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17

Tidal Mixing and Plankton Dynamics

Edited by Malcolm J. Bowman, Clarice M. Yentsch
and William T. Peterson

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PATTERNS OF PHYTOPLANKTON PRODUCTION AROUND THE GALAPAGOS ISLANDS

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INTRODUCTION

"The currents about these islands are very remarkable...."
Fitz-Roy (1839)

For the highly productive regions of the world's oceans, it is the pattern of physical processes that to a large extent determines the character and richness of the ecosystem. It has long been recognized that the ocean waters around islands are inherently more productive than waters far removed from land (Gilmartin and Revelante, 1974; Barber and Chavez, 1983). This increased productivity, which is often referred to in the literature as the Island Mass Effect (Doty and Oguri, 1956) depends primarily on the supply of nutrients to the euphotic zone brought about by enhanced vertical mixing around islands. Localized upwelling on the downstream sides of islands (LaFond and LaFond, 1971), topographically induced upwelling (Houvenaghel, 1978), the formation of island wakes (White, 1973), wind driven coastal or equatorial upwelling and tidal mixing (Kogelschatz et al., 1985) are some of the mechanisms that can produce vertical mixing around islands. Although the mechanisms may differ, the end result is often the same; an increase in the vertical transport of nutrients to the surface waters supporting enhanced levels of phytoplankton biomass and primary production.

Straddling the equator approximately 900 km to the west of the South American mainland, the Galapagos Islands (Figures 1 and 2) lie within the heart of the equatorial current system. Rising from the sea floor, the volcanic islands of the Galapagos are set on top of a distinctive platform. The main portion of the Galapagos Platform is relatively flat and less than 1000 m in depth. The steepest slopes are found along the western and southern flanks of the platform with a gradual slope toward the east.

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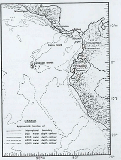

Figure 1. Map of the eastern equatorial Pacific Ocean showing the major features of the submarine bathymetry.

Numerous submarine banks and topographic features interrupt the flow of two of the major ocean currents of this region. The surface circulation around the Galapagos Islands is dominated by the generally westward flows of the South Equatorial Current (SEC). The strength and direction of flows associated with the SEC normally have a strong annual cycle which is related to the intensity of the Southeast Trade Winds (Halpern, 1983), westward surface flows associated with maximum westward winds (July through December) and eastward near-surface currents correlated with minimum westward wind or weak easterlies (March and April). The thickness of the SEC is minimal at the equator (20 to 50 m) deepening to the north and south. Below

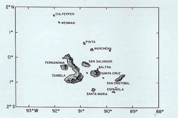

Figure 2. Chart of the Galapagos Islands in which the major islands of the archipelago are shown.

this shallow westward-flowing surface layer are the waters of the Equatorial Undercurrent (EUC), also called the Cromwell Current, which is a subsurface, eastward flowing current approximately 200 m thick with its high velocity core normally found at ∿75 m. The influence of these two opposing flow regimes makes the circulation patterns around these islands remarkably complex. The logs written by captains of 18th and 19th century sailing vessels are filled with references to the bewildering currents and winds they encountered as they explored, provisioned their vessels, or hunted the whales that were abundant in the waters around the Galapagos Islands.

Since the title of this volume is 'Tidal Mixing and Plankton Dynamics', it is appropriate at this point to discuss the influence of tides and tidal mixing in this region. Unfortunately, little is known and even less is written about the tides around the Galapagos Islands. What is known, however, is that the tides are predominantly semidiurnal, having two nearly equal high and low waters each day. The tidal range (approximately 1.5-2.5 m) varies from one location to another throughout the archipelago, and since the tidal currents in a particular area are often proportional to the range of the tide, it can be assumed that tidal currents also vary throughout the islands. Beebe (1926) wrote that

> *"The captain discovered the fact that at the surface at least there is a tidal current. On the lowering tide the current sets strongly north, and on the rising tide it turns and sets as strongly southward along the coast, at least ten miles out."*

Houvenaghel (1978) concluded that tidal mixing played a role in reducing water column stratification, while Kogelschatz et al. (1985) believed that the strongly periodic surface enrichment of nutrients they observed at their Academy Bay time series site may have been caused by tidal destratification. Clearly, more work needs to be done in order to fully assess the role of tidal mixing around the Galapagos.

