EOS

Transactions, American Geophysical Union
Vol. 67 No. 9 March 4, 1986

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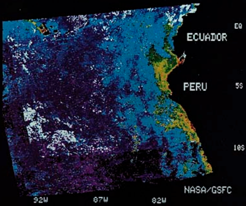

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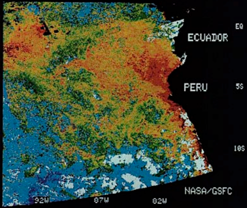

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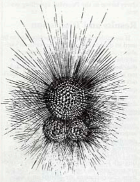
The Oceanography Report



Globigerina Bulloides, enlarged 150×, from a drawing in *Three Cruises of the Blake* by Agassiz (1888).

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Variability of the Productive Habitat in the Eastern Equatorial Pacific

Gene Carl Feldman

Introduction

There exists ample evidence supporting the link between ocean productivity and the intensity of upper ocean vertical motions [*Thompson*, 1981]. Where these motions increase the vertical transport of nutrients to the surface waters, regions of enhanced biological production often result. This relationship has been demonstrated quite clearly for one of the most highly productive regions of the world's ocean: the coastal upwelling zone along the western coast of South America. Investigations that relate changes in local winds, ocean circulation, and the vertical distribution of density and nutrients to the patterns of enhanced biological production have shown that relatively small changes in the physical environment have large consequences for the ecosystem [*Barber and Smith*, 1981; *Smith et al.*, 1983]. What is missing, however, is an understanding of the temporal and spatial scales of these processes and of the resulting variability in the distribution and abundances of phytoplankton. Not only do phytoplankton represent the first link in the food chain, but their patterns of distribution in time and space may provide clues as to how oceanographic processes regulate primary production [*Yentsch*, 1983].

This paper focuses on the eastern equatorial Pacific (Figure 1), which includes the coasts of northern Peru and southern Ecuador and extends offshore to the Galapagos Islands. This region is of particular interest because of its proximity to the equator; consequently, it is influenced by such features as the Equatorial Front and the Equatorial Undercurrent. One of the first scientific descriptions of the region was given by *Schott* [1931], in whose work the upwelling areas were classified by sea surface temperature, salinity, and current observations. *Love* [1972] used the extensive Eastern Tropical Pacific (EASTROPAC) data set to describe the major physical, chemical, and biological characteristics of the eastern equatorial Pacific. More recently, *Lukas* [1981] described the equatorial oceanic circulation patterns affecting this region, with particular emphasis on the Equatorial Undercurrent and its influence on the coastal upwelling area. A description of the hydrologic aspects of the main upwelling areas off Peru has been given by *Zuta et al.* [1978]. Specific descriptions of the northern Peruvian upwelling area between 4° and 6°S [*Fahrbach et al.*, 1981] and of the major upwelling center off Chimbote, Peru, at 9°S [*Guillen and Calienes*, 1981] have described the general physical characteristics of these regions, along with the observed variability in oceanographic, meteorological, and biological conditions.

This paper has two primary objectives. The first is to show that satellite ocean color data can be used to define the spatial extent of the region of enhanced biological production, referred to here as the productive habitat, in the eastern equatorial Pacific. The second objective is to determine the degree of interannual variability in the areal extent of the productive habitat and in the estimated primary production of the region.

Materials and Methods

Fourteen Coastal Zone Color Scanner (CZCS) images covering the eastern equatorial Pacific (5°N–15°S, 95°W–75°W) were processed on a satellite data and image processing system at NASA's Goddard Space Flight Center, according to procedures described by *Gordon et al.* [1983]. The changes in ocean color detected by the CZCS provide a quantitative measure of near-surface phytoplankton pigment concentrations. These concentrations, which for remote sensing applications represent the sum of chlorophyll a and phaeophytin a, are an index of phytoplankton biomass and may be empirically related to primary production [*Smith et al.*, 1982; *Platt and Herman*, 1983]. The depth to which the satellite measurements apply is inversely related to the concentration of phytoplankton and suspended material in the water column. The CZCS-derived values represent the average pigment concentration to a depth of 1 optical attenuation length (approximately the top 20–30% of the euphotic zone), the depth of which varies from approximately 17–1.6 m over the pigment concentration range of 0.1–10.0 mg/m^3 [*Smith and Baker*, 1978], respectively. The processed CZCS images that were used in this study were remapped to uniform spatial coordinates and then composited to produce the three "seasonal" mean pigment concentration scenes from which the data presented in Figures 3 and 4 were derived.

