

# Decorrelation Scales of Chlorophyll as Observed from Bio-optical Drifters in the California Current

Mark R. Abbott and Ricardo M. Letelier

College of Oceanic and Atmospheric Sciences  
Oregon State University  
Corvallis, OR 97331-5503

## ABSTRACT

The California Current System is characterized by intense mesoscale variability, with meandering jets that can create small regions of strong vertical motion that have velocities on the order of several tens of meters per day. To study physical and biological scales of variability, twenty-four near-surface drifters were released in this system, each equipped with a spectroradiometer to measure upwelling radiance. Sensors also measured downwelling irradiance as well as sea surface temperature (SST). Data were relayed to shore via satellite and processed into biological quantities, such as chlorophyll. Several drifters were trapped by mesoscale eddies, and the cross-correlation functions were calculated for both SST and chlorophyll. In general, changes in chlorophyll lagged changes in SST by one to two days. This was observed for both cyclonic and anticyclonic eddies and supports the hypothesis that the phytoplankton response to changes in the physical environment (and presumably the light/nutrient regime) may be governed by a “shift-up response.” Decorrelation time scales were calculated based on the first zero-crossing of the autocorrelation function, and the biological scales were compared with the physical scales. Time scales for all variables increased as the drifters moved from nearshore to offshore. Nearshore (defined as the region within 200 km of the coast) time scales were two days for both sea surface temperature (SST) and chlorophyll. In the region between 200 and 400 km offshore, the decorrelation scales were six days for SST and four days for chlorophyll. In the region more than 400 km offshore, the SST decorrelation scale was seven days and decreased to 2.5 days for chlorophyll. This pattern of decorrelation scales suggests that the processes regulating the distribution of temperature and chlorophyll are similar in the nearshore region and significantly different offshore. Similar calculations were made for fluorescence/chlorophyll, and the corresponding time scale increased steadily from less than one day nearshore to two days offshore. The rapid adjustments of fluorescence nearshore, relative to changes in pigment concentration, supports the notion that phytoplankton have adopted different strategies for growth in the nearshore versus the offshore region.

## INTRODUCTION

The California Current System (CCS) is a broad eastern boundary current that is characterized by strong mesoscale variability, especially during the upwelling season in spring and summer. This variability is especially intense off California where strong equatorward winds and positive curl in the wind stress lead to intense upwelling and a meandering coastal jet (Brink and Cowles, 1991; Strub et al., 1991; Abbott and Barksdale, 1991; Haidvogel et al., 1991; Batteen, 1997). Although this variability in the physical environment is manifested in the biological environment (Hood et al., 1990; 1991; Dugdale et al., 1989; Peláez and McGowan, 1986; Haury et al., 1986; Jones et al., 1988), there have been relatively few statistical analyses of this biological heterogeneity (Barale and Wittenburg-Fay, 1986; Michaelsen et al., 1989; Smith et al., 1989). Denman and Abbott (1988; 1994) studied time series of Coastal Zone Color Scanner (CZCS) and Advanced Very High Resolution Radiometer (AVHRR) imagery of phytoplankton pigment and sea surface temperature (SST) using cross-spectrum analysis. They showed that the temporal decorrelation scale was a strong function of spatial scale, and that these scales varied with location. Energetic regions, such as the upwelling filaments, had decorrelation scales of about three days for spatial scales of 50-100 km. Less energetic regions between filaments had scales of about a week (Denman and Abbott, 1994). In general, there was no observed lag between changes in the physical patterns (as indicated by SST) and changes in the biological patterns (as indicated by phytoplankton pigment), which led Denman and Abbott (1994) to conclude, based on the temporal and spatial resolution of the CZCS and AVHRR imagery, that phytoplankton was simply a passive scalar and that biological processes played only a minor role in determining the frequency and wavenumber spectra.

Although variability on such time and space scales clearly complicates any sampling scheme, the more interesting questions revolve around both the ecological and biogeochemical impacts of such variability. Beginning with Hutchinson (1941), the role of environmental variability has been thought to be an important component in structuring planktonic ecosystems. Harris (1986) provided a comprehensive review of the interaction of

environmental variability and physiological adaptation in aquatic systems. Drawing from both aquatic studies and general ecological theory, Harris argued that phytoplankton have evolved mechanisms to exploit the spectrum of environmental change. From an ecological perspective, environmental heterogeneity is thought to decouple the links in the food chain; for example, sudden blooms of diatoms can escape grazing pressure by zooplankton (e.g., Banse, 1996). Platt et al. (1989) suggested that small-scale patchiness in nutrient supply rates could be used to explain the apparent paradox between low primary productivity and high downward flux of carbon in the oligotrophic ocean.

Because of the scales associated with planktonic ecosystems, it has been extremely difficult to study these processes from a quantitative point of view. There have been numerous observations of variability in various components of the system (e.g., small-scale patchiness in phytoplankton pigment, time series observations of photosynthetic parameters, zooplankton patchiness), but there are relatively few systematic statistical analyses. One obstacle to such systematic observations is that our observing tools have their own characteristic time scales that are convolved with the underlying natural variability. Both Harris (1986) and Platt et al. (1989) note that common measurement techniques, such as chlorophyll fluorescence or sediment traps, are often applied to processes that have inherently different time and space scales. The result is that the observed variability is a complex mix of both natural variability and measurement resolution.

Implicit in these observations is that environmental variability is manifested in the degree to which the physiological state of the phytoplankton is removed from its equilibrium. That is, if a particular physiological parameter is slow to adapt to transient changes in the environment, then one would not expect to see a significant effect. On the other hand, some aspects of physiology may track environmental fluctuations quite closely, resulting in considerable variability in the signal. Cullen and Lewis (1988) and Lande and Lewis (1989) used these ideas on the time scale of adaptation to suggest that certain photoadaptive parameters could be measured and used to infer the degree of vertical mixing. For example, the maximum in the photosynthesis/irradiance relationship ( $P_{\max}$ ) is usually normalized by the chlorophyll concentration to give an assimilation number. As noted by Harris (1986) and Cullen (1990),  $P_{\max}$  may be independent of nutrient supply and is generally constant for populations from the well-lit regions of the ocean, but the evidence is not conclusive. However,  $P_{\max}$  has an inherent time scale of adaptation (usually several days) during which time it is not constant. To further complicate matters, chlorophyll has its own time scale of adaptation which is different than the  $P_{\max}$  time scale.

In an environment characterized by a broad spectrum of environmental fluctuations, phytoplankton have developed an equally broad range of strategies (Harris, 1986). Phytoplankton will attempt to maintain steady-state conditions, but there is a physiological price to be paid. For example, suppose the amount of available solar irradiance were to increase rapidly through a change in density stratification which reduced vertical mixing. The response might be to increase  $P_{\max}$  over several days, but the initial (or fast) response might be to increase the amount of fluorescence per unit chlorophyll since the number of photosynthetic units might not be able to handle the increased flux of captured photons (Cullen and Lewis, 1988). However, near-surface populations may rely on non-photochemical quenching such as photoprotective pigments which would protect the photosynthetic machinery from the effects caused by excess absorption of light. This process would be accompanied by a decline in fluorescence yield (Demmig-Adams, 1990; Mohanty and Yamamoto, 1995). The wide range of adaptation and forcing scales will complicate our analysis of environmental variability.