What all the descriptive and scientific evidence points to is the fact that this is an exceptionally dynamic region and that a great number of mixing processes are at work, any one of which could provide the vertical transport of nutrients necessary to support enhanced phytoplankton production. Not only do phytoplankton represent the first link in the oceanic food chain, but their patterns of distribution in time and space may indicate changes in the physical environment (Steele, 1978) and provide clues as to how oceanographic processes regulate primary production (Yentsch, 1983). Until recently, the limitations imposed by traditional sampling techniques and strategies have made it difficult to assess the variability of the biological response to changes in the physical environment. The development of satellite sensing systems (Hovis, 1981), notably the Nimbus-7 Coastal Zone Color Scanner (CZCS), has provided the synoptic perspective, the quantitative areal data and temporal coverage required for an accurate description of this region.

It is not the purpose of this paper to describe the mixing processes associated with these islands, but rather to show how mixing processes affect the distribution and abundance of phytoplankton in the surrounding waters. Satellite ocean color observations are used to describe the patterns of distribution and the degree of temporal and spatial variability of phytoplankton biomass around the Galapagos Islands. The relationship between temperature (where colder temperatures at the surface often indicate the injection of newly upwelled, or recently mixed waters rich in nutrients) and the distributions and abundances of phytoplankton will be described using sea surface temperature and ocean color imagery.

In addition it is shown that changes in the speed and direction of flows (winds and currents) past the islands produce significant variations in the patterns of phytoplankton distribution in the region and that these patterns are correlated with the seasonal cycle evident in the meteorological and oceanographic data. Finally, the satellite data are used to determine the spatial extent of the area of enhanced biological production, referred to here as the productive habitat, associated with the Galapagos Islands.

MATERIAL AND METHODS

Twenty Coastal Zone Color Scanner (CZCS) images of the Galapagos Islands covering the period from December 1978 through March 1983 were processed according to procedures described by Gordon et al. (1983). The subtle 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; Eppley, 1984; Feldman, 1985). The depth to which these 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 22% of the euphotic zone). Direct comparison between ship-measured and satellite-derived pigment concentrations have shown that over the 0.08-1.5 mg/m^3 concentration range, the algorithms used to relate the retrieved spectral radiances to phytoplankton pigment concentrations are accurate to within 30-40% (Gordon et al., 1983). The principal advantage to be gained by the use of satellites is the vastly increased spatial and temporal coverage possible as compared with that available from ships. The errors imposed by the inherent limitations of satellite measurements appear to be comparable to the errors caused by the spatial inhomogeneities in the biomass fields which are not accurately assessed by the ship surveys (Platt and Herman, 1983).

Five representative color-encoded maps of the phytoplankton pigment distributions around the Galapagos Islands are presented. In each case the islands are black and clouds white. The color scale representing specific pigment concentration ranges (e.g. dark green covers the concentration range from 0.41 to 0.50 mg/m^3) that was applied to each of the computer-processes CZCS images presented in this paper is included with the images. The CZCS images that were used in the statistical analyses were remapped to uniform spatial coordinates so that any given pixel (the smallest element resolved by the sensor) represents the same geographical location on the earth's surface in each image.

RESULTS AND DISCUSSION

CZCS data of the Galapagos Islands from Nimbus-8 orbit 739 taken on 16 December 1978 were processed to produce simultaneous, co-registered images of phytoplankton pigment concentrations (Plate 1a) and sea surface temperature (Plate 1b). Although direct observations of the oceanographic conditions around the islands are not available for December 1978, data gathered during the November 1978 cruise in the vicinity of the Galapagos by the research vessel Orion of the Oceanographic Institute of Ecuador (Arcos, 1981; Jimenez, 1981) provide surface information useful in the interpretation of the satellite images. The time difference between the ship survey and the satellite overpass makes direct comparisons difficult, however, a general agreement of the large-scale features does exist.

The satellite-derived sea surface temperature distributions (Plate 1b) show that warm waters (yellow) were found predominantly in the northern and southern regions of the archipelago. The warm, tropical surface waters to the north are separated from the generally cooler waters (blue) of the south by the Equatorial Front which extends zonally, and generally crosses the equator in the vicinity of the Galapagos Islands (Hayes, 1985). The Equatorial Front, sometimes referred to as the Galapagos Front in the vicinity of the islands, was very strong on the western side of the archipelago in November 1978 and was located just off the northern tip of Isabela.

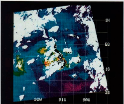

Plate 1a. Satellite ocean color image showing the distribution of phytoplankton pigments around the Galapagos Islands acquired on 16 December 1978 (Nimbus-7 orbit 739). Major islands are black and clouds white. The dotted line across the sharp color front located to the west of Isabela Island represents the trackline from which the data presented in Fig. 3 were derived.