A method to delineate regions of enhanced biological production, making use of both the qualitative and the quantitative information contained in the CZCS data, was developed. All the images were examined to determine the open ocean pigment concentration values for areas that were removed from probable coastal enhancement. Similarly, regions in which the maximum gradients in pigment concentrations occurred were also identified. These regions were generally associated with distinct mesoscale structures and features that

Cover. Satellite ocean color images showing the distribution of phytoplankton pigments in the eastern equatorial Pacific Ocean. These computer-generated images, color-coded according to concentration range, are time and space composites produced from data collected during the period December 1978–January 1979 (Dec 78–Jan 79) and December 1979–January 1980 using the Coastal Zone Color Scanner (CZCS) aboard the National Aeronautics and Space Administration Nimbus 7 satellite. Regions of high concentrations (above 1 mg/m^3) are yellow and orange; intermediate levels are green and light blue; lowest levels (less than 0.3 mg/m^3) are dark blue. The Ecuadorian and Peruvian coastlines are masked in black along the right sides of the images, and the Galapagos Islands can be seen along the equator near 92°W.

Mean phytoplankton pigment concentrations (an index of phytoplankton biomass) for the entire region increased by a factor of 3.5 from late 1978 to late 1979. The area of the productive habitat (defined as the region in which satellite derived pigment concentrations exceeded 1.0 mg/m^3 increased 14-fold over the same period and covered nearly 0.5×10^6 km^2. The 1982–1983 El Niño reduced the size of the productive habitat and the levels of primary production when compared with the Dec79–Jan80 period but, surprisingly, showed higher values of both parameters when compared with the Dec78–Jan79 period. Although significant mesoscale variability was observed over short time scales (daily to weekly), monthly CZCS composites retained the major mesoscale structures and dominant features of the region and were found to be the best means for quantifying the large-scale interannual variability. For more information, see the article "Variability of the productive habitat in the eastern equatorial Pacific" by Gene Carl Feldman, p. 106, in The Oceanography Report.

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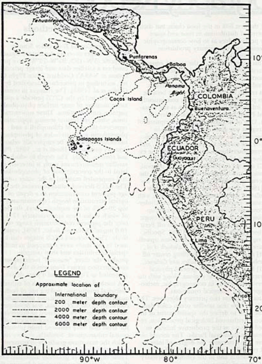

Fig. 1. Map of the eastern equatorial Pacific Ocean, showing the major features of the submarine bathymetry.

could most likely be attributed to coast- or island-induced processes. The images were then computer enhanced so that regions with values above and below a selected pigment concentration were clearly distinguishable. Setting the boundary at pigment concentrations in the range 0.8–1.5 mg/m^3 generally produced images that satisfied the criteria described above. For this study, the 1.0-mg/m^3 contour was selected as the most representative boundary separating the productive habitat from the open ocean region.

Recent work by *Platt and Harrison* [1985] has shown that in addition to this somewhat subjective choice of the 1.0-mg/m^3 pigment contour as a means of distinguishing between the productive coastal waters and the generally less productive waters further offshore, there may be biochemical evidence to support this value as well. Their data show that the relationship between new to regenerated production saturates at nitrate concentrations of approximately 1.0 μg atoms/L NO_3. New production is defined as the production resulting from the injection of new nutrients into the euphotic zone (e.g., through upwelling, vertical mixing, diffusion) rather than that production supported by nutrients that have been recycled within the euphotic zone itself [*Dugdale and Goering*, 1967]. Highly productive regions, of which upwelling systems are a good example, are characterized by the effective ratio of new production to total production being very high (roughly 80%, according to *Platt and Harrison* [1985]). In the Peruvian upwelling system, there is a general correspondence between the offshore 1.0 μg atoms/L NO_3 concentration and surface chlorophyll concentrations of 1.0 mg/m^3 (R.T. Barber, personal communication, 1985). This relationship, when considered in light of the findings of Platt and Harrison, tends to support the choice of the 1.0-mg/m^3 pigment concentration contour as representing the approximate boundary between productive habitat and the open ocean region.

