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The influence of horizontal and vertical displacements on phytoplankton assemblages in tropical upwelling systems

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ABSTRACT

The mechanisms by which pelagic communities are regulated in physically dynamic environments have only recently begun to be elucidated. Phytoplankton assemblages in upwelling regions are not only influenced by chemical and biological interactions, but are dramatically impacted by a three-dimensional advective regime. The "success" of a phytoplankton assemblage, as defined by its biomass, growth and persistence through time, is often primarily controlled by the combined effects of particle sinking and its interaction with the physical field. It is shown that the pattern of circulation deduced from surface drogues is usually not coherent throughout the euphotic zone. Samples for biological properties taken from below the cross-over depth would have significantly different histories than those from above. The vertical movement of an upwelled water parcel has the potential for rapidly changing the light field which phytoplankton experience, thereby substantially altering primary production within an upwelling system.

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RÉSUMÉ

Effet des déplacements horizontaux et verticaux sur les populations phytoplanctoniques dans les remontées d'eaux tropicales

Soumises à des variations des conditions physiques de leur environnement, les communautés pélagiques présentent des mécanismes de régulation dont la description est toute récente. Dans les remontées d'eau, les communautés phytoplanctoniques sont influencées par des interactions chimiques et biologiques, mais elles y sont principalement soumises à un régime advectif tridimensionnel. La « réussite » d'une population phytoplanctonique, définie par sa biomasse, sa croissance et sa durée de vie, est souvent contrôlée d'abord par les effets combinés de la sédimentation des particules et de la circulation des eaux. Cette étude montre que le schéma de la circulation superficielle, établi à l'aide de flotteurs dérivants, n'est en général pas conservé dans la zone euphotique. Des échantillons biologiques présenteraient des différences significatives selon qu'ils aient été prélevés au-dessous ou au-dessus de la profondeur d'inversion. Dans son mouvement vertical, une parcelle d'eau ascendante pourrait perturber rapidement le champ lumineux auquel le phytoplancton est exposé, et modifier notablement la production primaire dans le système de remontée d'eau.

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INTRODUCTION

All life in the oceans interacts with the physical and chemical environment in which it exists, and the results of this interaction ultimately determines the survival or death of the species over time. Many organisms have adopted life strategies which are keyed to physical processes of their localized environment. For example, fishes reduce advective losses of eggs and larvae by spawning inshore where advection is minimized (Parrish *et al.*, 1981). Krill (*Euphausia superba*) eggs in the Southern Ocean sink into a countercurrent and after larval metamorphosis migrate back into surface waters, thereby maintaining their position in productive waters (Everson, 1977). Copepods off the coast of Oregon appear to control their distribution by maintaining, *via* vertical migration, specific relationships between the upwelling circulation and their life stages (Peterson *et al.*, 1979). These adaptations to the localized advective regime insure the reproductive success of the species and hence its survival through time.

Phytoplankton, by virtue of their planktonic existence, are much less capable of regulating their vertical or horizontal position than higher trophic level organisms. Most species are more dense than seawater and hence sink; in addition, the range of sinking rates among different species of phytoplankton is great (Bienfang, 1981). In upwelling regions, if a species does not sink or migrate, it rapidly is advected away from the coast and ultimately must survive in a nutrient depleted environment. If a species sinks in upwelling regions, it then has the potential of being advected to the surface at the upwelling center, thus continuing its growth (Smith *et al.*, 1983). Such regions also can advect phytoplankton closer to the surface, hence increasing their photosynthetic rates (Smith *et al.*, 1983). Other phytoplankton species, for example some dinoflagellates, by virtue of their positive phototactic behavior and migratory ability, often are present in regions that exhibit three-dimensional circulation. Examples of phytoplankton assemblages which are dominated by dinoflagellates as a result of the interaction of diel movements of organisms and water are Bioluminescent Bay in Puerto Rico (Seliger *et al.*, 1970), Chesapeake Bay (Tyler, Seliger, 1978) and the Florida continental shelf (Haddad, Carder, 1979). *Mesodinium rubrum*, a holotrichous ciliate with cryptomonad endosymbionts, also has been shown to use its migratory and phototactic response in a manner similar to dinoflagellates to establish and maintain itself as the dominant member of the phytoplankton assemblage (Barber, Smith, 1981). Non-motile phytoplankton may also be entrained in areas with estuarine circulation by sinking into the return flow. Malone (1975; 1980) suggested that upwelling areas selectively retain large, rapidly sinking phytoplankton by entraining them in the three-dimensional circulation pattern. It was also demonstrated in the New York bight that diatoms which had sunk from the euphotic zone were upwelled to the surface by shelf-break upwelling (Malone *et al.*, 1983). However, Smith *et al.* (1983) were unable to demonstrate the occurrence of re-entrainment in the onshore/offshore component of flow for passively sinking particles during the 1977 upwelling season off Peru, although

