SMALL-SCALE DISTRIBUTIONS OF OCEANIC DIATOMS

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ABSTRACT

A sampling study was designed to investigate small-scale abundance fluctuations of diatoms over a distance of 10 miles. It was carried out at three depths in each of two oceanic environments of the North Pacific. Significant nonrandom distributions were observed. The intensity of aggregation varied with species and with depth.

An expression for the approximate confidence intervals for single observations was derived from the 5th and 95th percentiles of the observed frequency distributions.

Statistical analysis of the fluctuations of *Nitzschia turgiduloides* indicated a pattern of distribution with a scale of 1 mile. This may be associated with internal waves in the region of the thermocline.

Knowledge of small-scale distributions of organisms in the ocean is important for evaluation of data based on widely spaced samples, and, hence, is essential for design of efficient sampling programs. Moreover, abundance fluctuations on even the smallest scale relate directly to the ecology of the species, and an understanding of the magnitude and scale of such fluctuations is an important step toward the understanding of a species' relationship to its environment and to other species within its community.

Evidence indicates that the distribution of phytoplankton in the ocean may be highly aggregated (Bainbridge, 1957). A few attempts have been made to sample small-scale aggregations and to investigate quantitatively their density and spacing and the environmental factors which influence them (e.g., Hasle, 1954; Holmes and Widrig, 1956; Barnes and Hasle, 1957; Cassie, 1959a, b, 1960; Bernhard and Rampi, 1965). Although these studies applied a wide variety of statistical procedures to a range of spatial and temporal scales, all of the phytoplankton species studied were reported to have aggregated distributions. However, such studies have all been conducted in the nearshore environments. If, as has been suggested (Cassie, 1957), the contagious distributions of plankton reflect heterogeneities in the environment, then the results of such studies may not be applicable to the more homogeneous environments of the open ocean.

The study described in this paper was carried out in two oceanic environments of the North Pacific. While it was primarily designed to give a quantitative estimate of the precision of samples collected for an extensive study of oceanic diatoms, the results have general interest.

LOCATION OF STUDY

Closely spaced samples were taken twice during Scripps Institution of Oceanography Expedition URSA MAJOR, August-September, 1964. Station 23 (lat 49°07'N, long 155°31'W) was located in the Central Subarctic Pacific and Station 5 (lat 37°00'N, long 155°02'W) in the Central Pacific (Dodimead, Favorite, and Hirano, 1963); both regions were removed from the effects of either neritic environments or the North Pacific Transition Domain. The phytoplankton of the Central Subarctic consisted primarily of diatoms which reached densities in excess of 5,000 cells/100 ml. A total of 27 diatom species was recorded, of which *Nitzschia turgiduloides* comprised 68-92% of the population, and *Denticula seminae* an additional 9-20%. The maximum density of diatoms at the Central Pacific station was only 30 cells/100 ml. The dominant species, *Hemiaulus hauckii*, contributed 20% of the

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total diatom population, and 16 additional species were recorded. Subsequent samples from this region indicated that the major diatom population was below the depth range of the sampling study.

METHODS

At each location a line of stations was positioned with respect to a 10-m drogue. In the Subarctic Pacific, 10 stations were sampled; in the Central Pacific, 11. The stations were spaced at randomly ordered intervals of 0.5, 1.0, and 2.0 nautical miles, covering a total distance of 10.5 miles. At each station samples were collected from depths of 10, 35, and 50 m (wire out).

Samples were collected with 3-liter Van Dorn water samplers. The organisms in samples of 400 ml were preserved with 10 ml of 10% basic Formalin. Aliquots of 50 or 100 ml were settled for 24 hr and the diatoms identified and enumerated under the inverted microscope according to the sedimentation procedure of Utermöhl (1931). The species used for the analysis of distributions were those for which experience has shown the problems of identification and enumeration are negligible. In the case of chain-forming species, the statistical analyses were based upon the numbers of chains per aliquot.

STATISTICAL PROCEDURES

The variance of the cell counts includes the variability introduced into the data during the preparation and enumeration of the subsample, as well as any spatial heterogeneity. If these are independent, the sums of squares will be additive:

$$SS_{total} = SS_{subsample} + SS_{spatial}$$

and the total observed variance is given by:

$$s^2_{total} = SS_{total}/\text{degrees of freedom}.$$

In a brief preliminary study it was demonstrated that, for all species but one, the variability introduced into the data at either the initial or final subsampling stage was no greater than random (Poisson) expectation and may be approximated by the mean count. This agrees with the results of other workers (Holmes and Widrig, 1956; Lund, Kipling, and Le Cren, 1958). The single exception was *Nitzschia turgiduloides*, for which the total introduced variability was $35\bar{X}$.

