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Microscale and finescale variations of small plankton in coastal and pelagic environments

by R. W. Owen^{1,2}

ABSTRACT

Small-interval water sampling in oceanic subsurface layers in a variety of macro-environments for microplankton and for characteristics of their environment revealed concentration variations that often exceed errors of sampling and measurement. I report incidence and degree of microscale and finescale organism patchiness and their dependency on the local environment and on certain characteristics of the organisms themselves. Scale analysis indicates that patchiness occurs below as well as above the 20 cm intervals sampled. Incidence and degree of patchiness were about the same in separate eastern boundary regions, off California and Perú.

Effects of environmental characteristics on organism patchiness are clearly defined in this data set, which suggests influences by physical processes on local microplankton patches on the scale of a few centimeters (microscale) to a few meters (finescale). In the aggregate, finescale and microscale patchiness of microplankton populations was greater at lower wind speeds, during daylight than at night, and over continental slopes. Patchiness was greater in the more stable layers of the seasonal pycnocline, and under more oligotrophic conditions (lower concentrations of nutrients, particulates, and chlorophylls). Patchiness of organisms also was greater where nutrients and particulates were more patchy, but was unrelated to chlorophyll patchiness.

Intrinsic properties of the organisms less clearly affected microplankton patchiness. Population patchiness was greater for autotrophs and heterotrophs than for atrophs, and was slightly greater for larval fish competitors and predators than for their prey, and for more motile organisms. Reproductive capacity is indicated to dominate among intrinsic patch-forming attributes.

Smallscale patchiness of small plankton is a recurrent feature of the environment of small predators and may affect their growth and survival. Its incidence and degree appear to be specifiable over large domains from parameters of the mixing environment, e.g. wind stress and vertical stability. This would contribute to management of exploited stocks of marine organisms whose recruitment depends on food supply at early stages of their life-history.

1. Introduction

Starvation rate and growth of survivors in marine animal populations are determined by food supply. Intrinsic rate of natural increase of a population is often thus

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constrained. This supply is defined by encounter rate of predator with prey and by prey composition. Encounter rate is the product of the predator's search rate and the prey concentration. Encounter rate is enhanced where prey patchiness occurs on the scale of the predator's ambit. Prey composition, or "menu," depends on processes that determine the degree to which prey population patches are disjunct or concurrent.

Plankton concentrations are known to vary widely but, with a few exceptions, this knowledge derives from sampling volumes or intervals that greatly exceed those searched by small planktivores, and those over which other ecological processes occur. Models of production, growth, and recruitment that are based on feeding or environment may be futile if the interactions of organisms with one another and with the local environment are estimated from samples drawn at inappropriate intervals of space or time. The presence of small, subsurface patches of microplankton would alter a variety of interactions within and between populations; in particular, predation, competition and reproduction can be differentially affected in the presence of smallscale patchiness. A current hypothesis, for example, holds that small planktivores survive where their food rations appear too low by making use of adequate food patches too small to detect by conventional sampling (e.g. fish larvae: O'Connell and Raymond, 1970; Hunter, 1972; Vlymen, 1977; Lasker and Zweifel, 1978; Houde and Schekter, 1978; copepods: Mullin and Brooks, 1976). The menu, the rations and the consequent survival of predator populations may depend on incidence and degree of patchiness on scales of a few meters (finescale) or less than a meter (microscale).³ The margins of areas (or volumes) suitable for survival of predators can be considerably extended by the existence of such patchiness. Community characteristics are altered significantly where the living space fluctuates or becomes partitioned by populations so that organisms may co-exist in higher numbers and diversity (e.g. Hutchinson, 1961; Richerson *et al.*, 1970; Roughgarden, 1977). Finescale and microscale plankton patchiness can presumably be created, sustained or destroyed by mechanical processes, biological processes and interactions of the two (cf. Mackas *et al.*, 1985).

This report describes finescale and microscale patchiness of small plankton and of their environment in open waters off southern California and northern Perú on a scale similar to that explored by small fish larvae or copepods over the course of a few hours. I summarize the results of sampling to determine (1) if small predators and grazers encounter microplankton patches during short excursions in the mixed layer and seasonal thermocline of the open sea, and (2) to determine scale and degree of patchiness in the submeter transition between turbulent and molecular domination of diffusion and viscosity. Reported here are parameters of concentration variations detected among microplankton populations and environmental characteristics that were sampled over 2 m transects at 20 cm intervals at 65 sites. I also report sensitivity

3. The descriptive terms "finescale" and "microscale" approximately conform with current usage by oceanographers to describe structure and processes having these respective dimensions (e.g. Haury *et al.*, 1978).

of the variational parameters of organism concentration to environmental variables and to intrinsic characteristics of the organisms to indicate the mechanisms responsible for their patchiness.

a. Earlier observations. Work on finescale and microscale plankton patchiness has a rather brief history. Microscale plankton patchiness (using Cassie's 1958 definition) was well enough known to occur from direct observation. Published accounts of visual observations include those of Bainbridge (1952), Colebrook (1960), and Clutter (1969) on swarming crustacean populations, and of Owen (1966) on thaliaceans in surface convergences. Less formally, most of us who have paid attention in or near the water have seen plankton aggregations of small extent.

For practical reasons, plankton microstructure was first investigated in lakes. Whitney (1938) found turbid strata of submeter thickness and tens of meters in lateral extent to be common in several Wisconsin lakes. Ruttner and Sauberer (1938), from the correspondence of optical profiles with cell counts, attributed such microstrata in Austrian lakes to variations of phytoplankton and bacteria concentrations. Baker and Brook (1971) later demonstrated correspondence between lacustrine microlayers of turbidity and phytoplankton populations. The existence of small patches of less motile phytoplankton populations in the epilimnion of a California lake was attributed by Richerson *et al.* (1970) to their production rate, indicating that reproduction exceeded dispersion.

With the advent of the o-ring, indirect indications of microscale structure have been made in the open sea by *in situ* profiling of phytoplankton by pigment fluorescence (e.g. Derenbach *et al.*, 1979; Astheimer and Haardt, 1984) and of particulates by light scattering (e.g. Owen, 1972). The volume sensed by instruments deployed in these studies was less than 1 cm³, so their signal spikes may have been due to individual aggregates or colonies of plankters rather than to patches. Both methods integrate broadly over particle types.

Quantitative works on marine plankton variations based on submeter water sampling were summarized by Cassie (1963) and consist of studies by Cassie (1959, 1962) on horizontal variations of phytoplankton at the sea surface from water capture, and by Della Croce (1959) and Zaitzev (1961) on vertical variations of small zooplankton in the upper meter from net haul samples. Ragotzkie and Pomeroy (1957) found *Gymnodinium* cells confined mainly to the upper 10 cm layer during an estuarine bloom of this dinoflagellate. McAlice (1970) sampled at submeter intervals in the uppermost meter of two estuaries and presented evidence for the existence of coherent phytoplankton patches smaller than a meter. Owen (1981a,b) described variations within 2 m intervals from limited subsets of the data analyzed here. With the exception of these 1981 reports, literature on submeter plankton sampling has been confined to the sea surface (upper meter or less) and to bays, estuaries and lakes. Because plankton communities and physical processes are likely to be rather special in

the uppermost meter or in lakes and estuaries, results from these environments cannot reasonably be extended to subsurface, open-sea environments.

b. Regions and design. The Southern California Bight, where much of the sampling was conducted, affords conditions of low wind mixing and thus optimal conditions for maintenance and detection of open-sea microscale structure of plankton populations. The Channel Island groups and Tanner-Cortez Banks, extending southward from Point Conception, constitute a barrier that somewhat shelters the Bight interior from wind and surface wave mixing. A relatively shallow, stable pycnocline is created by insolation and geostrophic uplift, and is maintained by this sheltering effect. By contrast, the Chimbote Shelf off Perú is open to surface and subsurface mixing forces and is broad and shallow, sloping continuously to the shelf break about 100 km offshore. Vertical mixing and upwelling are correspondingly vigorous and physical stratification is weak.

Accordingly, I sampled for subsurface variations in concentration of small plankton and for certain environmental characteristics at 20 cm intervals in a variety of macroscale environments of the open sea. The work was designed to determine the incidence and intensity of microplankton variations in a variety of physical and biotic environments. All of the sampling reported here was conducted in regions of spawning by the sometimes extensive anchovy populations off California (58 casts) and Perú (7 casts). However, neither presence of larval fish nor estimates of larval fish prey were considered in the sampling design. All but four of the 65 casts sampled the vertical axis, over which the greatest degree of patchiness was anticipated. The four horizontal casts were paired with vertical casts to give an estimate of relative variability of patchiness along the two axes.

Sampling was conducted on the coastal shelf, near the shelf-break, and beyond the shelf-break within 200 km of the coast. Depth of the 2 m layer to be sampled was usually predicated within 20 min on results of CTD or chlorophyll profiles to sample the upper seasonal pycnocline, mixed layer, or chlorophyll maximum layer. Shifting of the target layer by internal wave passage may have occurred between CTD and water sampling, but target features usually were broad. Sampling was conducted in all seasons in daylight and at night under light or moderate winds, usually in the absence of waves that would produce surge during sampling (swell <2 m amplitude, <10 s period).

2. Methods

a. Sampling. Samples to assess microscale variations were obtained with a micro-patch sampler (MPS) (Owen, 1981) adapted for midwater use from a free vehicle bottom-water sampler design by Sholkovitz (1970). The MPS, shown in Figure 1, consists of a linear array of 4 cm i.d. sampler tubes spaced along a vaned frame fitted

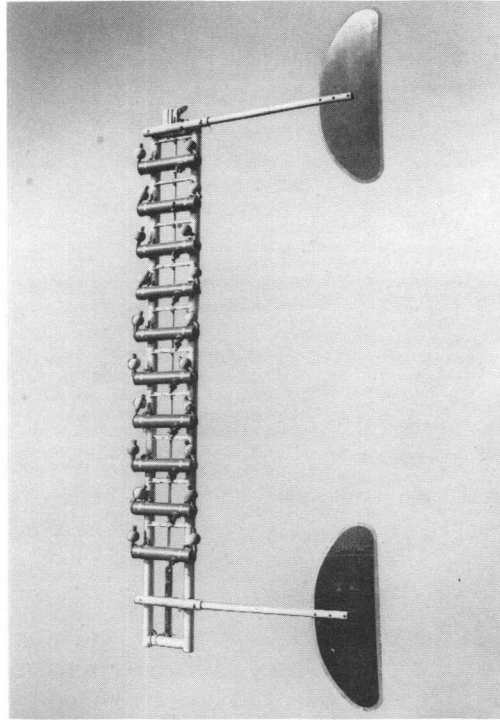


Figure 1. Micropatch sampler (MPS) with sample tubes open. Spring-loaded rod (center of frame) releases ball valve lanyards to close tubes when messenger weight strikes trigger on cable clamp atop MPS frame.

with cable clamps and a lanyard release mechanism. Water samples were retained by ball valves seated at either end of each tube and held by elastic cord connecting the valves through the tube center. Prior to deployment of the MPS, the ball valves were held clear of the tube mouths by lanyards hooked onto pins on the release mechanism.

