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Regulation of phytoplankton communities by physical processes in upwelling ecosystems

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ABSTRACT

Sinking rates of particles were superimposed on the x - z - t current field observed at 15S off the coast of San Juan, Peru in March–May, 1977 to calculate particle trajectories in the upwelling circulation. Vertical velocities were calculated by a modified variational objective analysis technique using the measured onshore and longshore currents in conjunction with the physical constraint of mass continuity. The calculated vertical flow showed considerable temporal and spatial variability, with the mean vertical transport varying by two orders of magnitude over the 16 km wide continental shelf. Changes in direction occurred rapidly (within 24 h) as has been observed for horizontal circulation in this region. The vertical velocity of water was much greater than the sinking rates of particles during the 52 day period, so that the net vertical transport of particles was controlled by the vertical velocity of the water. Reseeding of sinking particles from the surface offshore-flowing layer into the deeper onshore flow could not be demonstrated for this period, which may explain why the measured biomass and primary productivity were anomalously low in 1977. Vertical mixing greatly increased the possibility of reseeded by transporting material downward into the onshore flow. We suggest that recirculation of particles may normally occur in the Peruvian upwelling system, but that the continuity probably involves movement in the longshore as well as the cross-shelf direction.

1. Introduction

Coastal upwelling is a process in which surface waters are displaced offshore by a one-sided horizontal divergence caused by the longshore winds and are replaced by cold, nutrient-rich subsurface waters. Upwelling regions are characterized by substantial advective movement of water in both the longshore and onshore/offshore directions. The upwelling circulation also has significant components of temporal variation which occur over short (hours), intermediate (days), long (seasonal) and interannual time scales. Presently, it is uncertain to what degree communities utilize the physical structure of an upwelling system to enhance their growth or stability

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(Margalef, 1979), or whether the communities simply "withstand" the energetic physical conditions by adapting to the wide range of conditions that can occur.

Some populations and communities use the physical conditions of a particular habitat for their benefit. Estuarine dinoflagellate blooms can be maintained in both space and time by migration between the two layers in a region with typical estuarine circulation (Seliger *et al.*, 1970; Tyler and Seliger, 1978; Seliger *et al.*, 1981), and *Mesodinium rubrum*, a migratory photosynthetic ciliate, has been shown to maintain itself on the continental shelf during periods of active upwelling by a similar mechanism (Barber and Smith, 1981). Zooplankton also migrate between layers of water whose direction of flow is opposite in order to regulate their position (Peterson *et al.*, 1979; Wroblewski, 1982), and Mathieson (1982) hypothesized that anchoveta similarly utilize local currents to remain at one location. Use of currents by fishes and higher trophic level invertebrates at various stages of their life cycle has also been observed (Cushing, 1976; Parrish *et al.*, 1981). It appears that most trophic levels have members which utilize the prevalent current patterns to increase their reproductive success in a physically dynamic environment.

It has also been suggested that phytoplankton community composition is strongly influenced by the prevalent circulation patterns in upwelling systems. Malone (1975) suggested that "the high levels of net plankton productivity reflect the selective effects of circulation" and that small nanoplankton were selectively removed from upwelling areas by mass transport normal to the coast because of their low sinking rates. Migratory species also are selectively retained by utilizing the bilayered flow regime (Brink *et al.*, 1981; Barber and Smith, 1981). Therefore the size and composition of phytoplankton in both surface and source waters can be directly controlled by advective processes independent of biological (growth rates, grazing) processes.

The Peruvian upwelling region is a system in which changes in bottom topography and longshore wind stress result in upwelling which is enhanced locally, producing variations in water temperature, nutrients and plankton biomass alongshore as well as the expected changes offshore (Brink *et al.*, 1981; Huntsman *et al.*, 1981; Smith *et al.*, 1981). Plume structures are commonly observed (Kelley *et al.*, 1975) which increase or decrease in spatial extent through time depending on local wind stress, surface heating and longshore current interaction with the bottom topography. The region at 15S has persistent upwelling (Ryther *et al.*, 1971) and has received considerable study during the past two decades. In 1977 a series of current meter arrays were deployed off the coast, with a majority being moored at 15S (Brink *et al.*, 1978). The current meters were spaced within the water column so that both surface, intermediate and bottom flow could be measured on the continental shelf. In addition, arrays were deployed perpendicular to the coast to resolve the horizontal variations in the upwelling circulation. The resulting physical measurements provided a powerful data set with which to test the strength of the control of biological communities by physical processes.

