PATTERNING OF FLOW AND ORGANISMS IN THE LARVAL ANCHOVY ENVIRONMENT

by

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INTRODUCTION

This work reviews patterning of plankton populations and communities by their interaction with physical processes, with special reference to eastern boundary regions and their capacity to support early stages of engraulid fish populations. It describes patterning mechanisms and effects documented by case studies appropriate to a large range of scales and restates some old hypotheses. Coastal upwelling and its biological effects are treated in only a general way. The literature is extensive and is covered elsewhere in this volume (cf Bakun and Parrish).

By the time its yolk-sac is gone, an anchovy larva is a seeing animal with a functioning digestive system and an immediate need for food. It feeds by the hunt-and-peck tactic (Hunter, in press), selecting at first for rather specific particle types from the wide variety of organisms and detritus that it encounters. Favoured food particles are single, rounded plant cells or animals 20-120 mm in width which lack long spines (Arthur, 1976; de Mendiola, 1974). On the average, even in upwelling zones, it is unlikely to encounter enough particles to meet its metabolic needs (e.g., Lasker, *et al.*, 1970). This average, however, is known from methods that sample inappropriate volumes of water at inappropriate intervals. The interval immediately appropriate to a larva is the volume it searches in a day, and the path it takes to search this volume. These are as small as a litre and a few metres, respectively, as derived from Hunter's (1972) laboratory experiments, Smith's (1978) observations on plankton variability, and Vlymen's (1977) theoretical treatment of food concentration geometry and larval fish energetics. It is evident from work on inappropriately large intervals that larval food must occur in patterns in space and time to exceed concentrations larvae require, and that systematic approaches need to be taken to estimate the scale and degree of food patterning in the larval habitat in areas and at times of spawning if fishery models are to be realistically expected to specify recruitment under any particular measurable regime.

There is a considerable body of evidence that patchiness of plankton frequently and widely arises from patterned circulation. Environmental circumstances under which such patterns arise are often rather unexceptional, and thus may be more widespread than isolated case studies describe. There is also some promise of prediction of patterning and depatterning circulations, which would be of inestimable value in forecasting yield of fish stocks as affected by patterning of their food supply. Accounting for patterning of organisms should also enhance the accuracy of biological production models constructed for populations at any position in the food web.

MESOSCALE PLANKTON PATTERNING AND OFFSHORE ENRICHMENT BY EDDIES

Eddies arise from flow instability, uneven wind forcing and current deflection or separation at boundaries. They may be imbedded in the surrounding flow ("free"), or geographically stationary ("trapped"). Both free and trapped eddies can arise from frictional interaction with obstacles such as coastlines, islands and banks.

Planktonic communities, as well as some benthic and terrestrial populations, can be extended by eddy processes into otherwise marginal habitats, either continuously or ephemerally. The fate and dilution rate of anthropogenic products (e.g. MacGregor, 1974) and their effect on island, coastal and oceanic populations are also in part determined by eddy-like perturbations. Eddies also affect such local environmental conditions as temperature and nutrient distribution in the water and cloud cover in the atmosphere. Genesis, maintenance and lysis of eddies are of particular interest because organisms and substances in transit become differently distributed in space and time within and between eddies; concentrations of organisms and substances are locally maintained at higher levels and for longer periods, their trajectories are markedly different, and plankton populations which would not otherwise interact are juxtaposed. Eddies greatly amplify rates of transfer of materials (and energy) between nearshore upwelling zones characteristic of eastern boundary margins and pelagic regions well seaward of the continental shelf. Fronts that frequently bound upwelling zones cause slow subduction of surface waters into deeper, vertically stable strata of the offshore pycnocline. Eddy motion, whether the small-scale result of flow instability along the front or of mesoscale impingement from offshore, produces both surface and subsurface transport from upwelling zones.

Satellite imagery of thermal patterns at the sea surface off California indicate extensive seaward transport of cold water from upwelling zones by eddy motion. Thermal plumes can be traced for several hundred km offshore across the mean flow of the California Current (Bernstein *et al.*, 1977).

Cyclonic eddies larger than 10 km in diameters and a week's duration may have a major role in sustaining the higher biological concentrations and productivity which are characteristic of the inshore 200 km of the California Current System (CCS). Baroclinic eddies deform the density field. A cyclonic eddy or meander of sufficient size and intensity exhibits a detectable dome in surfaces of constant density to the depth where the eddy motion vanishes. Doming signals that the thermocline layer, which marks a sharp increase in water density with depth, has risen and displaced surface mixed-layer water. The displaced water is usually stripped of nutrients and often poor in phytoplankton as well. In eastern boundary regions, the thermocline is nutrient-laden and comparatively close to the sea surface. Elevation of the thermocline due to cyclonic motion thus results in upward flux of nutrients into the photic zone, which supports growth of phytoplankton. The new availability of nutrients is sustained by upwelling (here meaning upward flow across density surfaces) in and near the eddy centre and can be augmented by mixing and entrainment due to shear flow across the thermocline layer of the eddy. Additional nutrients are supplied in episodic fashion during storm activity which is either long or severe enough to erode the dome, with its relatively exposed pate (e.g. Blackburn, 1966).

The presence of a cyclonic eddy, however, does not assure photic layer enrichment. Such a case is provided by the transitory Hawaii Eddy phenomenon. Despite the large vertical displacement (50-150 m) of the thermocline attributable to doming (Patzert, 1969), nutrient-rich waters lie too deep for enrichment of the photic zone to occur. Water deeper than about 300 m would have to be raised more than 200 m to reach the bottom of the photic zone. McGary (1955) consequently found no evidence for photic zone enrichment that could be attributed to the Hawaii eddies. Other significant biological processes are, however, evidently affected; Sette (1955) describes evidence for the effect of the eddies on local fish populations.

If an eddy is stationary, e.g. topographically trapped, it can collect and locally conserve substances washed down from the boundary layer of the obstacle(s). Small eddies with short transit times thus extend the effective area of the boundary layer. Laboratory and field work with natural phytoplankton communities (recently, Thomas *et al.*, 1980; Estrada and Blasco, 1970) indicates that phytoplankton populations respond differentially to changes in nutrient flux and can create new sequences of community position on time scales greater than a few days. Transit times around mesoscale eddies are longer, so that new and distinguishable community compositions may arise at higher trophic levels as well as at the level of primary production. Thus seed populations in large trapped eddies can respond differentially and rapidly create new community sequences in transit. Close examination of biological effects of eddies seems warranted, for example, to determine whether eddy processes affect production of food organisms that support larvae and adults of the commercially and ecologically significant anchovy, *Engraulis mordax*. This may occur through effects of eddies on boundary layer extension, community structure, productivity and concentration of small plankton; all important factors in determining survival of the large numbers of anchovy spawned in such regions (Lasker, 1975; Smith, 1978).

Eddy genesis

In the vicinity of the island, bank and coastline systems, combinations of wind, current and topographic effects must be invoked to explain patterns of circulation (Pavlova, 1966; Arthur, 1965; Reid, 1965). The variability of flow impinging on obstacles couples with local topography to create or suppress eddy and front patterns. Wind patterns exercise significant control upstream by determining the impinging flow intensity and direction, and locally by augmenting or cancelling the topographic perturbations of water flow. Local-scale wind patterns are in turn affected by islands and coastlines. It is easy to understand why no theoretical treatment of flow consistently accounts for observed current patterns downstream of the islands, banks and coastlines of eastern ocean boundaries.

Large-scale eddy genesis by wind is indicated in Nelson's (1977) water transport calculations, derived from wind patterns off the west coast of North America. Flow directions are shown which are consistent with equatorward transport of the California Current, onshore transport south of the Southern California Bight, and nearshore poleward transport of the Southern California Countercurrent. These are elements of the Southern California Eddy, although Nelson's averaging scale is too large to resolve this eddy directly. On smaller scales, case studies (e.g. SIO 1962; Patzert, 1970) have shown that uneven wind distributions can create eddy circulations.

The distribution of wind speed and direction over the region of the Southern California Bight during northwest wind conditions (U.S. Dept. of Interior, 1978) may exhibit a two-jet system, consistent with wind retardation by the northern Channel Islands of a single jet impinging from the north. A high-wind zone is characteristic about 200 km off the California coast from April through August (Reid *et al.*, 1958; Alan Hancock Foundation, 1965). Its role in eddy genesis is unassessed as yet, although jet-like winds impart stress transport that would favour formation of small-scale mesoscale eddies.

Reports of atmospheric and oceanic eddy systems due to islands often taking the appearance of von Kārmān vortex wakes, have become well documented in recent years. Barkley's (1972) oceanographic study of Johnston Atoll's wake is the definitive example of vortex shedding of water by an island. As Barkley states, increasing reports of atmospheric marine effects are due to "... a special combination of circumstances: the wind, an obstacle, the right kind and quantity of cloud cover at the proper level, and a satellite overhead taking pictures; all must be present." Vortex wakes and other types of eddy patterns due to boundaries are apt to be common in ocean and atmosphere. Berger and Willie (1972) and Chopra (1973) review these phenomena and their dynamics. Of obstacles in the CCS, only Isla Guadalupe receives direct mention, but Chopra also reports effects of both smaller and larger islands elsewhere which show that obstacles of virtually any size may produce systematic flow deviations. Boundaries and direct wind effects are not prerequisities for eddy formation. Instability of flow can develop from current jets and convergences (e.g. Barkley, 1968) and eddies are commonplace in the open sea (Bernstein & White 1974). Uda and Ishino (1958) have identified patterns of enrichment resulting from free eddy systems off Japan. The eddies are comparable in scale to those off the Californias and Costa Rica. Areas of high concentrations of commercially and ecologically important fish, squid, whales, plankton and benthic fauna were found to coincide with areas of high eddy activity, both near to and far from land boundaries. Uda and Ishino distinguished between topographical and dynamic eddy systems and identified eddies affected both by topography and current collision (dynamic). Detection of eddies and their formation, persistence and decay by satellite sensing of sea temperature patterns shows particular promise (Bernstein *et al.*, 1977), although stratus clouds frequently obscure the sea surface in eastern boundary regions. Even in cloud-free periods, atmospheric path absorption effects need to be subtracted from sea-surface radiance patterns before satellite studies of eddies can proceed beyond qualitative detection.