To sample vertical variations, the MPS was clamped to the ship's hydro-wire ≈ 10 m above a 45 kg terminal weight, lowered with open sample tubes to the target depth and towed at ≈ 20 cm/s so that its vanes oriented the tube mouths into the induced current for complete flushing.⁴ To sample horizontal variations, the MPS was clamped sideways on the hydro-wire (tubes vertical), lowered below the target depth and retrieved slowly upward through the target depth. A messenger weight sent down the hydro-wire triggered the simultaneous release of lanyards that restrained the ball valves, whereupon the valves seated in the tube mouths and captured 0.6 l of seawater.

4. Direct observations of the instrument showed that the sampler remains within 5° of vertical when towed at 20–40 cm/s, and that discrete dye layers are sampled distinctly and are disturbed only in the wake of the instrument.

Upon retrieval of the MPS, water samples obtained from each tube were transferred to covered beakers, mixed thoroughly with a small plunger and then aliquoted for various combinations of analyses. Particular combinations depended on availability of people and equipment, and included plankton enumerations, phytoplankton pigments (chlorophyll-*a* and phaeo-pigments), Coulter particle counts, nutrient salts, and salinity.

To contrast variations along the sampler frame with variations at the same position on the frame, parallel samples were obtained from 40 of the 65 MPS casts by additional tubes strapped alongside the originals at 2–5 positions in the array. Parallel tube centers were 5 cm apart.

The first 37 casts were made with a 10-depth array of sampling tubes spaced at 20 cm intervals⁵ between tube centers. The remaining 28 casts were made with an array of sampling tubes spaced at five 20 cm intervals and two 40 cm intervals. (The interval sequence was 20, 40, 20, 20, 20, 20, 40 cm.) This arrangement permitted interspersing of fine-mesh plankton nets among the sampling tubes in the array; the results of their use are to be treated separately.

*b. Sample analysis.*⁶ Plankton preserved in 3% formalin prepared according to Beers and Stewart (1970) was concentrated by sedimentation overnight from known initial sample volumes and enumerated using the inverted microscope method of Utermöhl (1931). Counting was done by either of two methods; the entire slide surface was enumerated, or 20–35 randomly chosen fields were enumerated. Populous organisms usually were enumerated along single transects of the slide. Identical procedures were used when duplicating counts of the same sample to establish error of determination. Original sample volumes were usually 100 ml for enumerating phytoplankton and 400–600 ml for enumerating microzooplankton and rarer phytoplankton species. Organisms selected for counting exceeded 20 μm in longest dimension unless easily seen and identified at 100 \times using phase contrast on the Zeiss inverted microscope. Identification to species was not always possible, in which case organisms were classified to genus or higher taxon within defined size classes. This report treats only those species that usually occur as individuals except when dividing: colonial forms are ignored. Original microplankton enumerations and corresponding concentration factors are given by Owen and Kimbrell (1987).

Phytoplankton pigments were determined following the method and equations of Holm-Hansen *et al.* (1965). Water samples allocated for pigment analysis were filtered through Whatman GF/C glass fiber filters previously de-sized with distilled water. The filters were placed in vials with 10 ml of 90% aqueous acetone, sealed and extracted in cold and dark for 22–28 h. Fluorescence of phytoplankton pigments was

5. It seems more correct as well as convenient to consider MPS data as interval estimates rather than point estimates in view of the dimensions of the spaces sampled.

6. Reference to trade names in this section does not imply endorsement by the National Marine Fisheries Service, NOAA.

measured before and after acidification of the extracts with dilute HCl. The fluorometer was a Turner 111 with Sylvania F4T5 lamp behind Corning 5-60 excitation filter and red-sensitive Hamamatsu photomultiplier behind Corning 2-64 emission filter.

Particle concentrations were determined within an hour after sampling using a Coulter Ta counter with a 280 μm sensing pore to describe their variations in three size categories; 16–160 μm , 32–50 μm , and 51–160 μm equivalent spherical diameter. Total counts usually exceeded 50000 per sample. By overriding the Counter manometer (in the absence of ship's surge) I could analyze sample volumes of 20-100 cc to achieve higher total count levels.

Nutrient salt concentrations were determined by Technicon autoanalyzer or Beckman DU spectrophotometer using procedures of the Physical and Chemical Oceanographic Data Facility (PACODF) of the Scripps Institution of Oceanography (Atlas *et al.*, 1971). Samples either were analyzed within a few hours of collection, or were filtered and frozen for analysis ashore.

Salinity determinations were made ashore after each cruise with the Plessey or Autosal salinometers. Wormley water was used for primary standardization. Duplicate or triplicate determinations were averaged.

Conductivity/temperature/depth (CTD) casts were made at most stations using a Plessey 9040 CTD. To provide good resolution of structure in layers of interest, the CTD usually was fitted with a 300 d-bar pressure sensor and was lowered at 20 m/min. Where CTD casts were not made, Sippican XBT casts (with T-4 probes) were.

All sample analyses and measurements except temperature are expressed in concentration units.

c. Parameters of variation. A problem arises in treating the serial data obtained by the MPS because simple parameters of variation do not distinguish between samples drawn from a monotonic gradient and samples drawn from truly clumped distributions. To de-couple gradient effects from patchiness effects, I chose to characterize concentration variations in the following way. I derived the mean concentration gradient and the individual deviations about the gradient by linear regression of sample concentration (dependent variable) on sample depth (independent variable) for each organism population and each environmental characteristic in each MPS cast. The variance removed by the regression is termed finescale variation (*FSV*). *FSV* denotes the regression mean square over the 2 m interval and thus expresses variance accountable to the mean concentration gradient:

$$FSV = \Sigma(\hat{c}_i - \bar{c})^2$$

where \hat{c}_i is the predicted *i*-th sample concentration and \bar{c} is the cast mean concentration. *FSV* connotes meter-scale patchiness.

The residual variance, associated with the deviations of individual concentrations from the mean gradient, is termed microscale variation (*MSV*). *MSV* denotes the

mean square of deviations of the observed concentrations about the mean concentration gradient and thus expresses the detrended variance:

$$MSV = \Sigma(c_i - \hat{c}_i)^2 / (n - 2)$$

where c_i is the observed sample concentration and n is the number of intervals sampled. MSV connotes decimeter-scale patchiness.

Coefficient of variation (cv) was used to scale the variations between segments of the data set to allow comparisons among variational statistics of concentrations that occur at widely differing levels. The respective cv 's are thus the root mean square (rms) values of finescale and microscale variations divided by the cast mean:

$$cv-FSV = \sqrt{FSV} / \bar{c}$$

and

$$cv-MSV = \sqrt{MSV} / \bar{c}.$$

Coefficient of variation also stabilizes the variance, otherwise proportional to the mean value in patchy distributions, and is more intuitive and communicable than the variance value.

Coefficients of concentration variation were derived between depth intervals within casts using averaged parallel and duplicate values where these occurred, within the same sample (duplicate determinations) and between samples at the same depth interval from tubes in parallel. Parameters of organism concentration variations were derived from whole-slide and partial-slide counts. This presentation subsequently pools values derived from whole-slide and partial-slide concentrations because AOV showed no difference between them.

Variations due to error of sampling and determination were internally derived: coefficients were constructed for each environmental and population concentration by analysis of variance (AOV) on all parallel sample analyses (error of sampling) and on all duplicate analyses from the same sample bottle (error of determination + subsampling).

The coefficients of variation for parallel samples and duplicate determinations in Table 1 are used to contrast with cv values observed between depths in casts. Mean-square variation between organism concentrations from parallel samples exceeded that between duplicates by average factors of up to 15, depending on the count type and number of organisms counted. This disparity is also evident among the environmental determinations to roughly the same degree. Although the parallel samples were intended to provide an error term for contrast with the between-depth variations, some of the differences between parallel samples reflect real spatial variation due to the 5 cm separation between parallel sample bottles on the MPS frame. The use of mean-square variation between parallel sample determinations as an error term is correspondingly conservative and leads to underestimation of incidence

Table 1. Means (\bar{c}), coefficients of variation ($cv = s/\bar{c}$) and mean-square ratios (F) among pairs of parallel sample (parallels) values and duplicate determinations (duplicates) of individual microplankton populations and environmental characteristics. N is number of pairs.

Characteristic	N (pairs)	\bar{c} (no/1)	cv	F
Microplankton				
parallels	371	528	0.665	
duplicates	97	757	0.222	4.4
Chlorophyll- <i>a</i>				
parallels	89	2.005	0.131	
duplicates	9	1.657	0.080	3.9
Phaeopigment- <i>a</i>				
parallels	89	0.698	0.372	
duplicates	9	0.217	0.400	8.9
Coulter counts (16–160 μm)				
parallels	58	191	0.245	
duplicates	7	532	0.057	2.4
Coulter counts (32–50 μm)				
parallels	58	21.6	0.448	
duplicates	7	95.5	0.120	0.7
Coulter counts (51–161 μm)				
parallels	58	13.1	0.510	
duplicates	7	20.8	0.122	6.9
Nitrate + nitrite				
parallels	26	6.35	0.124	—
Nitrate				
parallels	10	2.50	0.212	—
Nitrite				
parallels	10	0.19	0.107	—
Ammonium				
parallels	17	1.04	0.231	—
Silicate				
parallels	27	702	0.176	—
Phosphate				
parallels	17	157	0.283	—
Salinity				
parallels	15	33.47	0.00053	—

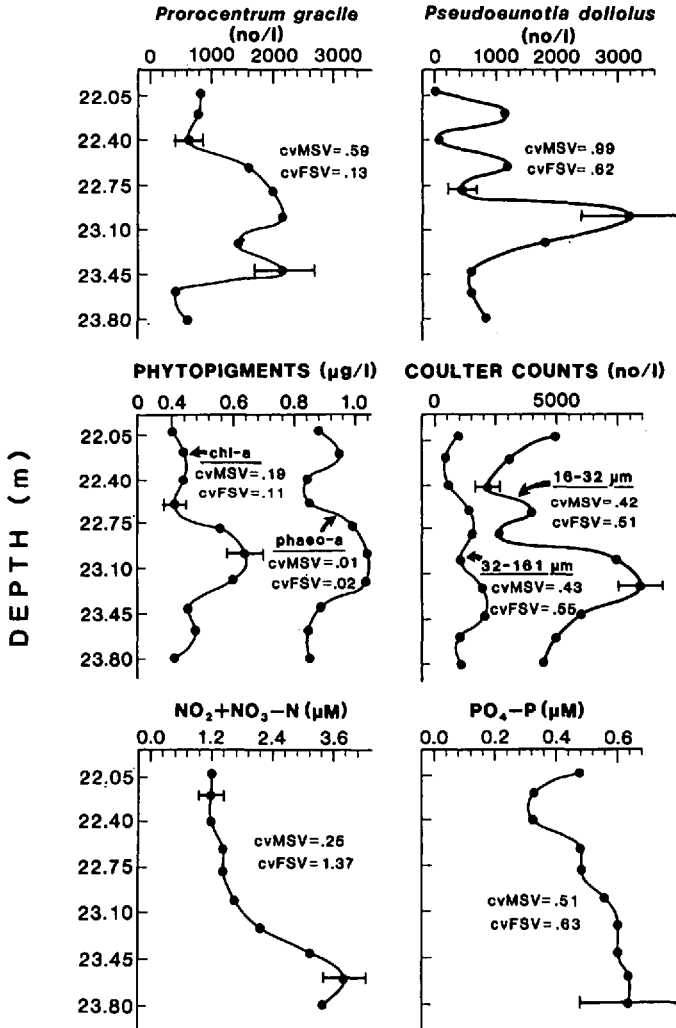


Figure 2. Profiles of organisms and environmental characteristics from a single MPS cast. Bars represent two standard deviations about the observed value.

and degree of finescale and microscale structure. The appropriate value of the error term lies somewhere between the value for duplicate and parallel sample values.