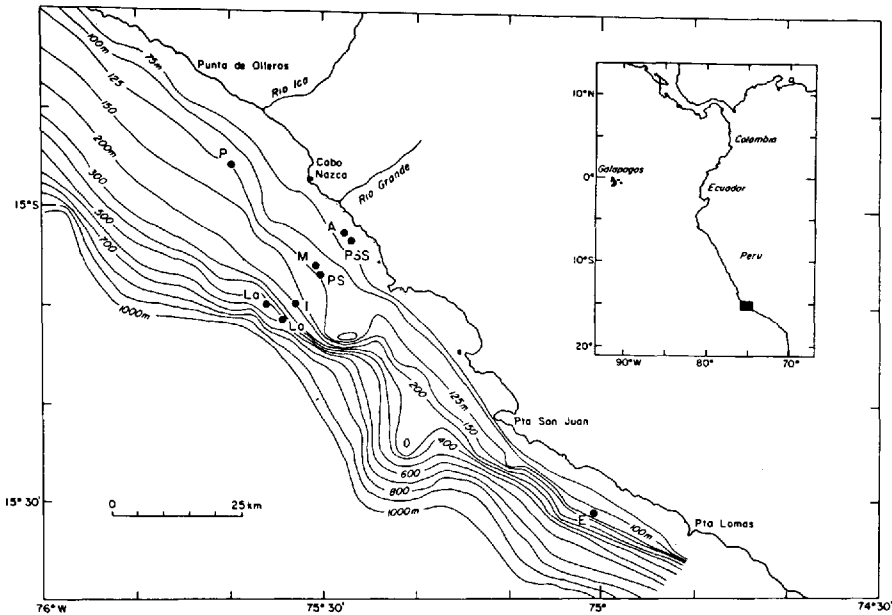


Figure 1. The location of the current meters used to measure horizontal velocities in the study area. PS and PSS were surface arrays, whereas Agave (A), Mila (M), Ironwood (I), Lagarta (La), Lobivia (Lo), Euphorbia (E) and Parodia (P) were positioned below 20 m.

2. Materials and methods

The region studied was at 15S off the coast of San Juan, Peru (Fig. 1) for 52 days from March–May, 1977. Five subsurface arrays of Aanderaa current meters (Agave, Ironwood, Lobivia, Lagarta and Mila, maintained by Dr. R. L. Smith, Oregon State University) and two additional arrays north and south of 15S (Euphorbia and Parodia) were moored for the entire period. Two surface arrays of VACM current meters (PS and PSS) were also monitored (by Dr. D. Halpern, PMEL/NOAA, Seattle) for the same period. The surface and subsurface arrays at 15S were as close as possible to each other but separated to prevent fouling. The data were low-pass filtered to remove diurnal tidal and higher frequency fluctuations; the half power point was 46.6 h with the half amplitude point at 40 h. A complete compendium of the data and methods of analysis is given in Brink *et al.* (1978).

The vertical velocity field was calculated by a variational calculus objective analysis method using the horizontal current meter observations. This variational method computes objectively adjusted values of both onshore velocities and longshore divergence through a cross-section such that the physical constraint of three dimensional mass continuity for an incompressible fluid is satisfied, i.e.,

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0$$

where u , v and w are the onshore, longshore and vertical velocity components in the x - y - z Cartesian coordinate system.

A modification of the variational formulation presented by O'Brien (1970) for calculating vertical motions in the atmosphere was the basis for the calculation of the vertical velocity estimates used here. The general formulation of the problem follows that of Sasaki (1958) and Stephens (1965). Let

$$F_k \left(e_i, \frac{\partial e_i}{\partial s}, \frac{\partial^2 e_i}{\partial s^2}, \dots, \frac{\partial^n e_i}{\partial s^n} \right)$$

be a set of constraints for certain initial estimates e_i . Also let $e'_i = e'_i(s)$, the i^{th} objectively modified estimate, and its derivatives be continuous in some region V and take on prescribed values on the boundary of V .

We can then define a difference functional

$$E(e'_i) = \int_V \left[\sum_i \kappa_i (e'_i - e_i)^2 + \sum_j \Gamma_j F_j \right] dV$$

where Γ_j are Lagrangian multipliers and κ_i are Gauss precision moduli. The latter are related to the variance of the estimates (Whittaker and Robinson, 1944) by

$$\kappa_i = \frac{1}{2\sigma_i^2}$$

Now, the objectively modified values can be computed by requiring the first variation of E to vanish.

For the study region estimates of the cross-shelf velocity components, were available from the current meter arrays at Agave/PSS, Mila/PS, and Ironwood (see Fig. 1). These arrays provided fairly high resolution in the vertical from near surface to near bottom. Furthermore, these arrays were all within the upwelling zone as defined by the internal Rossby radius of deformation (Hurlburt and Thompson, 1973). Thus, the areal coverage over the continental shelf in the plane normal to the coast was considered to be very good. The longshore divergence was initially estimated from the difference in the longshore velocity component between Mila and Parodia (Fig. 1). The vertical resolution at Parodia and the horizontal spacing of these arrays made the estimates of the longshore divergence much less precise and thus the weighting factors (i.e. the Gauss precision moduli) were adjusted to reflect this uncertainty in the accuracy of these initial estimates. Specifically, the weighting factor for the longshore divergence was related to the maximum variance (σ_{\max}^2) of the observations where as the cross-shelf estimates were related to the individual variances (σ_i^2) of the observations.