the effects of vertical motion on the assemblages' position in the water column was clearly shown. The importance of the advective regime (*i.e.* motion in both the vertical and horizontal planes) on the biomass of phytoplankton assemblages is paramount, especially in regions characterized by dynamic physical regimes.

In this paper the importance of horizontal and vertical advection to phytoplankton assemblages was investigated off the coast of Peru during a period in which the water column's biological properties (*e.g.* phytoplankton taxonomy, biomass, primary productivity, nutrient uptake, etc.) were intensively studied using conventional sampling techniques. We show that shear within the euphotic zone greatly complicates the analysis of biological data, and we describe the time scales of advection processes which have significant biological impacts. The importance of vertical displacements of water in Peru on phytoplankton distributions is demonstrated.

METHODS

Vertical velocities were calculated using the modified variational method described in detail by Smith *et al.* (1983). This method uses actual current meter data in conjunction with the assumption of mass continuity to compute objectively adjusted values of both onshore velocities and longshore divergence through a cross section. The current meter data were collected off the coast of Peru from March-May, 1977 at 15°S (Brink *et al.*, 1978); additional current meter data collected south and north of the 15°S section were used to obtain initial estimates of longshore divergence. Boundary conditions included zero flow at the coast and zero vertical motion at the sea surface. Therefore, the results of the analyses are cross-shelf (from the shoreline to 16 km offshore, the approximate location of the shelf-break) and vertical (from the surface to a depth of 160 m or the bottom) velocities computed at one-hour intervals. Actual bathymetry was used in the computations. Therefore, it is possible to follow the path of an individual water parcel within a vertical section normal to the coast, and to calculate the length of time it remains on the continental shelf.

It is also possible to superimpose the independent vertical motion of an organism onto that of the water and to determine its net movement (vertical and horizontal) through time (Smith *et al.*, 1983). In this analysis the organisms investigated were non-motile phytoplankton. The phytoplankton were given arbitrary, constant sinking rates which were estimated from those found in other eutrophic areas of the ocean (Bienfang, 1981; Johnson, Smith, 1986), and their resultant motion computed through time. Measured depths of mixing were also included in the analyses (Smith *et al.*, 1983). If a particle was within the surface mixed layer, its vertical position was reset to the bottom of the mixed layer. This maximized the chances for a particle to sink into the onshore-flowing layer and hence be entrained.

During the period that current meters were collected, a number of drogues (neutrally buoyant floats that are released at a known depth) were released and followed (MacIsaac *et al.*, 1985). The drogues, which had

small surface buoys to assist in detection, were set to follow the water at a depth of 5 m, and were tracked by the research vessel as they were moved by the water motion. The biological properties of the phytoplankton (*e.g.* phytoplankton biomass and taxonomy, nutrient uptake, primary production) in the water tracked by the drogues was determined at stations taken twice per day. We calculated the water movement during two of these drogues (Drogue I-2, sampled from March 27-29 and Drogue III-2, from May 2-4) to compare the observed flow of the drogues with that predicted by the trajectory analysis. We also compared the effects of differential flow within the

water column to distinguish between physiological responses induced by light and those induced by the differential flow itself.

