

The empirical cumulative distribution functions were constructed from the data by defining a random variable X as the sum of the percent of the total sediment weights retained in the sieve sizes <0.063, 0.063, and 0.124 mm. The random variable X takes a value of each sample, in each subarea, on each stratum. Thus, the empirical distribution functions constructed from this data characterized the sum of the weights of three finest sediment grades (and by subtraction from 100%, the three coarsest grades as well) for each stratum in each subarea. These three sieve sizes were grouped together because they constitute what may be called the finer grades of sediment and they probably have the greatest biological impact (Newell 1965). If the grain size which is of principal importance to the organisms is known, then the random variable could be chosen accordingly. There is much evidence that grain size is important to the organisms (e.g., see Loosanoff and Tommers 1948; Sanders 1958; Wieser 1959; Gray 1974). Subject to this limitation of comparing only the finer sediment groups, the sediment data may be statistically compared stratum to stratum in any one subarea, between subareas, or in combinations of these, both within or between seasons.

In each case, the null hypothesis for the K-S test on sediment was

$$H_0: F_1(x) = F_2(x) = \ldots = F_k(x) \qquad (1)$$

and the alternative

H_a: there is at least one inequality where $F_j(x)$ is the cumulative distribution function of the random variable X corresponding to area j.

The statistical analysis of the distribution of animal populations was based upon standard chi-square procedures (Conover 1971). Let the random variable Z have a multinomial distribution where the number of classes corresponds to the number of species types used, and the number of trials is the total number of individuals of all species. The chi-square test was applied to those

species types with entries in the expected value table which were either greater than unity, or at least, not far below unity. All species identified are listed, but, in certain cases, some species were grouped into families for the analysis; these are noted in the tables of data. Grouping of data is often advisable on statistical or biological grounds depending upon the objectives of the study. When data were grouped in this study, the grouping was dictated by sample sizes and was consistent with biological facts such as where the organisms occur in Garrison Bay, their modes of feeding, and their taxonomy.

The data were organized into contingency tables for a multinomial distribution. We denote the probability of a randomly selected value from the ith population as being classified in the jth class by P_{ij}. The columns of the table represent species (classes) while the rows represent populations, i.e., a particular stratum in a given subarea during a specific season. The null hypothesis may be stated as:

$$H_0: P_{1j} = P_{2j} = \ldots = P_{rj} \text{ for all } j; j = 1, 2, \ldots, c, \qquad (2)$$

and the alternative

H_a: there is at least one $P_{ij} \neq P_{kj}$ for some j and pair i, k where r equals the number of rows and c equals the number of columns. Under H_0,

$$P_{11} = P_{21} = \ldots = P_{r1} = P_1$$
$$\cdot$$
$$\cdot$$
$$\cdot$$
$$P_{1c} = P_{2c} = \ldots = P_{rc} = P_c$$

where $\hat{P}_j = C_j/N$; C_j = sum of observations in column j; N = total number of observations from all samples; and $\hat{P}_j$ estimates P_j. When a row or column of a particular contingency table equalled zero, it was not possible to reach a decision about the chi-square null hypothesis. To maintain consistent comparisons, no alteration of the contingency tables was made in such cases. The results of some of these tests of homogeneity are summarized in the next section.

RESULTS

The sampling data and the estimates of the variances of the sample means appear in Tables

1-3. It was necessary to pool the winter samples that were used to test for homogeneity (see Statistical Procedures) within each area. The samples in each area were considered to be from one subarea to correspond to the subareas used for the spring and summer sampling. The spring and summer samples were collected exclusively from subareas 1B, 2A, 3A, and 4A. The data in Tables 2 and 3 are for the species of bivalves and polychaetes which could be identified from the samples.

Sediment

The sediment data (Table 1) and statistical analyses confirm the existence of a particle size gradient from the closed (south) end to the open (north) end of the bay. Subareas 1B and 4A appear similar in Table 1, but subarea 1B is located in the closed end of Garrison Bay (Figure 1) which is much muddier with more fine grained particles and has poorer drainage than subarea 4A. Because the data suggest that subareas 1B and 4A contain approximately the same proportion of coarse grain particles (i.e., ≥1.981 mm), a qualitative description was used to supplement the quantitative analysis based on grain size composition by percentage weight: the 1.981-mm sieve in samples from subarea 1B contained large amounts of shell fragments, which will remain in suspension longer due to their flattened shape, while the same sieve size in subarea 4A contained mostly round pebbles, which settle more rapidly, and few shell fragments. Thus, despite their heavy weight, shell fragments were carried into the quiet part of the bay.