The selected boundary between oceanic and enhanced production also has significant ecological justification. *Walsh et al.* [1980] implied that chlorophyll concentrations of at least 0.7 mg/m^3 would be required to satisfy the daily carbon demand of first-feeding anchovy larvae in the Peruvian upwelling system.

Results and Discussion

If monthly or seasonal composites are to be used to quantify large-scale interannual variability, it is first necessary to determine whether or not significant coherence in the distributions and abundance of phytoplankton exists in both time and space for the periods to be covered by the composites. Frequency distributions of satellite-derived pigment concentrations represent one way of determining whether major changes in phytoplankton biomass have taken place from one period to the next. Changes in spatial distributions can best be assessed by a visual inspection of the satellite images. Frequency distributions of some of the CZCS images covering the December 1978 through January 1979 (Dec78–Jan79) and December 1979 through January 1980 (Dec79–Jan80) periods are presented in Figures 2*a* and 2*b*. The pigment concentrations are plotted on a logarithmic scale to show more clearly the contribution of each concentration range.

Although the patterns of phytoplankton distribution displayed significant mesoscale variability, there is sufficient similarity in the shapes of the curves within each time period to justify producing "seasonal" mean composites. These time/space composites retain the major features observed during their respective periods and appear to be the best means for quantifying the degree of interannual variability. A comparison between Figures 2*a* and 2*b* also shows that the interannual signal between these years was greater than that observed over the shorter time scales used to construct the composites. The frequency distributions for the individual CZCS images covering the December 1982 through February 1983 El Niño period (not presented) were similar to those from the Dec78–Jan79 period with the exception of a general increase in the 1.0–5.0-mg/m^3 range. As is discussed later, high levels of phytoplankton biomass were observed throughout the 1982 El Niño along a narrow coastal band.

Cumulative distributions (Figure 3) derived from the mean composited images document the large-scale interannual variability observed during the three time periods considered in this study. As described earlier, if it is assumed that the area of enhanced biological production is represented by those waters in which pigment concentrations exceeded 1.0 mg/m^3, the data show that this region constitutes less than 3% of the total study area in Dec78–Jan79, greater than 30% one year later, and roughly 10% during El Niño (also see Table 1).

The distributions for the Dec78–Jan79 and El Niño (Dec82–Feb83) periods are surprisingly similar, while their contrast with the Dec79–Jan80 period is striking. The major question raised by these findings does not revolve around El Niño but rather in trying to understand the reasons behind the apparent degree of interannual variability experienced between the Dec78–Jan79 and Dec79–Jan80 periods, two periods during which conditions throughout the region have been characterized as being close to normal [*Zuta and Quispe*,

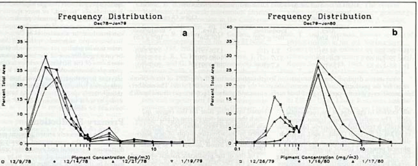

Fig. 2. Frequency distributions of satellite-derived phytoplankton pigment concentrations (in milligrams per cubic meters) versus the percentage of total cloud-free surface area covered by each concentration range for the region 0°–10°S, 87°–78°W, as observed by the Coastal Zone Color Scanner (CZCS). (*a*) Observations for December 9, 1978 (mean = 0.48 mg/m^3, standard deviation (SD) = 1.04 mg/m^3); December 14, 1978 (mean = 0.61 mg/m^3, SD = 1.62 mg/m^3); December 21, 1978 (mean = 0.53 mg/m^3, SD = 1.37 mg/mm^3); January 19, 1979 (mean = 0.38 mg/m^3, SD = 1.08 mg/m^3). (*b*) Observations for December 26, 1979 (mean = 1.04 mg/m^3, SD = 1.04 mg/m^3); January 16, 1980 (mean = 2.53 mg/m^3, SD = 2.88 mg/m^3); January 17, 1980 (mean = 1.54 mg/m^3, SD = 1.89 mg/m^3).