RESULTS

The drogue released on March 22 initially headed inshore and northward, but then moved offshore and ultimately returned southward, completing a large half-circle (Fig. 9 *a* in MacIsaac *et al.*, 1985). The onshore/offshore component of the drogue motion is shown in Figure 1. We calculated the trajectory of a

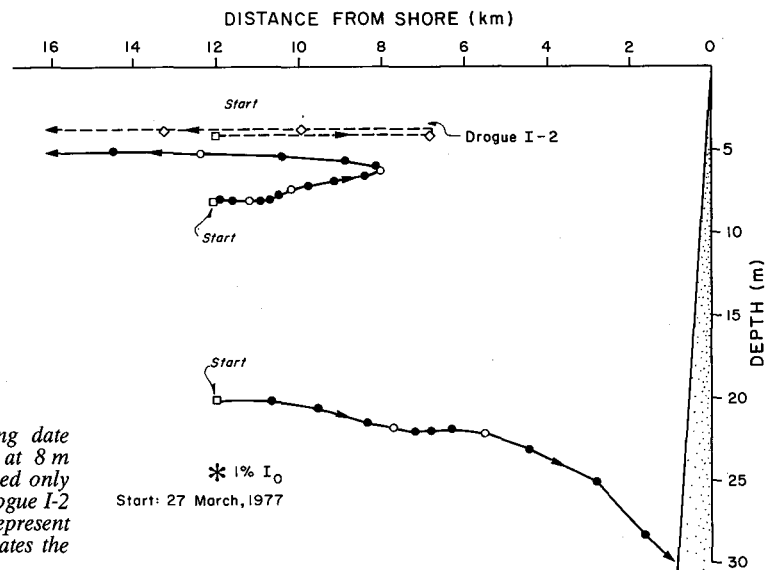


Figure 1

The vertical movement of phytoplankton at 15°S. Starting date March 27, 1977. The phytoplankton assemblage initially at 8 m moved inshore, then offshore; the assemblage at 20 m moved only inshore. Onshore/offshore component of movement of Drogue I-2 (diamonds; MacIsaac *et al.*, 1985) also shown. Closed dots represent 6-h intervals; open circles are 24-h intervals. Asterisk indicates the 1% light depth on starting date.

passively sinking phytoplankton assemblage initially at 12 km offshore (the same starting position of the drogue) but at a depth of 8 m rather than the stated depth of the drogue (4 m). This difference in starting depths is insignificant since vertical mixing during this period reached to 24 m (Smith *et al.*, 1983). The phytoplankton moved onshore (with a noticeable positive vertical component to the motion despite the assumed, uniform sinking rate of 1 m d^{-1}) but then reversed and was advected off the continental shelf (Fig. 1). The time the resident phytoplankton assemblage remained on the shelf was 107 hours; the residence time for the water sampled in the drogue study was approximately 96 hours. The similarity between the two residence times indicates that during this period there was a basic similarity among the onshore/offshore flow patterns within 25 km of the transect and that the biological characterizations (*e.g.* primary productivity, nutrient uptake) of surface waters (less than 10 m) were representative of a circulation pattern with mesoscale dimensions.

MacIsaac *et al.* (1985) also sampled water from the 1% isolume along the drogue track to determine the physiological adaptations occurring within the euphotic zone as it moves away from the center of upwelling. We calculated the trajectory of a phytoplankton assemblage initially at 20 m but at the same starting location as the drogue (Fig. 1). The depth of the euphotic zone (defined as the 1% light level) on that date was slightly deeper than this (26 m). The 20 m

assemblage moved inshore rapidly, was downwelled substantially, and would have "hit" the sediments near the coast after 66 hours. It should be pointed out that the trajectory analysis within two km of the coast is insensitive because of the large vertical and horizontal movements near the coastline as well as the lack of resolution near the boundary conditions within the model. The water obviously would not impinge directly on the sediments but would move parallel to the shoreline; nonetheless, the overall fate of the water and phytoplankton within it are the same. The large difference in the trajectories of phytoplankton at different depths within in euphotic zone emphasizes the importance of the vertical position in controlling the horizontal movement of phytoplankton. Water sampled at the 1% isolume after the start of the drogue would have had a completely independent trajectory from that at 4 m, so conclusions concerning the physiological processes at each depth must include effects of the water's advective history.