In the present context the estimates e_i are u_i (cross-shelf velocity component), $\partial v_i / \partial y$ (longshore divergence) and w_i (vertical velocity component). Since there were no measured vertical velocities, the initial estimates of w_i were set to zero. The boundary

conditions used were that $u = 0$ at the coast, $w = 0$ at the sea surface and no flow normal to the bottom. With these conditions and assumptions and using the physical constraints of three-dimensional mass continuity, the difference functional becomes

$$E\left(u'_i, \frac{\partial v'_i}{\partial y}, w'_i, \lambda_i\right) = \int_V \sum_i \left[\kappa_i (u'_i - u_i)^2 + \kappa^* \left(\frac{\partial v'_i}{\partial y} - \frac{\partial v}{\partial y} \right)^2 + \lambda_i \left(\frac{\partial u'_i}{\partial x} + \frac{\partial v'_i}{\partial y} + \frac{\partial w'_i}{\partial z} \right) \right] dV$$

$$\kappa^* = \frac{1}{2\sigma_{\max}^2} \text{ and } \kappa_i = \frac{1}{2\sigma_i^2}.$$

The vertical velocities were calculated by discretizing the functional, setting the first variation of the functional to zero and then solving the resultant set of linear equations numerically. One criterion for accepting the calculated vertical velocity estimates was that the adjusted cross-shelf velocity components could not vary more than one standard deviation from its initial value.

Depths of mixed layers were determined from the temperature records on the surface current meter arrays PS and PSS (Brink, 1979). Data were filtered with a half power point of two hours and decimated at hourly intervals. If the temperature recorded at a current meter agreed within 0.02°C with the shallowest instrument, then the mixed layer was assumed to extend at least to the depth of that current meter. If no temperature agreed with the shallowest to within 0.02°C , the depth of the mixed layer was assumed to be zero. Although density change would be a more accurate estimator of mixed layer depth, salinity-induced density changes are rare because salinity is nearly constant in the upper 25 m (Huyer *et al.*, 1978). Therefore temperature changes provided an accurate time series of mixed layer depths. The ΔT criterion used to define the mixed layer depth is arbitrary, but the patterns of mixing obtained are not substantially different when greater temperature differences are used (Brink, 1979).

Trajectories of particles over the continental shelf were computed by adding the vertical motion of a particle to the u -, v -, and w -velocities of the water and computing the distances moved in one-h intervals. Boundaries for the calculations were the shore, the bottom and 16 km offshore; the bathymetry is that used in numerical models for this region (e.g., Preller and O'Brien, 1980). The result is the calculated trajectory of a particle through time as it would have been influenced by the actual movement of water in 1977. All trajectories had the observed vertical mixing depths superimposed on them, so that if a particle was advected into the mixed layer its position was reset to the bottom of the mixed layer. The rationale for this step was to maximize the possibility of entrainment of a sub-population of phytoplankton by minimizing the distance through which particles must sink prior to entering the onshore flow. Biomass determinations within the upper 50 m showed the homogeneity of phytoplankton distribution within the mixed layer (Barber *et al.*, 1978). Molecular diffusive effects were not included because the diffusive time scale is large when compared to the advective time scale and would be important only in the viscous boundary layer, which is much narrower than the upwelling zone (Hurlburt and Thompson, 1973).

Table 1. Mean vertical velocities in m d^{-1} across the continental shelf. Positive values represent motion toward the surface.

Depth (m)	Distance from shore (km)								
	0	2	4	6	8	10	12	14	16
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	—	4.96	4.13	3.29	2.45	1.71	0.97	0.22	-0.52
20	—	8.53	6.98	5.43	3.89	2.64	1.41	0.17	-1.07
30	—	3.56	5.16	6.75	8.34	7.19	6.03	4.88	3.73
40	—	-0.48	2.73	5.94	9.17	9.05	8.95	8.85	8.74
50	—	-4.53	0.30	5.15	9.99	10.92	11.86	12.81	13.75
60	—	-3.89	0.02	3.92	7.83	10.40	12.96	15.52	18.09

3. Results

The calculated vertical velocities in the upper 60 m showed considerable cross-shelf variation (Table 1) as did the measured u - and v -components of flow (Brink *et al.*, 1978). A time series of the estimated vertical velocities at 20 m depth, 2 km from the shore (Fig. 3 in Brink *et al.*, 1980) showed the calculated estimates to be dynamically consistent with the longshore wind stress, longshore and cross-shelf velocity components, and the sea-surface temperatures. With the exception of the upper 20 m near the shelf break and the lower 20 m inshore, the mean vertical flow for the entire continental shelf was positive (i.e., upwelling occurred). The general trend reflected in Table 1 is that of a classical upwelling system: substantial vertical flux inshore and at intermediate depths, and little vertical displacement in surface waters as they move offshore in the Ekman layer.

The mean vertical flow is, however, not truly representative of the instantaneous water motion off Peru. Substantial variation occurs over the entire continental shelf (Table 2). All positions in the upper 60 m at some time experienced negative vertical transport (downward flow), and similarly, all experienced at some time substantial upward transport. Changes between the two extremes also occurred quite rapidly and may be associated with the passage of coastal trapped waves. An example of such a change occurred on March 25 (Fig. 2) following the passage of a wave trough around March 23 (Brink *et al.*, 1981). At hour 0 a strong reversal was occurring; i.e., onshore-flowing surface water and descending water near the coast. Maximum w -velocities were -44.0 m d^{-1} at 2 km offshore and a depth of 50 m. By hour 8 some offshore and upward flow had begun. By hour 16 the offshore and upward flow had deepened and strengthened, and by hour 24 strong positive vertical transport occurred throughout the upper 60 m from the coast to 14 km offshore. Horizontal flow also returned to a typical bilayered pattern by this time. It should be noted that equatorward (i.e., upwelling favorable) winds occurred throughout this entire period as well as the two weeks prior to March 25 (Brink *et al.*, 1981). Similar abrupt reversals of vertical and horizontal flow occurred throughout the 52-day period and can be related to similar wave events. Heburn (1980) used a three-dimensional numerical

Table 2. Minimum and maximum vertical velocities in $m\ d^{-1}$ across the continental shelf.