Baroclinic eddy incidence and size

The geostrophic method has been shown to apply in particular to representing eddy flow at mid-latitudes. Baroclinic representation of an isolated eddy of about 80 km diameter in the CCS corresponded well with drogue trajectories (Reid *et al.*, 1963). This study demonstrated coherence of the velocity and mass fields and so confirmed the adequacy of the baroclinic mode for representing eddy flow on the mesoscale and for identifying smaller eddies as well. Reid *et al.* pointed out, perhaps as a cautionary note, that the particular eddy they described would have "slipped through the mesh of the /‾CalCOFI_7 station grid" used for geostrophic description if it were not for a hydrographic station added to the grid in response to the discovery of the eddy by drogue work. This illustrates the general limitations of eddy detection by the geostrophic method, as ship surveys cannot be conducted continuously, nor sample all appropriate scales.

Eddies in the California Current System, as defined by one or more closed streamlines of baroclinic flow, have been enumerated from the charts of Wyllie (1966) by season in four size classes and four sectors off the Californias. I chose the sectors to represent segments of roughly equal area off the coastline between San Francisco Bay (38° N), Pt. Conception (35° N), Cabo Colnett (31° N), Pta. Eugenia (28° N) and Bahia Magdalena (25° N). The sectors were covered, in part or totally, by 112 CalCOFI survey periods from 1949-1965. Separate counts were made of cyclonic and anticyclonic eddies because of their presumably different biological effects and modes of genesis. As a matter of convenience, eddy incidence is expressed as the mean number occurring in ten years although the record used was 16 years in duration. Mean ten-year eddy incidences, corrected for gaps in coverage, are shown in Table 1 (from Owen, 1980). The estimations of incidence of 20-100 km eddies are the least accurate because some eddies of this size range obviously were missed by the CalCOFI survey timing and grid and because interval waves can create images of small eddies. Larger eddies also were missed when survey frequency was reduced.

Table 1 summarizes eddy incidence in four regions of the CCS and shows that eddies of all sizes detectable from the CalCOFI grid usually are present throughout the region off the Californias. Eddy incidence demonstrated no obvious seasonal variation except perhaps in the southernmost sector. Large eddies are rarer than small eddies in the Baja California sectors, but off California eddies larger than 200 km occur more often than those of 100-200 km diameter. In all areas and seasons, eddies smaller than 100 km occur most frequently. In the sector containing the Southern California Bight, eddy incidence is dominated by the consistent (but not constant) presence of the Southern California Eddy. In this sector there is a corresponding paucity both of large anticyclonic eddies and of small cyclonic eddies. The high incidence of small anticyclonic eddies in this sector, as well as of the two adjacent sectors, indicates that the small eddies could have derived from larger and predominantly cyclonic eddies, perhaps as a result of flow instabilities. The dominance of cyclonic over anticyclonic eddies is seen in Table 1 to occur progressively with increasing eddy size in each of the four sectors and in all four seasons.

Table 1. Mean 10-year incidence of eddies by size, type, area and season in the California Current System, 1949-1965, coast to 300 n. mi. offshore

Eddy diam (km)		20-100		101-150		151-200		>200		All sizes		%c= $100\frac{c}{a+c}$
Eddy type*		a	c	a	c	a	c	a	c	Σa	Σc	
Sector/Season**												
35-38°N	Winter	0.4	0.4	0.4	1.7	0	1.9	2.4	3.7	3.2	7.7	
	Spring	2.8	0.9	1.3	1.3	0.9	0.3	0	1.8	5.0	4.3	
	Summer	3.6	2.3	0.9	1.9	0.9	0.9	0	2.0	5.4	7.0	
	Fall	0.6	1.0	2.7	3.3	0	2.9	0.6	2.7	3.9	10.0	
	Annual	7.4	4.6	5.3	8.2	1.8	6.0	3.0	10.2	17.5	29.0	
	%c	38.3		60.7		76.9		77.3				62.3
31-35°N	Winter	5.0	2.0	1.0	1.1	1.0	3.7	0	7.2	7.0	13.9	
	Spring	3.7	2.3	0.2	1.3	0.9	2.6	0	6.4	4.9	12.7	
	Summer	6.2	1.9	0.3	1.6	0	1.0	0.3	9.2	6.7	13.6	
	Fall	3.0	2.1	1.6	2.4	0	0	0	7.3	4.6	11.9	
	Annual	17.9	8.3	3.1	6.4	1.9	7.3	0.3	30.1	23.2	52.1	
	%c	31.7		67.4		79.3		99.0				69.2
28-31°N	Winter	2.1	0.7	0.4	0.4	1.1	0	1.5	1.2	5.1	2.3	
	Spring	4.1	1.5	2.8	2.4	1.0	1.1	0.4	1.6	8.3	6.6	
	Summer	3.1	0.6	1.4	1.7	2.0	2.2	1.4	0.6	7.9	5.1	
	Fall	1.6	0.5	1.6	1.3	0.3	1.0	0	1.1	3.5	3.9	
	Annual	10.9	3.3	6.2	5.8	4.4	4.3	3.3	4.5	24.8	17.9	
	%c	23.2		48.3		49.4		57.7				41.9
25-28°N	Winter	1.1	1.4	0.7	1.0	0	0.7	0.3	0.3	2.1	3.4	
	Spring	3.2	0	1.8	0.5	0.7	0.9	0.3	0.3	6.0	1.7	
	Summer	4.0	2.2	1.8	2.1	0.3	2.7	0.3	1.0	6.4	8.0	
	Fall	3.3	6.1	2.3	3.3	0	2.0	0	3.8	5.6	15.2	
	Annual	11.6	9.7	6.6	6.9	1.0	6.3	0.9	5.4	20.1	28.3	
	%c	45.5		51.1		86.3		85.7				58.5
All areas 25-38°N		47.8	25.9	21.2	27.3	9.1	23.9	7.5	50.2	85.6	127.3	
	%c	35.1		56.3		72.4		87.0				59.8

*a = anticyclonic
c = cyclonic

**Winter = January, February, March
Spring = April, May, June
Summer = July, August, September
Fall = October, November, December

Eddy characteristics

The Southern California (SC) Eddy is the most resolvable of the eddies in the California Current System by virtue of its large scale and degree of permanence, which usually exceeds the threshold for detection of both the sampling grid mesh and frequency of CalCOFI survey observations. Examples of free eddies at least as large and intense as the SC Eddy have been detected in the main flow of the California Current (e.g. Wyllie, 1966), but have not been measured in detail because of their transitory character.

The SC Eddy is a composite flow pattern. The offshore limb of the Eddy is formed by flow diverging off the coast near Pt. Conception at about 35° N (Hickey, 1979) and extending southward beyond the Cortez-Tanner bank system and is sometimes demonstrated by jet-like flow imbedded in the California Current (Wyllie, 1966). The lower limb occurs as onshore flow between 30°-32° N, likely a result of wind-driven transport (Nelson, 1977).

The nearshore limb is defined by the northward flow along the Bight coast of the SC Countercurrent (Tsuchiya, 1980) which can diverge offshore at Pt. Conception, continue northward along the coast, or episodically disappear. The SC Eddy is quite variable in its extent and circulation strength and may occasionally disappear entirely, for example, at the peak anchovy spawning period in March-April, perhaps even flushing the SC Bight unless replaced by smaller, transitory eddies (Owen, 1980).

It is of interest to compare SC Eddy characteristics with those of large cyclonic eddies elsewhere in the Pacific, particularly one which has been investigated more intensively. The best example of baroclinic doming and eddy upwelling effects is provided by studies of the Costa Rica Dome, produced by a major deflection to the north and east of the North Equatorial Countercurrent as it impinges from the west on the American Continent (Wyrtki, 1964). The Dome is located in the bight of this deflection in a region where nutrients and thermocline both are close to the photic depth (Brandhorst, 1958; Thomas, 1970; Owen and Zeitzschel, 1970a). Its physical characteristics denote a trapped, cyclonic eddy large enough to demonstrate nutrient enrichment effects (Brandhorst, 1958; Broenkow, 1965; Thomas, 1970, 1977) and to detect elevated stocks of phytoplankton, zooplankton and small nekton (Blackburn *et al.*, 1970, Owen and Zeitzschel, 1970b).

Dimensions of several well-studied Pacific eddies and order of magnitude estimates of their mean vertical velocity and volume transport are compared in Table 2 (from Owen, 1980). Despite the varying eddy sizes, intensities and vertical velocities, vertical transport by upwelling is of the same order of magnitude in the SC Eddy, Hawaii Eddy, Costa Rica Dome and in a segment of the coastal upwelling domain 200 km in length (about the same distance along the California coast usually occupied by the SC Eddy). As may be seen from ambient nutricline and photic depths, nutrients are readily available for transfer up through the photic zone in all eddies considered except off Hawaii. Thus, the degree of enrichment and subsequent productivity of the SC Eddy is comparable to that of other major eddy systems. The SC Eddy appears only slightly less effective in total transport of nutrients into the photic zone than upwelling along a comparable segment of the California coastline. As noted above, the SC Eddy receives coastal upwelling products from the nearshore Bight as well as from Pt. Conception and north, although any biological consequences are only poorly understood from rather few and incomplete studies.

SC Eddy effects

During the time of the spring phytoplankton bloom and peak spawning of the northern anchovy (*Engraulis mordax*), the SC Eddy may periodically disappear for a month or more, flushing away the surface waters of the SC Bight. Flushing is episodic in character, most frequent in April (3 of 13 cases). The baroclinic representation of the eddy may also "dissolve" to such extent as to become an indeterminate field of flow. Such dissolution apparently often occurs in the same season as flushing (again, 3 of 13 April cases). The eddy can persist in the absence of the surface countercurrent. The countercurrent typically disappears in April-May, a period when the intensified California Current overrides the coastal countercurrent, to paraphrase Wyllie (1966). This pattern of events is corroborated by independent conclusions from drift bottle release-and-return statistics (Schwartzlose, 1962; Squire, 1977).