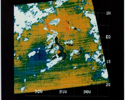

Plate 1b. Satellite-derived sea surface temperature distributions around the Galapagos Islands acquired on 16 December 1978 (Nimbus-7 orbit 739). Regions of warm waters (above 21°C) are yellow and red; intermediate temperatures (20 to 21°C) are light blue; coolest temperatures (<20°C) associated with the upwelling of the Equatorial Undercurrent are deep blue. Major islands are gray and clouds white.

One striking feature evident in the temperature image is the patch of relatively cold water (~19°C) located to the west of Isabela Island between the equator and 1.5°S. Jimenez (1981) reported that during November 1978 the axis of the eastward flowing subsurface Equatorial Undercurrent (EUC) was displaced slightly to the south of the equator; other studies (Bubnov and Egorikhin, 1981; Lukas, 1981) have given some indication of the behavior and the extent and period of the meandering of the axis of the EUC. Measurements have shown that subsurface waters belonging to the EUC upwell in the Galapagos area and influence the hydrology and productivity of the entire archipelago (Houvenaghel, 1978). Both Houvenaghel and Jimenez report the existence of a large patch of cold (19°) water to the west of Isabela Island. This patch, representing the topographically induced surfacing of the EUC, is clearly seen in Plate 1b. The satellite-derived temperature distributions seem to indicate that at the time of the satellite overpass, the EUC flowed primarily through the southern portion of the archipelago although its signature is not nearly as distinct as it is to the west. These data support the observations reported by others (Stevenson and Taft, 1971; Lukas, 1981; Hayes, 1985) that the EUC flows southward through the islands.

The CZCS-derived pigment concentrations for this period (Plate 1a) show that phytoplankton biomass was by no means uniformly distributed around the archipelago. Pigment concentrations were greatest on the western side of Isabela, particularly in Elizabeth Bay (located between Isabela and Fernandina Islands), while a small patch (~25 km) of relatively phytoplankton-rich water was found just to the north of Fernandina. The lowest concentrations are associated with the warm waters to the south of the islands and with the regions to the north of the reported position of the Equatorial Front. The region of relatively low pigment water located to the west of Isabela corresponds with the center of the EUC upwelling water as seen in the sea surface temperature image. It has long been recognized that newly upwelled water, although generally high in nutrients is usually low in phytoplankton biomass (Barber and Ryther, 1969). Jimenez's (1981) findings and the satellite data support this idea. Both show a sharp decrease in pigment concentrations where the EUC core upwells; however, the waters surrounding the upwelling center have some of the highest pigment concentrations in the region.

A particularly sharp and nearly coincident temperature and color front can be seen on the eastern edge of the EUC upwelling center. The bathymetry of the region (Figure 1) indicates that this front is located in waters with depths greater than 1000 m. Sea surface temperatures and pigment concentrations across this front (Figure 3) extracted from CZCS imagery along the dotted trackline shown in Plate 1a, show the sharpest gradient across the color front (0.4-6.1 mg/m^3) occurs between pixels 22 to 26 (a distance of approximately 3 km). Mean pigment concentrations on the east side of the front (0.95 mg/m^3) extending into Elizabeth Bay are significantly higher than those to the west (0.28 mg/m^3), which are generally within the newly upwelled EUC waters. The temperature data shows a marked, although less dramatic difference across the front. Temperatures were cooler (~18.8^{o}C) in the western region, increasing across the front and averaging 19.6^{o}C on the eastern side.

Pigment distributions on 11 June 1981 (Orbit 13288, Plate 2) show that although different in some respects to the patterns observed during December 1978, several features are clearly similar. Once again, the highest pigment concentrations are found on the

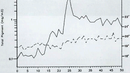

Figure 3. Satellite-derived sea surface temperatures (^{o}C, dashed line) and phytoplankton pigment concentrations (mg/m^3, solid line) versus distance (1 pixel = 825 meters) along the trackline depicted in Plate 1b extracted from the CZCS data acquired on 6 December 1978 (Nimbus-7 orbit 739).