Samples from subarea 2A often had added weight in the 1.981-mm sieve in the form of rocks of about 5 cm across. This is probably the result of the activities of early settlers or of recent anthropoligical investigations.

The K-S procedures ($\alpha = 0.10$) confirmed the existence of a north-south sediment gradient between similarly numbered strata in all seasons between all four subareas. All six of the null hypotheses (1) of equality were rejected.

The sources of this gradient were located by using the K-S procedure ($\alpha = 0.10$) to compare all combinations of subarea pairs and seasons for similarly numbered strata. This resulted in the testing of 36 null hypotheses (1) of no difference, of which 25 were rejected and the remainder accepted. Thus, a gradient may be said to be the result of

TABLE 1.—Average percent of total weight of sediment in each of six particle size categories: W = Winter, Sp = Spring, Su = Summer. The numbers in parentheses are estimates of the variance of sample means.

Particle size (mm)	Subarea 1B									Subarea 2A								
	Stratum 1			Stratum 2						Stratum 1			Stratum 2					
	W	Sp	Su	W	Sp	Su				W	Sp	Su	W	Sp	Su			
<0.063	6.7(1.0)	10.7(0.28)	6.7(1.0)	4.3(0.64)	9.5(4.9)	6.9(0.31)				10.4(2.6)	6.8(0.99)	7.9(1.5)	9.2(4.2)	5.0(0.04)	5.4(0.22)			
0.063	8.5(0.77)	11.2(1.3)	9.4(0.74)	5.6(1.4)	9.1(1.3)	9.4(0.43)				7.9(3.5)	7.1(1.2)	8.2(1.5)	8.0(1.7)	4.6(0.11)	5.9(0.10)			
0.124	13.7(1.3)	20.9(7.8)	15.6(1.5)	11.9(6.0)	19.4(5.2)	16.7(2.7)				10.3(10)	11.3(0.71)	11.8(1.8)	10.6(1.9)	7.5(0.05)	11.2(0.02)			
0.246	11.7(0.04)	15.5(4.8)	15.5(5.3)	10.9(3.0)	15.9(0.94)	16.5(6.5)				9.1(3.3)	11.5(0.33)	10.5(0.57)	9.2(0.35)	9.0(0.93)	12.4(0.15)			
0.495	16.2(1.0)	15.3(3.4)	18.5(0.58)	15.0(2.7)	15.1(1.7)	16.9(4.2)				13.2(1.4)	14.8(1.2)	13.2(3.1)	12.7(0.80)	11.7(0.51)	13.3(0.20)			
1.981	43.2(6.0)	26.2(21)	34.3(8.4)	52.3(59)	30.9(36)	33.5(48)				49.0(72)	48.8(11)	48.4(28)	50.2(20)	62.2(4.2)	51.8(2.1)			

Particle size (mm)	Subarea 3A									Subarea 4A								
	Stratum 1			Stratum 2						Stratum 1			Stratum 2					
	W	Sp	Su	W	Sp	Su				W	Sp	Su	W	Sp	Su			
<0.063	6.0(2.1)	10.9(1.5)	7.1(1.8)	8.0(3.2)	11.9(0.11)	9.2(1.2)				3.4(0.07)	4.6(0.39)	4.5(0.19)	3.0(0.11)	3.8(0.26)	4.8(0.49)			
0.063	14.6(7.4)	20.8(5.7)	16.9(4.6)	17.9(6.3)	22.0(2.6)	17.8(1.9)				9.9(0.80)	9.5(1.2)	9.2(1.6)	7.7(0.38)	9.8(1.4)	8.3(0.34)			
0.124	37.0(29)	36.1(6.0)	35.9(32)	39.2(7.3)	26.0(1.1)	30.6(1.7)				16.2(2.8)	20.2(4.6)	19.6(17)	9.1(0.19)	22.3(12)	22.6(4.8)			
0.246	12.5(1.7)	8.4(0.52)	11.8(9.1)	14.5(11)	10.6(0.13)	11.9(2.2)				3.4(0.27)	9.1(0.95)	6.6(0.83)	4.4(0.45)	10.4(5.5)	10.6(4.6)			
0.495	13.2(12)	7.7(0.55)	12.6(5.8)	10.5(3.1)	12.5(0.11)	12.5(1.9)				15.0(2.3)	14.9(0.25)	15.3(0.58)	14.6(0.72)	19.3(0.85)	20.2(0.81)			
1.981	16.7(33)	16.0(15)	15.6(37)	10.4(17)	16.9(5.5)	17.6(5.6)				52.2(8.8)	41.2(16)	44.8(37)	61.1(4.6)	34.6(39)	30.4(31)			

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different subareas being dissimilar in a season. In particular, it was found that: 1) in the spring, subareas 1B and 2A were significantly different on both strata, while only stratum 2 in those subareas was significantly different in the summer; 2) both strata in subareas 1B and 3A and subareas 3A and 4A were significantly different throughout all seasons; and 3) stratum 1 of subareas 2A and 4A were significantly different only in the spring, while stratum 2 in these subareas was different in each season.