Table 2. Parameters of Pacific eddies and California coastal upwelling

	Southern California Eddy[1]	Johnson Atoll[2]	Hawaii Eddy[3]	Costa Rica Dome[4]	Small CCS Eddy[5]	California Coastal Upwelling[6]
Effective obstacle diameter (km)	200	26	100 (wind) 300 (current)	-	-	200 (length**)
Eddy type	trapped	free vortex street	ephemeral wind-forced	trapped	free	(edge eddies occur)
Ambient* or incident flow (cm/sec)	20	60	30	55	20	20
Eddy flow (cm/sec) at 1/2 radius	30	80	50	40	20	-
Radius (km)	100	30	65	200	40	-
Decay time (dy to 1/e)	100	16	>65	-	>14	14
Vertical velocity (m/dy)	0.3	-	0.8(initial)	0.1	-	1.0
Upwelling volume (m^3/dy)	10^{10}	-	10^{10}	-		10^{10}**
Pycnocline elevation $\left(\frac{\text{ambient-dome}}{\text{ambient}}\right)$	0.3-0.5	-	0.4	0.7	0.1	0.4-0.6
Ambient* photic depth (m)	60	100	100	70	70	60
Ambient* nutricline depth (m)	30-70	75	300	40	40	20-60

Sources:
[1] McEwen, 1948; Wyllie, 1966; Wyllie and Lynn, 1971; Owen, 1974
[2] Barkley, 1972; Frederick, 1970
[3] Patzert, 1970; McGary, 1955; Frederick, 1970
[4] Wyrtki, 1964; Broenkow, 1965; Bennett, 1963; Owen and Zeitzschel, 1970a
[5] Reid *et al.*, 1963; Owen & Sanchez, 1974
[6] Bakun, 1973; Walsh *et al.*, 1974; McEwen, 1948; Wyllie and Lynn, 1971; Sverdrup and Fleming, 1941; Owen and Sanchez, 1974

* "ambient" refers to condition in absence of phenomenon.
** 200 km coastal strip 50 km wide for comparison with SC Eddy

Spatial variation of community structure and of population densities are evidently affected by the SC Eddy. Changes in community composition take place along flow streamlines: where such streamlines are closed, as in the SC Eddy, successive communities are inevitably juxtaposed. This is apparent from the observations of Allen (1945) and Sargeant and Walker (1948) showing that systematic changes occur in time and space from diatom species ensembles (characteristic of high nutrient injection by recent coastal upwelling) to dinoflagellate ensembles (characteristic of lower nutrient injection into older surface-layer waters). These ensembles were subsequently spatially juxtaposed into what may prove to be a characteristic state due to the Eddy. This effectively demonstrates (perhaps more crudely than actually occurs) the creation of community patchiness by stirring, as defined by Eckart (1948).

Patterns of high phytoplankton concentration which corresponds with that of the SC Eddy are shown by Owen (1974) and by Owen and Sanchez (1974) in terms of surface and depth-integrated chlorophyll a concentrations. These concentration patterns correspond spatially with patterns of higher surface layer and migrating nutrient concentrations of Thomas and Seibert (1974) and with higher zooplankton concentrations in Spring 1969 (Smith, 1974) when the Eddy was fully developed. Together with the evidence for persistence of the SC Eddy, these studies indicate that the observations of Allen and of Sargent and Walker are characteristic (rather than episodic) over the SC Bight. Primary production measurements within the Eddy are too sparse to demonstrate an enrichment effect. A single transect of such measurements (Owen, 1974, p. 98) showed primary production to be about six times greater within the Eddy than outside it. Obviously more observations are needed.

Effects of nutrient washdown into the SC Eddy are not likely confined to only the phytoplankton but certainly involve zooplankton and nekton as well. Arthur (1977) found maximum concentrations of copepod nauplii off the SC Bight at distances corresponding to the offshore limb of the SC Eddy. The maximum zone was associated with colder water, probably entrained from upwelling zones north of Pt. Conception. The pattern suggests that nutrient washdown enhanced reproduction by copepods, a response to their increased food supply.

From plankton surveys over the 1941 spawning season of one population of the California sardine (*Sardinops caerulea*), Sette and Ahlstrom (1948) determined that their eggs and larvae appeared to have been concentrated in an area corresponding closely to that of the SC Eddy and its characteristic elevated diatom densities (Allen, 1945; Sargent and Walker, 1948). This striking local correspondence suggests the susceptibility and possible sensitivity of the sardine stock to the Eddy. The surveys did not cover the entire range of spawning and it is probable that conditions beyond the SC Bight may also have supported spawning areas.

Since the change from dominance of the California sardine stocks to northern anchovy (*Engraulis mordax*), the CalCOFI plankton surveys have covered the spawning time and area of the anchovy. These have revealed (Smith, 1978) that the region inclusive of the SC Eddy, comprising about 12% of the spawning area of the anchovy's central subpopulation, contained 48% of their larvae on the average (1951-1975) and since 1966, 64%.

Berner (1959), in his study of food of anchovy larvae, noted that areas where larvae were found to be actively feeding corresponded to those of the copepod nauplii maximum as described by Arthur (1956). Comparison of areas of active larval feeding in the SC Bight, with corresponding charts of baroclinic flow (Wyllie, 1966, pp. 76, 79 and 82) show that the area of feeding larvae corresponded with the inshore limb of the SC Eddy, although Arthur (1977) subsequently showed that maximum concentration zones of copepod nauplii coincided with the SC Eddy axis or its offshore limb.

Brinton (1976) studied the population biology of *Euphausia pacifica*, a dominant species among the larger zooplankton of the SC Bight. He identified the SC Eddy and its associated upwelling regimes as a reproductive refuge for an identifiable population of the species.

Population persistence in benthic-dwelling organisms with planktonic life-history stages (usually larval) depends on their deposition at the end of the planktonic stage in waters shoal enough to permit survival on the sea bottom. Off the Californias, where flow frequently diverges from the coast, such populations depend on eddies and meanders in the mean flow to return a sufficient number of their meroplankton to appropriate habitat. Examples of this dependency include populations of the spiny lobster, *Panulirus interruptus* (Johnson, 1960) and the red crab, *Pleuroncodes planipes* (Longhurst, 1968). Both organisms spend extend periods as plankton in their early life history, yet maintain stationary and localized centers of the adult populations.

PATTERNING BY FRONTS

Within and between eddy systems, discontinuities known as "ocean fronts" occur which provide identifiable sites for smaller scale and more specific biological activity of likely significance to larval and adult fishes. Ocean fronts are line zones of laterally convergent flow that intensify vertical water motion. They occur singly or in series. Patterning of biological substances can occur mechanically, e.g., concentrating or dispersing organisms that move vertically through advection or convection. Patterning also occurs by indirect mechanisms: local nutrient enrichment and behavioural properties account at least qualitatively for localized responses to fronts by organisms including some types of phytoplankton, zooplankton, fishes, sea snakes, bird and whales.

Scales of variation of plankton tend to be much smaller in the presence of fronts as compared to patterns impressed by eddies. A basic and attractive tenet is that vertical displacements have greater ecological effects than similar horizontal displacements because environmental gradients of light, pressure, temperature, salinity, oxygen and nutrients are by far the steepest in the vertical dimension. Vertical motion in fronts is often vigorous and highly localized, whereas that in eddies is slower and spread over much larger areas. For this reason, coherent horizontal gradients of temperature, salinity and food supply are correspondingly sharper across convergent flows than across eddies. Their respective biological effects occur on accordingly disparate scales.

Scales on which ocean fronts have been observed to occur and to pattern organisms range laterally from 1 m - 10^5 m, persisting (depending on size) from hours to virtual permanence. The smallest-scale fronts are by no means ecologically insignificant since they may extend (in diverse patterns) over large ocean areas.

Bēnard and Langmuir Fronts

The smallest coherent frontal patterns that have been noted to collect organisms in the open sea were attributable to the Bēnard mechanism. Bēnard circulation occurs when cooling and salt gain through evaporation make surface water rapidly more dense: thermohaline circulation cells form a honeycomb pattern of surface convergences as the denser water exchanges with the less saline and warmer subsurface water. The resulting honeycomb pattern is easily deformed by wind or subsurface shear to form a series of small elongate, parallel fronts.

Surface convergences of this sort reported by Owen (1966) penetrated to less than a metre in depth, extended visibly for more than 30 m in unbroken length and were spaced at intervals of about 1.5 m. The patterns persisted in the absence of wind for at least two days. Taken singularly, such "micro-fronts" would have little ecological impact. However, this particular frontal system observed by Owen (1966) extended over several hundred km^2. Such fine-scale patterns can produce widespread alteration of concentration patterns and, presumably, concentration-dependent biological processes. In this instance, the surface convergences were marked by red bands less than 10 cm wide that consisted of upward swimming oikopleurans that had been highly concentrated in the upper 5 cm of the convergence planes. Their still-water swimming speed of about 0.2 cm/sec was used to set an upper limit on downwelling water speed in the convergence planes.

Under freshening and sustained winds, convergence systems of the better known and (usually) larger scale Langmuir circulation either develop into patterns like Bēnard cells or create their own patterns, detectable as parallel windrows. These windrows lie along the wind axis and are often marked by assemblages of floating organisms or substances. These are swept by convergent surface flow to the frontal zones. Trapping efficiency of buoyant materials is virtually 100% under steady winds of constant direction. Surface convergences can become strong enough on occasion to submerge even highly buoyant

Sargassum weed, requiring a downwelling circulation of 5-7 cm/sec (Woodcock, 1950). Organic films on the sea surface are also rapidly collected along such convergences to give windrows their most common streaked appearance. Under lower winds, collected oils dampen capillary waves to give the windrows the appearance of parallel slicks. At higher wind speeds the organics can be partly frothed and convergences appear as foam lines.

The size and circulation strength of these convection cells increase with time and wind speed. Spacings between convergence lines from several metres to over 100 m are typical, and downwelling speeds may exceed 10 cm/sec. Depth of penetration is some fraction of the distance between convergences, usually half or somewhat less.