Depth (m)	Distance from shore (km)											
	0	2	4	6	8	10	12	14	16			
0	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00	0.00 → 0.00			
10	— 19.42	-12.19 → 13.64	-6.95 → 13.64	-1.71 → 8.86	-3.49 → 6.40	-2.82 → 4.60	-2.15 → 2.81	-1.47 → 1.61	-2.54 → 0.69			
20	— 32.25	-22.07 → 32.25	-12.60 → 23.38	-6.11 → 16.64	-11.29 → 17.67	-8.81 → 12.61	-6.34 → 7.47	-3.86 → 3.58	-5.14 → 1.38			
30	— 35.43	-31.55 → 35.43	-19.54 → 29.21	-13.06 → 23.94	-12.33 → 27.83	-9.94 → 22.21	-7.55 → 16.59	-5.16 → 15.31	-7.72 → 15.00			
40	— 31.03	-37.22 → 31.03	-22.23 → 25.84	-19.95 → 24.30	-20.10 → 26.89	-10.63 → 24.49	-4.94 → 25.04	-9.97 → 26.85	-20.02 → 28.68			
50	— 26.62	-43.93 → 26.62	-26.60 → 22.48	-26.85 → 24.65	-29.66 → 30.14	-16.06 → 30.53	-5.23 → 34.45	-16.71 → 38.39	-32.32 → 44.44			
60	— 18.64	26.60 → 18.64	-19.68 → 18.08	-23.69 → 21.23	-28.30 → 29.09	-16.01 → 30.54	-4.05 → 40.07	-10.49 → 49.60	-23.68 → 59.13			

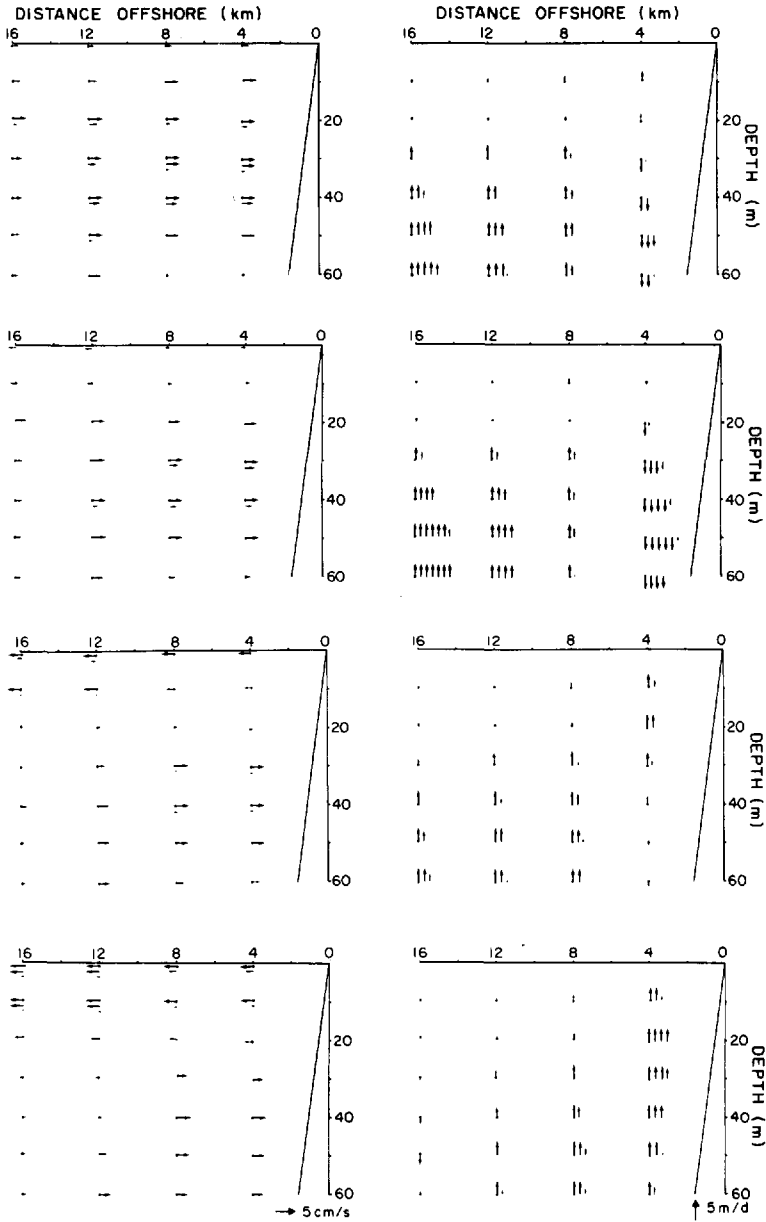


Figure 2. Changes in the u - and w -components (left and right panel, respectively) of flow at 6-h intervals on March 25, 1977. Actual bathymetry is shown. Each full arrow equals 5 cm s^{-1} for the horizontal velocity and 5 m d^{-1} for the vertical velocity.