The drogue released on May 3 (III-2) had an initial starting location *ca.* 10 km north of the current meter array. It initially moved offshore and after approximately 24 hours was advected rapidly to the north. The onshore/offshore component of the drogue movement is shown in Figure 2. The calculated trajectory of a phytoplankton assemblage starting 6 km offshore and at a depth of 4 m shows that the movement at the section where the current meters were deployed is noticeably different than those controlling the motion

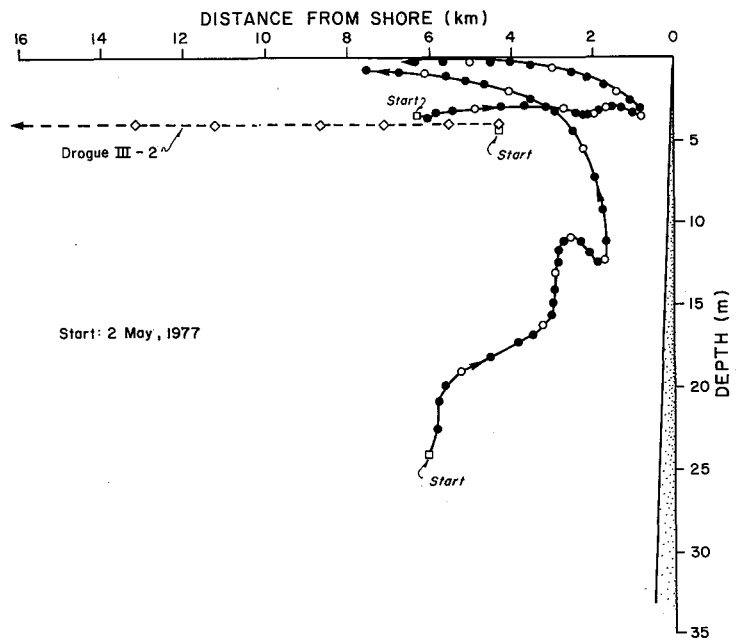


Figure 2
The vertical movement of phytoplankton at 15°S. Starting date May 2, 1977. An assemblage initially at 4 m is advected inshore and then offshore after being advected towards the surface. An assemblage at 25 m exhibited substantial positive vertical motion before being advected offshore; final position of both assemblages was approximately the same. Onshore/offshore component of movement of drogue III-2 (MacIsaac et al., 1985) also shown. Symbols as in Figure 1.

of the drogue. The assemblage moved inshore for 120 hours, and then began to move offshore (Fig. 2). An assemblage at 24 m was also advected inshore prior to moving offshore; it is also interesting that the phytoplankton undergo substantial net positive vertical motion despite the particles' rapid sinking, and after 204 hours (at that point the current meters were recovered and hence further trajectory analyses become impossible) the assemblage's calculated depth is 1 m. Therefore, in this case the starting depth had little effect on the ultimate position relative to the coast, but the upwelling velocities would have greatly impacted the depth distribution of any particles sus-

pending in the water column. Conclusions regarding water sampled only small distances from 15°S during this period cannot be extrapolated to larger areas.