Over the past decade, developments in smaller and less expensive instrumentation have allowed oceanographers to collect data sets at time and space scales that are difficult to observe from conventional platforms (Dickey, 1991; Dickey et al., 1991). Time series from a fixed point mooring are a combination of both temporal changes and spatial changes as new water masses are swept past the mooring. Free-drifting buoys that can be drogued to follow upper ocean circulation help separate temporal variations in a water mass from those that occur spatially. We can now begin to explore the time and space scales of variability in a systematic manner, as opposed to occasional campaigns. In addition, the quasi-Lagrangian approach may produce a more realistic estimate of patch size than the fixed point, Eulerian approach such as that used by Denman and Abbott (1988; 1994). However, the smaller scales that can now be observed are especially influenced by the interaction between physical variability and physiological response. Although Denman and Abbott (1994) asserted that phytoplankton were simply passive scalars in an intensely turbulent field, the physiological mechanisms that have evolved may allow phytoplankton to adapt to these changes in a manner quite different than a passive scalar.

Bio-optical drifters deployed in the California Current were initially used to examine physical and biological processes within a specific physical feature (Abbott et al., 1990; 1995). The advent of lower cost sensors as well as

the use of satellite data relay now allows the deployment of large numbers of drifters to conduct systematic studies of the statistical properties of the upper ocean bio-optical field (Abbott and Letelier, 1996; 1997). In this paper, our analyses followed two paths. First, we analyzed the impact of specific physical features on upper ocean biology. Second, we calculated large-scale statistics of some of the biological and physical fields. These results are discussed in the context of our current understanding of phytoplankton physiology and mesoscale variability.

## METHODS

Standard World Ocean Circulation Experiment (WOCE) surface drifters were modified by METOCEAN Data Systems to include a Satlantic spectroradiometer (model OCR-100) in the bottom of the surface float (Figure 1). This sensor measured upwelling radiance at 412, 443, 490, 510, 555, 670, and 683 nm. The surface float also included pressure and temperature sensors. A Satlantic narrow band irradiance sensor (model ED-100), centered at 490 nm, was mounted in the top of the surface float. A 40 m long drogue was attached below the surface float such that the drifter responded primarily to currents at 15 m depth. Data were averaged over 60 minutes and then transmitted. If a NOAA polar-orbiting satellite was in range, then the message was relayed to shore using Service Argos. Otherwise the message was updated the next hour and the new message transmitted. On average, approximately eight messages were received per day. The data set also includes housekeeping information from the drifter such as battery voltage, number of samples, and average time that the surface float was submerged.

Twenty-four drifters were released over a three-year period in the California Current. Four drifters failed soon after deployment (presumably due to high seas); the remainder had an average lifetime of six months with the maximum being nearly ten months. Figure 2 shows all of the drifter tracks collected between 1993 and 1995, and Table 1 shows the details of deployment location and schedule. Most of the drifters were deployed along a line at 39.5°N between 125° and 128°W. As expected, the general trend was for the drifters to move south and west with the prevailing summertime currents when most of the drifters were deployed (Paduan and Niiler, 1990; Brink et al. 1991; Swenson et al., 1992).

One of the problems with autonomous systems is quality control of the data which must rely only on the information contained within the data stream. Examination of the sensor or post-deployment testing is not possible as with more traditional sensor systems. Once the data were received, several screening tests were applied to eliminate low quality data points. Occasionally bits were dropped from the satellite data stream, resulting in unrealistic values in many of the drifter variables such as battery voltage, downwelling irradiance, etc. Screening for such out-of-bounds points is fairly straightforward. The position of the drifter was also determined by Argos using the Doppler shift of the transmission signal. Sometimes these positions were either missing or were obviously in error (sudden, large jumps in position). The Argos files also included the number of messages received during a given transmission from the drifter. If this number was small, then the probability of erroneous or corrupted data increased.

We limited our analyses to data that were obtained when the absolute solar angle (elevation) was greater than 20°. This constrained the study data set to observations collected with a few hours of local solar noon, reducing the effects of diel variability in properties such as fluorescence.

Bio-fouling is of particular concern, especially in the relatively productive waters of the California Current. In the past, various anti-fouling paints and mechanical devices have been used to keep optical surfaces free of contamination. However, many of the paints can significantly affect the optical performance of the sensor and in some cases actually enhance bio-fouling by providing a rougher surface for attachment (McLean et al., 1996). Mechanical scrubbers, such as those used by Wirick (1994), require more electrical power than is available in a small, autonomous drifter. Instead, we developed tests based on the optical measurements that could be used to indicate when bio-fouling had exceeded an acceptable threshold. The most robust test was based on the ratio of the radiances at 683 and 555 nm. As the radiance at 555 nm is relatively insensitive to changes in chlorophyll concentration and the radiance at 683 nm (which measures sun-stimulated fluorescence) is extremely sensitive to changes in chlorophyll content, then the ratio should be an excellent indicator of plant growth on the sensor. Figure 3 shows a time series from one of the drifters. Note that after 25 July 1994, the value of this ratio increases sharply and its level of variability increases as well. This was a consistent pattern for all of the drifters, although the time scale for the onset of bio-fouling varied from two to four months.

After screening, chlorophyll was calculated using the following equation:

$$chl = 0.56353 * \left( \frac{L_u(443)}{L_u(555)} \right)^{-0.595} \quad (1)$$

where  $L_u$  is upwelling radiance at a specific wavelength. This form is derived from earlier bio-optical models (Clark, 1981; Gordon and Morel, 1983), and the coefficients were based on comparisons with chlorophyll samples collected near an identical drifter that was deployed in Drake Passage in 1994 and with another identical drifter deployed off the Olympic Peninsula in 1996. Although the optical properties of Southern Ocean phytoplankton may differ from those in the California Current (Mitchell and Holm-Hansen, 1991), we only need relative chlorophyll values to calculate temporal statistics. However, these coefficients may change as a result of changes in species composition that are largely driven by changes in the physical environment (Abbott et al., 1995).