3. Results

Examples from an experience of small-scale sampling with the MPS are shown in Figure 2. This cast was made in the seasonal pycnocline at 22 m depth in 180 m of water 4 km off the California coast under calm winds and large ground swell. Similarities among profiles may be fortuitous: high correlations among populations are

Table 2. Incidence with which microscale variations (*cv-MSV*) and finescale variations (*cv-FSV*) of microplankton and environment exceeded parallel variations (*cv-prll*) and duplicate variations (*cv-dupl*) of Table 1. Values for organisms are from 29 casts. *N* is number of sets.

Characteristic	Parameters of variation				<i>N</i>
	<i>cv-MSV</i>		<i>cv-FSV</i>		
	> <i>cv-prll</i>	> <i>cv-dupl</i>	> <i>cv-prll</i>	> <i>cv-dupl</i>	
Organisms	61%	92%	53%	80%	471
Chlorophyll <i>a</i>	55%	71%	61%	76%	49
Phaeopigment <i>a</i>	20%	20%	45%	39%	49
Coulter 16–160 μm	42%	100%	70%	91%	33
Coulter 32–50 μm	32%	97%	44%	94%	34
Coulter 51–160 μm	32%	100%	47%	85%	34
Nitrate + nitrite	37%	—	53%	—	19
Nitrate	14%	—	71%	—	14
Nitrite	42%	—	66%	—	12
Ammonium	71%	—	85%	—	7
Silicate	25%	—	40%	—	20
Phosphate	5%	—	22%	—	18
Salinity	17%	—	42%	—	24

not commonplace in this data set. Finescale and microscale coefficients of variation are given to provide a sense of correspondence with actual concentration profiles.

Despite the more energetic mixing conditions observed off Perú, there is no evidence that small-scale variations were different from those off California. Cast means and standard deviations of Perú cast variation coefficients (*cv-MSV*, *cv-FSV*) are indistinguishable from those drawn from similar site and cast environments off California. Results of Perú and California MPS casts are therefore pooled with the caveat that the seven Perú casts, all made in austral spring on the Chimbote shelf and slope, probably under-represent the range of conditions to be found there.

a. Incidence and intensity of patchiness. The incidence with which coefficients of variation for smallscale patchiness exceeded the corresponding *cv*'s from parallel samples and from duplicate determinations is shown in Table 2, which indicates the rather commonplace occurrence of finescale and microscale structure of plankton populations and of their environment. By this criterion, concentration variations of one or more organism populations occurred in virtually all casts. Conversely, there were no casts in which every population or environmental characteristic showed high variation.

The incidence and degree of variations of organism concentrations and of environmental characteristics encountered in all 65 casts is given in Figures 3–10. Ratios of

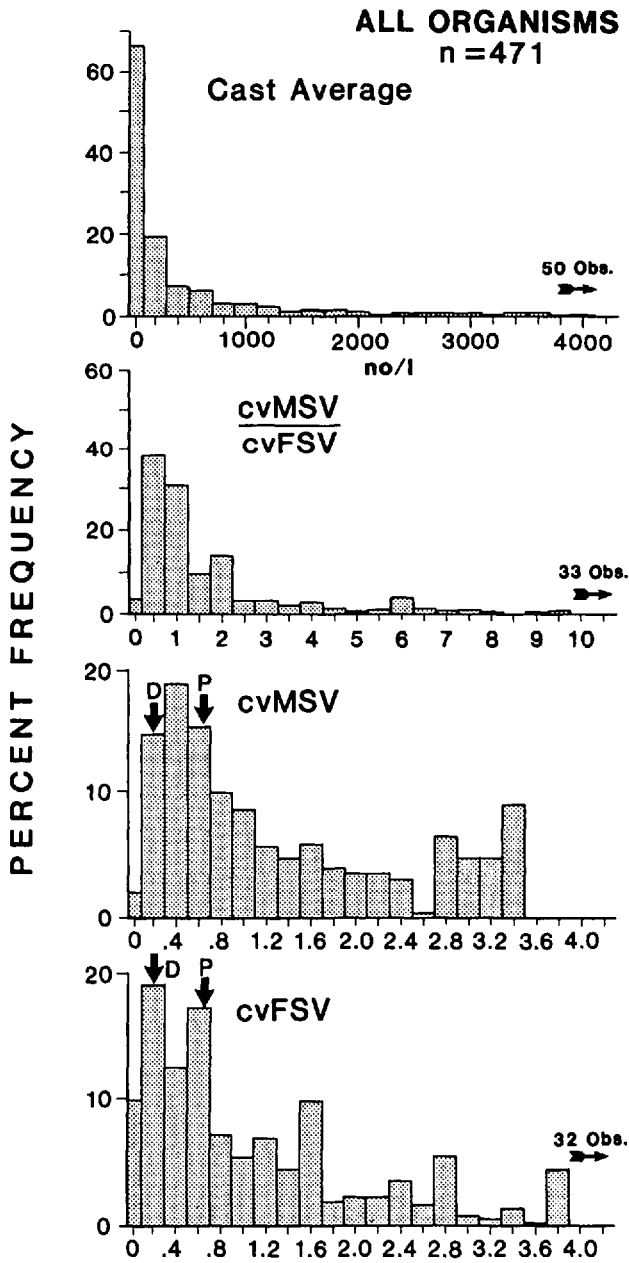


Figure 3. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for 471 organism populations in 29 MPS casts. Values for *cv*'s of determination (D) and parallel sampling (P) are indicated by arrows. Insets identify abscissas.

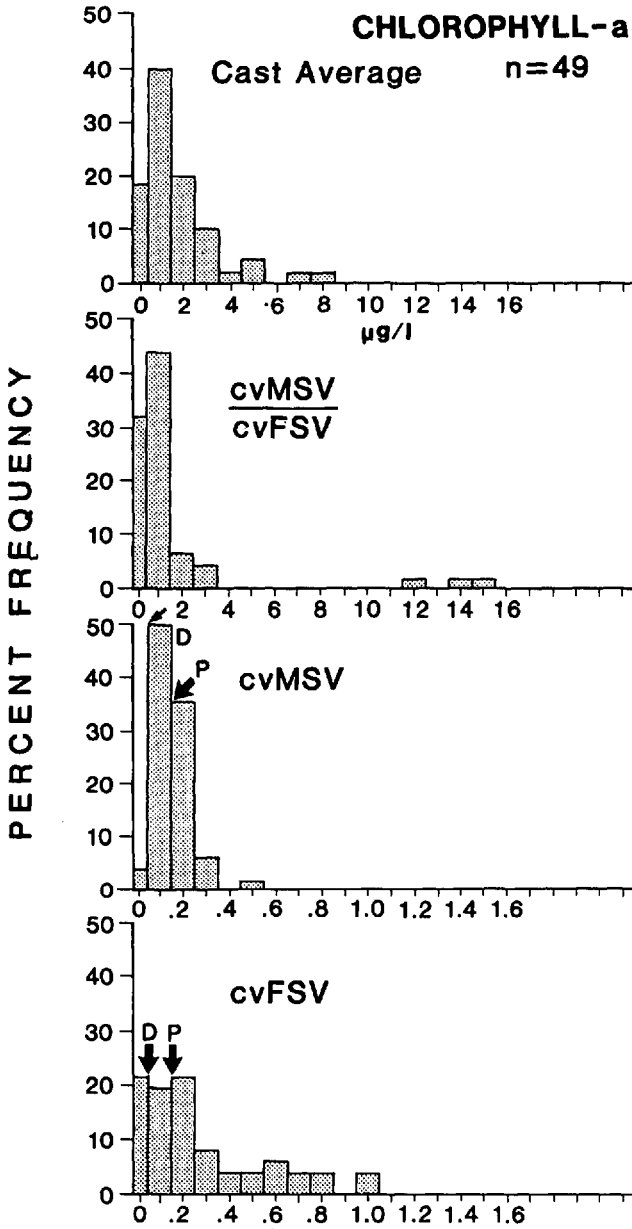


Figure 4. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for chlorophyll-*a* concentrations. Values for *cv*'s of determination (D) and parallel sampling (P) are indicated by arrows. Insets identify abscissas.

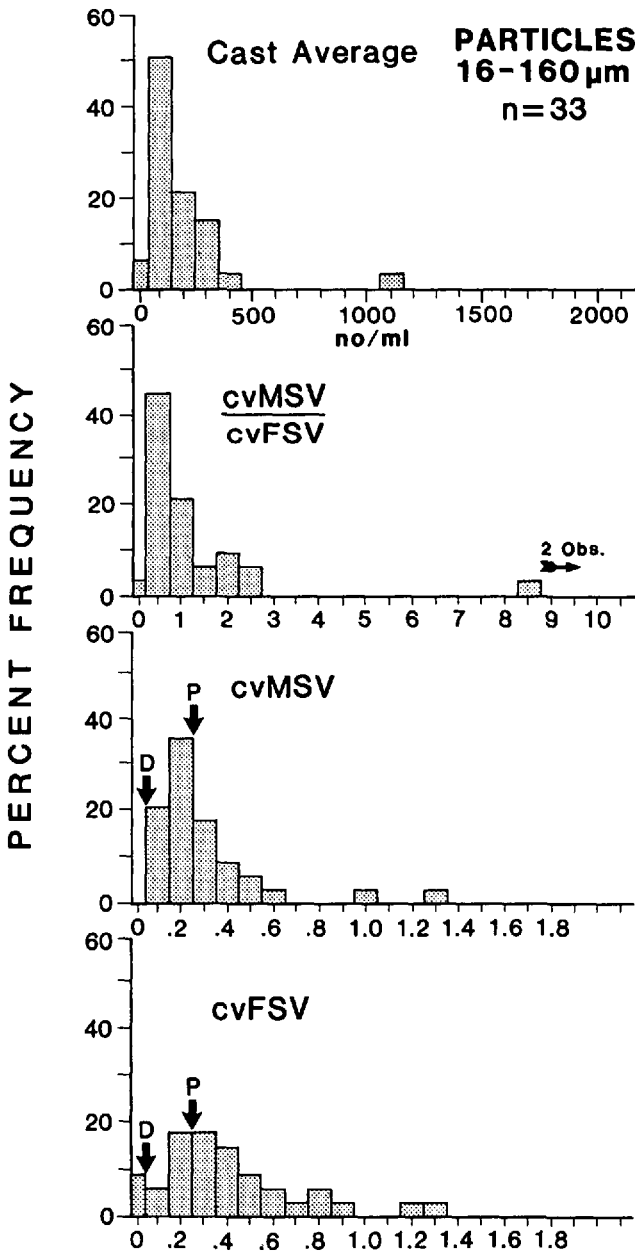


Figure 5. Frequency histograms of cast means, *cv*-ratios, *cv*-MSV and *cv*-FSV for Coulter counts of particles 16-160 μm diameter. Values for *cv*'s of determination (D) and parallel sampling (P) are indicated by arrows. Insets identify abscissas.