1981]. There is, however, evidence to suggest that there may have been significant large-scale oceanic and atmospheric differences between the two periods [*Sadler and Kilonsky*, 1981; *Donguy et al.*, 1982; *Mangum and Hayes*, 1984].

While data from which strong correlations between large-scale variations in circulation and interannual variability in phytoplankton production are particularly scarce for this region, a recent study by *Chelton et al.* [1982] of the California current system may provide some insight into this question. They conclude that large-scale changes in circulation patterns altered the nutrient supply available for primary production through either horizontal or vertical advection. Although it is not as well documented as the California system, significant variability in circulation patterns have been shown to occur in the eastern equatorial Pacific as well. *Lukas* [1981] demonstrated the variability in the strength of the Equatorial Undercurrent, which could be significant because of the undercurrent's role in supplying the Peru Undercurrent, which is the major source of water that upwells along the Peru coast. In addition to supplying the coastal upwelling system, variations in the strength, location, and timing of intensified undercurrent flows could alter the large-scale patterns of vertical mixing and nutrient supply, thereby influencing phytoplankton production. Recent improvements in large-scale ocean models (J. J. O'Brien, Florida State University, Tallahassee; personal communication, 1985) have begun to provide information about many of the parameters that could help explain the observed interannual variability in phytoplankton abundances throughout this region.

The Productive Habitat

The concept of a productive habitat is somewhat different from the traditionally defined coastal zone or, more specifically, coastal upwelling region. The coastal zone is often defined by submarine topography and gener-

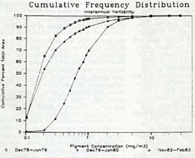

Fig. 3. Cumulative frequency distributions of satellite-derived phytoplankton pigment concentrations (in milligrams per cubic meter) versus the percentage of total cloud-free surface area covered by each concentration range for the eastern equatorial Pacific, as observed by the CZCS during December 1978–January 1979 (mean = 0.29 mg/m^3, SD = 0.80 mg/m^3); December 1979–January 1980 (mean = 1.04 mg/m^3, SD = 1.44 mg/m^3); November 1982–February 1983 (mean = 0.53 mg/m^3, SD = 1.52 mg/m^3).

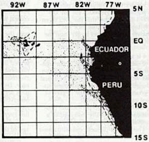

Fig. 4. The area of the productive habitat derived from Nimbus 7 CZCS images for the periods Dec78–Jan79 (darkly stippled), Dec79–Jan80 (lightly stippled) and Dec82–Feb83 (enclosed by dashed line). The coast of South America is in black along the right-hand edge of the image, and the Galapagos Islands are located on the equator at approximately 90°W.

TABLE 1. Surface Area and Estimated Primary Production

	Productive Habitat		Open Ocean	
	Area, 10^3 km^2	Production, 10^{10} g C/d	Area, 10^3 km^2	Production, 10^{10} g C/d
Dec 78–Jan 79	34 (3)	2.1 (10)	1326 (97)	19.2 (90)
Dec 79–Jan 80	468 (30)	27.7 (47)	1082 (70)	31.5 (53)
Dec 82–Feb 83	138 (9)	8.7 (30)	1379 (91)	20.7 (70)

Values to a depth of 1 optical attenuation length (approximately the top 22% of the euphotic zone) for the productive and open ocean habitats of the eastern equatorial Pacific. The numbers in parentheses give the percentage of total surface area and total production represented by each value.

ally extends to the edge of the continental shelf. The coastal upwelling region, however, generally is restricted to a narrow band within 50 km of the coast [*Smith*, 1968], its width dictated by the offshore extent to which the physical process of coastal upwelling can occur. The size that is ascribed to the upwelling area is particularly important when estimates of total ecosystem production based on discrete measurements of primary production are then extrapolated over the entire region. Although Smith cautioned against confusing the physical process of upwelling with its effects, most estimates of total ecosystem production for this region have relied upon the physical description of the upwelling zone rather than the area defined by levels of enhanced biological production resulting from these processes. It is this region that can now be defined and monitored through the use of satellite ocean color measurements.