The K-S procedure ($\alpha = 0.10$) was used to test sediment composition homogeneity both between the strata of a given subarea and among the three seasons for a single stratum. Over half of these null hypotheses were accepted. Therefore, sediment composition of the strata remained largely stable throughout the three seasons and apparently lacked a consistent zonation perpendicular to the water.

Polychaetes

Table 2 shows that the dominant polychaete species vary according to season and sediment type. These species were found to be: *Lumbrineris bicirrata, Dorvillea japonica, Scoloplos pugettensis, Cirratulus cirratus,* and *Capitella capitata.* In this study the dominant species is the species with the largest number of individuals.

Spatial and temporal dominance patterns may be seen. In subarea 2A, the dominant organism is generally *D. japonica* (in all seasons on stratum 2 and in the winter and spring on stratum 1). *Capitella capitata* is usually the dominant species in subarea 3A (*S. pugettensis* being dominant there only in the winter on stratum 1). The increase in this species during the summer, as compared to the spring, on both strata of subarea 3A may have been influenced by the presence of a dense algal mat of *Enteromorpha* sp. which covered large intertidal areas. Subarea 4A has the greatest fluctuation with respect to the dominant species. On stratum 2 of subarea 4A, *C. capitata* is dominant in the spring and summer, replacing *L. bicirrata,* the winter dominant. *Capitella capitata* is dominant only in the spring on stratum 1 of subarea 4A; *C. cirratus* is dominant in both winter and summer. Subarea 1B shows the smallest seasonal fluctuation of any subarea in both total polychaete assemblage and dominant species. *Cirratulus cirratus* is dominant on both strata in the spring and summer, replacing the winter

dominants *S. pugettensis* (on stratum 1) and *L. bicirrata* (on stratum 2).

No simple seasonal pattern is discernible on the strata of the various subareas (see Table 2). Stratum 1 in both subareas 1B and 3A shows a steady increase in total number of individuals between spring and summer. In the cases of subarea 1B (stratum 2), subarea 2A (strata 1 and 2), and subarea 4A (stratum 2), the largest number of individuals is present in the spring. Subarea 3A (stratum 2) and subarea 4A (stratum 1) have the largest number of individuals in the winter, due to *Cirratulus capitata* and *Capitella cirratus,* respectively. However, there is insufficient data to conclude that stratum 2 is uniformly sustaining the greatest total numbers of individuals seasonally (perhaps due to the small horizontal distance separating the strata in each subarea).

Table 2 shows that it is possible to rank the subareas, in descending order, with regard to number of species present: subareas 1B, 4A, 2A, and 3A; as well as with respect to the total number of individuals: subareas 1B, 2A, 4A, and 3A. There are occasional seasonal reordering of these ranks.

Statistical analysis using the chi-square procedures ($\alpha = 0.05$, 33 df) confirmed the existence of a within season polychaete distribution (for the 12 groups used in the analysis) on identically numbered strata, between the four subareas in five of these six comparisons. The one exception was the comparison of stratum 1, between the four subareas, during the winter. In that instance, a "no decision" result was reached.

To investigate the sources of this difference in distribution, the polychaete assemblage on similarly numbered strata, all combinations of subarea pairs and season were examined using chi-square tests ($\alpha = 0.05$, 11 df). Eleven of these 36 null hypotheses (2) resulted in a "no decision" conclusion while the remaining 25 were rejected using this analysis. In the case of stratum 2, the null hypotheses comparing subareas 1B and 2A, 1B and 3A, 1B and 4A, 3A and 4A, and 2A and 4A were rejected in all seasons. The fluctuation of this biotic distribution in time (season) and space (sample area) is apparent.