Extant theories that attempt to account for the Langmuir circulation include stability of vertical shear in the water, forcing by atmospheric vortices, wind-oriented thermal (Bénard) convection, wind profile modification by surface films, lateral radiation pressure on surface films, convergence of wave trains (reviewed by Scott *et al.*, 1969), and vertical decay of surface wave oscillations (Faller, 1969). Failure of data to support or rule out any single mechanism led Scott *et al.* (op. cit.) to conclude that combinations of mechanisms could occur. A subsequent study (Harris and Lott, 1973) lends support to the possibility of development of Bénard cells into Langmuir cells: mean downwelling velocities ranging from 2.1 to 9.4 cm/sec in Langmuir convergences correlated well with wind speed during net surface cooling but not as well during net surface heating. Despite the lack of agreement on mechanisms, the Bénard-Langmuir circulation is now widely held to be an important mechanism for vertical transfer of heat and substances in surface waters of lakes and seas. Large temporal variations, with a strong diel component (Woods, in press) may be expected in both Langmuir and Bénard circulations.

The theoretical and mathematical description of particle trajectories in cellular convections was formulated by Stommel (1949) and subsequently elaborated to include swimming (e.g., Stavn, 1971). Direct observations to date confirm the applicability of the model to real particles and plankters in such circulations, despite the rather large difficulties of field measurement and the less-than-ideal behaviour of both the fluid and plankton.

A number of field studies confirm the effectiveness of the Langmuir circulation in collecting and patterning organisms and substances. The most visible examples involve buoyant animals and substances such as *Physalia* (Woodcock, 1944), *Sargassum* weed (Faller and Woodcock, 1964; Woodcock, 1950) and surface films (Szekielda *et al.*, 1972). Sutcliffe *et al.* (1963) demonstrated that whitecapping and perhaps other wind action converts dissolved organics to particulate form available to zooplankton, and that a downwelling Langmuir convection, at 3-6 cm/sec, produced subsurface concentration zones of these particulates. The soluble inorganic phosphate concentration was also shown to be higher in such particulates. Sutcliffe *et al.* (1971) show, by detecting an increase in particle concentrations with increase in wind speed, that the process is highly effective. They found peak production to be particles of 6 um diameter. Higher concentrations of particles 2-13 μm diameter were shown to occur below convergence zones.

Patterning of phytoplankton and microzooplankton by Langmuir circulations has been more widely reported than one would expect from the mismatch of their reported speeds. Bainbridge (1957) reviews several observations of dinoflagellate concentrations in Langmuir scale patterns. The mobile and prolific ciliate *Mesodinium rubrum*, which can "zig-zag" at speeds up to 2 mm/sec and also occur in bloom ("red-water") concentrations, has been reported to gather in Langmuir convergences. Powers (1932) found *Mesodinium* in windrows off Maine, and Bary (1953) observed windrows of these ciliates to orient along a changing wind axis in New Zealand. Packard et al. (1978) describe *Mesodinium* windrows spaced at 100 m intervals under 10-20 knot winds, and their dispersion through the water column at winds over 30 knots.

Patterning of larger zooplankton in Langmuir circulations is less apparent and notoriously difficult to sample. The best examples of Langmuir patterning of zooplankton thus are from lakes, where populations of cladocerans and copepods migrate vertically into vortices in the epilimnion and concentrate in convergence planes (e.g., George and Edwards, 1973). Survival of Peru's larval anchoveta has been proposed by Ware et al. (in press) to be enhanced in the presence of small-scale patterning of their food supply in windrow circulations.

Internal wave effects

Internal waves, responsible for surface banding on continental shelves, do not actively produce organism patterns but may modify extant patterns. Interaction of waves with bottom topography, current shear, and diminished vertical stability can produce instabilities (and breaking waves) that disrupt pattern. Internal waves may interact with current boundaries and shelf-break fronts. Curtin and Mooers (1975) presented measurements that indicated generation of large amplitude, high frequency internal waves by breakdown of the semi-diurnal internal tide at the shelf-break front off Oregon. These induced major perturbation of a sonic scattering layer (organisms) inshore of the front. Earlier, Yasui (1961) presented a theoretical framework arguing for propagation of tidal-period internal waves along fronts of the sort encountered as Shiome, fronts due to current confluence, which are zones of high lateral shear as well as vertical circulation. Localized interaction between internal waves and eddies in mid-ocean also has been detected (Frankignoul, 1976), which may affect rates of vertical diffusion. As yet, these phenomena seem to be unexplored but may be expected to modify effects of fronts on populations of organism. Kamykowski (1975), for example, presented a mechanism by which phytoplankton can interact with the semi-diurnal internal tide to produce patterns of species concentrations. The biological result of internal wave interaction with fronts or eddies is obscure but may be significant. Internal waves are sensitive to current shear and to vertical density gradients, both of which vary at fronts and in eddies. It will not be surprising to find evidence of biological responses to these dynamic physical processes if adequate sampling techniques can be devised.

Tidal fronts

Simpson and Pingree (1978), Pingree et al. (1977) and Pingree et al. (1974) describe cases of genesis and decay of shallow sea fronts by variable tidal mixing on the European continental shelf. Surface convergent fronts of considerable physical and biological activity occur in zones where water types of different mixing histories impinge. Vertical mixing was induced in shallower waters by frictional dissipation on the bottom interface of (mainly) the principal lunar tidal component of flow and stratified cooler waters. In some areas of the shelf, such vertical mixing is sufficiently vigorous to prevent or override density stratification. Where tidally-mixed shoal water contacts stratified deeper water, a convergent front occurs. Thermal images of the Celtic Sea from the NOAA-5 satellite indicated the broad extent of tidal fronts like those examined in these studies have shown the genesis of a cold eddy from a frontal meander. Shipboard measurements of a similar front (Pingree et al., 1977) show its response to neap and spring tide cycles and its effect on phytoplankton chlorophyll concentrations in the stratified water well beyond the front. The study suggests that blooms of a dinoflagellate population offshore were caused by periodic release of nutrients from the destratified inshore side of the front by decay of the front during neap tides.

Admixture of water types at shelf fronts locally stimulates phytoplankton photosynthesis and thus sustains higher phytoplankton concentrations in the frontal zones. Savidge (1976) and Savidge and Foster (1978) describe such a process from surface measurements of chlorophyll, temperature and photosynthesis along transects on the European shelf between Ireland and Wales.

Zooplankton concentrated in shelf fronts is also commonly observed but descriptions from physical and biological measurements in such fronts are rare. Pingree et al. (1974)

describe activity in a vigorous tidal front of 15 km extent in the English Channel from temperature, salinity and current measurements and from direct underwater and surface observations of its effects on organisms and substances. Surface net hauls in the front showed greater concentrations of copepods, crustacean meroplankton, the euphausiid Nyctiphanes sp. and young fishes.

Plankton concentration at the front was confirmed by sub-surface visual observation. Underwater observation of motions of plankton and of dye injected at several depths also confirmed the turbulent, convergent character, which was apparent from temperature and salinity structure and from drogue measurements. The list provided of animals associated with floating macrophytes concentrated at the front consisted of a variety of post-larval fishes and crustacean species. Puffins, shear-waters and terns were seen feeding along the front, which also collected debris and oil lumps. The authors remark on the similarity of this front and its biota to the large, deep-ocean fronts described by Beebe (1926) and Amos et al. (1972).

Shelf-break fronts

Fronts of large extent commonly occur in the general vicinity of the shelf-break, i.e., where the slope of continental shelf steepens to become the continental slope (generally at about 100-300 m depth). Mooers et al. (1978) usefully distinguish between prograde fronts, those that separate more saline shelf water from offshore water; and retrograde fronts, those that separate less saline shelf water from offshore water. Shelf waters of both types are colder than offshore waters.

Prograde fronts arise by upwelling on the continental shelf. Seasonal and episodic wind-driven upwelling is characteristic of eastern boundary current systems, but occurs inshore of western boundary currents as well, where upwelling occurs by topographic deflection of currents. Retrograde fronts are due to shelf-water dilution from terrestrial runoff and thus predominate off large terrestrial water sheds. Their incidence and intensity usually vary with season.

Upwelling fronts

Prograde shelf-break fronts off upwelling zones bound the plankton-rich shelf waters. There is a dearth of studies that demonstrate higher plankton concentrations in these fronts than inshore, at least in part because field studies have been concerned more with the upwelling system as a whole and do not sufficiently sample frontal interfaces. Packard et al. (1978) describe the incidence and habitat of the pigmented ciliate, *Mesodinium rubrum* in an upwelling zone off Baja California. Surface-layer concentrations of this ciliate at prograde fronts appear to be facilitated by characteristics of its environment in combination with its phototaxic behaviour, rapid reproduction rate and ability to use both inorganics and organics for food.

Laurs (unpublished thesis), working with measurements of concentration of phytoplankton zooplankton and micronekton in and beyond the Oregon upwelling system, detected higher stocks near the frontal zone and in an anticyclonic eddy (phytoplankton only) outside the front. Bang (1973) describes a strong upwelling front extending northwest off Cape Town in the eastern boundary current off South Africa. Mixing cells occurred and episodic overturn at the front produced subthermocline sheets of homogeneous water. Higher concentrations of large zooplankton or micronekton were detected at the front by fathometer records.

Albacore make annual trans-Pacific migrations to feed on relatively high concentrations of large plankton and small fishes in the California Current, seaward of the coastal upwelling zones. The offshore extent of these upwelling zones are frequently denoted by prograde (upwelling) fronts. Albacore caught, tagged with ultrasonic transmitters and subsequently released, were tracked in the vicinity of such a front off Monterey Bay, California (Laurs *et al.*, 1977). Tracking results showed that such temperature fronts can influence local concentration of albacore; sonically tagged albacore moved about in the vicinity of the front, then moved away when the front weakened as upwelling ceased. These albacore also were seen to move more slowly when crossing fronts and to spend little time on the colder side ($T < 15^oC$), indicating a thermal barrier effect which would result in their collection at fronts. The enriching effects of large cyclonic eddies that predominate outside upwelling zones, and of eddies that transport substances away from upwelling zones (Owen, in press B) may also support higher forage levels beyond shelf-break.