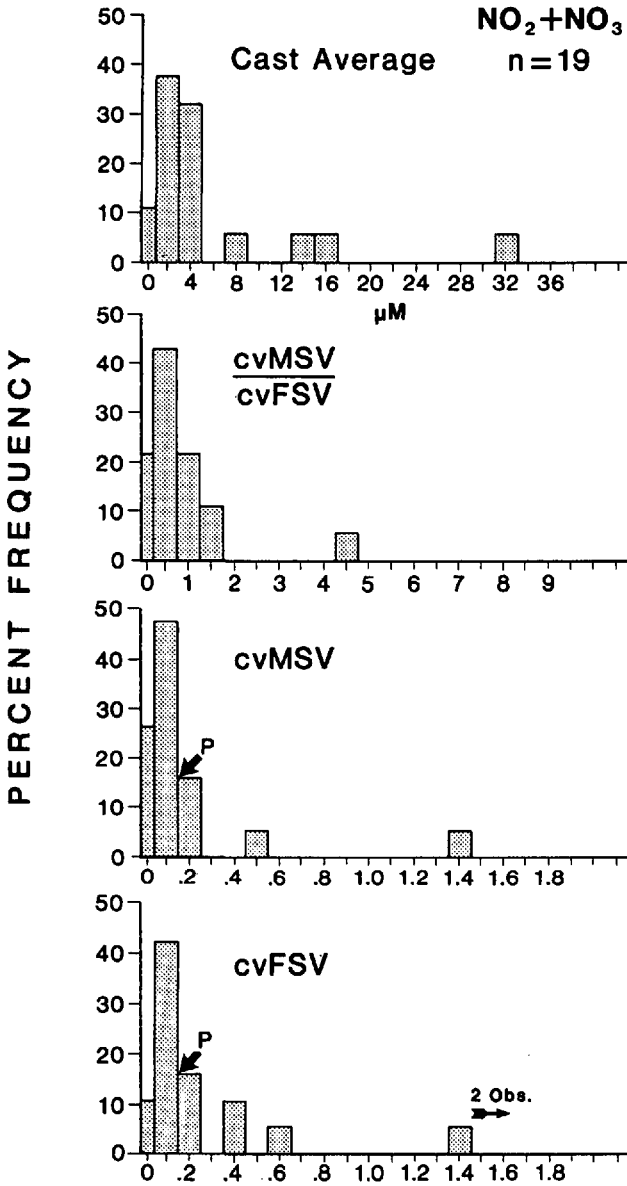


Figure 6. Frequency histograms of cast means, *cv*-ratios, *cv*-MSV and *cv*-FSV for nitrate + nitrite concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

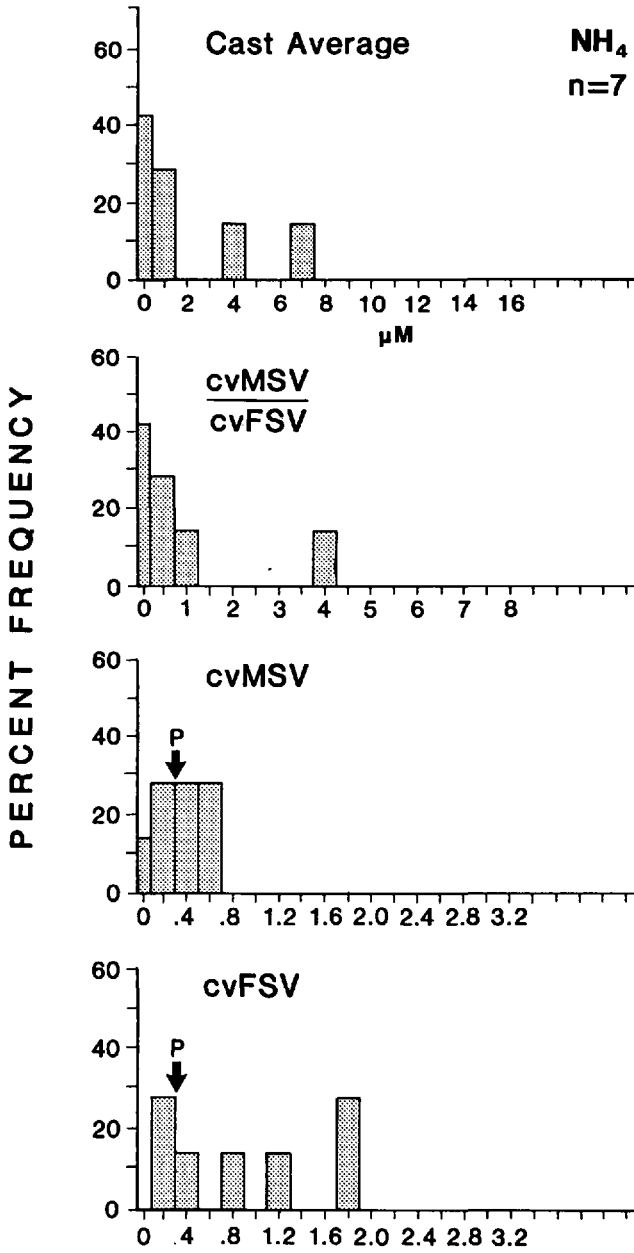


Figure 7. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for ammonium concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

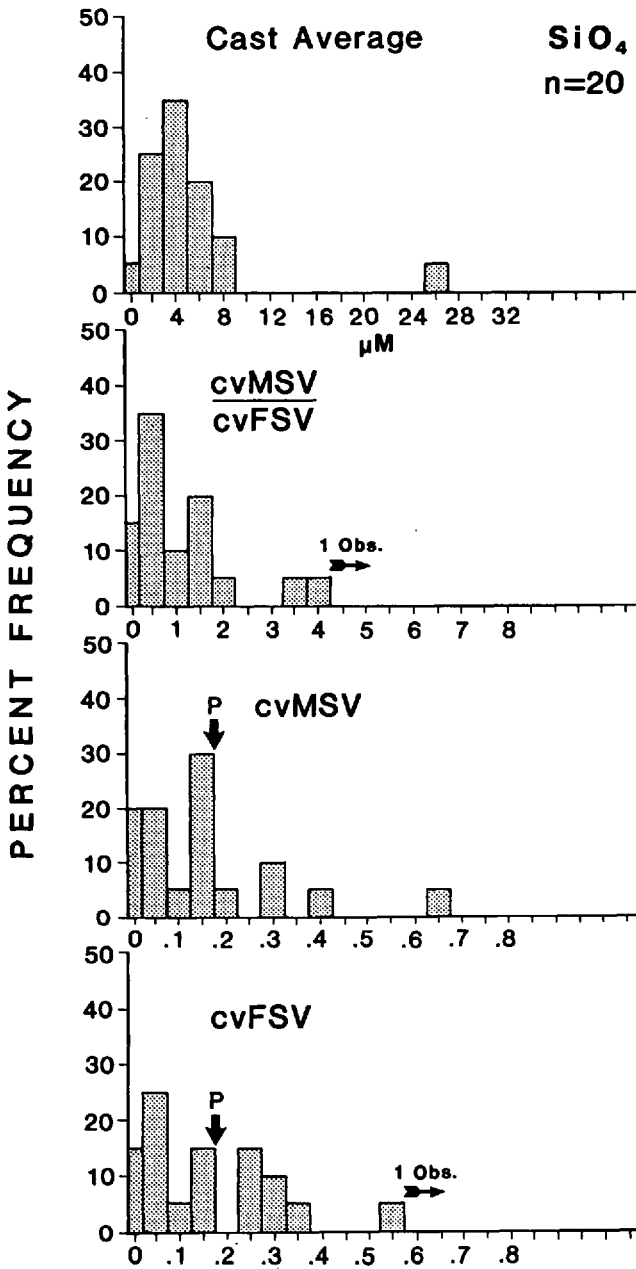


Figure 8. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for silicate concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

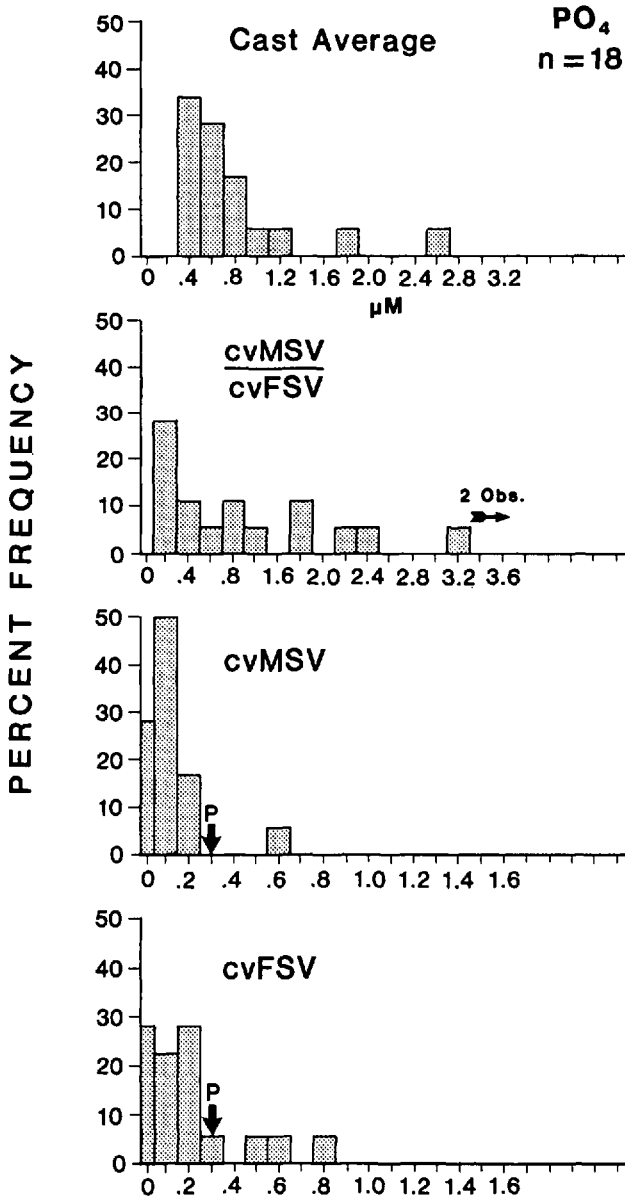


Figure 9. Frequency histograms of cast means, *cv*-ratios, *cv*-MSV and *cv*-FSV for phosphate concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