The homogeneity (2) of the polychaete assemblage between the three seasons for a single stratum was examined using chi-square tests ($\alpha = 0.05$, 22 df). Of the eight null hypotheses of homogeneity (2), six were rejected (i.e., both strata 1 and 2 in both subareas 1B and 3A, and stratum 2 in both subareas 2A and 4A). The two remaining

TABLE 2.—Total number of individuals of the eighteen common polychaete species in four samples: W = Winter, Sp = Spring, Su = Summer. The numbers in parentheses are estimates of the variance of sample means.

| Species - Number | Subarea 1B | | | | | | Subarea 2A | | | | | |
| | Stratum 1 | | | Stratum 2 | | | Stratum 1 | | | Stratum 2 | | |
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Harmothoe multisetosa - 1	2(0.08)	1(0.06)	0(0)	1(0.06)	1(0.06)	0(0)	1(0.06)	4(0.49)	4(0.17)	1(0.06)	3(0.06)	1(0.06)
Eulalia parvoseta - 2	0(0)	2(0.25)	0(0)	0(0)	4(0.49)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)
Gyptis brevipalpa[1] - 3	1(0.06)	4(0.49)	10(2.7)	2(0.08)	3(0.06)	3(0.23)	0(0)	0(0)	0(0)	1(0.06)	4(0.17)	2(0.00)
Ophiodromus pugettensis[1] - 4	1(0.06)	6(2.2)	10(2.4)	0(0)	7(0.39)	5(0.88)	0(0)	0(0)	1(0.06)	0(0)	4(0.99)	9(2.0)
Platynereis bicanaliculata - 5	2(0.08)	2(0.25)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)
Nephtys caeca - 6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Glycera capitata[2] - 7	4(0.17)	3(0.56)	3(0.23)	1(0.06)	2(0.08)	1(0.06)	4(0.50)	1(0.06)	2(0.08)	0(0)	1(0.06)	0(0)
Diopatra ornata - 8	0(0)	0(0)	0(0)	0(0)	2(0.08)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)
Lumbrineris bicirrata[2] - 9	8(3.9)	3(4.9)	64(26.6)	36(3.7)	75(4.5)	72(5.1)	39(3.4)	55(39)	22(3.5)	20(1.5)	64(21)	45(18)
Dorvillea japonica[2] - 10	10(1.7)	50(22)	81(6.2)	15(1.1)	85(30)	36(13.7)	78(49)	96(36)	48(28)	35(11.6)	165(119)	56(61)
Scoloplos pugettensis[2] - 11	27(1.5)	26(8.8)	42(12.3)	6(1.4)	8(0.99)	4(0.49)	15(3.2)	43(25)	52(27)	9(1.1)	20(4.4)	1(0.06)
Naineris quadricuspida[2] - 12	0(0)	2(0.25)	7(2.0)	0(0)	5(0.06)	2(0.08)	25(9.3)	12(0.83)	14(1.4)	5(0.41)	39(38)	5(0.39)
Cirratulus cirratus[1] - 13	7(0.39)	124(193)	127(148)	17(3.5)	133(182)	110(56.2)	6(0.41)	24(4.5)	51(15)	2(0.08)	27(3.8)	21(2.7)
Armandia brevis[2] - 14	4(0.33)	6(0.74)	3(0.23)	1(0.06)	3(0.23)	1(0.06)	3(0.23)	16(5.1)	0(0)	1(0.06)	5(0.23)	0(0)
Capitella capitata[2] - 15	18(5.4)	94(135)	65(41)	10(0.41)	82(49)	66(12.6)	20(2.1)	36(11.6)	56(49)	3(0.23)	36(7.1)	13(0.23)
Axiothella rubrocincta[2] - 16	0(0)	0(0)	2(0.08)	7(1.4)	7(1.1)	5(1.5)	0(0)	0(0)	0(0)	1(0.06)	1(0.06)	2(0.25)
Owenia fusiformis[2] - 17	0(0)	2(0.08)	7(0.72)	8(1.2)	4(0.49)	9(1.1)	0(0)	1(0.06)	1(0.06)	0(0)	0(0)	1(0.06)
Thelepus crispus[2] - 18	8(2.8)	27(8.9)	34(13.3)	8(0.50)	19(3.4)	52(37.7)	4(0.33)	4(0.33)	5(0.39)	2(0.08)	18(2.7)	18(6.2)