Traditionally derived sea surface temperature maps (i.e., from ships) are severely limited in their ability to estimate the offshore extent and variability of the upwelling region. Unfortunately, very little reliable satellite-derived sea surface temperature information is available for the early periods that are being considered in this study. The information that is available, however, reveals a general correspondence between the patterns of upwelling observed in the sea surface temperature field and the regions of enhanced biological production [*Feldman*, 1985]. Specific comparisons between coincident satellite-derived sea surface temperature and phytoplankton pigment distributions for the December 1978 period show that the area of enhanced phytoplankton abundance was approximately 1.1–1.5 times larger than the area identified as cold, recently upwelled water.

Figure 4 is a graphical representation of the area of the productive habitat in the eastern equatorial Pacific. Although many of the fine details were lost in going from the actual satellite images (see cover) to this representation, the general features and the degree of interannual variability are seen.

During the Dec78–Jan79 period, the productive habitat was generally restricted to a narrow coastal band approximately 50–75 km in width. The highest pigment concentrations (5.0–10.0 mg/m^3) were found within 20 km of the coast, near the Chimbote upwelling center (9°S). Associated with this region was a plume of pigment-rich water extending nearly 250 km offshore. A similarly sized plume can be seen at 5°S (Paita). Although the offshore extent of these plumes was generally greater than had been previously thought, the region of biological enhancement was primarily near shore. This is in general agreement with the traditional definition of the coastal upwelling zone for this region, in which the spatial distribution of phytoplankton biomass has been shown to be determined by the advective supply of new nutrients to the surface layer [*Barber and Chavez*, 1983].

The size of the productive habitat observed during the Dec79–Jan80 period was nearly 14 times larger than was observed during the preceeding year. Enhancement appears to have occurred on a much broader scale, with the offshore boundary of the productive habitat extending nearly 400 km from the coast at 10°S and nearly 1000 km from the coast at 2.5°S. These values agree quite well with the "potential upwelling region" described by *Yoshida* [1967] for the eastern Pacific. The spatial distribution of phytoplankton biomass during this period suggests that processes other than coastal upwelling may have been responsible for supplying the nutrients necessary to support the levels of phytoplankton biomass observed at that time.

The size of the productive habitat was reduced during the Dec82–Feb83 phase of El Niño when compared with Dec79–Jan80; a similar reduction was observed during the 1975 El Niño [*Cowles et al.*, 1977]. Although its offshore extent closely resembles that observed during Dec78–Jan79, there are three notable exceptions. While high levels of phytoplankton biomass along a narrow coastal band (less than 50 km) were still observed during El Niño, the offshore extent of the plankton-rich plumes was greatly reduced. Shipboard estimates of the mean chlorophyll concentrations in the 100-km-wide Peruvian coastal band for Jan–Feb 1983 (1.04 mg/m^3, according to *Guillen* [1985]) agreed quite well with the satellite estimate (1.01 mg/m^3, standard deviation 0.32 mg/m^3). In place of the gradual transition from enhanced to open ocean pigment concentrations that was observed in previous years, waters with very low pigment concentrations were found closer to the coast during El Niño than at any other time. During the non–El Niño periods, distinct regions of enhanced production were observed to the west of the Galapagos Islands (see cover). During this phase of El Niño, however, the region of enhancement appeared to shift from one side of the archipelago to the other (Figure 4), reflecting the changing patterns of ocean circulation observed during that time [*Feldman et al.*, 1984].