Given the near-surface measurements of upwelling radiance, it is necessary to correct the radiance measurement at 683 nm for solar backscatter. This is in contrast to the usual measurements that are done at depth and where the solar contribution is small (e.g., Kiefer et al., 1989). The correction was performed based on the absorbance of pure seawater (Smith and Baker, 1981) and chlorophyll over the top 0.5 m of water since the radiometer is located 0.5 m below the sea surface. We calculated the absorbance at 670 nm and at 683 nm as:

$$abs_{670} = (0.43 + chlor.*0.0182) * 0.5 \quad (2)$$

$$abs_{683} = (0.45 + chlor.*0.0114) * 0.5 \quad (3)$$

These absorbances were then used to calculate a backscatter correction following Kirk (1994):

$$backscatter = \frac{abs_{683}}{abs_{670} * 0.5326} \quad (4)$$

This correction was applied as:

$$fluor = L_u(683) - (L_u(670) / backscatter) \quad (5)$$

where  $L_u$  refers to the upwelling radiance measured at a specific wavelength.

SST was measured directly by the sensor package, and no further calculations were necessary. Drifter speed was calculated from the quality-controlled drifter position information. Distance between successive positions was based on a great circle calculation and then divided by time between positions to estimate speed.

Once the data files were cleaned and the various derived quantities were calculated, we estimated decorrelation scales from the drifter data set. We first calculated a “daily average” for the variables of interest: SST, chlorophyll, fluorescence/chlorophyll, and drifter speed. Some of the data records were too short or too gappy for further statistical analyses. However, the majority of the drifters were nearly complete with only occasional missing data points. These gaps were filled using linear interpolation between adjacent days. A linear trend was removed from each time series, and the autocorrelation function was calculated. The decorrelation scale was estimated as the point at which this function first became insignificantly different from zero. Figure 5 shows a typical pair of autocorrelation functions for SST and chlorophyll from one drifter. Cross-correlation functions were calculated in a similar manner between detrended time series of SST and chlorophyll.

## RESULTS

Of the 20 drifters that survived the initial deployment, the average length of the bio-optical time series was 73 days before fouling became evident. Some drifters lasted well over 90 days before there was any evidence in the bio-optical signals that fouling had occurred. For these long time series, it was possible to divide the record into two parts, each one covering a different season. After checking the quality of the bio-optical measurements, 16 were selected for further analysis. The other 4 had time gaps greater than several days in the data records that compromised the quality of any time series analysis.

### ***Pigment Packaging***

One of the concerns raised by Carder et al. (1991) was that the amount of chlorophyll “packaging” would significantly affect light absorption by chlorophyll, thus resulting in serious errors in the radiance ratio model for chlorophyll. Packaging encompasses several processes that govern how chlorophyll is distributed and bundled within the phytoplankton cell (Nelson et al., 1993). Carder et al. (1991) showed that rapidly-growing phytoplankton are often characterized by high levels of packaging, thus causing serious errors in chlorophyll estimates that are based on static radiance ratio models. Results presented by Carder et al. (submitted) indicate that phytoplankton in the waters off the California coast are typically characterized by highly packaged pigments. To investigate this effect, Carder et al. (submitted) suggest plotting the ratio of the remote sensing reflectance (defined as the ratio of upwelling radiance to downwelling irradiance for a particular wavelength) at 412 nm to that at 443 nm versus the ratio of the remote sensing reflectance at 443 nm to that at 555 nm. This first ratio encapsulates the relative absorption by colored dissolved organic matter (CDOM) at 412 nm to the absorption by chlorophyll at 443 nm. A low ratio corresponds to high CDOM:chlorophyll. The second ratio (443 to 555 nm) is inversely proportional to chlorophyll concentration; that is, we expect this ratio to decrease as chlorophyll concentration increases. In the case of packaging, the 412:443 ratio will increase because the effective decrease in reflectance at 443 nm will be larger than the decrease at 412 nm (Carder et al., submitted). Similarly, the ratio of 443:555 will decrease because reflectance at 443 nm will decrease faster than the reflectance at 555 nm.

When these two reflectance ratios are plotted, one would expect there to be a positive slope in the relationship. That is, as chlorophyll decreases, the ratio of 443:555 will increase and the amount of CDOM relative to chlorophyll will also decrease, thus increasing the ratio of 412:443. However, the package effect will significantly alter this relationship as will changes in vertical transport since CDOM generally accumulates at depth and is photo-oxidized in near-surface waters (Siegel and Michaels, 1996). In fact, the slope of the relationship may be reversed. At high chlorophyll concentrations, the absorption by chlorophyll may increase significantly faster than absorption by CDOM even though the ratio of CDOM to chlorophyll may not change. This will lead to an apparent increase in the 412:443 ratio as the 443:555 ratio decreases.

The bio-optical drifters did not measure remote sensing reflectance, but ratios of the upwelling radiances will provide similar information, as long as we restrict the optical data to periods around local solar noon. Figure 4 shows the ratio of 412 nm to 443 nm radiance plotted against the ratio of 443 nm to 555 nm radiance. These values are within the range expected for upwelling systems (Carder et al., submitted), but note that the slope is decidedly negative. We plotted these numbers as a function of SST as well as a function of the distance from the coast to determine if there were large-scale spatial changes in these optical characteristics. There was no significant difference in these relationships from that depicted in Figure 4. Thus we conclude that the phytoplankton were indeed highly packaged, as noted by Carder et al. (1991). However, this should not affect the statistical analyses as there were no consistent large-scale spatial shifts in packaging.

### ***Eddy Observations***

One of the observations noted by Denman and Abbott (1994) was the lack of a lag time between changes in chlorophyll and changes in SST. In one subregion, they observed that there was a two-day lag consistent with other observations in upwelling systems where freshly upwelled water does not immediately result in increased chlorophyll values. Instead, phytoplankton require a few days to “shift-up” their nutrient utilization capabilities to take advantage of these higher nutrients (MacIsaac et al., 1985; Jones et al., 1988; Dugdale et al., 1997). However, Denman and Abbott (1994) only found such a lag in a location adjacent to an upwelling center that presumably had strong horizontal advection as well. In general, they did not observe such a lag in the satellite time series of SST and phytoplankton pigments.

In contrast, many of the drifter deployments revealed that changes in SST led changes in chlorophyll by roughly 1-2 days, especially those that sampled ocean eddies. Figure 6 shows the track and cross-correlation function for drifter 22622 that made nearly two complete circuits around a large anticyclonic eddy. Changes in SST led changes in chlorophyll by one day (negative lag between the two series). Drifter 20139 made two circuits around a smaller, cyclonic eddy. Data from this drifter is presented in Figure 7. Note that in this case, the negative correlation (at near zero lag) is much larger in the anticyclonic eddy (Fig. 6) than in the cyclonic eddy (Fig. 7). For all of the eddies sampled by drifters, the negative correlation at this one to two day negative lag was generally larger in anticyclonic versus cyclonic eddies. The cyclonic eddy shown in Figure 7 has positive lobes at -7 and +2 day lags and negative lobes at -15 and +9 day lags. The lag time scale of the positive correlation (five days) corresponds to

one-half of the travel time around the eddy (cold water, high chlorophyll on one side of the eddy and warm water, low chlorophyll on the other). The anticyclonic eddy (Fig. 6) has larger positive lobes at -10 and +5 days which implies a travel time of about 15 days (versus 10 days for the cyclonic eddy). The presence of a lag of 1-2 days was also consistently observed in both cyclonic and anticyclonic eddies, with changes in SST leading changes in chlorophyll.