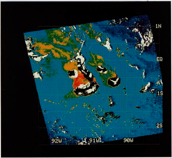

Plate 2. Satellite ocean color image showing the distribution of phytoplankton pigments around the Galapagos Islands acquired on 11 June 1981 (Nimbus-7 orbit 13288).

western side of Isabela in Elizabeth Bay. The sharp color front seen in December 1978 also appears in the June 1981 image, although its position is displaced approximately 20 km to the east. A small patch of pigment-rich water is again found off the northern tip of Fernandina Island. The most notable differences between the two scenes are (1) the appearance of phytoplankton-rich plumes extending to the northwest from most of the islands in June 1981 and (2) an overall increase in pigment concentrations in the waters around the archipelago. The overall mean pigment concentration for the entire region covered by the CZCS image increased from 0.26 mg/m^3 in December 1978 to 0.42 mg/m^3 in June 1981. This increase is particularly evident in the offshore waters, indicating the possibility of either a large-scale seasonal or interannual effect. The seasonal influence will be addressed later in this paper, whereas Feldman (1985) has discussed the interannual variability in phytoplankton biomass and production experienced by this region.

Oceanographic measurements of the large-scale circulation patterns which are available for the June 1981 period, proved useful in interpreting the patterns seen in the satellite image. The trajectories of four satellite-tracked drifting buoys deployed to the east of the Galapagos Islands (Pazos and Paul, 1984) during the latter half of June 1981 are presented in Figure 4; the tic-marks along the trajectories represent successive ten day intervals. The horizontal displacements of the buoys have been interpreted as providing a measure of the velocity and direction of water movement in the upper layer (~50 m) of the ocean (Hansen and Paul, 1984). The trajectories show that the surface waters to the north of the equator around the Galapagos Islands were moving in a generally west-northwest direction, and in a west-southwest direction for the waters to the south. The plumes of pigment-rich water seen in Plate 2 therefore, are forming on the downstream sides of the islands.

Simpson et al. (1982) and Simpson and Tett (this volume) described the mixing processes associated with flows around islands. It was noted that at times when significant non-tidal residual flows were present (4-20 cm/sec was reported by Simpson et al. for the waters around the Scilly Isles), mixed water would be swept away from the island and produce a plume downstream. Houvenaghel (1978) reported that in the Galapagos, newly upwelled waters of the EUC were mixed with and carried along by the flows of the South Equatorial Current. The appearance of distinctive island waters in many of the ocean color images of the Galapagos clearly indicates the presence and significance of the mean surface flows in determining the patterns of phytoplankton distribution around these islands.

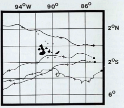

Figure 4. The trajectories of four satellite-tracked drifting buoys deployed to the east of the Galapagos Islands during the third week of June 1981. The deployment locations are indicated (closed circles) and the tic-marks along the trajectories represent subsequent ten-day intervals (after Pazos and Paul, 1984).

The trajectories given in Figure 4 indicate that the buoy to the north of the islands traveled further during the same period of time than did the buoy to the south. For the second ten-day interval, the period when the buoys were closest to the islands, the northern buoy covered approximately 54 km/day (-63 cm/sec) while the southern buoy averaged only 35 km/day (-41 cm/sec). The slower westward movement of this southern buoy may possibly be due to the influence of the eastward flows of the EUC, particularly if, as seen in Plate 1a, the major portion of the EUC flows were through the southern part of the archipelago.

Buoy displacements can also be used to help interpret the patterns of phytoplankton distribution observed on 20 August 1980 (Orbit 9211, Plate 3). In this scene, the large-scale spatial resolution of the CZCS is utilized to show the extent to which the Galapagos Islands enhance the production of the surrounding waters. Although the islands themselves are obscured by clouds (Isabela and Fernandina are masked in black), the plumes of phytoplankton-rich

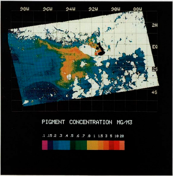

Plate 3. Satellite ocean color image showing the distribution of phytoplankton pigments around the Galapagos Islands acquired on 20 August 1980 (Nimbus-7 orbit 9211). This image is presented at full swath resolution (~1500 km wide) so that the spatial extent of the area of enhanced phytoplankton production associated with the Galapagos Islands can be assessed. Although the islands are obscured by cloud cover, the locations of Isabela and Fernandina have been masked in black.

waters can be seen extending nearly 600 km towards the west. The twin plumes observed in the satellite image appear to reflect the drifting buoy trajectories for this period as described by Pazos and Paul (1984) which were primarily westward to the north of the equator and in a generally southwesterly direction to the south. This image will be discussed in more detail in a later section of this paper where the spatial extent of the area of enhanced biological production (the productive habitat) associated with islands is estimated.