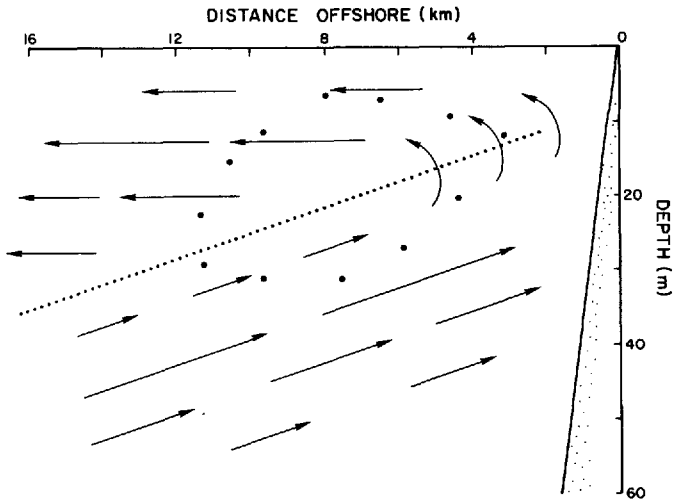


Figure 3. Hypothetical cross-shelf reseeding mechanism. Phytoplankton (solid circles) are advected offshore in the surface layer but sink into the onshore-flowing layer. They then are moved inshore and upwelled to the surface where a new bloom is initiated. The dotted line represents the observed mean depth of zero onshore/offshore motion.

model with a parameterization of the longshore currents to demonstrate the influence of coastal trapped waves on the vertical motion of the pycnocline in the Peruvian upwelling system. Figures 17 and 18 in Heburn (1980) showed good agreement between the estimated vertical velocities derived by the variational technique and the vertical motions predicted by the numerical model. A comparison of the estimates from this method and those derived from drogue experiments (Fig. 4 in Stevenson *et al.*, 1980) also showed good qualitative and quantitative agreement. These comparisons indicate that the calculated vertical velocities appear to be reasonable estimates of the flow during this period.

Trajectory analyses were computed to test the hypothesis that phytoplankton sink from the offshore-flowing Ekman layer, enter the onshore-flowing waters and are carried to the surface by vertical transport. A hypothetical illustration of this process is shown in Figure 3. This mechanism has been suggested as a means of "reseeding" newly upwelled waters with certain species of phytoplankton (Malone, 1975; Walsh *et al.*, 1980; Brink *et al.*, 1981) which increases the relative proportion of large, rapidly sinking species independent of growth rates or grazing pressures. However, the offshore-flowing surface layer deepens and slows as the distance offshore increases (Brink *et al.*, 1978), which effectively reduces the spatial extent over which such a reseeding might occur.

For the entire 52-day period we were unable to demonstrate a single occurrence of a particle moving offshore (beyond 8 km from the coast), sinking from the surface Ekman layer, entering the onshore flow, and finally being upwelled to the surface near

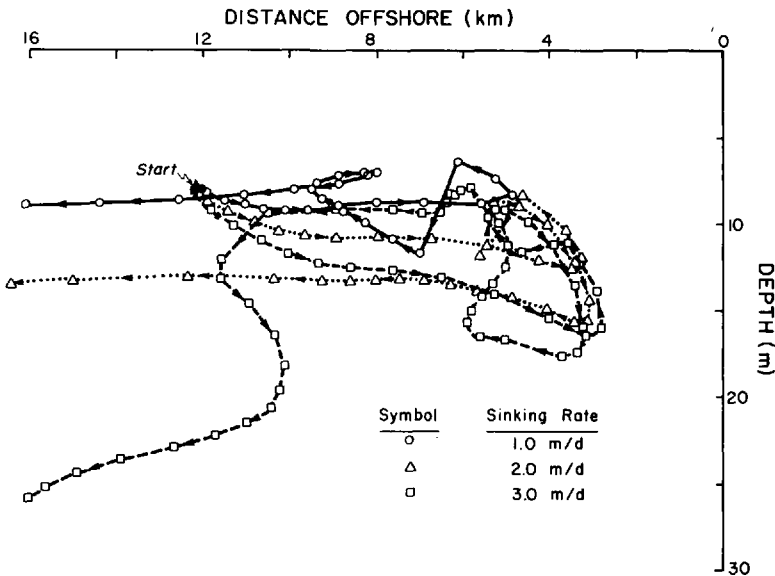


Figure 4. Trajectory of particles with different sinking rates beginning March 22, 1977. The particles move onshore, are upwelled toward the surface, and then are advected off the continental shelf. Arrows indicate that the population was completely mixed to the position indicated. Each symbol represents a 6-h time interval.

the coast. Although complete “loops” were not observed, it was observed that particles did enter the onshore-flowing water, were transported upward into the surface Ekman layer, and advected offshore and ultimately off the continental shelf. One example of this type of trajectory occurred on March 22 (Fig. 4). This pattern illustrates the effects of currents and their variability on the movement of planktonic organisms within the defined ecosystem boundaries. But the total absence of reseeding and relative infrequency of the pattern illustrated in Figure 4 emphasizes the lack of two-dimensional biological continuity during this period.