Of the 20 drifters that transmitted their position over a period of two weeks or longer, 11 made at least one complete transit around an eddy. Figure 8 shows the tracks for one of the drifters (in addition to the two shown in Figures 6 and 7) which traced out eddy patterns in the northern part of the study region. Huyer et al. (this volume) reviewed high resolution surveys that were conducted at the time of the drifter deployments in 1993. They noted the presence of a warm core, anticyclonic eddy at the location of the eddy in Figure 6 one year earlier in August 1993. The drifter track in Figure 8 also traversed a large anticyclonic eddy in this northern region. Although the eddy in Figure 6 is not the same as the one sampled by the ship survey, many of the characteristics are similar. Huyer et al. (this volume) suggested that the 1993 eddy formed nearshore in early spring and then moved offshore at a rate of about 1-5 km/day. The tangential velocity of this eddy was about 25 cm/s, and the eddy diameter was about 150 km in August 1993. The August 1994 eddy in Figure 6 had a diameter of about 110 km (assuming that the drifter was following the outer edge of the eddy). The tangential velocity was about 25 cm/s, and the westward propagation speed was a little over 1 km/day.

Huyer et al. (this volume) also suggest that a pair of eddies (one anticyclonic and one cyclonic), observed near 38° N between 126° and 127° W, were moving westward as a pair. Evidence of this pair can be seen in the track shown in Figure 8. In this case, these drifters were deployed in summer 1993 so it is likely that these are the same eddies as those observed by Huyer et al. Interestingly, one of the drifters traversed both eddies, first going around the anticyclone and then going around the cyclone to the west.

The stronger negative correlation between chlorophyll and SST at near-zero lag in the anticyclone (Fig. 6) should be expected in such a warm core eddy. Although Huyer et al. noted that this northern anticyclone was more heterogeneous than the southern anticyclone in 1993, the relatively well-behaved cross-correlation function in Figure 6 suggests that this anticyclone may have been more homogeneous in August. In contrast, the cross-correlation function for the cyclone (Fig. 7) has more small-scale structure. The weaker negative correlation at near-zero lag between SST and chlorophyll is also expected for this cold core eddy. Although freshly upwelled water should be both colder and more chlorophyll-rich than older upwelled waters, this relationship is not constant. Intense upwelling may bring up water that is both cold and chlorophyll-poor, if it comes from sufficient depth. Similarly, solar heating will both warm the upwelled waters and stimulate phytoplankton production. Abbott and Zion (1985) examined a sequence of AVHRR and CZCS images during an upwelling event in this same region. As the upwelling developed, the inverse relationship between SST and chlorophyll strengthened in the warmer, offshore waters whereas it became more complex in the cooler, nearshore waters.

Although the ship survey took place in 1993 and the drifter deployments covered both 1993 and 1994, the general patterns of eddies were similar. Based on drifter tracks, the northern anticyclone near 39° N, 126° W was nearly identical in location and physical characteristics in both years. More complex eddy patterns were apparent to the south, although recurrent eddies also are a common feature. The apparent exchange between an anticyclone/cyclone eddy pair (Fig. 8) suggests that this might be a mechanism to move material offshore in the surface waters.

Occasionally, two drifters would follow the same path, although one would be following the other several days later. Such opportunities allowed us to compare sensor performance. Drifter 22622, which sampled the anticyclonic eddy, was followed somewhat later in time by drifter 20140. The drifters were deployed at 39°33'N, 124°55'W (drifter 20140) and 39°25', 126°27'W (drifter 22622). Although these drifters were released approximately 130 km apart, they followed the same circulation path over a period of 50 days with an average separation time of 18 hours and average distance of 62 km between drifters (Fig. 9 top).

The temperature records produced by the instrument packages appear to be sampling different water masses over the first 30 days (Fig. 9 middle). After day 245, the temperature records are similar in magnitude and trend, suggesting that both drifters are sampling the same water mass. During this period, the distance between both drifters was reduced to an average of 18 km (Fig. 9 top). Furthermore, estimates of chlorophyll concentration are also similar during this period (Fig. 9, bottom). In this particular case, these results suggest that the principal physical and biological processes controlling phytoplankton biomass over temporal scales of days appear to be acting over large spatial scales (1-100 km). Similar scales were noted by Huyer et al. (this volume).

### *Decorrelation Scales*

The temporal decorrelation scale averaged over the 16 drifters was longest for SST at 6.3 days. The decorrelation scale for chlorophyll was 3.7 days, 2.3 days for fluorescence/chlorophyll, and 3.3 days for drifter speed. These results are within the range for the same region off northern California as reported by Denman and Abbott (1994) where the time scales were between one and seven days, depending on length scale. Note that the SST time scale was significantly larger than the chlorophyll time scale, which is not consistent with the results of Denman and Abbott (1994) who found no significant differences in the statistics of these two fields. However, the drifter speed decorrelation scale was quite similar to the chlorophyll time scale. This suggests that SST may not be an especially good indicator of the overall statistics of the physical circulation in this region. The similarity between the chlorophyll and speed scales is consistent with the interpretation of Denman and Abbott (1994). Our estimates of the near surface current time scales is similar to that estimated in a more comprehensive analysis of drifter tracks by Davis (1985). Although the drifter speed time scale is much smaller than the SST time scale, this is not surprising. Drifter speed can change as a result of many physical processes, such as inertial motions, that have relatively short time scales. SST is a non-conservative tracer, and small-scale fluctuations may be smoothed out by large-scale processes such as air/sea fluxes. In addition, SST responds to large-scale forcing such as coastal upwelling which may impose longer time scales.

Although these overall scales are useful, examination of the raw data records suggested that the nature of the variability changed as the drifters moved offshore. We recalculated the decorrelation scales as a function of the average distance offshore. We divided the distance offshore into three categories: <200 km (nearshore), >200 km but less than 400 km (transition), and > 400km (offshore). These domains are similar to those described by Simpson et al. (1986) based on an analysis of CZCS and AVHRR imagery. Simpson et al. (1986) noted that the “transition zone” was dominated by mesoscale eddies that tended to recur at specific locations. Figure 5 shows the decorrelation scale for SST, chlorophyll, fluorescence/chlorophyll, and drifter speed as a function of these three domains. Five drifter tracks were included in the nearshore zone, nine in the transition zone, and ten in the offshore zone. Note that these add up to more than the 16 drifters that delivered useful data. This is a result of subdividing some of the drifter tracks into two seasonal subsets. There is a general trend for the time scales to increase as one moves offshore. Both the SST and fluorescence/chlorophyll time scales increase offshore, from 2 days to 7.5 days for SST and from 0.25 to 2 days for fluorescence/chlorophyll (Fig. 10). However, the pattern is more complex than a simple cross-shore gradient. The decorrelation scale for drifter speed is nearly constant across the entire domain (around 4 days), with perhaps a small increase in the offshore region. The time scale for chlorophyll increases from 2 days to four days from the nearshore to the transition region and then decreases to 2 days in the offshore region.