The distributions of phytoplankton pigments observed on 26 April 1980 (Orbit 7608, Plate 4) are dramatically different from those found in the previously described scenes. Although the mean pigment concentration for the entire region was only slightly lower in April 1980 than during June 1981 (0.37 vs. 0.42 mg/m^3), the greatest difference is seen in the patterns of phytoplankton distribution around the islands. The regions of highest phytoplankton biomass are no longer located on the western side of Isabela, but rather are found to the south and east. Mean pigment concentrations for the waters around Elizabeth Bay were only 0.35 mg/m^3 while those between Isabela, San Salvador and Santa Cruz were 0.74 mg/m^3.

A question that can be asked is what differing oceanographic conditions existed during these periods that could possibly explain the contrasting patterns of phytoplankton distributions observed in the satellite image. One possibility is the altered circulation patterns observed during April 1980. Near-surface (15 m) current meter measurements taken at 0°, 110°W for the period February 1980 through September 1981 are presented in Figure 5a (Halpern, pers. comm.). Although these observations were made nearly 2100 km to the west of the Galapagos Islands, they document the dominant oceanic circulation features of the region during the times of three of the satellite overpasses presented in this paper. Coincident sea level records from the Galapagos Islands are presented in Figure 5b (Hayes, pers. comm.). A recent study (Hayes and Halpern, 1984) has shown that for the period March 1980 to July 1981 sea level at the Galapagos was highly correlated with the currents measured at 0°, 110°W. Specifically, they found that eastward flows, expressed as vertically averaged zonal velocities, resulted in rising sea level at the Galapagos.

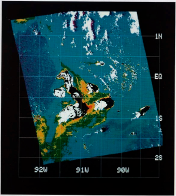

Plate 4. Satellite ocean color image showing the distribution of phytoplankton pigments around the Galapagos Islands acquired on 26 April 1980 (Nimbus 7 orbit 7608). Note that phytoplankton pigment concentrations are greatest in the waters to the east of Isabela Island and that relatively low phytoplankton abundances (pigment concentrations less than 0.4 mg/m^3) are observed in Elizabeth Bay.

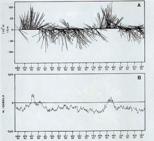

Figure 5. A) Daily vector-averaged current meter records showing speed and direction at a depth of 15 m measured at 0°, 100°W (Halpern, pers. comm., 1984). Eastward direction is upward. B) Low pass filtered and detided sea level record from the Galapagos Islands (recorded at the northern tip of Isabela Island) for the same period covered by the current meter data (Hayes, pers. comm., 1984). In this presentation, pressure changes can be related to sea level fluctuations assuming 1 cm = 0.01 db.

Enhanced eastward surface flows and elevated sea levels are clearly seen during the March through May periods of each year. By the latter part of April 1980, sea level at the Galapagos had been rising rapidly and strong eastward flows had been recorded throughout the preceding month. This is in sharp contrast to the conditions that were observed during August 1980 and June 1981 during which time sea levels were low, and surface flows although variable, were in a generally westward direction.

The position of the Galapagos Islands near the eastern end of the equatorial waveguide, subjects them not only to perturbations in local forcing, but also to disturbances generated in the central and western Pacific (Kogelschatz et al., 1985). These propagating disturbances, the most dramatic of which are associated with El Niño, have been shown to have profound effects on the biota of these islands. A recent investigation utilizing satellite ocean color observations and complemented with coincident oceanographic measurements demonstrated the tight coupling that exists between the distribution of phytoplankton biomass around the Galapagos Islands and the oceanographic and atmospheric conditions observed during the 1982-83 El Niño (Feldman et al., 1984).

The CZCS data presented in Plate 5 was acquired on 8 November 1982 (Orbit 20406) during the onset phase of El Niño. When the overall mean pigment concentration for the entire archipelago was computed in the same manner as the other CZCS scenes presented in this paper, an interesting fact emerged; the mean pigment concentration calculated for the November 1982 scene (0.23 mg/m^3) was not significantly lower than was calculated for December 1978 (0.26 mg/m^3), which supposedly represents the non-Niño conditions. In fact, the sharp color front and highest pigment concentrations are once again found outside of Elizabeth Bay. What is particularly striking about this scene, however, is the large region to the north of the islands where waters with exceptionally low pigment concentrations were observed. In the satellite-derived sea surface temperature distributions of the eastern equatorial Pacific on 8 November 1982 presented in Philander et al. (1985), two features appear which are also observable in the CZCS image of that day. The Equatorial Front was in a position very close to that observed in the CZCS image as the boundary between the low pigment waters to the north and the richer waters to the south. The front is displaced to the south during El Niño (Barber and Chavez, 1983; Hayes, 1985) and it appears as if the 8 November CZCS image caught the front just as it reached the Galapagos. The sea surface temperature data also indicates a plume of relatively cool water extending to the south of Isabela. A similar plume of pigment-rich water can be seen in the CZCS image. It is not known whether the plumes were generated locally or swept around the island from the west as a result of the changing oceanographic and meteorological conditions at the time. Although locally high levels of phytoplankton biomass were observed around the Gala-