There is evidence to suggest that phytoplankton abundances after the 1982–1983 El Niño were some of the highest observed and that the region of plankton-rich water extended several hundred kilometers offshore (R. T. Barber, personal communication, 1985), in many ways similar to the change that took place between the December 1978 and December 1979 periods. One interesting line of speculation is that perhaps the system is periodically "purged," or more specifically, periods during which primary production is low throughout most of the region significantly reduce the abundances of the primary herbivores (i.e., copepods, anchovies). Such a reduction in grazing pressure, which would be prolonged because of the longer generation times of the herbivores relative to the phytoplankton, would then allow for a large increase in phytoplankton abundances if accompanied by sufficent nutrient levels. Although this is speculative, it would be interesting to see if such "boom and bust" scenarios could be identified.

Primary Production

The use of remotely sensed pigment measurements for the estimation of primary production on a regional and even global scale is growing. The principal advantage to be gained by the use of satellites is the vastly increased spatial and temporal coverage possible, in comparison with that available from ships. The errors imposed by the inherent limitations of the satellite measurements appear to be comparable to the errors caused by the spatial inhomogeneities in the biomass fields that are not accurately assessed by ship surveys [*Platt and Herman*, 1983]. The quantitative information contained in the satellite images allows the primary production to be estimated for the entire study area, as well as the production arising specifically from the open ocean and enhanced regions.

For the purposes of this study, primary production was estimated by

$$P = C_{\mathrm{SAT}} \times A \times D \times \mathrm{PI}$$

where P is the total primary production (in milligrams of C per day) calculated to a depth of 1 optical attenuation length, C_{SAT} is the satellite-derived pigment concentration (in milligrams of chlorophyll per cubic meter), A is the total surface area (in square meters) covered by that pigment concentration, D is the optical depth (in meters) to which the satellite measurement applies (as estimated from the work of *Smith and Baker* [1978]), and PI is the productivity index for this region (50 mg of C per milligram of chlorophyll per day) based on measured values from *Barber and Smith* [1981] and *Barber and Chavez* [1983]. The use of a single value for the productivity index throughout the entire region obviously neglects much of the physiological variability in phytoplankton production. Region specific productivity indices based upon temperature, seasonal variability in solar insolation, and perhaps a better knowledge of the spatial and temporal variability in mixing [*Eppley et al.*, 1985] should significantly improve our large-scale productivity estimates.

The results presented in Table 1 therefore represent a first approximation of satellite-derived primary production for this region. It must be emphasized that these values represent the primary production to a depth of 1 optical attenuation length, the depth from which the satellite measurements actually apply. Inferences beyond this depth to the base of the euphotic zone (approximately 4.6 optical depths) are based upon regressions derived from vertical profile data [*Brown et al.*, 1984]. The values given in Table 1 represent approximately 40% of the total water column production that is estimated when the relationship between C_{SAT} and total production, as described by *Eppley* [1984, Figure 2] is applied.

The satellite-derived production estimate for the productive habitat during El Niño (8.7×10^{10} gC/d) is similar to the estimate of 12×10^{10} gC/d presented by *Chavez et al.* [1984] in which the area of the coastal zone (assumed to extend 50 km offshore) was estimated at approximately 78×10^3 km^2. However, if their productivity estimates are extrapolated over the satellite-derived area of the productive habitat given in Table 1, the estimated total primary production is then 20.7×10^{10} gC/d. The estimated production given in Table 1 is roughly 40% of this value, or what the relationship between total water column production and upper optical depth production appears to be, based on *Eppley*'s [1984] findings.

The 1982–1983 El Niño was the best documented and most intensively sampled event of its kind. It is not surprising, therefore, to find such a close agreement between the primary production estimates from ship sampling during this period and those from the satellite data which are presented here. What is evident from this discussion, however, is that the increased spatial coverage offered by satellites may significantly reduce the errors associated with regional primary production estimates. If nothing else, satellite observations can reduce these errors by merely providing a more accurate assessment of the region itself.

Acknowledgments

Research support was provided by National Aeronautics and Space Administration Graduate Researchers Fellowship Grant 33–015–802. The author gratefully acknowledges those who reviewed the early drafts of this report for their helpful comments and suggestions. This is contribution 505 from the Marine Science Research Center, State University of New York, Stony Brook.

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