The comparisons between the biological quantities (chlorophyll and fluorescence/chlorophyll) and the physical quantities (SST and drifter speed) are more complex. In the nearshore domain, the time scales for both SST and chlorophyll are nearly identical. The time scale for fluorescence/chlorophyll is much smaller (several of the autocorrelation functions were not significantly different than zero beyond zero lag). The time scale associated with drifter speed was nearly twice as large as for SST and chlorophyll, and it was also considerably more variable (note the size of the standard deviation). In the transition region, the scales of SST and chlorophyll began to diverge as the increase in the decorrelation scale for SST was larger than the increase in the chlorophyll decorrelation scale. Interestingly, the decorrelation scale for drifter speed was essentially the same as for the inshore region, although its variance was much smaller. In the offshore domain, the SST scale was significantly longer than the chlorophyll scale (7 days versus 2.5 days). In contrast, the time scales for drifter speed and fluorescence/chlorophyll were nearly the same as the chlorophyll scale. Note that the variability in the drifter speed scale is much smaller than in the other two regions (Figure 10).

As noted before, some of the drifters provided useful data over more than one season (Table 1). We calculated decorrelation scales for these different seasons, but there was no consistent seasonal pattern. In part, this was the result of deploying nearly all of the drifters in summer so that spring and winter were poorly sampled. However, we expect that a more thorough program of deployments may reveal a consistent seasonal pattern in these scales.

### **DISCUSSION**

Temporal and spatial variability in planktonic ecosystems has been a focus of oceanographic research for several decades, with continuing debate over the relative importance of physical and biological processes. For example, Bennett and Denman (1985) argued that the only mechanism that could cause biological patterns to deviate from the spatial patterns of mesoscale physical processes would be spatial heterogeneity in growth rates. Without this

persistent source of variance, the spatial statistics of phytoplankton would be overwhelmed by mesoscale turbulence and one could not distinguish the two. Support for this view came from a variety of sources, including Denman and Abbott (1994) who showed that the temporal and spatial statistics of SST and chlorophyll were indistinguishable over time scales of 1 day to 1 month and space scales 25 km to 100 km. Thus much of the debate over spatial and temporal heterogeneity and its impacts on sampling and ecological processes has focused on the perceived dominance of physical forcing. For example, the Joint Global Ocean Flux Study (JGOFS) time series at Bermuda and Hawaii are thought to be aliased by unresolved mesoscale variability (e.g., Dickey et al., 1993). This problem was pursued in a numerical model of the Bermuda ecosystem by Lawson et al. (1995; 1996) who showed that the present JGOFS sampling might not be adequate to resolve ecologically important processes that were associated with this physical forcing.

Ecological processes such as predation and competition are often thought to be relatively unimportant in regions such as the California Current where physical disruption of the environment is thought to occur too frequently to allow such processes to develop (McGowan, 1974). However, more “stable” environments such as the central North Pacific are thought to be more strongly influenced by such biological processes (Venrick, 1982; McGowan and Walker 1985). On long time scales (years to decades), even stable environments can shift as a result of large-scale changes in forcing and ocean circulation (e.g., Karl et al., 1995).

The debate over physical or biological control depends strongly on our assessment of whether the planktonic ecosystem is in equilibrium or not (Harris, 1986). That is, we implicitly assume that stable systems are in equilibrium and therefore ecological processes such as competition can govern ecosystem structure. Systems that are in a non-equilibrium state are assumed to be regulated by the physical environment. At this point, the debate shifts to the role of physiological processes and how organisms “perceive” environmental heterogeneity. As argued by Harris (1986), phytoplankton have evolved to exploit various scales of variability, resulting in a system where “equilibrium” and “non-equilibrium” are ambiguous terms. That is, the physiological responses of phytoplankton (e.g., nutrient uptake, light utilization) can respond to changes in the environment at different scales (Cullen and Lewis, 1988; Lande and Lewis, 1989). Whether the phytoplankton are in equilibrium or not depends on the overall time scales of the physiological response and the characteristic scales of the environmental fluctuations. For example, phytoplankton respond to changes in irradiance as a result of high frequency surface gravity waves (which cause focusing and de-focusing of sunlight) and the low frequency internal waves (which raise and lower entire phytoplankton layers). In the first case, we expect there to be a negligible effect on overall productivity as the phytoplankton will effectively average over these fluctuations whereas the internal wave case may have a significant impact (Denman and Powell, 1984).

Our results show that physical processes have a strong influence on the time/space distribution of phytoplankton (as indicated by chlorophyll concentration). The prevalence of both warm core and cold core eddies clearly affect chlorophyll distributions, as revealed in the cross-correlation functions between SST and chlorophyll (Figures 6 and 7). Even though there is an element of randomness in the eddy field, our results support earlier studies that showed that such eddies in the California Current are often predictable (Simpson et al., 1986; Haury et al., 1986; Peláez and McGowan, 1986; Lagerloef, 1992; Hickey, 1979). The anticyclone in the northern portion of the study area (around 39° N, 126° - 127° W) had very similar properties in both 1993 and 1994. Paired eddies such as those observed in the southern portion (Huyer et., this volume, Simpson et al., 1986) are a common occurrence. Thus while individual features may be uncommon, there is a fairly high level of predictability concerning the statistics of these eddies. This may be sufficient to support the evolution of more than one strategy to exploit these physical environments that may have distinct spectra of environmental fluctuations.

The presence of large, negative correlations between SST and chlorophyll in warm core eddies compared with the weaker (and noisier) cross-correlations in cold core eddies suggests that the usual SST/chlorophyll relationship is more stable in these warm core eddies. Small increases (decreases) in SST are correlated with small decreases (increases) in chlorophyll content. The cold core cyclones are characterized by a less stable relationship between SST and chlorophyll. Processes such as upwelling of deep waters with low chlorophyll content or rapid heating of surface waters may break this simple linear model. In the former case, phytoplankton are apparently tracking physical fluctuations so we would suspect that they may be close to equilibrium. In the cold core eddies, the scale of environmental variability is too short so consequently phytoplankton cannot track every fluctuation. The population may then be farther away from equilibrium in such a physical environment.