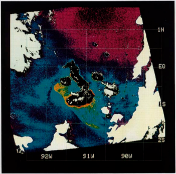

Plate 5. Satellite ocean color image showing the distribution of phytoplankton pigments around the Galapagos Islands acquired on 8 November 1982 (Nimbus-7 orbit 20406) during the onset of the 1982-83 El Niño. Note the sharp boundary between waters very low in phytoplankton abundances (pigment concentrations less than 0.1 mg/m³) in the northern portion of the image and the generally richer waters to the south.

pagos Islands during El Niño (Feldman et al., 1984; Kogelschatz et al., 1985), the productivity of the offshore waters was significantly reduced (Barber and Chavez, 1983).

Patterns of Production and the Seasonal Cycle

The satellite ocean color images presented in this paper demonstrate the degree of spatial and temporal variability of phytoplankton biomass around the Galapagos Islands. One of the first things evident from the satellite images is that some areas around the Galapagos appear richer than others. To quantify this observation, I divided the archipelago into nine sampling regions (Figure 6). Since,

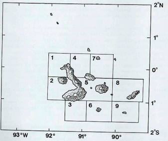

Figure 6. Chart of the Galapagos Islands showing the location of the nine mesoscale sampling regions used to assess the spatial and temporal variability of phytoplankton biomass around the archipelago.

as has been previously noted, all the images are remapped to the same spatial coordinants, the geographic area covered by each sampling region is the same in each image. The mean pigment concentration for each sampling region could then be calculated.

Several additional kinds of information can be obtained through this approach. First, by comparing the individual regions within a single scene, the spatial variability in phytoplankton biomass around the islands can be determined. Second, a given sampling region or group of regions can be compared from one image to the next, giving an indication of the temporal variability. Third, images can be composited to develop an overall as well as seasonal mean. Twelve CZCS images of the Galapagos Islands spanning the period from December 1978 through November 1981, including the images presented in this paper, were composited to produce the data presented in Table 1, in which the overall mean pigment concentration for each sampling region, along with the minimum and maximum values are given.

The range of mean pigment concentrations for each of the sampling regions indicates that the greatest variability was found in the maximum values. The minimum values for all nine regions were surprisingly similar (0.12-0.21 mg/m^3) whereas the maximum values ranged from 0.25-2.05 mg/m^3. Individually, sampling regions 6, 8, and 9 had the lowest overall mean concentrations and the smallest ranges. The sampling regions in the eastern portion of the archipelago appear more oceanic in character, with low, and relatively uniform pigment concentrations. The description of the western regions of the archipelago as being the most productive (e.g. Maxwell, 1974; Jiminez, 1981) is confirmed by the satellite data, particularly when any seasonal influences are not considered as is the case in the composited data just described. The seasonal influence on the distributions and abundances of phytoplankton around the Galapagos, however, appear to be significant.

Seasonal variability in the oceanic and atmospheric parameters affecting the Galapagos Islands has been described by many authors; however, the transition periods from one season to the next are often poorly defined and to a large extent based upon the data set being described. Palmer and Pyle (1966) noted a distinct annual variation between a wet season from January to April and a dry season during the rest of the year. The wet season is characterized by increased

Table 1. Overall mean phytoplankton pigment concentrations (mg/m^3) for each of the nine mesoscale sampling regions derived by compositing twelve CZCS images of the Galapagos Islands for the period December 1978 through November 1981. The maximum and minimum mean pigment concentration for each region is also given.

	Sampling Region								
	1	2	3	4	5	6	7	8	9
MEAN	0.41	0.83	0.29	0.26	0.38	0.21	0.25	0.23	0.18
MAX	0.95	2.05	0.50	0.43	0.74	0.31	0.48	0.35	0.25
MIN	0.16	0.16	0.15	0.15	0.21	0.13	0.14	0.17	0.12

air and sea temperatures and a weakening of the southeast Trade Winds which, during this season, are often replaced by calms or periods of westerly winds. The wet season, also referred to as the warm season by some authors, is the time when heavy rains fall on the typically arid Galapagos. The dry season is characterized by cooler air and sea temperatures, strong southeast Trade Winds and less frequent periods of rainfall. Distinct annual variations in the intensity and duration of both seasons have also been noted. Houvenaghel (1978) places the warm season from February until April; Hayes (1984) from February to May; while others (Maxwell, 1974; Kogelschatz et al., 1984) extend it from January through May.