| Species - Number | Subarea 3A | | | | | | Subarea 4A | | | | | |
| | Stratum 1 | | | Stratum 2 | | | Stratum 1 | | | Stratum 2 | | |
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Harmothoe multisetosa - 1	0(0)	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	4(0.99)	3(0.23)	3(0.23)	2(0.08)	1(0.06)
Eulalia parvoseta - 2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Gyptis brevipalpa[1] - 3	0(0)	1(0.06)	2(0.25)	3(0.06)	2(0.08)	0(0)	1(0.06)	5(0.89)	2(0.25)	3(0.55)	3(0.06)	3(0.06)
Ophiodromus pugettensis[1] - 4	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	2(0.25)	1(0.06)	2(0.25)	2(0.25)	8(0.17)	3(0.56)
Platynereis bicanaliculata - 5	0(0)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	13(1.1)	1(0.06)	0(0)	0(0)	5(0.23)
Nephtys caeca - 6	0(0)	0(0)	0(0)	2(0.08)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Glycera capitata[2] - 7	4(0.33)	4(0.33)	1(0.06)	2(0.08)	4(0.17)	1(0.06)	0(0)	2(0.08)	2(0.08)	2(0.08)	5(0.39)	1(0.06)
Diopatra ornata - 8	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Lumbrineris bicirrata[2] - 9	1(12.5)	6(0.91)	6(2.2)	0(0)	4(0.49)	6(0.91)	77(0.7)	8(1.9)	17(9.3)	40(3.8)	13(0.22)	15(2.7)
Dorvillea japonica[2] - 10	10(0.70)	130(0.54)	6(0.91)	5(0.88)	23(0.54)	15(3.2)	9(1.7)	17(2.9)	7(0.39)	14(2.7)	14(12)	5(0.56)
Scoloplos pugettensis[2] - 11	46(0.40)	18(0.41)	290(0.70)	56(4.5)	31(0.70)	19(2.4)	5(0.88)	5(0.39)	9(1.7)	6(1.4)	8(0.33)	2(0.25)
Naineris quadricuspida[2] - 12	2(0.25)	6(0.41)	4(0.17)	1(0.06)	5(0.23)	2(0.08)	40(0.48)	0(0)	3(0.56)	5(0.88)	1(0.06)	1(0.06)
Cirratulus cirratus[1] - 13	1(0.06)	19(2.2)	28(1.4)	4(0.99)	9(2.5)	2(0.25)	187(3.1)	16(1.2)	94(2.2)	6(0.74)	24(1.1)	24(0.66)
Armandia brevis[2] - 14	6(0.41)	2(0.08)	0(0)	8(0.08)	7(1.4)	1(0.06)	2(0.25)	21(0.06)	41(1.2)	4(0.33)	12(1.3)	8(1.8)
Capitella capitata[2] - 15	9(2.7)	31(0.54)	97(1.5)	104(1.4)	52(1.1)	85(1.9)	35(3.2)	59(4.1)	41(1.2)	28(4.1)	104(1.1)	43(0.22)
Axiothella rubrocincta[2] - 16	0(0)	0(0)	1(0.06)	0(0)	2(0.25)	3(0.23)	0(0)	24(1.6)	13(0.38)	17(2.4)	17(2.7)	9(1.2)
Owenia fusiformis[2] - 17	2(0.08)	2(0.25)	4(0.17)	4(0.49)	0(0)	3(0.23)	0(0)	0(0)	0(0)	2(0.25)	5(0.54)	0(0)
Thelepus crispus[2] - 18	0(0)	3(0.20)	0(0)	0(0)	5(0.56)	2(0.08)	1(0.06)	19(2.2)	5(0.39)	1(0.06)	0(0)	8(0.83)

[1] Treated as one group in the statistical analysis.
[2] Used in the statistical analysis.

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null hypotheses resulted in no decision. The data from Table 2 indicate that the apparent variation does occur in these two cases (stratum 1 in both subareas 2A and 4A) as well.

The homogeneity (2) of the polychaete assemblage between strata, in a given subarea, in a given season was also examined using chi-square tests ($\alpha = 0.05$, 12 df). Five of the 12 null hypotheses were rejected (i.e., subarea 4A in the winter, subareas 1B, 2A, and 3A in the spring, and subarea 1B in the summer). A no decision result was reached in the remaining cases.

Bivalves

The sampling data collected on the bivalve populations in Garrison Bay are given in Table 3. The data are organized as follows: 1) *Protothaca staminea*, *Venerupis japonica*, and *Saxidomus giganteus* were grouped as one into the Veneridae; 2) *Macoma inconspicua*, *M. irus*, and *M. nasuta* were grouped as one into the Tellinidae; 3) *Transennella tantilla*, *Clinocardium nuttalli*, *Mya arenaria*, and *Mysella tumida* were considered individually; and 4) *Macoma secta* was considered apart from the Tellinidae because of its usual occurrence in clean sandy environments.

The size and the number of sampling units in this study were generally inadequate for sampling most mature bivalves. As a consequence, hypotheses for small bivalves, such as *T. tantilla* and *M. tumida*, are best represented by the data in this study. Indeed, large densities of *T. tantilla* were found in all four subareas, with the largest numbers in subarea 3A, and *M. tumida* was found in large numbers only in subarea 4A.