The initial depth of the particle or assemblage in the water column has a large impact on its ultimate position (both vertical and horizontal) in an upwelling system. For example, trajectory analyses of neutrally buoyant particles (e.g. cyanobacteria, small diatoms) initially at 5, 15 and 25 m clearly show that the length of time that the particle is retained on the continental shelf as well as its ultimate fate is dependent on its initial depth (Fig. 3). For this time period starting March 19, the particle at 5 m is advected off the shelf

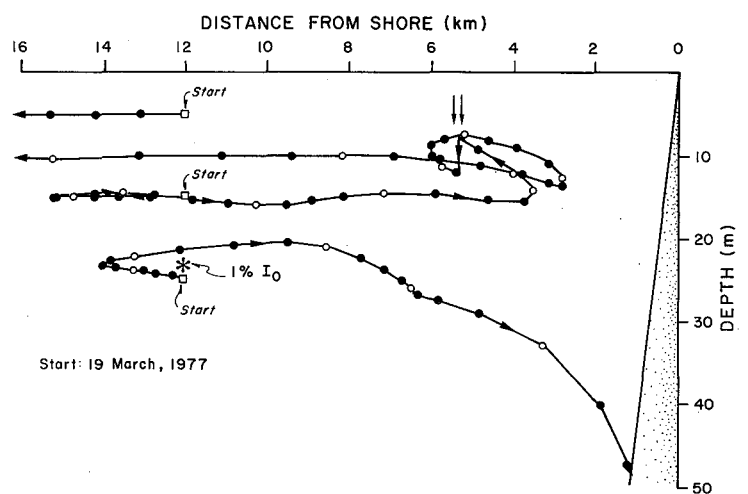


Figure 3
Trajectory of phytoplankton with initially different vertical positions on March 19, 1977. Assemblage at 5 m moved rapidly offshore; that at 15 m moved offshore, then inshore, then offshore. Assemblage at 25 m moved inshore and substantially downward. Symbols as in Figure 1. Arrows indicate mixing events.

in less than 24 hours; the particle at 15 m is also advected off the shelf, but has undergone transport inshore and upwards prior to offshore movement. The total time spent on the shelf by the 15 m water parcel is 267 hours. In addition to a long residence time, the assemblage has been within the mixed layer near the coast, and therefore probably enriched with nutrients. Such an event may serve to increase the growth of the assemblage relative to its initial state. The particle at

25 m is advected inshore, undergoes significant downward transport, and is advected into the sediments after 126 hours. It should also be noted that on May 2 the 1% light depth 12 km offshore was 24 m; therefore, the variable displacements all occurred from positions initially within the euphotic zone.

A similar, dramatic effect of initial water column depth was observed for the time period beginning

April 12 (Fig. 4). The phytoplankton assemblages at 10 and 15 m were rapidly advected off the shelf, but that at 20 m was advected inshore where it was repeatedly transported vertically towards the surface and mixed downward. It should be pointed out that the method used to calculate trajectories when influenced by mixing is the most conservative, *i.e.* it results in minimal estimates of the length of residence

on the shelf. A more realistic procedure might involve the incorporation of stochastic movements within the mixed layer to mimic turbulent transport. In this computation the water parcel ultimately rose to less than 5 m and was advected offshore. The water parcel at 25 m was advected inshore and into the sediments very close to the coast. Again, all starting depths were initially within the euphotic zone (31 m).