It has been shown (Venrick, 1971) that the expected total variance of a series of counts from a randomly distributed population is given by:

$$\sigma^2 = \Big\{(n_{al}-1)\,(n_{ss})\,(n_{pop})\,(1-\tfrac{1}{f_1})\,\bar{X}_{al} + [(n_{ss}-1)\,(n_{pop})\,(1-\tfrac{1}{f_2}) \times (\bar{X}_{al} + \tfrac{n_{al}}{f_2}\bar{X}_{al})] + (n_{pop}-1)\,[\bar{X}_{al} + \tfrac{n_{al}}{f_2}\bar{X}_{al} + \tfrac{n_{al}\,n_{ss}}{f_1\,f_2}\bar{X}_{al}]\Big\} / [(n_{al})\,(n_{ss})\,(n_{pop}) - 1]$$

where n_{al}, n_{ss}, and n_{pop} are the numbers of aliquots per subsample, the numbers of subsamples per sample, and the number of samples collected from each depth; f_1 is the ratio of sample volume to subsample volume, f_2 is the ratio of subsample volume to aliquot volume; and $\bar{X}_{al}$ is the mean number of cells (or chains) per aliquot. Substituting $n_{al} = 1$, $n_{ss} = 1$, and $f_1 = \frac{3000}{400} = 7.5$, the expression simplifies to:

$$\sigma^2 = \bar{X}_{al} + \frac{1}{f_2}\bar{X}_{al} + \frac{1}{7.5\,f_2}\bar{X}_{al},$$

where $f_2 = 8.0$ for 50 ml aliquots and 4.0 for 100 ml aliquots. For *N. turgiduloides*, the appropriate expected variance is:

$$\sigma^2 = 35\bar{X}_{al} + \frac{1}{7.5\,f_2}\bar{X}_{al}.$$

At each depth, the observed variance, s^2, may be compared with the expected variance, σ^2, and the probability of departure from random expectation determined by means of the ratio

$s^2/\sigma^2 = \chi^2/\text{df}$. For 10 and 11 samples $\chi^2(0.05)/\text{df}$ values are 1.88 and 1.83 respectively. Species for which the s^2/σ^2 ratio exceeds the χ^2/df value are considered to have aggregated distributions. Ratios greater than 1.63 and 1.60 respectively were significant at the 0.10 level.

With the small number of degrees of freedom involved, the maximum variance attainable by species with mean counts less than 0.2 is too small to give an s^2/σ^2 ratio significant at better than the 0.10 level. For rarer species, a runs test on presence and absence (Tate and Clelland, 1959) was used to give additional information about distribution patterns.

RESULTS

The detection of aggregation in a population is influenced by interaction between volume and spacing of field samples and the scale of aggregation of the population (Grieg-Smith, 1964), and by the proportion of the initial sample which is ultimately enumerated (Venrick, 1971). Thus, the specific results of this study are strictly pertinent only to this sampling design, and they must be interpreted accordingly.

The results of these studies are presented in Tables 1 and 2. Within the Subarctic region, 8 of the 24 distributions were significantly aggregated at the 0.05 level, and two additional species at the 0.10 level. At every depth the species with contagious distributions were the most abundant ones, with the exception of *N. turgiduloides* at 10 m. It is likely that spatial variability of this species was obscured by the large sampling error. Aggregations of the dominant species would result if they had outgrown, in situ, the other species. The fewest aggregated distributions occurred at 10 m. This was the only sampled depth within the mixed layer, and presumably, wind-driven turbulence was sufficient to keep all but the most rapidly dividing species distributed randomly.

Within the Central Pacific, only 3 of the 20 distributions were significantly nonrandom, at the 0.05 level. The runs test, significant at the 0.10 level, indicated that five additional species were aggregated. In this region, aggregation did not appear to be related to the abundance of the species.

Concordance tests were used to investigate the agreement of species with respect to fluctuations of abundances between samples. At Subarctic Station 23 there was significant concordance ($P < 0.05$) between all species at each of the three depths, indicating that species tended to respond to, or be influenced by, their environment in the same manner. In contrast, there was no concordance between species at any depth at Central Pacific Station 5.