The oceanographic conditions around the Galapagos, in particular the two main current systems which influence this region, also exhibited pronounced seasonality. The strength of the Equatorial Undercurrent varies annually (Wyrtki, 1974; Lukas, 1981; Leetma and Molinari, 1984) and is generally stronger during the early part of the year. Halpern (1983) found that the near-surface flows of the South Equatorial Current have a strong annual cycle with predominant westward flows from July-December, eastward flows during March-May (Fig. 5), with February and June being transition periods between the two.

Although there are reports of the interannual variability in phytoplankton biomass and productivity around the Galapagos Islands (Barber and Chavez, 1983; Kogelschatz et al., 1985) the identification of a distinct seasonal cycle has been hampered by the difficulty in making synoptic measurements of this highly dynamic region using traditional ship sampling techniques. Maxwell (1974) reported that seasonal differences in productivity were evident in Galapagos waters with the cold season (June-December) being more productive than the warm season (February-May). Houvenaghel (1978), however, reported that no distinct seasonal cycle in either phytoplankton biomass or productivity could be deduced.

The satellite data presented here provide both the synoptic perspective and the temporal coverage required to address more effectively the question of whether or not a seasonal cycle in phytoplankton abundance does exist, and if so, to what factors may it be related. The mean pigment concentrations for each of the nine sampling regions for the twelve CZCS images (December 1978-November

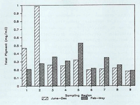

Figure 7. Seasonal mean phytoplankton pigment concentrations (mg/m^3) for each of the nine mesoscale sampling regions based upon a seasonal grouping of twelve CZCS images of the Galapagos Islands for the period December 1978 through November 1981.

1981) were grouped according to season and the seasonal mean concentration for each region was calculated. These values are presented in Figure 7.

The first conclusion that can be drawn from the data is that there appears not to be a statistically significant difference in pigment concentrations between seasons for the archipelago as a whole. The mean concentration for the June through December period (0.34 mg/m^3) was just slightly greater than that for the February through May period (0.31 mg/m^3). The major difference between the two seasons, however, is the dramatic and definitely significant decrease in pigment concentrations in the western half of the archipelago (regions 1 and 2) from the June through December to the February through May period. The mean concentration in region 2 decreased nearly 4-fold while the mean concentration in region 1 during February through May was less than half of that recorded during June through December. Also seen in Figure 7 along with the decrease in pigment concentrations to the west of the archipelago during February through May, is a corresponding increase in concentrations for all regions to the east.

It is this seasonal redistribution or, more specifically, a shift in the areas of increased production, that the satellite images have allowed us to identify. From the data presented, it appears that the patterns of phytoplankton distributions revealed in the satellite ocean color observations reflect features of, and changes in, the large-scale oceanic and atmospheric circulation systems. Although to draw conclusions based upon twelve CZCS images spanning 2.5 years may be tenuous, it appears as if interannual variability is seen predominantly by an increase or decrease in pigment concentrations over the region as a whole, while seasonal variability more specifically affects the distribution of phytoplankton around the islands. Obviously, increasing the number of images from which these kinds of analyses are based will greatly improve our understanding of these relationships. Also, the increasing amount of meteorological and oceanographic data that will be gathered as part of the ten year observational and modeling program designed to study the interrelationships between the tropical oceans and the atmosphere (TOGA) will vastly expand our knowledge of the physical environment of this region.

The Productive Habitat of the Galapagos Archipelago

To what extent do the Galapagos Islands enhance the production of the surrounding waters? Making use of both the qualitative and quantitative information contained in the CZCS data, it is possible to determine the spatial extent of the area of enhanced biological production, referred to here as the productive habitat (Feldman, 1985), associated with the islands. The relationships among biomass, growth, and production are complex. Yentsch (1984) has argued that the pigment distributions observed by the CZCS reflects the net growth processes of phytoplankton and not merely the redistribution of abundance. He hypothesizes that it is vertical mixing, resulting in the periodic injection of nutrients into the surface waters, that is responsible for the growth and, therefore, the abundance of phytoplankton evident in the satellite images. The colder, subsurface waters around the Galapagos are generally rich in nutrients; thus the appearance of cold water at the surface is, in this case, an indicator of nutrient rich water. The relationship between temperature and the distribution and abundance of phytoplankton presented in this paper (i.e. the newly upwelled water seen in Plate 1b and Figure 3) support Yentsch's hypothesis. In general, it is fair to say that the areas of increased phytoplankton biomass seen in the satellite ocean color images reflect a period of increased phytoplankton production.