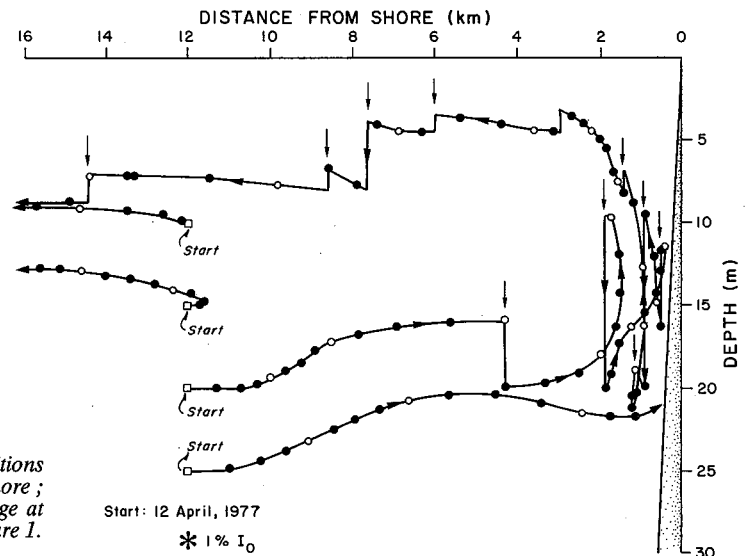


Figure 4

Trajectory of phytoplankton with initially different vertical positions on April 12. Assemblages at 10 and 15 m moved rapidly offshore; that at 20 m moved inshore, upward, then offshore. Assemblage at 25 m moved inshore and into the sediments. Symbols as in Figure 1. Arrows indicate mixing events.

DISCUSSION

The results of the trajectory analyses emphasize that in physically dynamic environments such as upwelling systems, it is extremely difficult to understand the history of phytoplankton assemblages sampled at one point in time, as well as to accurately predict their growth within the euphotic one. Net biomass change is a function of losses (due to grazing, advection, respiration, excretion, migration and sinking) and gains (increases potentially can result from photosynthesis, migration and advection). In upwelling regions, advection is often the dominant factor in regulating phytoplankton biomass (Huntsman *et al.*, 1981). Because the time/space relationships within the vertical and horizontal circulation patterns of upwelling systems are complex, understanding the transport of biological material is exceedingly difficult. However, as real-time models become more sophisticated, budgets of particulate materials and biota may be incorporated and the practices of theoretical and experimental biological oceanography may be merged.

The analyses of physiological responses of phytoplankton within a water column tracked by a drogue are greatly complicated by differential flow and shear within the euphotic zone because the history of an assemblage at the base of the euphotic zone probably is greatly different than that of a surface assemblage. Surface assemblages are influenced by vertical mixing induced by wind, which causes physiological responses on a number of time scales (Harris, 1978). Assemblages at the base of the euphotic zone off Peru may have had a completely different environmental history than those within the mixed layer. For example, an assem-

blage at 25 m might have recently (within hours) been mixed to that depth from the surface and entrained by the onshore-flowing water (Fig. 4), or it might have been at that depth for a number of days (Fig. 3). Clearly the physiological adaptations in these two hypothetical cases would be greatly different. The study by MacIsaac *et al.* (1985) demonstrated markedly different responses by assemblages sampled from high and low environments (50 and 1% of surface irradiance). Although there were periods when the movement of surface water along the coast was similar to that calculated by the trajectory analysis, undoubtedly there would be few cases in which that was true for low light (*i.e.* below the crossover point in the horizontal circulation pattern) assemblages. Thus the responses MacIsaac *et al.* (1985) observed may have been a result of different physiological conditions, but they also must have been strongly influenced by the past history of the assemblages, and that history was not only influenced by surface mixing events but the differential flow within the water column. Most likely the responses observed were a combination of both factors, since the time scale of water movement was slightly greater than that normally associated with metabolic changes of phytoplankton (Steemann Nielsen, Park, 1964; Eppley, 1981; Falkowski, 1983). Nonetheless, conclusions from drogue studies in regions with significant shear within the euphotic zone should be examined closely.

It is illustrative to look at the spatial scales which the variational analyses predict significant effects of vertical and horizontal movement on phytoplankton. Vertical motion can be very rapid: for example, on April 16 the phytoplankton assemblage nearshore was advected from 20 to 10 m in 24 hours (Smith *et al.*,