PRECISION OF SINGLE SAMPLES

ESTIMATES OF ABUNDANCE

If the frequency distribution of organisms in the field can be fitted to a theoretical distribution, confidence limits on single observations can be derived from the variance of that distribution. Some workers (e.g., Winsor and Clarke, 1940; Barnes and Hasle, 1957) have successfully used logarithmic transformations to normalize abundance data. This procedure was successful for some of the diatom species under consideration in this study. (Normality was tested with normal-probability paper.) The transformation, however, was not successful for all species at all depths and thus a general use of parametric statistics on log-transformed data was not justifiable.

The observed frequency distributions of the aggregated species were satisfactorily predicted by the negative binomial distribution (Anscombe, 1949). Values of k (estimated from the expression $k = \bar{X}^2/(s^2 - \bar{X})$ for the aggregated species ranged from 0.15 to 13.30. The comparisons between the predicted and the observed cumulative frequency distributions were made with Kolmogorov-Smirnov tests (Tate and Clelland, 1959); none were significantly different at the 0.10 level. There are available transformations which normalize negative binomial distributions (Anscombe, 1948). However, these transformations depend upon knowledge of the value of k and thus are applicable only to this particular set of data and not to observations of other species or observations from other environments.

TABLE 1.—Results of sampling study at Subarctic Pacific Station 23.

Species	$\bar{X}_{al}$	σ^2	s^2	s^2/σ^2	P
I. 10-m depth					
Nitzschia turgiduloides[1]	513.5	17,981.23	20,764.30	1.15	--
Denticula seminae[1]	53.8	61.44	271.28	4.42	<0.001
Chaetoceros atlanticus[1]	8.4	9.59	8.26	0.86	-
Dactyliosolen mediterraneus[1]	4.4	5.02	9.30	1.85	<0.10
Coscinodiscus marginatus	2.1	2.40	0.76	0.32	-
Rhizosolenia alata[1]	1.6	1.83	2.26	1.23	-
Thalassiothrix longissima	1.5	1.71	1.16	0.68	-
Rhizosolenia hebetata hiemalis	1.3	1.48	1.56	1.05	--
Corethron criophilum	1.1	1.26	0.98	0.78	--
II. 35-m depth					
Nitzschia turgiduloides[1]	801.0	28,048.62	122,374.22	4.36	<0.001
Denticula seminae[1]	119.3	136.24	1,966.23	14.43	<0.001
Dactyliosolen mediterraneus[1]	23.1	26.38	367.11	13.92	<0.001
Chaetoceros atlanticus[1]	3.0	3.43	17.55	5.12	<0.001
Thalassiothrix longissima	1.5	1.71	3.16	1.85	<0.10
Rhizosolenia hebetata hiemalis	1.4	1.60	2.04	1.28	--
Rhizosolenia alata[1]	0.9	1.03	0.76	0.74	--
Corethron criophilum	0.9	1.03	0.98	0.95	--
Coscinodiscus marginatus	0.8	0.91	1.28	1.41	--
III. 50-m depth					
Nitzschia turgiduloides[1]	330.6	11,581.91	291,104.04	25.13	<0.001
Denticula seminae[1]	39.0	50.04	279.33	5.58	<0.001
Dactyliosolen mediterraneus[1]	7.7	9.88	65.30	6.61	<0.001
Corethron criophilum	0.7	0.90	1.13	1.26	-
Coscinodiscus marginatus	0.6	0.77	0.93	1.21	-
Chaetoceros atlanticus[1]	0.2	0.26	0.40	1.54	--
Rhizosolenia hebetata hiemalis	0.1	0.13	0.10	0.77	--

[1] Statistics based on numbers of chains per aliquot.

The expression which was ultimately chosen to estimate the precision of single observations was derived empirically from the 5th and 95th percentiles of the frequency distributions. For any single count, x, of a nonrandomly distributed species at a single depth, it was found that the expression

$$0.3x \leqslant \bar{X} \leqslant 3.2x$$

included the observed population mean X 90% of the time. The expression was conservative for species with nonaggregated distributions. When all species were considered, the expression included the population mean 95% of the time. The expression gave satisfactory results for estimates of mean numbers of cells of chain-forming species ($P \sim 0.13$) and for mean total diatom abundances ($P \sim 0.14$).

The use of this expression is demonstrated in Table 3, where it has been applied to two samples from 35-m depth at Subarctic Station 23.

TABLE 2.—Results of sampling study at Central Pacific Station 5.