One potential mechanism to produce particle reseeding is by vertical mixing events which “inject” organisms into the onshore-flowing waters from the surface layer, thereby completing the cycle. This potential can be seen in the trajectories of particles for April 15 (Fig. 5). The particle initially was at the bottom of the mixed layer (20 m) at 6 km offshore. It is advected onshore, is mixed to the bottom of the mixed layer twice, and after approximately 150 h is advected into the offshore-flowing surface layer. It’s calculated trajectory was off the continental shelf; however, if a mixing event had occurred 11 km offshore, the particle would have then entered the onshore-flow again and ultimately returned inshore. The potential for increasing net vertical transport of organisms by mixing events into a layer with opposite flow may be large and the effect on the entrainment process may be substantial.

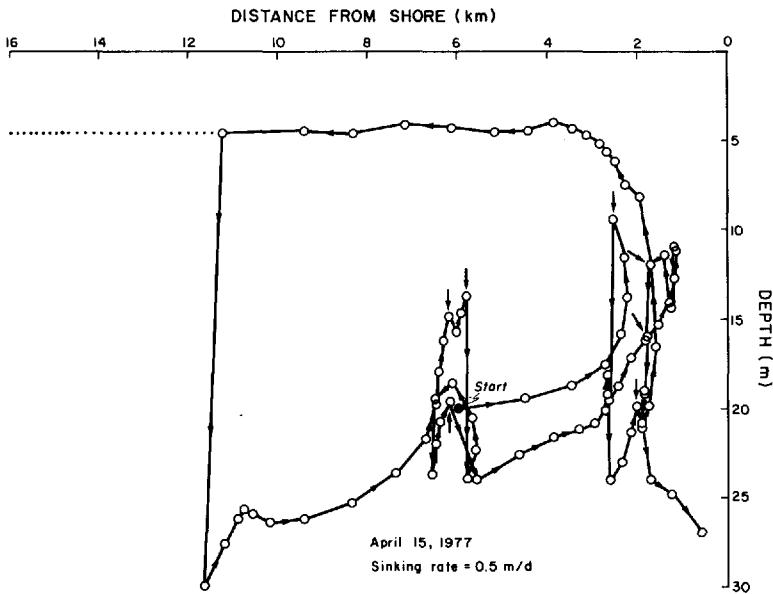


Figure 5. Trajectory of particle starting April 15, 1977. Arrows indicate that the population was completely mixed to the depth indicated. The dashed line indicates the actual trajectory; the solid line thereafter represents the trajectory of the population after a hypothetical mixing event. The mixing modifies the trajectory and increases the net downward vertical transport of particles, thereby allowing reseeding to occur.

The calculated vertical transport in most cases over-ride potential differences in sinking rates of different sized particles (Fig. 6). The period beginning April 16 was characterized by high rates of upward flow which caused even rapidly sinking (up to 6 m d^{-1}) particles to rise in the water column. Very little difference existed among particles with regard to their final position, which indicates the importance of water flow to the positioning of organisms within the water column.

4. Discussion

It presently is not possible to directly measure vertical velocities. Estimates have been made in the past based on the vertical displacement of isotherms or isopycnals (Saito, 1954 in Wooster and Reid, 1963), vertical estimates of horizontal divergence (Wooster and Reid, 1963; Federov, 1977; Stevenson *et al.*, 1980), and the distribution of chemical properties (Broecker *et al.*, 1978). All of these methods involve assumptions which reduce the precision and usefulness of the estimates, and due to limitations in temporal sampling, cannot be used to continuously analyze rapid changes of vertical velocities which occur in space and time. In contrast, the temporal and spatial resolution of the variational method is dependent only on the resolution of the horizontal currents measured and therefore is able to estimate the rapid changes which

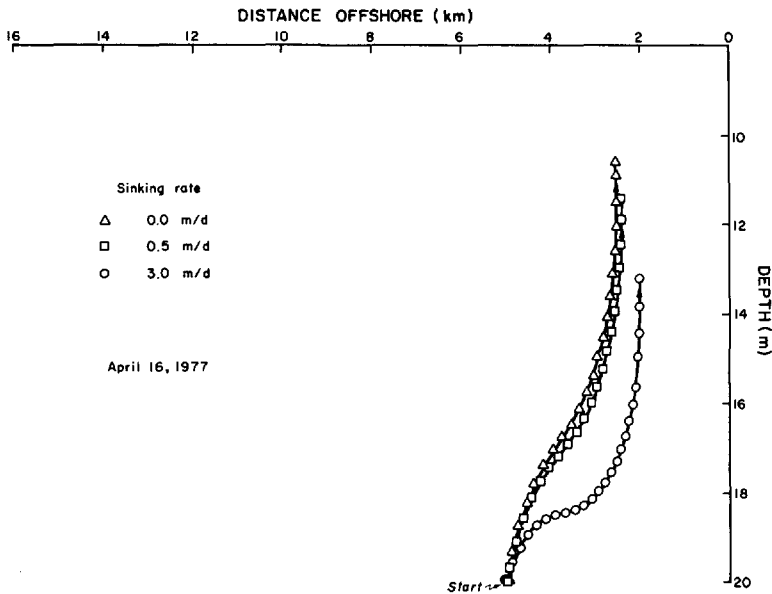


Figure 6. The effect of the vertical velocity of the water on the net vertical transport rates of particles with different sinking rates. All particles were initially at 20 m. Little spatial separation among particles with different sinking rates occurred.