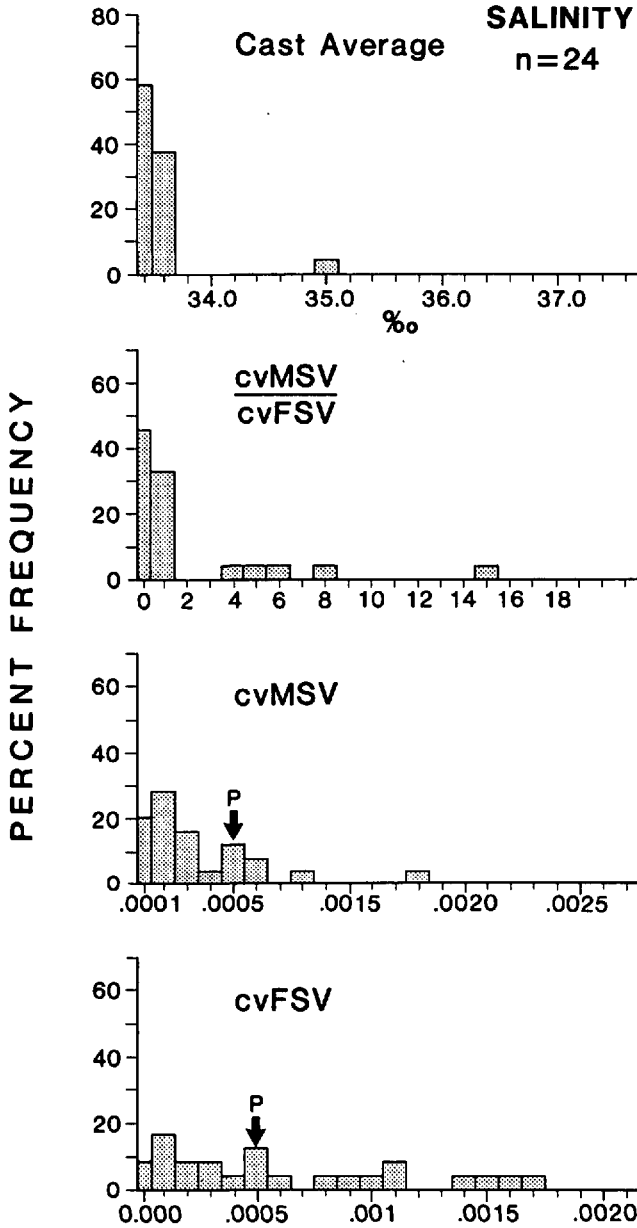


Figure 10. Frequency histograms of cast means, *cv*-ratios, *cv*-*MSV* and *cv*-*FSV* for salinities. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

the variation coefficients, $cv\text{-}MSV:cv\text{-}FSV$, are shown to give a sense of the relative contribution of each to the total variation.

Figure 3 gives distributions of these parameters for every set of organism populations. The distribution of cv -ratios shows that microscale variation frequently exceeded the corresponding finescale variation of the same population. Distributions of microscale and finescale coefficients show that values frequently exceed twice the "error" levels.

Distributions of chlorophyll-*a* and Coulter count parameters (Figs. 4 and 5) show less variation on both microscale and finescale than those of organism populations, and more contribution to total variation from finescale gradients than from microscale patches. As discussed below, parameters for chlorophyll and particle variations reflect the effect of integration over individual population variations.

Distributions of variation parameters of nutrient species (Figs. 6–9) are comparable to those of chlorophyll and Coulter counts. Among the nutrients, ammonium showed somewhat higher incidence and degree of patchiness, silicate and phosphate showed the lowest. Nitrite patchiness was greater than that of nitrate. Finescale gradients of nutrients usually contributed more to total spatial variation than did microscale patches.

Salinity variations (Fig. 10) usually were dominated by finescale gradients. Large ratios of microscale to finescale coefficients occurred only where finescale gradients were very small. Coefficients of salinity variation are small because mean salinity is large compared with its variance.

b. Aliasing by organic aggregates. A special case of organism patchiness arises from association of organisms with macroscopic aggregates of detritus ("marine snow"), shown by Wiebe and Pomeroy (1972), Silver *et al.* (1978), and Beers *et al.* (1986), to occur for a variety of microplankton and types of snow. Such "nanoscale" discontinuities are embedded in the viscous regime dominated by Fickian (molecular) processes. This source of variation is not evaluated by sampling with the MPS because the aggregates are either small or few per liter, and are dispersed during sampling and sample processing. Associations of organisms with snow would, however, alias variational parameters if large, populated aggregates were caught by some bottles but not others. This effect could explain part of the higher variations seen between parallel samples than between duplicate determinations of organism concentration determinations.

In this data set, association of an organism population with snow would be indicated by a relationship of its concentration to detrital concentration. All five casts for which detrital particles were enumerated by microscope displayed high levels of microscale detrital variation between sample depths. Of 46 kinds of organisms enumerated among these casts, six display correlation coefficients higher than 0.5 with detritus concentration. Of the six, two appear categorically fortuitous—crustacean eggs and small

post-naupliar copepods. The others are three diatoms, *Eucampia zoodiacus*, *Nitzschia seriata* group, *Thalassiosira* sp. *B*, and one dinoflagellate species, *Ceratium breve*, any of which have been associated with snow (op. cit.). As previously noted (Owen, 1981a), high correlations between ciliates and detritus among parallel samples in two MPS casts indicate other examples of this association.

Divers deployed to the depths of 10 daytime MPS casts off Southern California in September, 1979 estimated snow concentration at several hundred per liter, sufficiently high to denote minimal effects of uneven sampling by individual water bottles. Snow size never exceeded 3 mm equivalent spherical diameter. Variational characteristics of organisms and environmental characteristics at the dive sites were typical of those elsewhere.

c. Finescale and microscale variation by particle type. I determined patterns of finescale and microscale variation among functionally similar kinds of organisms (Table 3). To construct similar groups of organisms, I assigned each taxon to a class of trophic mode, degree of motility, and ecological relation to larval anchovy. Trophic mode classes consist of obligate heterotrophs (e.g. crustacean larvae, ciliates, *Noctiluca* and peridinnid dinoflagellates), autotrophs (diatoms and other dinoflagellates), atrophs (eggs, pollens and unidentified spheres), and detritus (strings, flakes and amorphous blobs). Motility classes consist of passives (detritus, eggs, centric diatoms), weak motiles (pennate diatoms and other forms capable of directed movements of m/dy), motiles (dinoflagellates, ciliates, crustacean nauplii, m/hr), and fast motiles (oikopleurans, small chaetognaths, small crustaceans, m/min). Larval fish interaction classes consist of prey, competitors with prey, predators, and noninteractives. "Prey" types meet the following criteria, from Rojas de Mendiola (1974) and Arthur (1976): ingestible dimensions ($20 \mu\text{m} < \text{width} < 150 \mu\text{m}$), absence of long spines or setae, and some degree of motility (except that eggs of ingestible size are included). "Competitors with prey" are autotrophs and auto-heterotrophs other than prey, "predators" are organisms that kill fish larvae, and "inactives" are inedible atrophs and detrital substances. It must be emphasized that the "predator" category excludes larger or faster organisms that are under-represented by the collection methods by virtue of rarity or escapement ability. On the other hand, all "prey" types are capturable by the collection methods.

Aggregates of finescale and microscale coefficients for each population and cast were formed according to these rules, rather than computing coefficients for summed taxon concentrations. Even so, pooling heterogeneous populations by single attributes may have caused underestimation of patchiness differences among classes of organism attributes.

Trophism (Table 3a). Atrophs, chiefly calanoid copepod eggs, and detritus showed the least patchiness on both finescale and microscale. Autotrophs and heterotrophs showed about the same degree of finescale and microscale patchiness, well above that

Table 3. Microscale patchiness (*cv-MSV*) and finescale patchiness (*cv-FSV*) of plankton populations classified by motility, trophism and interaction with small fish larvae. *DF* is degrees of freedom, *SS* is sums of squared deviations, *MS* is mean squared deviation SS/DF , *F* is treatment-*MS*/error-*MS*, *N* is number of population sets in the 29 MPS casts, *MEAN cv* is mean coefficient of variation in the designated class, *STDEV* is the standard deviation of *MEAN cv*.

(a) Trophism

analysis of variance on <i>cv-MSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
trophism	3	25.48	8.49	7.85 $p < .001$
error	547	591.75	1.08	
total	550	617.23		
Level	<i>N</i>	<i>MEAN cv</i>	<i>STDEV</i>	
autotroph	297	1.502	1.049	
heterotroph	195	1.396	1.080	
repro. product	37	0.918	0.921	
detritus	22	0.607	0.658	
analysis of variance on <i>cv-FSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
trophism	3	16.54	5.51	3.26 $p < .05$
error	547	925.35	1.69	
total	550	941.89		
Level	<i>N</i>	<i>MEAN cv</i>	<i>STDEV</i>	
autotroph	297	1.454	1.329	
heterotroph	195	1.332	1.339	
repro. product	37	1.033	1.136	
detritus	22	0.692	0.611	

(b) Motility

analysis of variance on <i>cv-MSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
motility	3	5.17	1.72	1.54 $.5 > p > .2$
error	547	612.06	1.12	
total	550	617.23		
Level	<i>N</i>	<i>MEAN cv</i>	<i>STDEV</i>	
passive	140	1.240	1.032	
m/day	70	1.344	0.922	
m/hr	296	1.452	1.098	
m/min	45	1.516	1.064	

Table 3. (Continued)

analysis of variance on <i>cv-FSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
motility	3	7.64	2.55	1.49
error	547	934.25	1.71	$.5 > p > .2$
total	550	941.89		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
passive	140	1.174	1.200	
m/day	70	1.311	1.016	
m/hr	296	1.415	1.392	
m/min	45	1.557	1.440	

(c) Interaction with fish larvae

analysis of variance on <i>cv-MSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
larv. interaction	3	15.18	5.06	4.60
error	547	602.04	1.10	$p < .01$
total	550	617.23		

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
inactive	84	1.154	0.996
prey	220	1.280	1.063
competor	229	1.564	1.060
predator	18	1.611	0.972

analysis of variance on <i>cv-FSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
larv. interaction	3	16.50	5.50	3.25
error	547	925.38	1.69	$p < .05$
total	550	941.89		

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
inactive	84	1.034	1.104
prey	220	1.306	1.340
competor	229	1.477	1.303
predator	18	1.821	1.608

of nonfeeding particulates. AOV indicated significant effects on finescale and microscale patchiness associated with trophism classification.

Motility (Table 3b). Mean values of finescale and microscale organism patchiness increased monotonically with degree of motility. Amotile and weakly motile forms such as eggs and diatoms displayed a lower degree of microscale and finescale

patchiness than did faster motiles such as dinoflagellates and small crustaceans. AOV, however, indicated no significant differences between motility classes, even after combining the two faster and two slower classes.

Interaction with fish larvae (Table 3c). Populations of larval fish prey were less patchy on average than their competitors and more patchy than noninteractive forms. Predators on larvae were the most patchy. (As noted above, the "predator" category does not include larger or faster organisms that are under-represented by the collection methods by virtue of their rarity or escapement ability.) Differences in degree of patchiness were more pronounced at the microscale level than at the finescale level. Classification of microplankton by their relation to larvae pools organisms with disparate attributes, which probably minimizes statistical distinctions between categories.

d. Finescale and microscale variation by environment. To test the hypothesis that organism patchiness is related to the environment, each MPS cast was classified according to the site environment (bottom depth, mixed layer depth, wind speed and lighting at the place and time of the cast); according to the cast environment (temperature gradient, chlorophyll concentration, nutrient concentration, and Coulter particulate concentration over the 2 m interval subtended by the MPS cast); and according to the sample environment (degree of microscale variation of chlorophyll, nutrients and particulates from the MPS cast samples). Casts were grouped according to this classification and the corresponding coefficients of variation of organism populations were compared by AOV to determine environmental effects on finescale and microscale plankton patchiness (Table 4).

Chlorophyll and particulate concentrations are used here to express characteristics of the organisms' environment. Although presumably somewhat affected by the density of some types of the organisms enumerated, chlorophyll and Coulter particle measurements characterize the environment rather than organism density because they were dominated by particles smaller than those enumerated, and because detritus constituted a large fraction of particulates sensed by the Coulter counter. For these reasons, chlorophyll and particulate concentrations usually were not well correlated with concentration estimates of organisms within casts.