The north-south bivalve distribution, as constructed from these data, is somewhat different from that found in the polychaetes. The data in Table 3 show that the subareas may be ranked in descending order with respect to the total numbers of individuals as follows: subareas 3A and 1B and subareas 2A and 4A are about the same. However, occasional seasonal reorderings do occur. The high densities in subarea 3A are probably due to the presence of large numbers of *T. tantilla*. In terms of the number of species present, subarea 1B generally ranks highest and the remaining three subareas are almost indistinguishable.

Differences in the bivalve distributions within a season, on like-numbered strata, and between subareas were examined using chi-square tests

TABLE 3.—Total number of individuals of the seven groups of common bivalves in four samples; W = Winter, Sp = Spring, Su = Summer. Numbers in parentheses are estimates of the variance of sample means.

Species or family - Number	Subarea 1B						Subarea 2A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Veneridae[1] - 1	1(0.06)	6(0.41)	3(0.23)	3(0.06)	7(1.1)	4(0.33)	2(0.08)	2(0.25)	4(0.17)	2(0.25)	3(0.23)	2(0.08)
Tellinidae[1] - 2	10(2.4)	3(0.06)	3(0.23)	17(1.7)	3(0.06)	8(0.17)	8(1.2)	5(0.06)	2(0.08)	10(0.74)	3(0.23)	7(0.40)
Transennella tantilla[1] - 3	4(0.99)	13(3.2)	0(0)	8(0.83)	11(5.8)	6(0.08)	6(0.74)	16(1.5)	10(0.74)	9(1.7)	6(1.4)	2(0.08)
Macoma secta - 4	4(0.33)	1(0.06)	2(0.08)	2(0.08)	0(0)	1(0.06)	0(0)	1(0.06)	2(0.25)	0(0)	0(0)	0(0)
Clinocardium nuttalli - 5	1(0.06)	2(0.25)	0(0)	1(0.06)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mya arenaria - 6	0(0)	0(0)	1(0.06)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mysella tumida - 7	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

Species or family - Number	Subarea 3A						Subarea 4A					
	Stratum 1			Stratum 2			Stratum 1			Stratum 2		
	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su
Veneridae[1] - 1	3(0.06)	0(0)	1(0.06)	1(0.06)	2(0.08)	0(0)	6(0.08)	1(0.06)	6(0.41)	1(0.06)	4(0.50)	5(0.89)
Tellinidae[1] - 2	3(0.06)	10(0.41)	9(0.23)	13(0.72)	10(0.74)	10(0.41)	9(0.39)	12(0.83)	11(2.4)	11(0.06)	12(0.50)	7(0.72)
Transennella tantilla[1] - 3	23(6.0)	9(0.56)	69(128)	27(1.5)	3(0.23)	35(30)	5(0.88)	3(0.23)	2(0.08)	0(0)	1(0.06)	0(0)
Macoma secta - 4	1(0.06)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Clinocardium nuttalli - 5	0(0)	1(0.06)	0(0)	0(0)	1(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mya arenaria - 6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Mysella tumida - 7	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	7(0.23)	4(0.17)	0(0)	12(1.1)	6(0.74)

[1]Used in the statistical analysis.

($\alpha = 0.05$, 6 df). All six of the null hypotheses (2) were rejected. Thus the bivalve distributions between subareas are different. To investigate the sources of this difference in distribution, the bivalve assemblage on similarly numbered strata, in all combinations of subarea pairs and season were examined using chi-square tests ($\alpha = 0.05$, 2 df). Nineteen of these 36 null hypotheses of homogeneity (2) were rejected. Thus, the bivalve distribution is not consistent in either time (season) or space (sample subareas).

The homogeneity (2) of the bivalve assemblage between the three seasons for a single stratum was examined using chi-square tests ($\alpha = 0.05$, 4 df). Four of the eight null hypotheses were rejected. The homogeneity (2) of the bivalve assemblage between strata, in a given subarea, in a given season was also examined using chi-square tests ($\alpha = 0.05$, 2 df). Two of the 12 null hypotheses were rejected. Thus, a definitive statement about the dependence between bivalve presence and season cannot be made. Furthermore, the differences between the strata of a single subarea are apparently minimal.

DISCUSSION

The sediment and macrofauna data collected in the Garrison Bay study were analyzed under the assumption of intrasample independence within each subarea (i.e., the contents of one sampling unit neither predicts nor influences the contents of any other unit). The assumption is based upon the homogeneity of macrofauna and sediment composition within study subareas. Macrofaunal homogeneity is defined here as meaning that all members of a given species on a given stratum are described by the same spatial probability distribution. Although specific probability distributions were not fit to the data, chi-square and Kolmogorov-Smirnov tests are legitimately applied to the sample data.