occur in an upwelling region. Although the 52-day mean vertical velocities (Table 1) are not different than might be expected in an upwelling system, large variations occurred in the upward flux of waters both in space and time (Table 2). The maximum positive displacement rate in the upper 50 m was -44.4 m d^{-1} ($-5.1 \times 10^{-2} \text{ cm s}^{-1}$; negative velocities represent onshore flow), which is considerably greater than the rate generally considered to occur in upwelling regions (e.g., 1 m d^{-1} or $10^{-3} \text{ cm s}^{-1}$; Wooster, 1981). The mean for the entire shelf (upper 60 m) was 5.65 m d^{-1} ($6.53 \times 10^{-3} \text{ cm s}^{-1}$). However, it must be remembered that the region at 15S exhibits persistent, enhanced upwelling, so that vertical transport in this region is probably larger than the mean w -velocity for the entire Peru coast. In view of this, the calculated vertical fluxes appear to be reasonable estimates of the actual vertical transport which occurred during this period.

Although it has been hypothesized that the bilayered circulation pattern of upwelling regions might act as a "reseeding" mechanism for plankton populations (Brink *et al.*, 1981), we were unable to show a single occurrence during the 52-day period tested. This generally resulted from the sinking rates of particles being much smaller than the vertical transport. Therefore a particle inshore was generally advected toward the surface and carried offshore in the surface Ekman layer. At offshore locations the upward transport was less and the particles sank in the water column but because the shear zone between the opposite-flowing layers was deeper offshore (Brink

et al., 1978), the particles did not sink fast enough to enter the onshore-flowing waters, and the hypothesized reseeding mechanism did not function. We do not know how the currents of other time periods compare to this 52-day period in 1977, but there is some evidence to indicate that in April–May, 1976 the shear layer was much shallower (ca. 10 m, Brink *et al.*, 1980). It is also interesting to note that the surface biology in 1976 was dominated by massive blooms of the migratory dinoflagellate *Gymnodinium splendens* (Dugdale *et al.*, 1977). Huntsman *et al.* (1981) concluded that the increase in population size of the dinoflagellate was due to advection from offshore and not solely *in situ* growth. We suggest that coupled with advection and growth that the dinoflagellates were concentrated by utilizing the near-surface bilayered flow regime (i.e., periodically migrating into onshore-flowing waters), thereby maintaining and concentrating the population on the shelf. Such a concentration could only occur if the dinoflagellates were able to migrate through the shear zone into onshore-flowing waters. Because migration rates of up to 1 m h^{-1} have been observed for dinoflagellates (Eppley *et al.*, 1968; Heaney and Eppley, 1981), it appears feasible that such a concentration mechanism was operative during 1976.

The reseeding hypothesis is highly dependent on the magnitude of sinking rates. Early work (see Smayda, 1970) indicated that sinking rates of phytoplankton were highly variable and strongly dependent not only on cell size but on physiological state. More recent work using sensitive isotopic techniques has shown that in both cultures and natural populations phytoplankton sink very slowly, usually less than 2 m d^{-1} (Bienfang, 1979, 1981). In this study a wide range of sinking rates were tested ranging from 0.0 to 24.0 m d^{-1} , but no sinking rates resulted in reseeding. It should also be noted that the tested sinking rates were held constant throughout. It is possible that elevated sinking rates occurred offshore as a result of nutrient depletion and a change in physiological state, thereby allowing cells to sink more rapidly and enter the onshore-flowing waters. However, we do not believe this occurred because nutrient conditions were nearly always near saturating levels over the entire shelf, so that nutrient depletion would have been rare. Furthermore, because nitrate uptake is generally a function of light uptake (McCarthy, 1981), it is not clear that sinking rates would be reduced once cells entered the onshore-flowing, nutrient-rich waters. Because the depth of zero flow averaged 24 m at 12 km offshore (Brink *et al.*, 1978), cells would be experiencing very low light levels (Barber *et al.*, 1978) which would reduce nutrient uptake. If sinking rates were not rapidly and markedly reduced, the particles would soon settle to the sediment surface.