Because the classification treatment does not account for interaction of organism behaviors with the environment, patchiness differences in contrasting environments may be underestimated.

Effects of site environment (Table 4a). I expected finescale and microscale plankton patchiness to show the influence of processes that affect the upper 30 m of the water column. AOV was performed on finescale and microscale patch parameters at levels of light, wind, layer and bottom depth.

Microscale patchiness of organisms was significantly greater in daylight than in darkness. Possible mechanisms are diurnal variation of patchiness due to dark/light

Table 4. Microscale patchiness (*cv-MSV*) and finescale patchiness (*cv-FSV*) of organism populations by site, cast, and sample environment. *DF* is degrees of freedom, *SS* is sums of squared deviations, *MS* is mean squared deviation SS/DF , *F* is treatment-*MS*/error-*MS*, *N* is number of population sets in the 29 MPS casts, MEAN *cv* is mean coefficient of variation in the designated class, *STDEV* is standard deviation of MEAN *cv*.

(a) General (site) environment

Ambient lighting

analysis of variance on <i>cv-MSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
light	2	18.14	9.07	8.22 $p < .001$
error	578	638.09	1.10	
total	580	656.23		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
night	142	1.044	0.892	
crepuscular	81	1.285	1.069	
day	358	1.463	1.103	
analysis of variance on <i>cv-FSV</i>				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
light	2	10.13	5.06	3.02 $.1 > p > .05$
error	578	967.95	1.67	
total	580	978.08		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
night	142	1.078	1.169	
crepuscular	81	1.430	1.454	
day	358	1.371	1.303	

Wind speed at 10 m above sea level

analysis of variance on <i>cv-MSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
wind	1	13.02	13.02	11.72 $p < .002$
error	579	643.21	1.11	
total	580	656.23		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<10 m/s	508	1.393	1.082	
>10 m/s	73	0.941	0.834	

Table 4. (Continued)

analysis of variance on <i>cv-FSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
wind	1	5.01	5.01	2.98
error	579	973.08	1.68	$.2 > p > .1$
total	580	978.08		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<10 m/s	508	1.343	1.318	
>10 m/s	73	1.063	1.133	
<i>Mixed layer vs. pycnocline casts</i>				
analysis of variance on <i>cv-MSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
layer	1	13.02	13.02	11.72
error	579	643.21	1.11	$p < .002$
total	580	656.23		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
mixed layer	73	0.941	0.834	
pycnocline	508	1.393	1.082	
analysis of variance on <i>cv-FSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
layer	1	5.01	5.01	2.98
error	579	973.08	1.68	$.2 > p > .1$
total	580	978.08		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
mixed layer	73	1.063	1.133	
pycnocline	508	1.343	1.318	
<i>Bottom depth</i>				
analysis of variance on <i>cv-MSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
bottom	2	32.98	16.49	15.29
error	578	623.26	1.08	$p < .001$
total	580	656.23		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<100 m	189	1.015	0.945	
100–500 m	361	1.521	1.103	
>500 m	31	1.138	0.766	

Table 4. (Continued)

analysis of variance on *cv-FSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
bottom	2	17.98	8.99	5.41 $p < .01$
error	578	960.10	1.66	
total	580	978.08		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<100 m	189	1.147	1.267	
100-500 m	361	1.434	1.328	
>500 m	31	0.821	0.884	

(b) Local (cast) environment*Local vertical temperature gradient*analysis of variance on *cv-MSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
temperature grad.	2	31.85	15.93	14.74 $p < .001$
error	578	624.38	1.08	
total	580	656.23		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<0.1 °C/m	307	1.167	0.990	
.1-.18 °C/m	159	1.340	1.064	
>.18 °C/m	115	1.783	1.131	

analysis of variance on *cv-FSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
temperature grad.	2	11.32	5.66	3.38 $.1 > p > .05$
error	578	966.76	1.67	
total	580	978.08		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<.1 °C/m	307	1.180	1.228	
.1-.18 °C/m	159	1.406	1.394	
>.18 °C/m	115	1.512	1.319	

*Nitrate + nitrite concentration*analysis of variance on *cv-MSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
ave [N]	2	22.15	11.07	9.35 $p < .001$
error	310	367.08	1.18	
total	312	389.23		

Table 4. (Continued)

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
<2 μM	162	1.567	1.106
2–5 μM	112	1.732	1.145
>5 μM	39	0.862	0.802

analysis of variance on *cv-FSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
ave [N]	2	9.66	4.83	2.75
error	310	543.79	1.75	
total	312	553.45		

 $.2 > p > .1$

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
<2 μM	162	1.612	1.417
2–5 μM	112	1.378	1.263
>5 μM	39	1.096	1.068

*Coulter particle concentration*analysis of variance on *cv-MSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
ave particles	2	42.77	21.39	19.02
error	281	315.92	1.12	
total	283	358.69		

 $p < .001$

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
<70/ml	116	1.905	1.102
70–165/ml	126	1.609	1.116
>165/ml	42	0.728	0.708

analysis of variance on *cv-FSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
ave particles	2	29.39	14.70	8.56
error	281	482.67	1.72	
total	283	512.06		

 $p < .001$

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
<70/ml	116	1.642	1.345
70–165/ml	126	1.598	1.402
>165/ml	42	0.715	0.843

Table 4. (Continued)

Chlorophyll concentration

analysis of variance on <i>cv-MSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
ave chl	2	43.16	21.58	20.15 $p < .001$
error	521	557.96	1.07	
total	523	601.12		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<1 $\mu\text{g/l}$	273	1.681	1.099	
1-2.5 $\mu\text{g/l}$	115	1.089	0.936	
>2.5 $\mu\text{g/l}$	136	1.122	0.980	
analysis of variance on <i>cv-FSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
ave chl	2	21.21	10.61	6.27 $p < .005$
error	521	880.85	1.69	
total	523	902.07		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<1 $\mu\text{g/l}$	273	1.529	1.348	
1-2.5 $\mu\text{g/l}$	115	1.033	1.090	
>2.5 $\mu\text{g/l}$	136	1.267	1.363	

(c) Microscale (sample) environment*nitrate + nitrite patchiness*

analysis of variance on <i>cv-MSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
<i>cv-MSV</i> :nitrogen	1	10.23	10.23	8.20 $p < .01$
error	282	351.79	1.25	
total	283	362.02		
Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>	
<.1	103	1.344	1.088	
>.1	181	1.739	1.133	

Coulter particle patchiness

analysis of variance on <i>cv-MSV</i> of organisms				
Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
<i>cv-MSV</i> :particles	1	37.47	37.47	32.90 $p < .001$
error	282	321.22	1.14	
total	283	358.69		

Table 4. (Continued)

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
<.4	42	0.728	0.708
>.4	242	1.751	1.117

*Chlorophyll patchiness*analysis of variance on *cv-MSV* of organisms

Source	<i>DF</i>	<i>SS</i>	<i>MS</i>	<i>F</i>
<i>cv-MSV:chlorophyll</i>	1	0.70	0.70	0.61 <i>p</i> > .5
error	522	600.42	1.15	
total	523	601.12		

Level	<i>N</i>	MEAN <i>cv</i>	<i>STDEV</i>
<.15	232	1.365	1.055
>.15	292	1.439	1.086

cycles of directed organism movement or of reproduction (cf. Olson *et al.*, 1986; Chisolm, 1981). However, this result does not denote a behavioral response because, intuitively, patchiness during hours of darkness could be diminished by increased convective mixing, which would disrupt patches formed during the stabilizing period of daytime insolation.

Wind stress, which drives mixing and stirring of the upper ocean layers, similarly affects microscale variation. Wind speeds above 10 m/s (at 10 m above sea level), produced significantly less microstructure of organism populations, although wind mixing never managed to obliterate structure in mixed layer or pycnocline.

Casts in the seasonal pycnocline showed greater microstructure than casts in the mixed layer, again due to increased vertical lability of waters of the upper layer.

Casts at sites where bottom depth was less than 100 m displayed less finescale and microscale structure of organisms than did casts at deeper sites. This treatment produced the greatest separation of finescale and microscale coefficients (see *F*-ratios), perhaps because "bottom depth" is the net expression of a number of effects that operate on patchiness. Upwelling, breaking internal waves, and interaction of flow with the bottom all contribute to increased levels of vertical mixing at shallower depths, which would produce the observed result.

Effects of cast environment (Table 4b). Sources of spatial variation were expected to operate on plankton within finescale layers of the water column. AOV was performed on finescale and microscale parameters of variation to determine their sensitivity to degree of vertical stability, (estimated by the 2 m temperature gradient, grad *t*, at the cast depth), and trophic state of the water (as specified by mean concentrations of chlorophyll-*a*, Coulter particulates and nitrate + nitrite from the cast). Finescale and microscale parameters grouped according to cast environment levels show increased microscale patchiness and larger finescale gradients in more stable layers (larger thermal gradients) and in more oligotrophic layers (diminished levels of nutrients,

small particles and chlorophyll). Effects on microscale variations are particularly pronounced.

Patchiness parameters follow a pattern one would expect of the influence of vertical stability on vertical exchange rates: patchiness was greater in more stable layers where contemporaneous disruption by vertical exchange was minimal.

Microscale variations of organisms were also affected by levels of nutrients, particles and phytopigment. Oligotrophic layers, those with reduced concentrations of nitrate and nitrite, particulates and chlorophyll, displayed markedly increased levels of microscale patchiness of small plankton.

Effects of sample environment (Table 4c). The microscale environment also would be expected to affect the patchiness of microplankton. Degree of microscale patchiness of the nutrient, particulate and chlorophyll fields, specified by their respective variation coefficients, accords with degree of microscale patchiness of organisms. AOV results showed microscale organism differences to be significant for nutrient and particulate patchiness but not for chlorophyll patchiness. The relationship of finescale organism parameters to microscale environment parameters is not reported because there is no reason *a priori* why microscale variation of the environment should affect the mean gradient of organisms. The accordance of organism patchiness with environmental patchiness does not necessarily denote a cause-effect condition because physical events are as likely to have given rise to both.

Environmental factors and organism characteristics considered here affect microscale patchiness more than finescale patchiness. For each determinant in Table 3 and 4, ratios of the factor mean square to the error mean square (*F*-values) indicate greater effects on *cv-MSV* (the microscale coefficient) than on *cv-FSV*. Each determinant thus accounts for more of the microscale variance than of the finescale variance.

Overall, effects of environment on organism patchiness are more pronounced than are effects of intrinsic organism behaviors. This is reflected by the consistently larger mean-square ratios (*F*-values) throughout the environment treatments of Table 4, as compared with those of organism characteristics of Table 3. This connotes dominance of physical determinants over biological determinants of smallscale patchiness, but it may also reflect an artifact arising from pooling organisms with differing behaviors.

e. Patterns within MPS casts. Tests to determine the incidence of pattern within the 2 m cast interval were conducted. I computed serial correlations on original and detrended (residual) values of organism concentrations and of environmental characteristics using the "mean-square successive difference test" described by Zar (1974). The test statistic is

$$S = 1 - s(d)^2/s^2$$

where $s(d)^2$ is the sum of squared successive differences in concentration through a sample set divided by $2(n - 1)$, and s^2 is the variance of the sample set.