Species	$\bar{X}_{al}$	σ^2	s^2	s^2/σ^2	P
I. 10-m depth					
Hemiaulus hauckii[1]	2.4	3.08	3.45	1.12	--
Asterolampra marylandica	1.0	1.28	1.00	0.78	<0.10 (r)
Rhizoselenia hebetata semispina[1]	0.7	0.90	3.42	3.80	<0.001
Asteromphalus heptactis	0.4	0.51	0.45	0.88	--
Chaetoceros dadayi[1]	0.4	0.51	0.45	0.88	<0.10 (r)
Nitzschia sicula	0.3	0.38	0.21	0.55	--
Mastogloia rostrata	0.3	0.38	0.41	1.08	--
II. 35-m depth					
Hemiaulus hauckii[1]	1.2	1.54	4.56	2.96	=0.001
Nitzschia sicula	0.7	0.90	0.42	0.47	<0.10 (r)
Asteromphalus heptactis	0.6	0.77	0.45	0.58	-
Mastogloia rostrata	0.4	0.51	0.27	0.53	<0.10 (r)
Bacteriastrum sp.[1]	0.4	0.51	1.45	2.84	<0.01
Chaetoceros bacteriastroides var.	0.4	0.51	0.45	0.88	--
Chaetoceros bacteriastroides	0.4	0.51	0.45	0.88	--
Asterolampra marylandica	0.1	0.13	0.09	0.69	--
Chaetoceros dadayi[1]	0.1	0.13	0.09	0.69	--
III. 50-m depth					
Nitzschia sicula	0.9	1.15	1.70	1.48	--
Hemiaulus hauckii[1]	0.8	1.03	1.17	1.14	<0.10 (r)
Chaetoceros bacteriastroides[1]	0.4	0.51	0.27	0.53	--
Asteromphalus heptactis	0.2	0.26	0.16	0.62	--
Bacteriastrum sp.[1]	0.2	0.26	0.16	0.62	--
Chaetoceros bacteriastroides var.	0.2	0.26	0.16	0.62	--
Asterolampra marylandica	0.1	0.13	0.09	0.69	--
Mastogloia rostrata	0.1	0.13	0.09	0.69	--

[1] Statistics based on numbers of chains per aliquot.
r Nonrandomness indicated only by runs test.

For the more abundant species, the 95% confidence limits which can be placed around a single sample are extremely broad. However, without replicate samples, this interval cannot be significantly reduced. For species represented in a sample by fewer than five cells, the confidence interval given by the empirically derived expression is smaller than that obtained from the assumption of a Poisson distribution. For these rarer species, it is recommended that the confidence interval around a single sample be derived from the assumption of a Poisson distribution (Fisher and Yates, 1957).

ESTIMATES OF DIVERSITY

The variability of individual species in the field determines the precision with which a

single sample estimates the structure of the assemblage. The phytoplankton association within the Subarctic Pacific had a low diversity and significant concordance between species. As a result, the species showed a high degree of consistency of relative abundances within samples. In every sample *Nitzschia turgiduloides* was the numerically dominant species, *Denticula seminae* was the second dominant, and one of two species, *Chaetoceros atlanticus* or *Dactyliosolen mediterraneus* was third in abundance. Thus, a single sample appeared to give a precise estimate of the structure of a less diverse assemblage, even though the large between-sample variability decreased the precision of the estimate of absolute abundances of single species.

In contrast, the phytoplankton association in the upper 50 m of the Central Pacific had a high diversity and lacked concordance between species. At 10, 35, and 50 m, respectively, three, seven, and five species were dominant in at least one sample. Thus, a single sample from a diverse assemblage gave an imprecise estimate of the relative abundances of the component species.

TABLE 3.—Confidence interval about single samples. (95% confidence intervals about single samples, x, calculated from the expression $0.3x - 3.2x$ and compared with the population mean density as estimated by the mean of 10 samples, $\bar{X}$.)

Species		$\bar{X}$	Substation e[1]		Substation h[1]	
			x	Confidence interval	x	Confidence interval
Station 23, 35 m; 50-ml aliquots						
Nitzschia turgiduloides	cells	3,018.0	1,481	444.3-4,739.2	4,654	1,396.2-14,892.8
	chains	801.0	484	145.2-1,548.8	1,252	375.6- 4,006.4
Denticula seminae	cells	395.8	175	52.5- 560.0	624	187.2- 1,996.8
	chains	119.3	87	26.1- 278.4	169	50.7- 540.8
Dactyliosolen mediterraneus	chains	23.1	8	2.4- 25.6	64	19.2- 204.8
Chaetoceros atlanticus	cells	7.7	3	0.9- 9.6	25	7.5- 80.0
	chains	3.0	1	0.3- 3.2	11	3.3- 35.2
Rhizosolenia hebetata hiemalis	cells	1.6	0	-- --	3	0.9- 9.6
	chains	1.4	0	-- --	2	0.6- 6.4
Thalassiothrix longissima	cells	1.5	2	0.6- 6.4	1	0.3- 3.2
Corethron criophilum	cells	0.9	1	0.3- 3.2	1	0.3- 3.2
Total cells		3,491.1	1,704	511.2-5,452.8	5,445	1,633.5-17,424.0

[1] Substations e and h separated by 3.5 nautical miles.