As demonstrated for tidal fronts, an important aspect of upwelling fronts may be their periodic relaxation, their decay, and subsequent release into offshore water of nutrients and plankton previously accumulated in the shelf water. Frontal relaxation occurs upon cessation of upwelling. This can occur either seasonally or episodically depending on the wind system. Breaching, or destructuring dissipation occurs more locally than does relaxation. The causes of breaching have not been defined but likely involve meanders and eddies formed by local instabilities of frontal currents, impingement of eddies from outside the fronts, and perhaps wave interactions with the fronts. When clear weather permits, breaching is clearly evident in thermal images of sea surface temperature fields off California transmitted from satellites. Bernstein *et al.* (1977) demonstrate the possibility of using such infrared images to follow the genesis, lysis and incidence of fronts as well as eddies and upwelling zones in the California Current System.

Estuarine fronts

Retrograde estuarine fronts exhibit salinity gradients, because freshwater sources dilute surface waters on one side of such fronts. Iizuka and Arie (1969) showed concentrations of *Trichodesmium* (flagellate) for 80 km along an estuarine front off Japan. LeFevre and Grall (1970) showed similar convergent aggregations of *Noctiluca scintillans* off Brittany and also emphasized local competition that was apparent between *Noctiluca* and copepods for diatoms in the convergence area.

Owen (1968) studied effects of the Columbia River plume, which albacore encounter in their summer arrival off Oregon. Based on research vessel catch rates and oceanographic data, results showed that albacore moved through the outer plume boundary, defined by the $32.2^o/oo$ isohaline that defined the outer boundary of the salinity gradient of the plume-sea front (Owen, 1967). Albacore catches were somewhat lower in mid-plume than in the vicinity of its frontal limits, indicating an attraction to forage in fronts per se and possibly a combined attraction/aversion to the warmer temperatures/lower salinities of the plume core. Catch rates were higher near the seaward limit than inshore, where even stronger thermohaline fronts resulted between plume coastal upwelling zones.

Tsujita (1957) showed seasonal cross-shelf movements of stocks of the Japanese sardine off western Japan. Spawning and hatching occurs at depth in oceanic water off a retrograde (estuarine) coastal front. Larvae move shoreward through the shelf-break front, seek nearshore feeding grounds, grow to 7-10 cm length and diffuse seaward in summer in the upper layer of the shelf waters.

MICROSCALE PLANKTON PATCHINESS

Patterning of plankton occurs on the sub-metre scale. Cassie (1959a, b) demonstrated high variation of plankton concentrations at the sea surface, and Owen (in press b) showed similar variations at sub-surface depths. The role of circulation in the patterning process is obscure, particularly since this approaches the scale of turbulent dissipation. This section discusses some new measurements made to determine if small predators and grazers encounter food patches in excursions of less than 2 m extent. Variation in food supply available to fish populations is commonly examined to help determine causes of large interannual fluctuations frequently experienced in the availability of fish to fisheries. Yet concentrations of food of rist-feeding northern anchovy (*Engraulis mordax* Girard) seem frequently to be too low in the California Current System for larval survival and growth (Lasker *et al.*, 1970). This may be because conventional sampling with plankton nets, which integrate over depth, distance and volume, has little relation to the comparatively tiny volumes searched by single larvae (Hunter, 1972). Survival of such larvae may, in fact, depend on the existence of food particle patchiness on scales considerably less than 10 m and 1 week (Vlymen, 1977).

Regions sampled

Southern California Bight waters tend to high vertical stability by virtue of characteristically slow flow (reduced shear) and year-round net heat gain, except in December, by the ocean's upper layer (Clark *et al.*, 1974). The mixed layer is relatively shallow (<30 m), due to the combined influences of wind shattering, heat gain, the California Current and the Southern California Eddy. Large temperature gradients predominate over salinity gradients in determining vertical stability. Maximum stability occurs in the upper pycnocline in the absence of steady winds. These characteristics are favourable to the development of small-scale patchiness but are episodically reversed by storm winds of a few days duration, which destroy shoaler layering (Lasker, 1978). Episodic upwelling, internal waves, and eddies may destratify the water column locally along the narrow shelf of the Southern California Bight margain and in even more restricted areas near islands and capes.

The region studied off Peru is functionally similar to the S.C. Bight in having a shoal pycnocline, destratification on the shelf, and high production rates of forage and fish. Differences between the sampled regions are mainly of magnitude: Peru's shelf is 1-2 orders of magnitude broader, the margin is more exposed to storm activity, and processes of destratification are more dynamic, somewhat more consistent, and more broadly effective than in the SC Bight. The role of eddy processes in the Peru region is unassessed. Well-defined prograde fronts are found on and near the Peru shelf. These frequently separate stratified from unstratified zones but cellular fronts also occur on smaller scales, e.g. Bēnard-Langmuir on sized cells.

One would thus expect off Peru both a lesser degree of vertical microstructure of plankton and environment, and a lesser need of such microstructure by the larval fishes due to the increased general productivity compared to the Southern California region.

Microscale measurements

Samples to assess microscale patchiness at each site were obtained using an array of water samples on a varied frame. The micropatch sampler (MPS) sampled either in the mixed layer or in the upper pycnocline in the main chlorophyll maximum layer, as defined by pigment fluorescence in a water stream provided by continuously lowered pump and hose. Clamped either vertically or horizontally to the ship's hydro-wire and lowered to the depth desired, the MPS captured water at ten intervals on 20 cm centres in 5 cm (i.d.) tubes of 600 ml capacity by simultaneous messenger-activated release of lanyards which restrain ball valves from their seats at either end of each sample tube. Replicates were obtained on some casts by strapping another sample tube alongside the original. When sampling vertically, vanes oriented the sample tube mouths to face a current of ~50 cm/sec induced by moving the ship slowly ahead. This minimized vertical mixing of the water by the MPS. When sampling horizontally (tubes vertical), the tubes were closed while raising the array. Water was aliquoted for various analyses from the well-stirred contents of the MPS tubes upon recovery aboard ship. Plant pigment determinations were made by the fluorometric method on acetone extracts, particle concentrations by Coulter T_A, nutrients by autoanalyzer and salinity by inductive bridge. Samples for microscope analysis were preserved in <5% buffered formalin spiked with strontium chloride. These were counted ashore by the sedimentation method of Utermohl (1931).

Microstructure of organism populations

Results of microscope counts are summarized in Table 3 as coefficients of variation, V = 100 x variance/mean, of concentrations determined over the 10 intervals sampled to represent the 2 m span. Where replicate samples were counted, average values between replicates were used in the computation. Coefficients are shown for population counts exceeding 10 in at least one of the samples in the set. Trends (i.e. mean gradients) over the 2 m span are represented by the coefficients, as are variations within the span (i.e. deviations from mean gradients). Both sources are taken to indicate microstructure degree because sampling was done in the absence of conventionally detectable biological gradients (i.e. in mixed layer and chlorophyll maximum). The V statistic was chosen because it scales variances for comparability and because it is widely used and understood. A measure of sampling and counting error is provided from counts on four MPS sets each consisting of five replicate sample pairs. The average coefficient of variation between replicates for 15 taxonomic groups counted was 10.9 (range was 4.0 - 18.5), not including the coefficient for ciliates associated with marine snow at two sites (7703J-MS1, MS2).

V-coefficients are considered to indicate significant microstructure if they exceed the average replicate V-coefficient by at least a factor of 3, Table 3 shows that:

- Microscale patchiness is apparent (V > 33) at all but one of the 13 Southern California Bight sampling sites and at both Peru sites for one or (usually) more kinds of organisms enumerated.

- Most types of organisms suitable as larval anchovy food display significant degrees of microaggregation. Non-food organism types are also aggregated, in many cases to an even greater degree, and not necessarily in the same zones as the presumed food organisms.

- Vertical profiles in the upper mixed layer of the SC Bight (the latter defined by absence of density gradients determined from standard STD casts) showed significant microscale patchiness for 5 of 8 food types and 3 of 8 non-food types at one site or the other, both occurred during the anchovy spawning season under calm wind conditions. At the shelf edge off Peru, in the lower part of the mixed layer under 20 kt winds, microscale patches of ciliates, copepod eggs and the diatom *Corethron* were detected.

- Microscale variation was usually greatest in the pycnocline and in the vertical axis for most food and non-food types alike (but see *Exuviaella* sp. C - this flagellate species behaves rather differently on the microscale, being more randomly dispersed vertically than horizontally in the pycnocline and apparently capable of forming small patches in the mixed layer).

- Non-motile or weakly motile organisms (cf. *Nitzschia*, *Thalassiosira* and pennate diatom categories) may show as much or more patchiness as motile organisms (cf. *Exuviaella*, *Prorocentrum* and ciliate categories).

- There is no evidence for a difference in degree of vertical microstructure in the pycnocline between periods of peak and minimal spawning activity (mean V = 49.3 and 50.0, respectively). This is perhaps partly due to too few comparable categories since species composition changed between periods sampled, complicating relevant interpretation regarding appropriate larval anchovy food.

Table 3. Coefficients of variation of organism concentrations sampled at ten 20-cm intervals (interval replicates averaged where obtained) in the mixed layer and upper pycnocline of the coastal shelf of the Southern California Bight and Peru (7711).