The decorrelation statistics from the drifters can also be interpreted in this context. In the overall statistics of the drifter data set, the SST time scale was greater than either the drifter speed or the chlorophyll time scales (roughly 6

days versus 3 days). If physical processes completely controlled biological distributions, we might expect the time scales to be similar for both SST and chlorophyll. Although the SST time scale is much larger (over the whole study domain), this result is consistent with the view that at some time scales, biological and physical processes are in synchrony while at other scales the two are disconnected. In this case, the difference in decorrelation scales could be interpreted to mean that at large time scales, processes other than physics are controlling the temporal distribution of chlorophyll. Earlier research using variance spectra (Denman and Platt, 1976; Powell et al. 1974; Denman et al., 1977) suggested that biology should control abundances at these large scales while at some smaller critical length (or time) scale, physics became the controlling factor. Evidence for this interpretation can be seen in the results from individual eddies. At near-zero lag, there is a strong relationship, but this becomes more complex (and less consistent) at longer time separations (Figures 6 and 7). However, the shift at larger time scales could simply be a shift in the physical processes that control SST at these scales rather than a shift from physical to biological control in chlorophyll. Although SST is controlled by physics, it is not a conservative tracer, just as chlorophyll is not a conservative tracer.

The cross-shore patterns of decorrelation time scales (Fig. 10) provide more insight into these processes. In the nearshore domain (within 200 km of the coast), SST and chlorophyll have identical decorrelation scales. In contrast, the drifter speed scale is significantly larger, and the fluorescence/chlorophyll scale is significantly smaller. This suggests that in this nearshore region, the processes that control the temporal statistics of SST and chlorophyll are the same and that they are quite variable. A three-day decorrelation scale is about the scale of synoptic forcing of upwelling events. The longer drifter speed time scale suggests that horizontal speeds of the upper ocean may be driven by larger scale processes and these speeds do not respond as rapidly as SST. Current meter records, such as those from the Coastal Ocean Dynamics Experiment (Winant et al., 1987), have time scales of days to weeks. The short fluorescence/chlorophyll time scale (recall that many of these records showed little significant autocorrelation even at scales of one day) implies that the phytoplankton light harvesting (as represented by chlorophyll content) and light utilization (as represented by fluorescence) are not in balance. That is, fluorescence per unit chlorophyll is changing extremely rapidly so that although phytoplankton are harvesting light, they are not able to utilize this light in photosynthesis and must re-emit some of it as fluorescence (Kiefer and Reynolds, 1992).

In the transition region (between 200 and 400 km offshore), all of the time scales increased, except for drifter speed. In this region (which was dominated by eddies), the SST and chlorophyll scales began to diverge (though not significantly). The fluorescence/chlorophyll time scale became more similar to the chlorophyll scale, suggesting that the processes of harvesting and utilization were becoming more in balance. The longer time scales of both SST and chlorophyll are likely the result of eddy processes. As noted earlier, these eddy scales were in the range of 5 to 15 days. These scales are longer than the average statistics shown in Figure 10 because drifters in the transition zone were not always following eddies, and some of the eddies were smaller than those shown in Figures 6 and 7. The key point is that the time scales in the transition zone are longer than those nearshore, and that this difference is probably the result of prevalence of eddies in this region (Simpson et al., 1986).

The offshore region (> 400 km offshore) is significantly different from the two regions closer to shore (Fig. 10). The SST time scale is much longer than the others, which are nearly identical with each other. As discussed earlier, we could interpret this difference in SST and chlorophyll to be the result of biological control at large scales and physical control at small scales. An alternative explanation is that the physical processes that govern SST variability offshore no longer govern the variability of chlorophyll. The fluorescence/chlorophyll time scale may help us to differentiate between these two explanations. The nearly identical time scales between this and chlorophyll imply that light harvesting and light utilization are in balance. As the amount of chlorophyll (which to first order controls light capture) changes, the amount of fluorescence (which represents a loss of energy that might otherwise be available for photosynthesis) changes as well. Since the drifter speed scale is nearly the same as both the chlorophyll and the fluorescence/chlorophyll scales, this suggests that there is a change in the physical processes that control phytoplankton growth and abundance in the offshore region, and that these processes occur on time scales that allow phytoplankton to adapt. In the nearshore region (and to some extent in the transition region), the environment varies more rapidly, leading to a lack of coherence between light capture and use. This environmental variability controls both SST and chlorophyll in the nearshore region.

In this examination of cross-shore differences, it is worth recalling our analysis of phytoplankton chlorophyll packaging. Large spatial scale changes in the effective light absorption by chlorophyll might lead to similar patterns of decorrelation scale. Given the large shifts in phytoplankton community composition from nearshore (dominated by diatoms) to offshore (dominated by small green flagellates) as noted by Hood et al. (1991), we might expect the package effect to change as well. However, we could find no evidence of a change in the degree of packaging either

as a function of distance offshore or as a function of SST. The entire study region showed the same level of packaging.

The shift in time scales and earlier observations on shifts in species composition and growth rate (e.g., Hood et al., 1991) supports the idea that nearshore and offshore environments not only have different physical environments with different scales of variability, but that the phytoplankton communities are characterized by different ecological strategies. Rather than a simple distinction between physical or biological control, it appears that the physical environment sets the basic time and space scales. However, the physiological scales of the phytoplankton (e.g., nutrient uptake, light harvesting and utilization, etc.) as well as the scales of the grazers and other components of the ecosystem determine how this variability is perceived. Organisms that can respond rapidly to small-scale changes in light or nutrients may well be close to equilibrium in a highly variable environment. Therefore the interaction between physical scales and physiological scales will determine in part whether the phytoplankton are in equilibrium or not. Moreover, as noted by Harris (1986), the degree of equilibrium may vary according to species, but on the broad scales observed by the drifters, we can resolve only two communities. The nearshore community is not in equilibrium with the physical environment that is largely driven by processes related to upwelling. This community is dominated by chain-forming diatoms (Chavez et al., 1991; Hood et al., 1991) which typically are at an advantage in variable environments (Margalef, 1978). The offshore community is closer to an equilibrium state, and earlier field studies have shown it to be dominated by smaller species, primarily flagellates and prokaryotic forms.

These ideas of equilibrium versus non-equilibrium have been explored in oceanography for many years (e.g., Margalef, 1978; Harris, 1986). Communities that are close to equilibrium tend to be closely coupled to grazing and dominated by recycling processes (e.g., Banse, 1996). On the other hand, non-equilibrium communities are generally characterized by episodic blooms that can outstrip grazing pressure. Such differences clearly can affect biogeochemical processes such as downward carbon flux. Platt et al. (1989) argued that the apparently high flux in the central gyres was the result of unresolved bloom events that escaped grazer control, leading to high rates of downward carbon flux. Apart from these episodic events, the ecosystem was in balance with tight coupling between phytoplankton growth, grazing, and recycling.