ANALYSIS OF PATTERNS

In the analysis of patchiness and its causal factors, the size and shape of a patch often receives primary consideration. This approach is hampered by the difficulty of accurately defining a patch, particularly where, as in the ocean, one can rarely see the patch as a physical entity. An alternate approach is to examine the scale on which a population shows consistent spatial distribution, regardless of the degree of contagion. Since the detection of nonrandomness depends upon the interaction of the size and distribution of the samples with the population distribution, if the scale of sampling is systematically altered, the observed population variance may change, and those sampling scales which produce maximum variances may indicate scales of heterogeneity in the population distribution.

The six sets of 10 and 11 samples were considered as sets of 45 and 55 pairs of samples separated by intervals of 0.5, 1.0, 1.5, . . . 10.5 miles. For all nonrandomly distributed species, the variance was calculated between each possible pair of samples and averaged for each interval. Thus, for the set of 10 Subarctic samples, in which three pairs were separated by 0.5 mile, four pairs by 1.0 mile, two pairs by 1.5 miles, etc., $\bar{s}^2_{0.5}$ is an average of three variances, $\bar{s}^2_{1.0}$ an average of four variances, $\bar{s}^2_{1.5}$ an aver-

age of two variances, etc. The average variances were plotted against the sampling interval, i.

In the case of one species, *N. turgiduloides*, this technique revealed a periodicity of $\bar{s}_i^2$ with peaks separated by 1-mile increments of the sampling interval (Figure 1 b-d). This indicates a pattern of heterogeneity on a scale of 1 mile which was not apparent from a direct plot of abundances (Figure 1a). The periodicity was best developed at 35 m (runs test significant at $P < 0.001$) where it centered about the population variance, as measured by the total variance of the 10 samples. The periodicity was also highly significant (runs test, $P = 0.01$) at 10-m depth. At 50 m the variance showed significant periodicity ($P = 0.10$) only when the sample from substation h was omitted from the calculation. The high population densities of *N. turgiduloides*, and other species, encountered at substation h were comparable to densities observed at shallower depths, and may represent another scale of patchiness imposed upon the deeper populations by vertical mixing.

The horizontal pattern observed in *N. turgiduloides* was most highly developed along the top of the seasonal thermocline, which, at Station 23, extended between 30 and 50 m. Internal waves travelling along the thermocline produce a regular series of vertical displacements, which may occur on a scale of 1 mile. In species with strong vertical gradients of density at the top of the thermocline, such circulation patterns would produce regular horizontal fluctuations of abundance, such as were observed in the present study. The effect of vertical displacement on the less strongly stratified species may have been obscured by their horizontal variations.

This technique has been successfully used to investigate patterns of terrestrial vegetation (Grieg-Smith, 1964). Once scales of heterogeneity have been defined, those environmental parameters that vary on scales of similar magnitude may be sought as possible determinants of the species patterns. Because this approach is not limited to factors which can be measured simultaneously, it is very flexible. It is applicable not only to parameters in effect at the time of sampling, but also to those whose effect on phytoplankton was exerted some time in the past, and which cannot therefore be directly correlated with abundance. It may for instance prove to be a useful tool for examining the effect of vertically migrating herbivores on the standing stock of phytoplankton.

SUMMARY AND CONCLUSIONS

Of the distributions examined in the present study, less than half showed significant aggregation. For these species the 90% confidence interval about a single sample, x, could be estimated from the interval $0.3x$ — $3.2x$. This expression was conservative for the nonaggregated species.

The inability to establish contagion for the majority of the species investigated in the present study does not prove randomness on this or other scales. However, the prevalence of nonaggregated distributions lends support to the hypothesis that the oceanic environment is less complex than that of the nearshore region. In the oceanic environment, the numerous processes which bring about local variations in abundance of phytoplankton appear to proceed more slowly relative to the randomizing turbulent processes. In such an environment, only the most important local processes produce a measureable effect, and, thus, these may be relatively easily isolated for further study.