Table 5. Incidence of significant values of runs tests among original values and residuals about the mean gradient of organism and environmental concentrations within MPS casts. *N* is number of serial data sets tested.

Characteristic	<i>N</i> (sets)	Percent significant	
		originals	residuals
		(95% level)	
Organisms	607	13	5
Chlorophyll- <i>a</i>	49	33	10
Phaeopigment	49	31	6
Particles 16–160 μm	34	21	0
Particles 32–50 μm	34	18	6
Particles 51–160 μm	34	15	3
Nitrate + nitrite	18	39	17
Nitrite	11	27	9
Nitrate	13	54	23
Ammonium	16	37	6
Phosphate	6	25	0
Silicate	18	22	11
Salinity	24	39	8

The results (Table 5) indicate a low incidence of significant serial correlations among organism populations (13% for originals and 5% for residuals). Thus organism patch sizes usually were at or below the interval sampled by the MPS, i.e. less than 2 m. The incidence of significant serial correlations among original values of all environmental characteristics was higher than that among organism populations. In 285 sets of environmental characteristics, *S*-values were significant in 30% of the original sequences. Finescale gradients were more common among environmental variables than among organism populations, indicating that environmental characteristics were often arranged in gradients greater than 2 m in vertical extent. Among residual series of the environmental concentrations, the incidence of significant *S*-values was higher for nitrate, silicate and chlorophyll, indicating a somewhat coarser submeter scale of patchiness among these than among organisms or other environmental characteristics.

f. Patch intensity and size. Manipulation of the small-structure parameters reveals some characteristics of dimension and intensity of organism patchiness. As shown by Lloyd (1967), the nondimensional contagion parameter, *k*, of the negative binomial distribution expresses the reciprocal proportion by which mean crowding, c^* , exceeds mean concentration, \bar{c} , over a defined domain:

$$c^*/\bar{c} = 1 + 1/k.$$

Mean crowding and the k -parameter were computed for each population in each MPS cast from the organism concentration files. The k -parameter is related to the unpartitioned coefficient of variation (over the entire cast) by the equation

$$k = 1/(cv^2 - 1/\bar{c}). \quad (1)$$

Small k values thus imply patchiness, and large values imply random distributions. Values for k range from 0.097 ($c^*/\bar{c} = 11.3$) to 301 ($c^*/\bar{c} = 1$) among 552 records; the median value is 1.031 ($c^*/\bar{c} = 1.97$). Lloyd's expression above approximately gives the relationship of concentration in patches to mean concentration. The median value suggests that patch concentrations most commonly are twice the mean concentration. The range over all records suggests that patch concentrations can exceed mean concentrations by more than 10-fold.

The finding that microplankton populations occur in small clusters substantiates the conclusion from theory by Vlymen (1977) that prey patchiness must occur on the scale of optimum foraging strategy by anchovy at pre-schooling larval stages.

Vlymen (1977) gives expressions from which patch geometry and frequency can be derived. Using the median value in Vlymen's expression (his Eq. 23) for patch size, k and mean concentration in this data set yields geometric patch diameters of 4 cm at organism concentrations of 5/ml, and 12 cm at 50/ml. The median patch size was 27 cm. Corresponding inter-patch distances, computed from Vlymen's Eq. 24, were 8 cm and 15 cm, respectively.

Patchiness at submeter intervals appears frequently to attain the optimum intensity ($c^*/\bar{c} = 11$) for larval anchovy feeding that is derivable from Vlymen's model: eighteen percent of all microplankton populations fell between $c^*/\bar{c} = 10.5$ to 11.3. This model was based on food densities used to sustain laboratory-reared larvae: because larvae may require more food in tanks than in the sea, the incidence at sea of adequate food concentrations may be higher than that derived from the model.

g. Simulations of patchiness. The experiences of sampling on the submeter scale are summarized by vertical sections of concentrations of a hypothetical microplankton population (Fig. 11). The figure portrays the sensitivity of microscale patchiness to wind, an easily monitored parameter of the mixing environment: patchiness is comparably sensitive to vertical stability and to the diurnal convection cycle. The cut-off wind speed value of 10 m/s represents the onset of turbulent vertical mixing (Simpson and Dickey, 1981).

Organism concentration fields portrayed in Figure 11 were simulated from negative binomial distributions, each with a mean value of 100 organisms/l and with contagion parameters derived from Table 4a through Eq. 1 for microscale patchiness under low and high wind conditions. Finescale gradients are not represented. Horizontal scale of patchiness is assumed to be four times that of the vertical. This ratio is based on mean ratios of patchiness coefficients of organism populations and environmentals from four

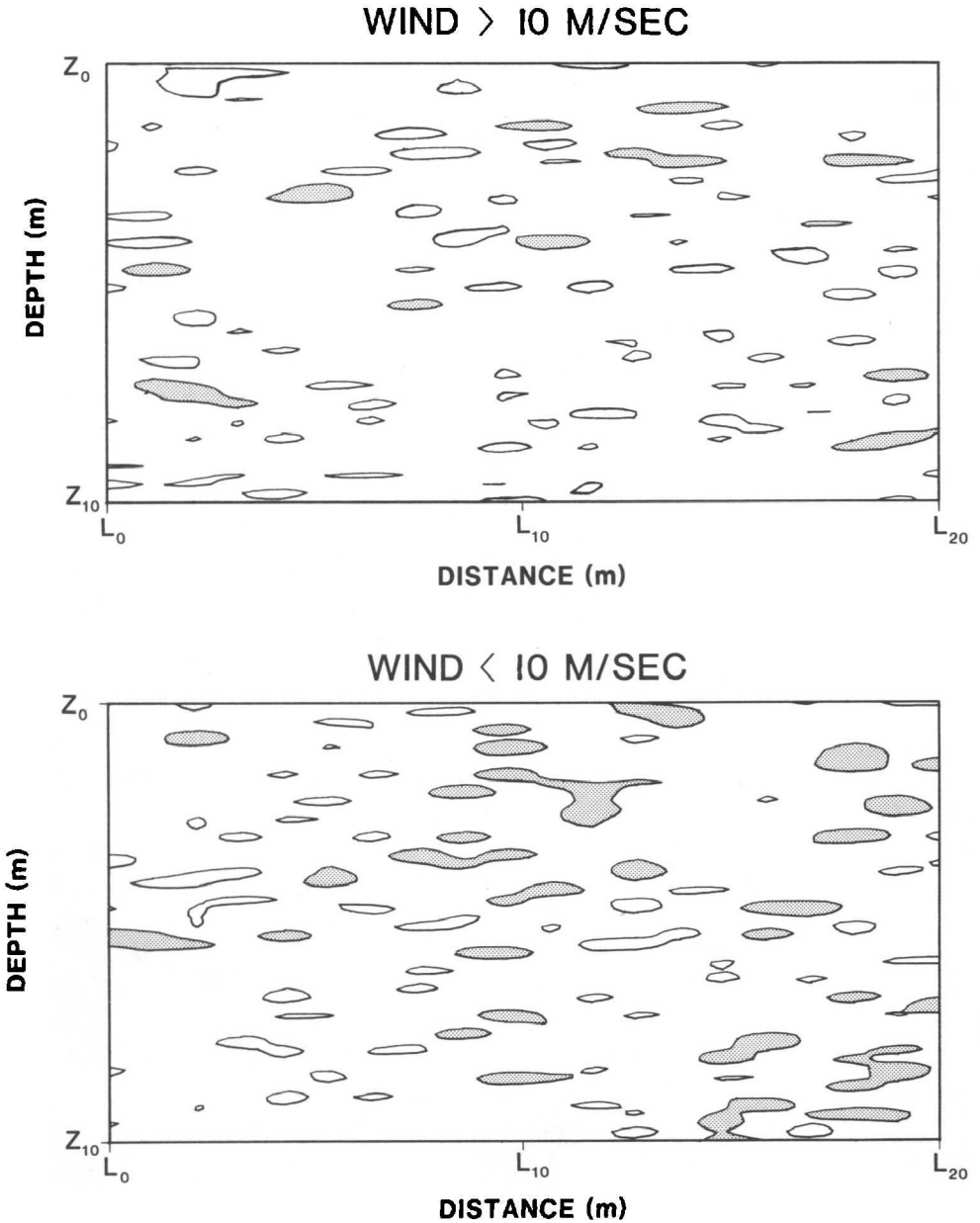


Figure 11. Vertical sections of microscale organism patchiness simulated under contrasting conditions of wind speed. Contours delimit zones where organism concentrations exceeded twice the mean value. Shading denotes zones where maximum concentrations exceeded four times the mean value.

Table 6. Individual and aggregate population statistics for microscale coefficients of variation (*cv-MSV*) in all MPS casts. Summed populations, chlorophyll-*a* and particulates represent aggregate characteristics. *cv-error* values are from Tables 1 and 2. *N* is number of data sets used.

	<i>N</i>	Mean	S.D.	Min.	Max.	<i>cv-error</i>
Individual populations	522	1.39	1.06	0.08	3.35	.22
Summed populations	29	0.26	0.15	0.06	0.14	.22
Chlorophyll- <i>a</i>	49	0.14	0.08	0.03	0.46	.08
Particulates 16–160 μm	33	0.30	0.25	0.08	1.32	.06

pairs of horizontal and vertical casts and is in close agreement with corresponding ratios of smallscale chlorophyll variations measured *in situ* by Derenbach *et al.*, 1979.

In these simulations (Fig. 11), patch incidence is no higher at low wind speeds: the number of patches is about the same under high and low winds. Patch intensity, however, is markedly affected: patches under low winds are larger and contain more organisms.

Also apparent from these simulations is the improbability either of representing typical concentrations or of detecting extreme concentrations from point sampling of the water column at large intervals. Integrative sampling by net hauls or pumping water is equally unlikely to yield more than rough estimates of the average concentration. Average concentration, however, has virtually no meaning to predators, which experience wide deviations from average feeding conditions over short distances.

h. Population aggregates and concentration dependence. Early explorations of organism population data failed to reveal any consistent relationships among population concentrations within MPS casts. This indicated that populations had disjoint distributions at finescale and microscale dimensions, and that small foragers encounter a variable selection of prey types in their ambits over short distances.

Whereas individual populations frequently exhibit finescale and microscale patchiness, in the aggregate they do not. The evidence for this lies in comparison of coefficients of variation from individual population concentrations with coefficients from measures of aggregate concentrations, i.e. summed populations, chlorophyll and Coulter particle counts (Table 6). The mean coefficient of variation of individual populations exceeds five times that of summed populations, nine times that of chlorophyll concentration, and over four times that of Coulter particulate concentration.

Whether by physical or biological means, the microplankton community more completely occupies available space in the water column than any of its constituent populations. Thus microhabitat spaces appear to be occupied by a variety of partially segregated population patches. Partitioning of the living space is thus denoted which may operate to the advantage of all populations present. This would increase the

capacity for kinds of organisms to co-occur. As stated by Richerson *et al.* (1970), the biological system exhibits a state of contemporaneous disequilibrium.