1983). If the attenuation coefficient was $.158 \text{ m}^{-1}$ (that found on that date farther offshore; Barber *et al.*, 1978), then the vertical motion would increase the light available for photosynthesis from 4 to 21 %. Such a rapid change might cause photoinhibition prior to photoadaptation, although the time scale of movement is similar to that reported for photoadaptation (Prezelin, 1981). Photosynthesis definitely would be expected to increase in a linear fashion at those light levels, and therefore the primary production and growth rate of the assemblage in the nutrient replete waters would also be expected to increase as well. Similar downward fluxes were observed (see Fig. 3), so that vertical velocity changes in the system can be expected to have significant impacts on phytoplankton growth as well as distribution. The time scale of vertical motion is not as rapid as that of vertical mixing, which is a function of depth of mixing (h) and the coefficient of eddy viscosity in the vertical plane (K_z) such that

$$T = h^2/2K_z,$$

where T is the time scale of mixing (Gallegos *et al.*, 1983). However, vertical motion due to advection is much more rapid than simple sinking of phytoplankton (see Fig. 5; Smith *et al.*, 1983) and of the same magnitude as vertical incursions due to internal waves (Kamykowski, 1976). The effects of vertical displacements in upwelling systems are clearly important in structuring the biomass distribution within the water column.

It has been suggested that sinking from the euphotic zone is extremely important in allowing a diatom assemblage to persist in upwelling systems (Smetacek, 1985). He argued that rapid sinking would seed populations into nutrient-rich, deep water that is ultimately transported to the surface. He also pointed out that some colonial diatom species (*e.g.* *Thalassiosira* spp., *Chaetoceros sociale*) grew rapidly prior to nutrient depletion, and the colonial matrix tended to disintegrate upon senescence giving rise to individual cells. Smetacek (1985) hypothesized that such behavior not only increases the probability of these species remaining in the upwelled waters (*i.e.* becoming entrained), but that disintegration of colonies slows sinking and provides for the dispersal of cells over a wide area. Based on our trajectory analysis, we suggest that such behavior might increase the chances of entrainment by the following mechanism: Colonies are advected offshore and sink rapidly, but upon disintegration of the colonial matrix, the individual cell's sinking rate is greatly decreased, allowing it to be transported onshore in the return flow and ultimately upwelled to the surface. Such a hypothesis requires that the positive vertical displacements of the water inshore be offset by negative phytoplankton motion (*i.e.* net sinking) offshore. We have found that although the spatial and temporal variations of vertical motions are great (Smith *et al.*, 1983), the "average" conditions in 1977 were such that the magnitude of the vertical velocities of water over the entire shelf were

much greater than those which could reasonably be attributed to phytoplankton sinking. For example, on April 16 rates up to 3.0 m d^{-1} still resulted in positive motions of phytoplankton (Smith *et al.*, 1983). If cells had large enough sinking rates to sink rapidly through the surface, offshore-flowing layer, then they also sank rapidly through subeuphotic depths despite being advected onshore. Thus the fate of rapidly sinking particles was to sink to the sediments of the continental shelf. Disintegration within the water column of colonial diatoms such as *Chaetoceros* and *Thalassiosira* spp. (which are commonly observed off Peru; MacIsaac *et al.*, 1985) would provide a mechanism to produce variable sinking rates for these species and increase their chances for survival and reproduction in the upwelling system. Whether such a mechanism is of sufficient magnitude to increase the probability of reseeding is unknown.

In physically dynamic environments such as tropical upwelling regions advection plays a dominant role in regulating biological communities. Despite this generalization, little attention has been given to delineating the various physical-biological interactions in the ocean. We suggest that serious consideration be given to designing programs which directly or indirectly measure vertical velocities in the water column in concert with vertical turbulence rates, since these movements play a major role in the distribution and flux of heat and biota. We also suggest that biological oceanographers consider the advective regime within the euphotic zone (even if quantitative knowledge is lacking) prior to sampling so that the observed experimental responses can be placed in context of the entire flow field.

CONCLUSIONS

We conclude that in tropical upwelling systems the role of vertical transport on biological processes has been underestimated. Transport is of such magnitude to alter the phytoplankton assemblage's environment rapidly and produce variations in biomass, distribution and production of plankton. Furthermore, the three-dimensional circulation pattern produces a complex history of particles within the water column, and this history may complicate the interpretation of measurements of rate processes. Conclusions drawn from measurements made on whole-water samples should be made with caution in such physically dynamic regions.

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