Our results suggest that even in an eastern boundary current environment characterized by highly packaged pigments, there are strong differences in ecological strategies along a cross-shore gradient. However, note that this interpretation cannot be based solely on measurements of SST and chlorophyll, as were used in the analysis by Denman and Abbott (1994). Although SST and chlorophyll time scales diverge as one moves offshore, one cannot unambiguously assign this divergence to a shift from physical to biological control. Moreover, the SST and drifter speed time scales also diverge. Thus we can only say that the nature of the physical variability has shifted as one moves offshore, and that SST may not necessarily be a particularly accurate indicator of the physical environment offshore. However, consideration of the time scales of fluorescence/chlorophyll suggests that the biological community and the nature of its response to environmental changes as one moves offshore. Thus the results of Denman and Abbott (1994) who argued that phytoplankton behaved merely as a passive scalar in this region are apparently not applicable to the entire domain. We suspect that in the nearshore domain that indeed phytoplankton (as represented by chlorophyll) and SST are closely linked and respond to similar physical forcing. However, in the transition and the offshore domains (which were not especially well-sampled by the satellite imagery used by Denman and Abbott because of increased cloudiness), SST is controlled by different physical processes than chlorophyll, and the phytoplankton community shifts from one characterized by non-equilibrium processes to one that is characterized by equilibrium processes.

Chlorophyll fluorescence varies on a wide range of time scales and is sensitive to changes in nutrient stress and species composition (Falkowski and Kolber, 1995). Although this change in the quantum yield of fluorescence greatly complicates the use of fluorescence to estimate phytoplankton biomass, this variability may be used to bridge the gap between the small scales associated with physiological adaptations and the longer scales associated with ecosystem function (Falkowski and Kolber, 1995). In regions of strong vertical motion (such as in areas of active upwelling in the nearshore region), we expect that fluorescence per unit chlorophyll will change rapidly. Our results have implications for primary productivity models that are based on remote sensing observations. Behrenfeld and Falkowski (1997) demonstrate that the performance of productivity models depends strongly on optimal assimilation efficiency (a measure of photoadaptation). If fluorescence quantum yield is an indicator of photoadaptation (Falkowski and Kolber, 1995), then our results suggest that there may be different strategies of photoadaptation as phytoplankton communities shift from non-equilibrium to equilibrium. In other words, phytoplankton may always be “tracking” an optimal photosynthetic efficiency, but the closeness of this tracking may vary significantly. Our results support the conclusion of Behrenfeld and Falkowski (1997) that more effort must be placed on understanding

the linkages between phytoplankton physiology and environmental variability.

These results have applications to other studies. Optimal interpolation and various data assimilation techniques require estimates of temporal and spatial decorrelation scales (e.g., Denman and Freeland, 1985; Mariano and Brown, 1992; Bennett, 1992). These results also show that various measurement techniques have different effective resolution scales. For example, because fluorescence per unit chlorophyll changes very rapidly in the nearshore region, its use as an indicator of chlorophyll content would be limited to small scales as well. Platt et al. (1989) discussed the similar impacts of measurement scales in the oligotrophic ocean.

Although bio-optical drifters present their own set of challenges in terms of data processing and analysis, they can provide a more systematic approach for the study of time scales of biological processes in the upper ocean. In the California Current, they reveal that physical forcing may be the ultimate cause that drives variability in the phytoplankton community, but the ecological strategies adopted by the community can significantly modify its impact. Moreover, we cannot neglect the physiological processes in the various species that are at the heart of the community response. Thus future studies of environmental variability must continue to elucidate both bulk measures of phytoplankton (such as chlorophyll) as well as more species-specific measures.

*Acknowledgments*-We thank the many people who assisted with deployment of the drifters. We especially thank Dick Limeburner, Bob Beardsley, and Ken Brink of Woods Hole Oceanographic Institution, Mike Kosro, Jane Huyer, Jack Barth, and Tim Cowles of Oregon State University, and Jeff Paduan of the Naval Postgraduate School. Brett Barksdale, Curt Vandetta, Ganesh Gopalan, and Anand Sankaran assisted with programming and data base management. This research was supported by the Office of Naval Research (Grant N00014-92-J-1536), and the National Aeronautics and Space Administration (Contract NAS5-31360).

## REFERENCES

- Abbott, M. R., and P. M. Zion (1985) Satellite observations of phytoplankton variability during an upwelling event. *Continental Shelf Research*, **4**, 661-680.
- Abbott, M. R., and B. Barksdale (1991) Phytoplankton pigment patterns and wind forcing off central California. *Journal of Geophysical Research*, **96**, 14,649-14,667.
- Abbott, M. R., K. H. Brink, C. R. Booth, D. Blasco, L. A. Codispoti, P. P. Niiler and S. R. Ramp (1990) Observations of phytoplankton and nutrients from a Lagrangian drifter off northern California. *Journal of Geophysical Research*, **95**, 9393-9409.
- Abbott, M. R., K. H. Brink, C. R. Booth, D. Blasco, M. S. Swenson, C. O. Davis and L. A. Codispoti (1995) Scales of variability of bio-optical properties as observed from near-surface drifters. *Journal of Geophysical Research*, **100**, 13,345-13,367.
- Banse, K. (1996) Low seasonality of low concentrations of surface chlorophyll in the Subantarctic water ring: underwater irradiance, iron, or grazing? *Progress in Oceanography*, **37**, 241-291.
- Barale, V., and R. Wittenburg-Fay (1986) Variability of the ocean surface color field in Central California near-coastal waters as observed in a seasonal analysis of CZCS imagery. *Journal of Marine Research*, **44**, 291-316.
- Batteen, M. L. (1997) Wind-forced modeling studies of currents, meanders, and eddies in the California Current system. *Journal of Geophysical Research*, **102**, 985-1010.
- Behrenfeld, M. J., and P. G. Falkowski (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, **42**, 1-20.
- Bennett, A. F. (1992) *Inverse Methods in Physical Oceanography, Monographs on Mechanics and Applied Mathematics*, Cambridge University Press, New York, 346 pp.
- Bennett, A. F., and K. L. Denman (1985) Phytoplankton patchiness: inferences from particle statistics. *Journal of Marine Research*, **43**, 307-335.
- Brink, K. H., and T. J. Cowles (1991) The coastal transition zone program. *Journal of Geophysical Research*, **96**, 14,637-14,647.
- Brink, K. H., R. C. Beardsley, P. P. Niiler, M. Abbott, A. Huyer, S. Ramp, T. Stanton and D. Stuart (1991) Statistical properties of near surface flow in the California coastal transition zone. *Journal of Geophysical Research*,

96, 14,693-14,706.

Carder, K. L., S. K. Hawes, K. S. Baker, R. C. Smith, R. G. Steward and B. G. Mitchell (1991) Reflectance model for quantifying chlorophyll *a* in the presence of productivity degradation products. *Journal of Geophysical Research*, **96**, 20,599-20,611.

Carder, K. L., S. K. Hawes and Z. Lee (1997) SeaWiFS algorithm for chlorophyll *a* and colored dissolved organic matter in subtropical environments. *Journal of Geophysical Research*, submitted.