There are K different systematic samples, each of size n, that could be chosen (recall $N = nK$); one of these is selected at random. The sample mean of the ith such systematic samples, $\bar{y}_i$, and the population mean, $\overline{Y}$, are defined respectively as:

$$\bar{y}_i = (\sum_{j=1}^{n} y_{ij})/n \text{ and}$$

$$\overline{Y} = (\sum_{i=1}^{K} \sum_{j=1}^{n} y_{ij})/nK$$

where y_{ij} is the attribute of interest in the sample

(e.g., the number of individuals of a given species in the jth sample). Since systematic sampling is a probability sampling scheme, a valid expression for the variance of the sample mean is

$$\text{var}(\bar{y}_i) = (\sum_{i=1}^{K} (\bar{y}_i - \overline{Y})^2)/K \qquad \text{(Sukhatme and Sukhatme 1970).}$$

Alternative expressions of this quantity have been derived (Cochran 1963). No difficulties arise in using any of these forms of var ($\bar{y}_i$) in theoretical studies, but in applications of systematic sampling, no reliable estimate of var ($\bar{y}_i$) is known from taking only one sample of size n from an area. This is a disadvantage of SSS. In practice, approximations to var ($\bar{y}_i$) are used as estimators of this statistic. The texts by Cochran (1963:224-227) and Sukhatme and Sukhatme (1970:369-370) present several methods to approximate var ($\bar{y}_i$) from a single systematic sample. However, if m (≥ 2) independent systematic samples (each of size n) are taken on the same stratum at the same time, an exact (as opposed to an approximate) estimate of var ($\bar{y}_i$) is possible. Letting $\bar{y}_i$ represent the sample mean from one of the m systematic samples, then

$$\text{var}(\bar{y}) = \sum_{i=1}^{n} (\bar{y}_i - \bar{y})^2/m(m-1)$$

where $\bar{y} = (\sum_{i=1}^{m} \bar{y}_i)/m$ \qquad (Sukhatme and Sukhatme 1970).

In this study the estimate of the variance of the sample means was approximated by the variance calculated for a simple random sample (Cochran 1963). This is reasonable because of the within-area homogeneity of the sediment and macrofauna in each of the four study areas. Of course, it is preferable to take at least two independent systematic samples, each of size n.

Cochran (1963) discussed the difference in precision between random and systematic sampling based on the results of these methods upon certain types of population data. Special attention should be given to data which is either inherently periodic or subject to a periodic input, e.g., tidal forces. Under these circumstances, K must be carefully selected. Periodic variation in the north-south direction in Garrison Bay is considered to be unlikely.

The use of SSS allows strata to be placed at tidal heights where experimental interest is focused. Thus, samples may be taken at fixed tidal levels as

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in FLTS and statistically valid estimates of means and variances on a stratum found. Furthermore, no greater physical effort is required in SSS than in FLTS. SSS also provides a method to quantify species-presence gradients. Hence, SSS is free of some of the disadvantages of FLTS while maintaining the advantages often ascribed to FLTS plans.

There is a sediment gradient in the bay in the sense of a gradual increase in coarseness (silt to sand) south to north over the four areas for all seasons. Over all seasons, subarea 1B generally contained the largest number of bivalve species and, were it not for the abundance of *Transennella tantilla* (which is discussed later), subarea 1B would have the largest number of bivalves also. In addition, in almost all seasons subarea 1B contained the largest number of individuals and species of polychaetes. Thus, there is a distribution in bivalve and polychaete presence, from high density and species numbers to low as the sediment becomes more coarse. The sediment composition, as measured by average percentage composition by weight of various grain sizes, is a necessary factor to consider in predicting macrofauna population dynamics, but it is not a sufficient predictor by itself. This viewpoint is based on the necessity of employing qualitative information concerning the types of material retained by the 1.981-mm sieve (see Results section), and the role we attribute to the algae *Enteromorpha* sp. in the population dynamics of *T. tantilla* (see later discussion).

Newell (1965) found a higher number of microorganisms in areas composed of finer grades of sediment and an associated higher number of the deposit feeders (*Hydrobia ulvae* and *Macoma balthica*). He concluded that the large number of microorganisms was a result of the greater surface area of fine sediment grades which is related to the amount of organic nitrogen (protein) available to deposit feeders. The polychaete data from Garrison Bay, and subsequent statistical analyses, suggest that Newell's (1965) hypothesis can be extended to incorporate a statement about the biological effects of different sediment compositions in the presence of temporal heterogeneity. Recall that the sediment data show that subarea 4A, the most exposed subarea, experiences greater interseason fluctuations than does subarea 1B, the most sheltered subarea. Furthermore, the polychaete assemblage in subarea 1B shows the smallest seasonal fluctuation with regard to both total