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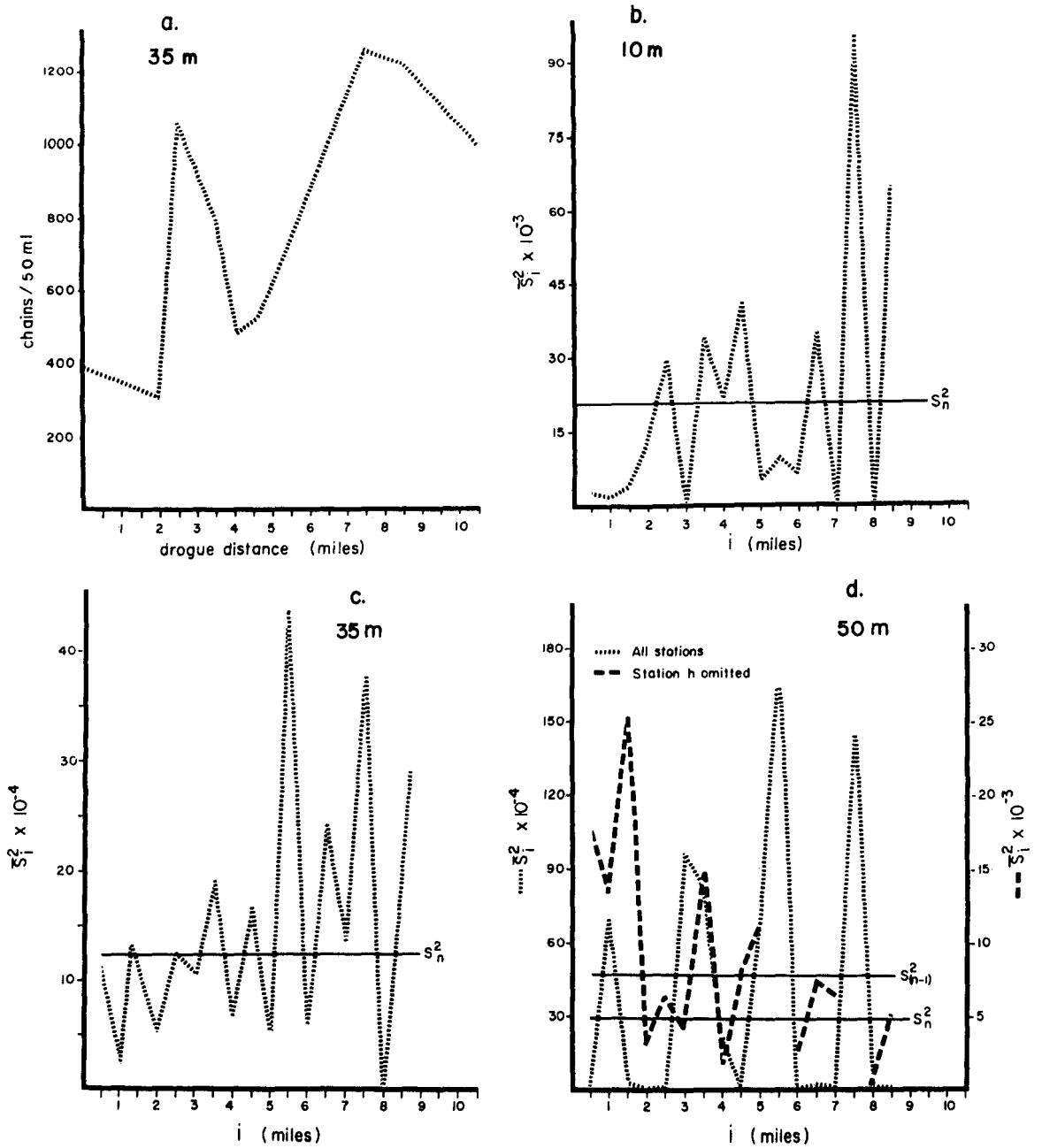

FIGURE 1.—Small-scale distribution patterns of *Nitzschia turgiduloides*. (a) Fluctuations in the abundance of chains, 35 m. (b-d) Fluctuations of the mean, two-sample variance, $\bar{s}_i^2$, with increasing sample interval, *i*, compared with total variance, s_n^2, of 10 samples: (b) 10 m; (c) 35 m; (d) 50 m; analysis run with (dotted line) and without (dashed line) substation h.

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