If the open ocean phytoplankton concentrations observed in areas not influenced by probable island-induced enhancement represent nutrient-limited conditions (Simpson et al., 1982), then the increased nutrient supply generated by mixing processes around the Galapagos should produce regions of enhanced phytoplankton production. Such regions are evident in all the CZCS images, but in particular, the twin plumes extending nearly 600 km downstream from the islands in the 20 August 1980 scene (Plate 3) are particularly impressive.

To calculate the area of enhancement associated with the Galapagos, it was assumed that the regions in the CZCS images where pigment concentrations were less than 0.4 mg/m^3 (blue) represented open ocean, unenhanced conditions. The next step was to select a pigment concentration value which delineated most clearly the boundary separating the enhanced conditions (productive habitat) from the open ocean region. The actual plumes appeared to be very well defined by the yellow (>0.7 mg/m^3) contour. However, aside from the plumes themselves, there appeared to be somewhat less distinct regions of enhanced phytoplankton abundances obviously associated with the islands, perhaps representing the diffusing outer edges of the plumes. These regions were best delineated by the 0.4 mg/m^3 contour and are colored green in the images. The areas of the productive habitat calculated from five large-scale CZCS images of the Galapagos Islands are given in Table 2. What is particularly striking about these findings are the size and variability of the region influenced by the Galapagos and the ability of the satellite ocean color data to assess it.

It is perhaps more meaningful to compare the actual areal extent of the productive habitats, rather than their percentage of the total because the cloud-free surface area varied considerably between images. A visual inspection of the images reveals for instance that the areal extent of the plume (>0.7 mg/m^3) in the August 1980 image may have been underestimated by at least 12,000 km^2 because of cloud

Table 2. Total cloud-free surface area (10^3 km^2), the areas of ocean surface containing phytoplankton pigment concentrations greater than 0.4 mg/m^3 (wake) and 0.7 mg/m^3 (plume), and the overall mean pigment concentration (mg/m^3) and Standard Deviation (SD) computed from five large-scale Coastal Zone Color Scanner images of the Galapagos Islands. The numbers in parentheses are the percentage of total surface area represented by each value.

Date	Area ($10^3 km^2$) >0.4	Area ($10^3 km^2$) >0.7	Total cloud-free-area ($10^3 km^2$)	Overall mean pigment concentration
2-19-79	55 (21%)	9 (3%)	267	0.30 (0.29)
11-24-79	110 (57%)	18 (10%)	192	0.45 (0.36)
4-26-80	46 (14%)	9 (3%)	318	0.29 (0.43)
8-20-80	80 (26%)	25 (8%)	313	0.37 (0.69)
6-11-81	31 (10%)	6 (2%)	317	0.28 (0.44)

cover. The largest plumes and consequently, the largest productive habitats (November 1979, August 1980) appear to be associated with times of maximum trade wind strength and strong westward flows of the South Equatorial Current. Buoy displacements (Pazos and Paul, 1984) indicate that surface flows of approximately 50 cm/sec were found in the vicinity of the northern plume during the August 1980 period. This would mean that a water parcel brought to the surface at the Galapagos, would take between 10-15 days to reach the westernmost tip of the plume.

It is interesting to speculate as to whether or not a steady state system exists, with nutrients being supplied by mixing processes at the Galapagos supporting enhanced phytoplankton production along the axis of the plume. The horizontal (downstream) extent of the plume may be limited by several factors including (1) rate of nutrient supply, (2) advective and diffusive losses, (3) nutrient depletion resulting from phytoplankton uptake, (4) grazing by zooplankton, or (5) sinking losses. There is also the possibility that the residence time in the plume may be longer than estimated because of the complex circulation patterns and numerous trapping mechanisms, including eddies that form on the downstream sides of islands (Hamner and Hauri, 1981; Wolanski et al., 1982). The topic of island plumes and wakes is of considerable interest both from a physical and biological perspective and deserves further study. An island plume model (Okubo, pers. comm.) is being developed which will make use of the satellite data to study the processes associated with plume formation and decay and to more fully assess the impact of islands and island groups on the productivity of the surrounding waters.

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