There exists a potential for vertical mixing events to act as a mechanism whereby surface plankton are mixed into shoreward-flowing water, thus increasing the net vertical transport of particles and increasing the probability of entrainment. Mixed layer depths varied both spatially and temporally off Peru which resulted in a heterogeneous environment for the biological communities (Fig. 7). Although large diurnal and event-scale variations occur (Brink, 1979), the average mixed layer depth at PSS (6 km offshore) was 5.58 m and was significantly greater than that at PS (12

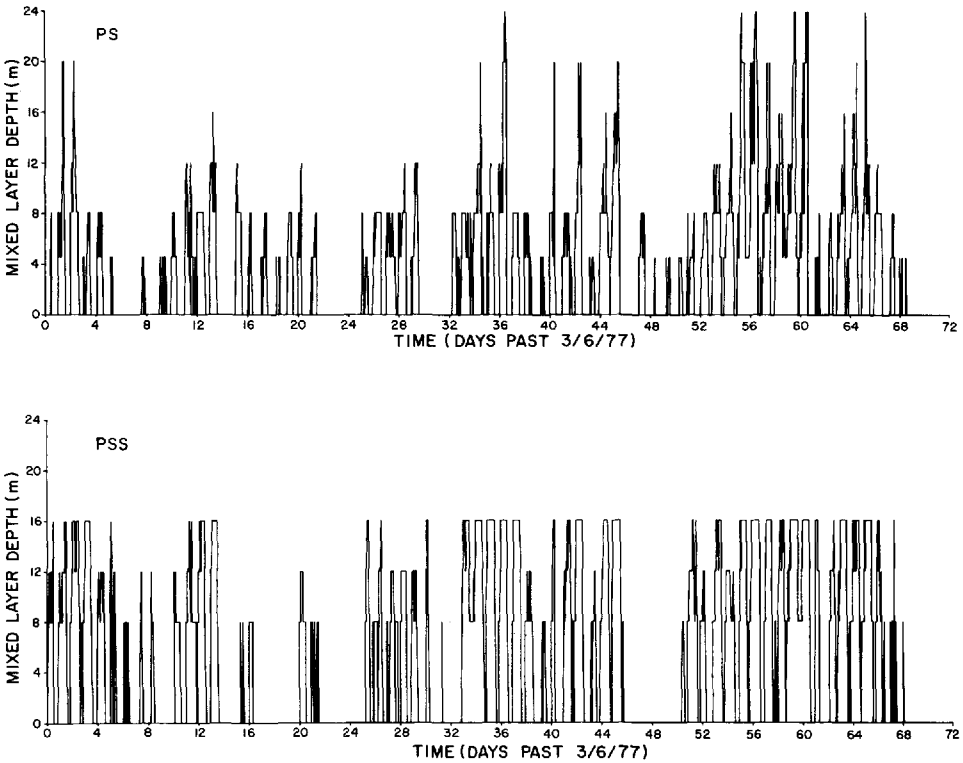


Figure 7. The temporal variations in mixed layer depths at 6 (PSS) and 12 (PS) km offshore.

km offshore) where the mean mixed layer was 3.75 m ($p < .001$; t-test). This difference occurred even though the maximum possible mixed layer depth we could measure at PSS was 16 km due to the vertical arrangement of sensors. The mixed layer depths at the two locations were also significantly correlated in time ($r = .80$, $p < .001$), which implies that similar forces were controlling both. The alongshore component of winds was slightly higher at PSS (Brink *et al.*, 1978), so that the difference in mixed layer depth could simply be the result of greater wind stress inshore. Cross-shelf variations in mixed layer depth also have biological implications. For example, shallow offshore mixed layers reduce the potential for substantial increases in the downward flux of particles; conversely, relatively deep mixed layers inshore suggest that the downward movement of populations may be occurring in spite of the large positive vertical transport of the water. We observed numerous occasions in which particles move back and forth within the inshore region (8 km), but the hypothesized reseeding pattern (Fig. 3) was obscured by repeated vertical mixing. If reseeding were occurring within the inner shelf region, it would further emphasize the importance of mixing as a mechanism to increase downward vertical flux of

phytoplankton as well as the importance of the w -velocities of the water and the insignificant contribution of passive sinking to the vertical positioning of phytoplankton.

Phytoplankton biomass and productivity were anomalously low during 1977, even though nutrient concentrations and growth rates were high over the entire shelf (Barber *et al.*, 1978). We suggest that the major reason for the low productivity and biomass was that the newly upwelled waters had reduced levels of phytoplankton biomass due to a disruption in the reseeding mechanism. The causes of such a disruption are uncertain, although Brink *et al.* (1981) suggested that one potential mechanism might be coastal trapped waves, and Heburn (1980) showed that coastal trapped waves play an important part in the Peruvian upwelling dynamics. Unfortunately it is impossible to test the importance of this and other potential disruptions without data to test the occurrence of reseeding in "normal" years, but reseeding has been suggested as an important mechanism for controlling the size of phytoplankton in upwelling systems (Malone, 1975). Further work is needed to demonstrate the positive relationship between recirculation and phytoplankton cell size.

Although much effort, both observational and experimental, has been placed on the effects and interactions of nutrients (e.g., Parsons and Takahashi, 1973; Tilman, 1977) and grazing (e.g., Frost, 1972; Eppley *et al.*, 1978) on phytoplankton community structure, our results indicate that the advective processes in upwelling systems are the dominant forces controlling the biomass and potentially the composition of phytoplankton communities. These effects occurred rapidly and over-rode any biotic interactions which were present. In systems where energetic physical processes occur (e.g. coastal regions, polar seas), it is imperative that a thorough appreciation of the physical forces be determined in order to correctly interpret the biological processes of the ecosystem.

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