		Vertical casts in pycnocline at chlorophyll maximum layer									$\bar{V}$	Horizontal casts in pycnocline			$\bar{V}$	Vertical casts in mixed layer			$\bar{V}$
TOP DEPTH (m)		22	23	25	29	20	20	14	20	15		17	18	21		10	10	15	
DATE (Year/Month)		7509	7509	7509	7509	7603	7603	7703	7708	7711		7603	7603	7603		7603	7703	7711	
MPS No.		1	2	4	5	1	5	2	1	3		3	10	11		2	1	2	
FOOD TYPES	Exuviaella sp.C					22.7	17.3					27.4	29.1	21.8		12.8	76.6		
	Oxytoxum septrum						27.7												
	Prorocentrum gracile	69.8	52.6	138.4		45.4										37.6			
	Peridinium (2 spp.)					50.9							19.2			25.4			
	Peridinium minutum					174.1		25.0					35.2			35.5	21.2		
	Cochlodinium catenatum	28.4		51.2	44.9				22.0										
	Gymnodinium sp. S					22.2													
	Torodinium robustum								29.8										
	naked flagellate 30x50 µm					67.4			14.5			27.3	21.4	17.3			41.6		
	tintinnids 100 µm						98.6			51.9						22.2:	34.2		
	free ciliates			54.6	44.2	64.1	11.5	63.2				26.2	14.3	24.4		9.9	23.4	43.2	
	copepod nauplii					32.0	25.4						29.6			10.7	31.8		
	Prorocentrum micans									59.5									
	Copepod eggs, 35-80 µm									30.7	49.6				24.5			123.0	36.6
NON-FOOD TYPES	Nitzschia seriata					51.8	44.9						35.7			29.2			
	Eucampia zoodiacus							115.7								31.0			
	Thalassiothrix frauenfeldi															25.1			
	Thalassiosira sp.A							27.3											
	pennate diatom 30 µm			158.2	92.2														
	silicoflagellate			55.3	60.4														
	Ceratium kofoidii	39.1				58.4						39.2							
	Dinoflagellate spp. 5x10 µm					27.9							31.1			27.0			
	Pseudoeunotia doliolus	95.7	10 .6	56.8															
	Thalassiosira sp.B								28.9					37.3					
	Skeletonema costatum															40.1			
	pollen grain 70x40 µm																65.6		
	oikopleurans															52.4			
	Noctiluca sp.					29.0	21.2									21.5			
	Corythron sp.																	33.9	
	Pleurosigma elongatum									59.5									
	Pleurosigma nicobaricum									86.9	63.9				33.5				36.2

In the 15 microsampler sets enumerated by microscope, 20 species of phytoplankton, 6 categories of microzooplankton, and 4 size categories of detritus were sufficiently populous to examine their microscale variation. Microstructure occurred in 94% of profiles of phytoplankton species, 92% of microzooplankton profiles, and 85% of detritus profiles in 3 size categories ranging from 16 to 200 µm.

The maximum concentrations of food and non-food organisms do not usually coincide on the microscale. A characteristic experience is shown in Figure 1, taken from a vertical MPS cast in the pycnocline, in the vicinity of the main chlorophyll maximum. This effect may augment the increase in availability of food organisms due to microstructure by reducing local abundance of undesirable strike targets in zones where food organism concentrations are highest. The argument assumes varying degrees of distinguishability and desirability among the food types by the fish larvae, as there are no consistent patterns apparent between food and non-food organism distributions on this scale.

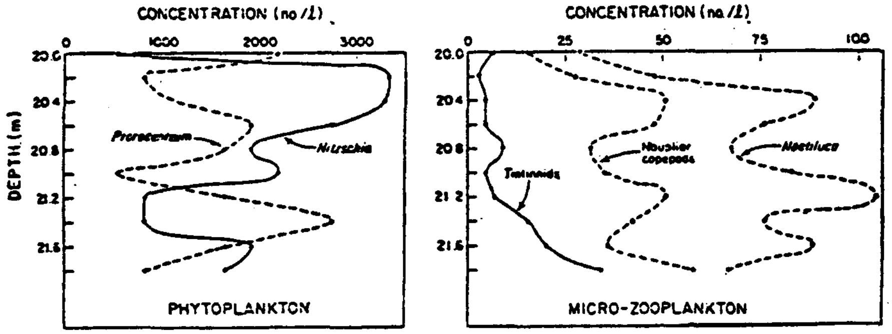

Figure 1. Microscale variation of larval anchovy food and non-food organisms in the pycnocline of the Southern California Bight

Concentrations of suitable food in one MPS cast of 13 analyzed from the SC Bight exceeded the "critical concentration" criteria of Lasker and Zweifel (1978) for survival and growth of anchovy larvae. This incidence would likely be higher if (1) all food type organisms had been enumerated rather than those selected only for clear identification and abundance, or if (2) high plankton standing stock had been among criteria for choosing sampling sites.

Patch shape

Results of four casts made horizontally at depths comparable to those of vertical profiles permit a rough estimate of the *in situ* shapes of particle patches. Variation in concentration of the more numerous components of the microplankton community present averaged three to five times greater in the vertical sets than in the horizontal sets, as measured by the coefficient of variation, $s/\bar{X}$, of counts made on these components. This leads me to speculate that populations were concentrated in partly overlapping lenticular patches with horizontal dimensions three to five times greater than vertical dimensions. This geometry provides an interesting contrast with shapes of plankton patches discerned on larger scales, whose characteristic vertical dimensions are reported in metres and horizontal dimensions are reported in km (e.g. Bainbridge, 1957). This indicates a marked tendency towards isotropy with diminishing scales and bears further investigation for confirmation.

The observations suggest no simple relationship between organism types, but show a large degree of variation on short intervals. Results confirm Vlymen's (1977) postulate that some degree of small-scale patchiness (on the scale order reported here) must necessarily occur to support even the minimum fraction of anchovy larvae surviving to recruitment size. The results also suggest sampling precautions to be taken wherever minimum or maximum plankton concentrations need to be known or where "critical concentrations" need to be detected.

Microstructure of bulk properties and organisms

Vertical sampling of the water "column" by water-capturing devices at intervals usually spaced more than 5 m apart or by continuously-lowered pump and hose, both underestimate the *in situ* variations of concentration and thus lead to underestimates of the maximum concentrations actually present. The degree to which this can occur is shown in Figure 2, where a small inversion in plant pigment concentration, detected *in vivo* by fluorescence of a sample stream from a pump profiling system, was resampled within 5 minutes by the microsampler array and acetone extracts of filtered samples analyzed by fluorometer for chlorophyll and phaeopigment concentrations. Unlike determinations from filtered, extracted samples from the microsampler, the *in vivo* measurement does not differentiate between chlorophyll *a* and phaeopigment (photosynthetically inactive degradation products of chlorophyll). Hence both are shown in the insert. Noting that the pigment concentration scales are the same for pump and microsampler array, the degree of averaging by the pump system is apparent: the variation of pigment concentration over the 0.6 m depth interval was an order of magnitude greater as sampled by microsampler than by the pump. This case displays the greatest disparity yet encountered between pump and MPS profiles of plant pigment.

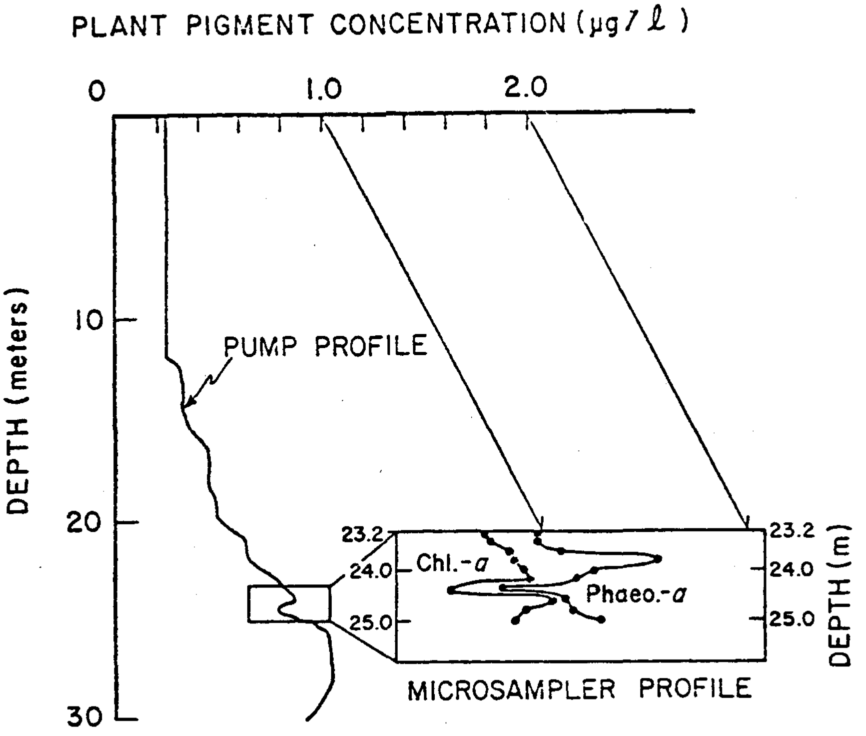

Figure 2. Comparison of small-scale change of phytoplankton pigment concentration by pump profiling and by 20-cm discrete sampling in California coastal waters. Pigment concentration scales are the same for both displays.

To date, 33 vertical and 4 horizontal microprofile sets have been obtained from mixed and stratified coastal waters in the Southern California Bight and on the Peru shelf under all but full-storm conditions. Of these, all except a horizontal set made in the mixed layer exhibited variations beyond sampling and measurement error of one or more of the parameters measured over the 2 m interval. As examples, two microprofile sets are shown in Figure 3. Also shown (lower panel) are concentration profiles of chlorophyll, an integrative measure of phytoplankton density; phaeopigments, photosynthetically inactive derivatives of chlorophyll; particulates 16 to 160 μm diameter, indicative of detrital particle load in this region; and inorganic nitrate, important for phytoplankton growth. Both were obtained from the SC Bight in the density-stratified portion of the water column where the bottom depth was about 200 m. They were selected because most parameters in these two sets displayed small-scale variations that exceeded sampling and measurement error. Greater variation existed within any single parameter in other sets. Concentration profiles of a motile phytoplankter, *Exuviaella* sp. C; oligotrich ciliates; and copepod nauplii were selected to depict microscale variations of species and of functionally similar groups (upper panel). Each is a food item of larval anchovy.