Microscale partitioning of the habitat could be related to population densities. Concentration dependence would be expected to occur when population members are competing, even temporarily, for local resources. To test the hypothesis that higher population concentrations produce increased patchiness, I regressed mean concentrations of each population (independent variable) against the square root of respective values of the population's micro- and finescale parameters, *MSV* and *FSV*. Expressions for the relationships are:

$$\sqrt{MSV} = \text{rms}(\text{microscale}) = -9.8 + .344 \bar{c}$$

$$\sqrt{FSV} = \text{rms}(\text{finescale}) = -181 + .339 \bar{c}$$

where \bar{c} is mean concentration in no/l. Microscale patchiness was positively dependent on mean population concentration ($r^2 = 0.92$). A lower degree of concentration dependence was shown for finescale variation ($r^2 = 0.70$).

4. Mechanisms and ecological consequences

Because a variety of processes may evoke finescale and microscale plankton distributions, it is useful to consider which are the more likely to be responsible and how they affect microplankton and predators.

a. Sources of patchiness. Organism characteristics can determine larger-scale vertical patterns (Cullen and Eppley, 1981). There is evidence from the present data treatments that reproduction dominates over motility in its influence on patchiness at small scales. Mean patchiness levels increase with organisms' motility level (Table 4b) but patchiness differences are not statistically significant ($p > 0.2$). By contrast, patchiness differences among trophic classes of populations are significant ($p < 0.05$, Table 4a). The latter separation is due mainly to patchiness differences between atrophs and feeders (autotrophs and heterotrophs), with atrophs displaying less patchiness (Table 4a). Atrophs have no motility ("passives" in Table 4b) and no reproductive capability. If differences in patchiness between atrophs and feeders are not due to differences in motility (Table 4b), perhaps they are due to differences in reproductive capacity.

Microstructure of biological particles more clearly reflects recent or current events of mixing and stirring. The conclusion of Frontier (1978–1979) for larger plankton and scales of sampling, that the mean statistics of plankton abundance correspond with the statistics of passive particles suspended in a turbulent medium, may thus extend to submeter scales for small plankton. The physical controls of plankton patchiness at scales upward of 10 m, reviewed by Denman and Powell (1984), are here extended to dimensions in the inertial subrange (ca. 0.1 m to 1 m), the transition regime between the buoyancy and viscous domains (cf. Mackas *et al.*, 1985).

Energy for mechanically redistributing plankton on small scales arises from a variety of sources, including shear and internal wave instability, wind stress, free vertical convection, lateral thermohaline intrusion and salt fingering.

Shear instability—Billow turbulence events attributed to Kelvin-Helmholtz instabilities have been detected in the upper layers of the seas and apparently are commonplace. Signatures of billow turbulence have been observed directly from the behavior of dye layers on sheets of submeter vertical extent in the seasonal thermocline (Woods and Fosberry, 1967; Woods, 1968a), and indirectly from high-resolution thermal profiles in the main and seasonal thermocline, which display zones of large temperature variations on submeter scales (Wiley, 1972; Gregg, 1980 and references therein; Gallagher, 1976; Hogg *et al.*, 1978). A current discussion concerns whether such signatures are relicts of rare, powerful events (Gibson, 1982), or whether they represent frequent, contemporaneous events in the upper thermocline (Gregg, 1980).

A current hypothesis holds that mixing in the interior of the ocean is dominated by internal waves (Garrett and Munk; 1972, 1975): at critical values of the shear forces, internal waves break and generate turbulence that is detectable by perturbations of the vertical temperature gradient. Measurements of these signatures have shown that mixing events are not random but occur in patches of high activity that vary from centimeters to tens of meters in vertical extent (e.g. Gregg, 1980). Smaller patches are the more common. According to theory and observation, such patches are more likely to occur at preferred sites that are definable from the internal wave field and vertical stability.

Several reports suggest that physical variations of small vertical extent can be laterally coherent for hundreds of meters and temporally coherent for hours to days (e.g. Woods and Fosberry, 1967; Simpson, 1971; Osborn and Cox, 1972; Kullenberg, 1974—at <100 m depth; Williams, 1976—deeper). Others suggest that this is usually not the case (e.g. Gargett, 1975; Hayes, 1975), that such signatures are more highly intermittent in space and time. Persistence and extent of the physical signatures of turbulence thus are probably variable. The existence of such signatures, however, suggests that other substances, including small plankton redistributed by the same turbulent events, may also exhibit similar lateral coherence for periods that would depend on the organism's behavior.

The attenuation of microscale plankton patchiness where sea floor depths are less than 100 m (cf. Table 4a) may reflect the higher incidence of billow turbulence on the continental borderland as incoming internal waves encounter either the bottom or the relatively destratified waters above the shelf.

Salt fingering—Local sources of microscale turbulence at ocean mid-depths include double diffusion (salt fingering), which occurs across pronounced vertical decreases in salinity. CTD profiles, taken at most MPS sites, exhibited low salinity gradients (0.33‰ in 10 m was maximum), and MPS-sampled salinity differences in 24 MPS casts never exceeded 0.055‰ in 2 m or 0.023‰ in 20 cm. In the absence of strong vertical gradients of salinity and of temperature inversions in the regions of concern

here, salt fingering alone is unlikely to produce signatures that dominate over shear-induced sources of variation.

Lateral intrusions—Thermohaline intrusions, on the other hand, commonly occur in the regions sampled for plankton microstructure (Reid, *et al.*, 1958; Gregg, 1975; Johnson *et al.*, 1978). Dissipation of kinetic energy was found by Gregg to be particularly high at boundaries of intrusion zones off Baja California, and due to intense fluctuations at submeter scales. Johnson *et al.*, working with finescale CTD records, concluded that wave-induced vertical straining dominated over thermohaline intrusion to determine finestructure. Records from CTD profiles at most MPS cast sites show evidence of shallow intrusions with thicknesses greater than 5 m, usually at depths below the seasonal pycnocline. Within the 1 m limit of depth resolution of these CTD casts there was seldom any indication of intrusions of small vertical extent. Although direct effects on organism patchiness by smallscale intrusions are discounted, fluctuations associated with intrusions in the buoyancy subrange may have affected smallscale patchiness.

Surface sources—Wind stress and convective mixing transfer surface-generated momentum to deeper layers and destroy solar-induced gradients in the mixed layer or, at higher rates, erode and deepen the seasonal thermocline (e.g. Price *et al.*, 1986; Denman and Gargett, 1988). Yet they may or may not destroy larger-scale discontinuities in plankton concentrations. For example, Lasker (1975) documents the [Eulerian] disappearance of the main chlorophyll maximum layer with the passage of a storm off Southern California, whereas Mullin *et al.* (1985) describe the preservation of vertical stratification of plankton with the passage of another storm. At yet smaller scales, Owen (1981b) describes the persistence of plankton microstructure in the face of windy conditions at the continental shelf-break off Perú.

Microscale variation of small plankton decreases with increasing wind stress unless sheltered by local temperature gradients (Table 4a,b). As seen in day-night differences (Table 4a), microscale variation also decreases with the increased convective mixing that ensues during darkness, as reported by Woods (1968b). On the other hand, microstructure was not obliterated even at the highest mixing conditions encountered, whereas finescale variation was not detectably different under the various mixing regimes.

It is likely that genesis and exodus of plankton patches parallel the cascade of turbulent energy from larger to smaller scales. In other words, large patches, formed for example by baroclinic instabilities, are milled into progressively smaller patches as stirring proceeds by flow irregularities of smaller scale. At some scale smaller than that of concern here, patchiness must become isotropic and then disappear.

b. Ecological implications. This work suggests that physical forcing of population and community characteristics operates through its influence on plankton patchiness. Microplankton patch incidence and intensity are sensitive to physical mixing processes

in the turbulent domain. The presence of microplankton patches alters interactions among individuals and populations; e.g., small planktivores, which depend on rate of prey encounter, are more likely to survive and grow where their food rations are patchy on the scale of their foraging ambit because the prey menu and rations available are enhanced at higher incidence and intensity of patchiness. Widespread effects on predator populations are possible because large areas suitable for survival of small predators can be created or deleted by large-scale processes that determine microscale patchiness. Community characteristics are altered in ways depending on whether strongly dominant populations emerge from vigorously mixed environments or whether competing populations co-exist in higher numbers and diversity by virtue of a minutely structured living space.

Processes of formation and maintenance of microscale patchiness are likely to affect mortality and growth of larval fishes, and must be included in our perception of factors governing their well-being. One body of evidence suggests that foraging, even by smaller organisms in the sea, is highly episodic and of limited duration. Despite the widely held view that pelagic fish larvae need high densities of microplankton (e.g. Vlymen, 1977; Lasker and Zweifel, 1978; Houde and Schekter, 1978; Lasker, 1978), transience in the co-occurrence of fish larvae and their prey has been noted at larger scales by Govoni *et al.* (1985) for sciaenid larvae, by Fortier and Leggett (1984) for capelin larvae, and by Arthur (1976), O'Connell (1980), Methot (1981), and Brewer and Kleppel (1986) for anchovy larvae. This transience may be due to infrequency of encounters of predators with prey patches if patches are ephemeral or widely spaced. More likely, the coincidence of predators with prey patches is underdocumented because it mostly occurs on small scales: prey patches are most often small, and special circumstances or new methods are needed to detect their co-occurrence in time and space.

Whether fish larvae seek or otherwise respond to prey patches in the natural habitat is thus unanswerable at present. An indication that they may is furnished by Hunter and Thomas (1974), who describe laboratory observations of a behavioral mechanism whereby larvae remain longer in small patches of higher food concentration: larvae swim shorter distances and turn more frequently in zones with larger numbers of strike targets. By this mechanism, larvae would collect in prey patches even in the absence of directed movement of larvae to a patch.

c. Resource management implications. Finescale and microscale patchiness of biological materials can be indexed from a combination of easily monitored physical and biological field values over larger domains than could ever be surveyed directly. This would satisfy a current need for assessing the incidence and intensity of plankton patchiness to specify regions and periods of adequate foraging conditions for larval fishes over the entire time-space domain of adult fish spawning. An indication of the power of such an approach to fishery management is provided collectively by Peterman

and Bradford (1987), Wroblewski (1984) and Vlymen (1977). These works addressed Lasker's (1975) hypothesis that wind mixing dissipates the large-scale chlorophyll maximum layer where prey is more abundant on average, leading to increased mortality of fish larvae by starvation. Peterman and Bradford concluded that timing, intensity and duration of wind mixing events accounted for most of the interannual variations of mortality rates of anchovy larvae, more than offshore transport or cannibalism by adults. Wroblewski concluded that the lowest mortality of anchovy larvae must occur in prey patches, and Vlymen concluded that such patches were necessarily small. Together with this paper, these works provide a basis for regional specification of anchovy survival from environmental effects at the microscale.

5. Summary

Whereas feeding conditions for small predators in the sea often appear subsustaining on average, zones of a meter or less usually exist where microplankton concentrations are much above (and much below) average. According to field sampling results, small predators moving two meters vertically are 95% likely to encounter noncolonial microplankton populations that range 240% above or below their average concentration in the seasonal pycnocline and 144% above or below their average in the upper mixed layer. Such patchiness depends upon levels of wind mixing, ambient lighting, local temperature gradient and oligotrophy, and upon the microscale environment. Less clearly, microplankton patchiness depends upon organisms' reproduction capacity and population density. Population patches are spatially disjoint: thus the menu of small predators is more diverse and, whether by physical or biological means, the microplankton community more completely occupies available space than its constituent populations in a biological system that exhibits a state of contemporaneous disequilibrium.

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