numbers of individuals and species as compared with subarea 4A. Subareas 2A and 3A also show smaller seasonal variations in both polychaete assemblage and sediment composition than does subarea 4A. All of this suggests that mixed fine sediment grades (silty areas) may act as insulators for certain infauna against seasonal stresses. That is, fine sediments with their larger total surface area to volume ratio retain larger quantities of nutrients (organic nitrogen) and hold more interstitial water. If the areas composed chiefly of fine sediment grades occur in the cul de sac of an embayment, where wave action is minimal, then these areas are more likely to retain larger numbers of individuals and species than other areas within the embayment. Thus, despite the periodic fluctuations in many environmental parameters of the intertidal zone, a constant sediment particle composition contributes to a high degree of environmental predictability. Slobodkin and Sanders (1969), Levinton (1972), and Gray (1974) considered aspects of the consequences of temporal predictability for deposit and suspension feeders.

The bivalves and polychaetes listed in Tables 2 and 3 represent both suspension and deposit feeders. Rhoads and Young (1970) advanced the hypothesis that animals of one trophic level modify the environment and affect the dynamics of members of another trophic level, and called it trophic group amensalism. They found suspension feeders in the subtidal to be generally restricted to sandy or firm mud bottoms, and deposit feeders to be more numerous in soft silty substrates. The polychaete results generally support this hypothesis. An exception noted by Young and Rhoads (1971) was the case in which it was hypothesized that tube-building polychaetes (both suspension and deposit feeders) make it possible for higher densities of bivalve and polychaete suspension feeders to coexist with deposit feeders in silty sediments because of their ability to bind particles together and thereby stabilize sediments. This hypothesis may be useful in explaining why suspension feeders, e.g., the tube builder *Owenia fusiformis* and the members of the Veneridae, are so numerous in subarea 1B, as well as why the tube building terebellid *Thelepus crispus*, a surface level deposit feeder, reaches its maximum density in subarea 1B. The combination of tube building coupled with the feeding behavior of suspension feeders may provide these organisms a survival advantage in this otherwise soft

silty area. Further studies are being conducted to develop hypotheses for Garrison Bay.

Newell's (1965) hypothesis does not appear to explain the abundance and apparent sediment preferences of *T. tantilla*. Maurer (1969) found *T. tantilla* to be ubiquitous in a bay with a sediment gradient similar to that of Garrison Bay, while attaining its greatest numbers in a region composed principally of finer sediment particle sizes. Excluding subarea 3A, similar results follow for *T. tantilla* in Garrison Bay. The increased abundance of this bivalve in the summer on both strata of subarea 3A indicates that the principal response of *T. tantilla* may be to something other than just sediment composition. The extensive covering of subarea 3A by a dense algal mat of *Enteromorpha* sp. is probably involved in the population explosion. *Transennella tantilla* would gain protection from some physiological stresses such as elevated temperatures and increased water evaporation by the sun and wind. Similar dense mats of *Enteromorpha* sp. were not found in the other three areas at the sampling times.

The polychaete assemblage in Garrison Bay is described by a distribution which is apparently sediment and season dependent. The limited data on the distribution of bivalves does not have the same patterns. Preliminary analyses from an investigation (Gallucci)[7] involving the collection of large numbers of bivalves in Garrison Bay substantiates the lack of a simple gradient relationship for bivalves. Life in a calcium carbonate shell seems to allow for greater independence from environmental fluctuations than life near the sediment surface without such a shell.

Although the effects of seasonal and sediment type variations are often evident, causal links must be established by the examination of specific factors, e.g., competition, predation, food availability and selection, salinity, and temperature. Toward this end, Hylleberg and Gallucci (1975) and Gallucci and Hylleberg (1976) have examined the role of food availability and sediment composition upon the growth of the deposit feeder *Macoma nasuta* in Garrison Bay. Garrison Bay daylight summer surface water temperatures are about 1°C higher in the closed end than in the open end (Gallucci, unpubl. data), and short stretches of intertidal areas sustain a

subsurface freshwater runoff.

In this paper we have developed an appropriate sampling method for marine studies and the statistical machinery for testing certain relevant hypotheses. We have applied these methods in an intertidal study. The biological results pertain to sediment and animal gradients under seasonal change. Conclusions are based upon statistical comparisons in which the null hypothesis was rejected, tempered by extensive biological studies.

The data and results of the Garrison Bay study have obvious significance for shellfish culture. Factors such as the selection of sediment type in which to establish seed beds, interspecies associations, the season in which to make population assessments, and the sampling techniques should all be considered if sound management decisions are to be made.

ACKNOWLEDGMENTS

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