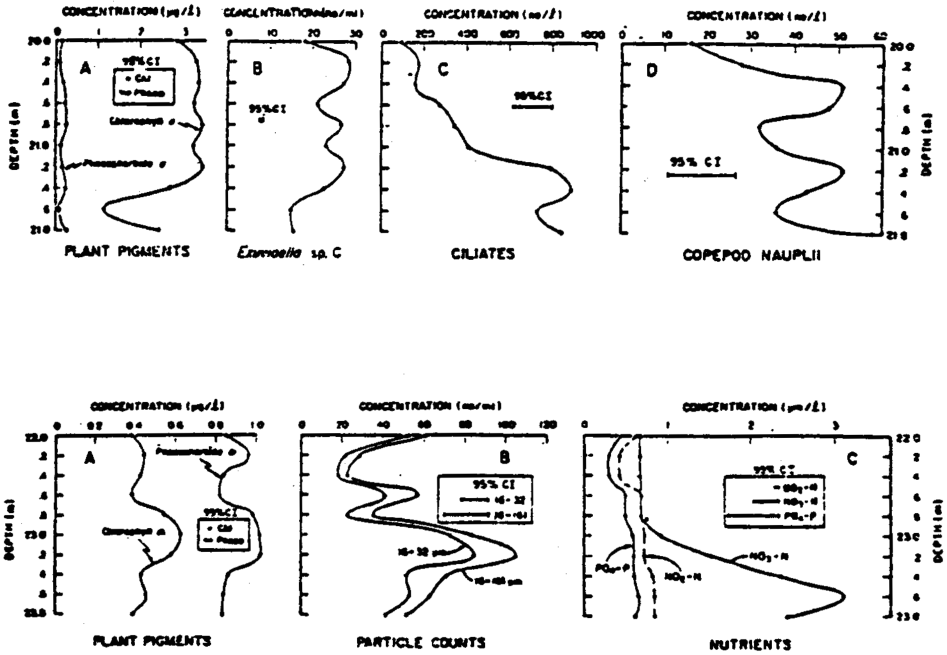

Figure 3. (Upper panel). Microscale variation of plant pigments and three organism types from the pycnocline in the Southern California Bight in March (7603/MPS-1). (Lower panel). Microscale variation of plant pigments, particles and nutrient salts from the pycnocline in the Southern California Bight in September (7509/MPS-1).

Results of a September cast in the SC Bight demonstrates the small-scale variation commonly present in plant pigments, particle concentration and nutrients. The incidence of microstructure was high; significant fine-structure existed in 16% of 22 particle profiles and 11 of 21 nitrate profiles and in both of two ammonium profiles. The particle coincidence of particle and plant pigment maximums centered at 23.2 m is fortuitous; virtually all particle profiles were independent of the corresponding plant pigment profiles (15 sets). Incidence of plant pigment microstructure was quite high. All 23 sets analyzed showed variation of chlorophyll concentration indicating microstructure of the phytoplankton community as a whole. Fewer (19%) showed cm-scale variation of phaeopigments. In the set shown in Figure 3 (lower panel), the phaeopigment profiles resembles that of chlorophyll a. However, of 23 such profiles, 14 exhibited unrelated profiles of chlorophyll and phaeopigments and 4 exhibited inverse relationships. This inconsistency demonstrates a degree of independence on the microscale which is not apparent in pigment concentration profiles from the usual sampling intervals of 5 to 10 m. This independence may be due to local effects of grazing or to differential rates of local production and sinking of the two particle types. These measurements thus may reflect the spatial scales on which these processes are first apparent.

Microstructure was not, of course, always detected. Sample series from the wind-mixed upper layer of the SC Bight showed less variation of organisms, particulates and nutrients than did sample series from density-stratified waters. However, significant microstructure of motile and non-motile organism populations, as well as of detrital particles, was detected in 2 of 4 casts made within the mixed layer in the absence of measurable density gradients, when mixing by wind was not in progress. The nutrient salts phosphate and nitrite-nitrate exhibited low incidence of microscale variation over distances less than 2 m in both regions sampled. Widely varying values of silicate concentration suggest microstructure for that nutrient but occasional wide disagreement between replicate samples vitiate the case for silicate microstructure. Salinity (5 sets) varied monotonically in the presence of nutrient and organism microscale variation. Temperature microvariation was not measured.

Peru microscale

Microstructure of biological materials apparently occurs under a variety of environmental conditions. Off Peru during Project ICANE (Doe, 1978), MPS-3/7711 sampled 5 km from shore near Chimbote below a surface layer stabilized by surface layer heating after recent weakening or cessation of upwelling. Large quantities of the "weed" diatom *Chaetoceros* were present at the surface and at the sampled depths. Microstructure of two types was evident among populations enumerated from 15-17 m depth. Concentrations of the diatoms *Pleurosigma elongatum* and *P. nicobaricum* exhibited nearly monotonic, stepwise decreases with depth (Fig. 4, upper panel), whereas spheres, tintinnid ciliates and *Prorocentrum micans* exhibited yet smaller-scale variations by pronounced maxima and minima between 15 and 17 m (Fig. 4, lower panels). Nutrient salt concentrations, nitrate-nitrite, ammonia, phosphate and silicate at this site exhibited no microstructure (Fig. 5). Particle concentrations, by Coulter Counter, indicated significant microstructure of particulates likely dominated by detrital substances (Fig. 6). By contrast with stabilized conditions at the coastal site, MPS-2/7711 sampled 10 km seaward of the shelf-break at about the same latitude (9°S) as MPS-3. More labile conditions prevailed at this site; MPS-2 sampled from 15-17 m in the virtually isopycnal layer that extended from the sea surface to 21 m depth under 20 kt winds. Standing stocks of phytoplankton were less than at the coastal station, tintinnids were supplanted by oligotrich ciliates, and copepod nauplii were more abundant.

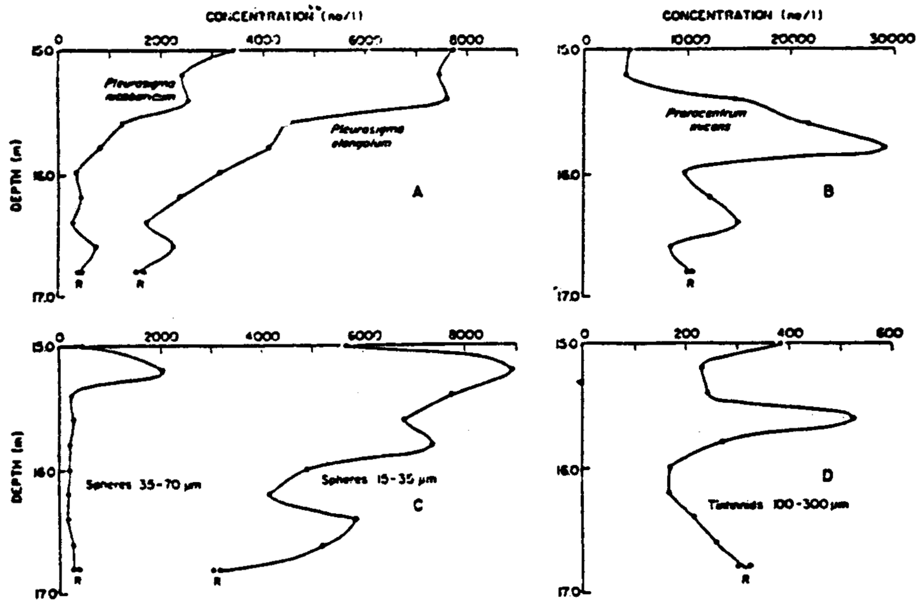

Figure 4. Microscale variation of larval anchovy food and non-food organisms in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

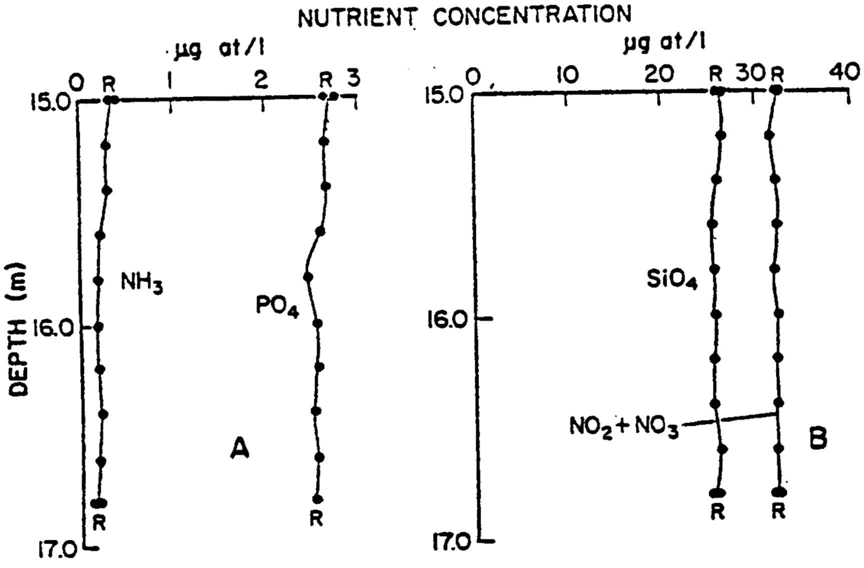

Figure 5. Microscale variation of nutrient salts in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

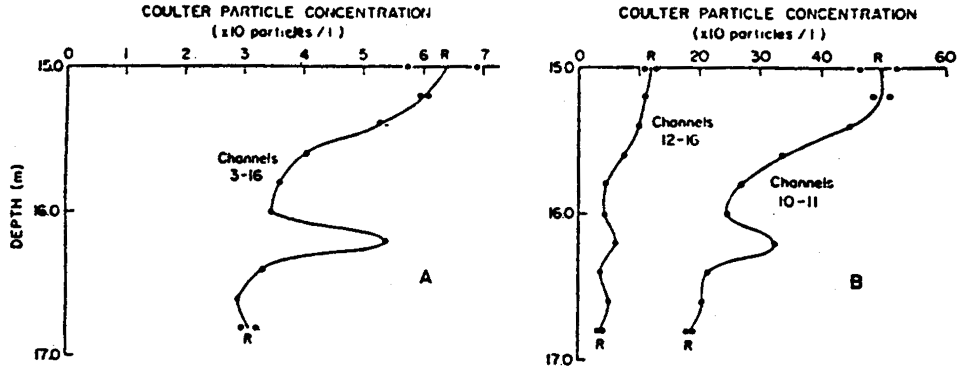

Figure 6. Microscale variation of particle counts (Coulter TA) in the pycnocline near Peru's coast in November 1977 (7711/MPS-3).

Despite the dynamic conditions encountered, microstructure of the several organisms was at least as pronounced in the "mixed layer" near Peru's shelf-break as in the more stable layer at the same depth near the coast. None of the variations were in the form of stepped trends but were all of sub-metre extent (Fig. 7). Small ciliates (20-50 μm) were less numerous and covaried with the small ciliates.

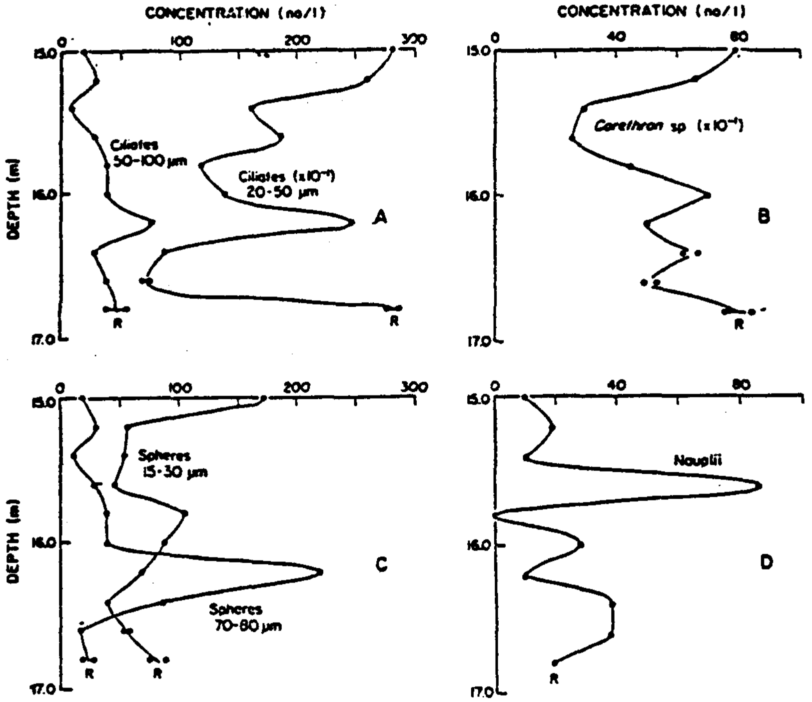

Figure 7. Microscale variation of larval anchovy food and non-food organisms off Peru's shelf-break in November 1977 (7711/KPS-2).

Covariation with ciliates of 70-80 µm sphere concentrations indicates that ciliates had actively associated with copepod eggs in the stratum between 16.0 and 16.6 m or alternatively that these spheres were actually ciliates (an artifact of sample preservation). The former seems more likely, as the spheres were quite smooth and regular in shape, and of nearly uniform size.

Copepod nauplii, also food items, exhibited large vertical variation and close replication. A pronounced maximum of their concentration was detected 60 cm above the presumed "egg" maximum, and 20 cm above a sample containing no nauplii.

Microscale variation of nutrients was greater at the slope station than at the coastal station, despite the difference in layer stability (Fig. 8). Nutrients were lower than at the coastal station but not limiting to phytoplankton growth. Microscale variation was not as pronounced as in the SC Bight, but was detectable for silicate (which covaried with the diatom *Corethron*) and perhaps for ammonia and phosphate. Nitrite-nitrate was constant over the 2 m interval.

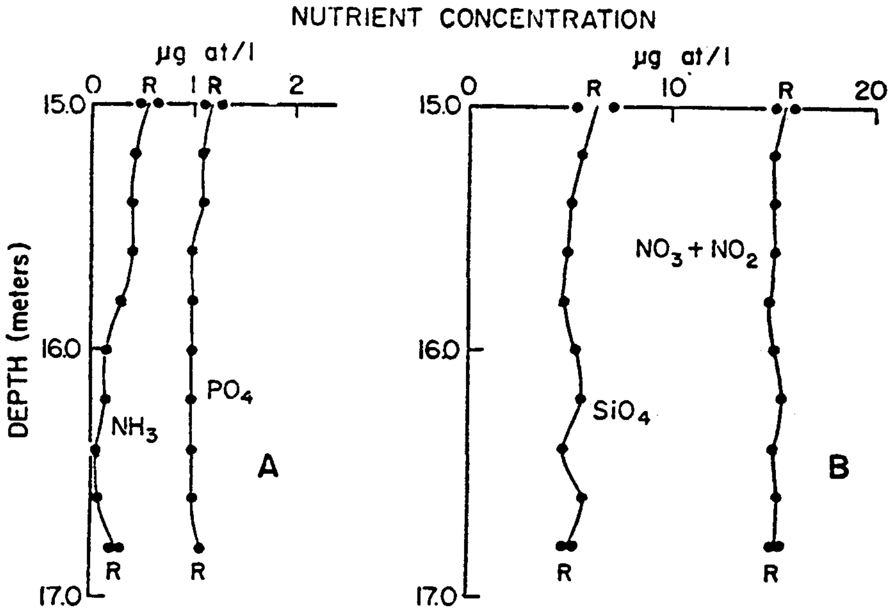

Figure 8. Microscale variation of nutrient salts off Peru's shelf-break in November 1977 (MPS-2).

Particle concentration counts from Coulter Counter was lower and less variable with depth than at the coastal station, except for the 16-50 µm category, which also showed variation on the 5 cm scale (Fig. 9). Chlorophyll a and phaeopigments, by contrast with Fig. 5, varied reciprocally with depth (Fig. 10) indicating either physical control by fine-scale lateral interleafing or biological control by localized grazing. No particular correspondence is evident between plant pigment concentration and variation of the population enumerated.

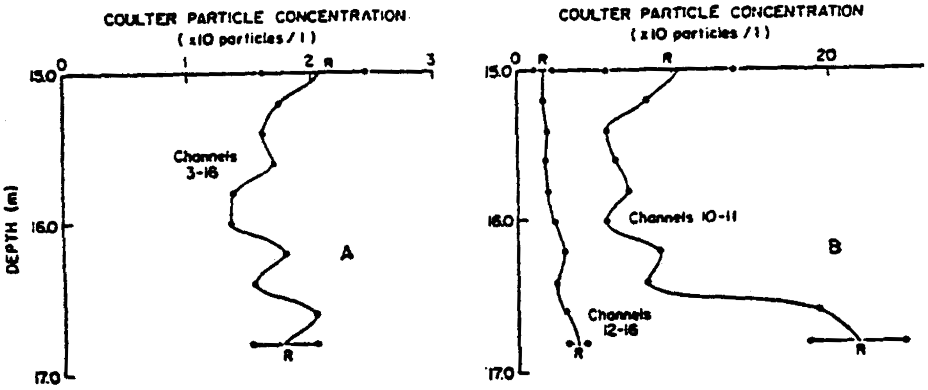

Figure 9. Microscale variation of particle counts (Coulter TA) off Peru's shelf-break in November 1977 (7711/MPS-2).

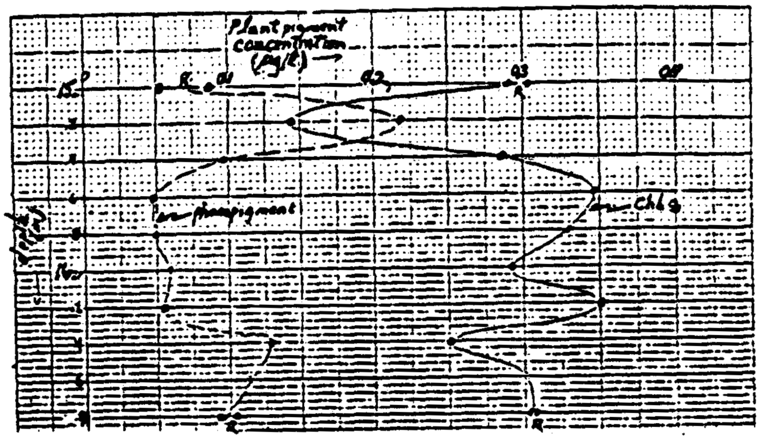

Figure 10. Microscale variation of phytoplankton pigment concentration off Peru's shelf-break in November 1977 (7711/MPS-2).

DISCUSSION

Association of plankton and biologically active substances with macroscopic flocs ("marine snow") has been reported and represents micro-distribution on the sub-cm scale. This work is of interest because it suggests yet another dimension to the complex ecological structure of the mixed layer and thermocline, e.g. organisms residing on marine snow are not available to the same predators or grazers as free-living individuals. The seaward extent of influence of marine snow is not known. My work indicates the presence of flocs affected concentrations of ciliates and detritus within 1 to 2 km of the coast but not beyond. This is confirmed by the lower incidence of aggregates in water of recent offshore origin than in neritic water, as reported by Trent *et al.* (1978).

Yet to be determined is the extent to which physical mixing mediates the microstructuring process. Dye studies by Kullenberg (1974) and Woods (1968) conducted elsewhere in density-stratified waters, show that layers of sub-metre thickness scale can persis for at least a day in the absence of storm-force winds and that disruptive processes can operate on the same scale. Only broad agreement was found during this study between degree of microstructure and estimates of vertical diffusivity from current shear and density stratification spanning layers in which microstructure was measured off California. The current meters, however, were separated vertically by 20 m. It is likely that any important mixing processes occurred on smaller scales.

The micro structure sample data suggest that small planktonic organisms overcome dispersive processes such as diffusive mixing to a degree sufficient to form laminae on the cm scale. Their vertical variation is pronounced in density-stratified water but detectable in the mixed layer as well. By water movement, reproductive rate and behaviour, plankton become differentially layered in what may prove to be microniches. The existence of the microniche is indicated in my work by the accompanying cm-scale variation of non-living particulates and of nutrient salts, particularly that of nitrogenous nutrients, which are commonly limiting to phytoplankton growth in these waters. Spatial partitioning of microplankton populations likely increases the capacity of the habitat to support greater community diversity and higher standing stocks because interspecific competition for resources is reduced, in much the same fashion as in terrestrial communities. Unlike terrestrial communities, however, such partitioning in the sea is inherently less stable on the short term. As examples, increased mixing during wind storms would modify if not destroy fine-scale variation, and the nearly synchronous diel reproduction (at times depending on species) of diatom and dinoflagellate populations likely produces daily changes in plankton microstructure. How such processes of mixing and restructuring of layers affect development and evolution of plankton communities is a topic of considerable interest.

It now appears that niches for plankton organisms may identifiably occur in midwater on a variety of spatial scales. For example, Reid *et al.* (1978) were able to distinguish between coastal phytoplankton communities of the upper mixed layer and the density-stratified layer from larger scale, vertically integrative pump samples, and below the sub-metre niche proposed here is the sub-centimetre niche created by marine snow for both phytoplankton and small zooplankton, as identified by Alldredge (1972) and by Silver *et al.* (1978).

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