Chavez, F. P., R. T. Barber, P. M. Kosro, A. Huyer, S. R. Ramp, T. P. Stanton and B. Rojas de Mendiola (1991) Horizontal transport and the distribution of nutrients in the coastal transition zone off northern California: Effects on primary production, phytoplankton biomass and species composition. *Journal of Geophysical Research*, **96**, 14,833-4,848.

Clark, D. K. (1981) Phytoplankton pigment algorithms for the Nimbus-7 CZCS. In: *Oceanography from Space*, J. F. R. Gower, editor, Plenum Press, New York, pp. 227-238.

Cullen, J. J., (1990) On models of growth and photosynthesis in phytoplankton. *Deep-Sea Research*, **37**, 667-683.

Cullen, J. J., and M. R. Lewis (1988) The kinetics of algal photoadaptation in the context of vertical mixing. *Journal of Plankton Research*, **10**, 1039-1063.

Davis, R. E. (1985) Drifter observations of coastal surface currents during Coastal Ocean Dynamics Experiment: The statistical and dynamical view. *Journal of Geophysical Research*, **90**, 4756-4772.

Demmig-Adams, B. (1990) Carotenoids and photoprotection in plants: a role of the xanthophyll zeaxanthin. *Biochimica et Biophysica Acta* **1020**, 1-24.

Denman, K. L., and T. Platt (1976) The variance spectrum of phytoplankton in a turbulent ocean. *Journal of Marine Research*, **34**, 593-601.

Denman, K. L., and T. M. Powell (1984) Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanography and Marine Biology Annual Review*, **22**, 125-168.

Denman, K. L., and H. J. Freeland (1985) Correlation scales, objective mapping and a statistical test of geostrophy over the continental shelf. *Journal of Marine Research*, **43**, 517-539.

Denman, K. L., and M. R. Abbott (1988) Time evolution of surface chlorophyll patterns from cross-spectrum analysis of satellite ocean color images. *Journal of Geophysical Research*, **93**, 6789-6798.

Denman, K. L. and M. R. Abbott (1994) Time scales of pattern evolution from cross-spectrum analysis of advanced very high resolution radiometer and coastal zone color scanner imagery. *Journal of Geophysical Research*, **99**, 7433-7442.

Denman, K. L., A. Okubo and T. Platt (1977) The chlorophyll fluctuation spectrum in the sea. *Limnology and Oceanography*, **22**, 1033-1038.

Dickey, T. D. (1991) The emergence of concurrent high-resolution physical and bio-optical measurements in the upper ocean and their applications. *Reviews of Geophysics*, **29**, 383-413.

Dickey, T. D., J. Marra, T. Granata, C. Langdon, M. Hamilton, J. Wiggert, D. Siegel and A. Bratkovich (1991) Concurrent high resolution bio-optical and physical time series observations in the Sargasso Sea during the spring of 1987. *Journal of Geophysical Research*, **96**, 8643-8663.

Dickey, T. D., T. Granata, J. Marra, C. Langdon, J. Wiggert, Z. Chai-Jochner, M. Hamilton, J. Vazquez, M. Stramska, R. Bidigare and D. Siegel (1993) Seasonal variability of bio-optical and physical properties in the Sargasso Sea. *Journal of Geophysical Research*, **98**, 865-898.

Dugdale, R. C., A. Morel, A. Bricaud and F. P. Wilkerson (1989) Modeling new production in upwelling centers: A case study of modeling new production from remotely sensed temperature and color. *Journal of Geophysical Research*, **94**, 18,119-18,132.

Dugdale, R. C., C. O. Davis and F. P. Wilkerson (1997) Assessment of new production at the upwelling center at Point conception, California, using nitrate estimated from remotely sensed sea surface temperature. *Journal of Geophysical Research*, **102**, 8573-8585.

- Falkowski, P. G., and Z. Kolber (1995) Variations in chlorophyll fluorescence yields in phytoplankton in the world oceans. *Australian Journal of Plant Physiology*, **22**, 341-55.
- Gordon, H. R., and A. Y. Morel (1983) *Remote Assessment of Ocean Color for Interpretation of satellite Visible Imagery: A Review*. Springer, New York, 114 pp.
- Haidvogel, D. B., A. Beckmann and K. S. Hedstrom (1991) Dynamical simulations of filament formation and evolution in the coastal transition zone. *Journal of Geophysical Research*, **96**, 15,017-15,040.
- Harris, G. P. (1986) *Phytoplankton Ecology: Structure, Function, and Fluctuation*. Chapman and Hall, New York, 384 pp.
- Haury, L. R., J. J. Simpson, J. Peláez, C. J. Koblinsky and D. Wiesenhahn (1986) Biological consequences of a persistent eddy off Point conception, California. *Journal of Geophysical Research*, **91**, 12,937-12,956.
- Hickey, B. M. (1979) The California Current system - hypotheses and facts. *Progress in Oceanography*, **8**, 191-279.
- Hood, R., M. R. Abbott, P. M. Kosro and A. E. Huyer (1990) Relationships between physical structure and biological pattern in the surface layer of a northern California upwelling system. *Journal of Geophysical Research*, **95**, 18,081-18,094.
- Hood, R. R., M. R. Abbott and A. Huyer (1991) Phytoplankton and photosynthetic light response in the coastal transition zone off northern California in June 1987. *Journal of Geophysical Research*, **96**, 14,769-14,780.
- Hutchinson, G. E. (1941) Ecological aspects of succession in natural populations. *American Naturalist*, **75**, 406-418.
- Huyer, A., J. A. Barth, P. M. Kosro, R. K. Shearman and R. L. Smith (1997) Upper-ocean water mass characteristics of the California Current, Summer 1993. *Deep-Sea Research*, this volume.
- Jones, B. H., L. P. Atkinson, D. Blasco, K. H. Brink and S. L. Smith (1988) The asymmetric distribution of chlorophyll associated with an upwelling center. *Continental Shelf Research*, **8**, 1155-1170.
- Karl, D. M., R. M. Letelier, D. V. Hebel, T. Tupas, J. Dore, J. Christian and C. Winn (1995) Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991-1992 El Niño. *Nature*, **373**, 230-234.
- Kiefer, D. A., and R. A. Reynolds (1992) Advances in understanding phytoplankton fluorescence and photosynthesis. In: *Primary Productivity and Biogeochemical Cycles in the Sea*, P. G. Falkowski and A. D. Woodhead, editors, Plenum Press, New York, pp. 155-174.
- Kiefer, D. A., W. S. Chamberlin and C. R. Booth (1989) Natural fluorescence of chlorophyll *a*: Relationship to photosynthesis and chlorophyll concentration in the western South Pacific gyre. *Limnology and Oceanography*, **34**, 868-881.
- Kirk, J. T. O. (1994) *Light and Photosynthesis in Aquatic Ecosystems*. 2<sup>nd</sup> edn, Cambridge Univ. Press, Cambridge, U.K., 509 pp.
- Lagerloef, G. S. E. (1992) The Point Arena eddy: A recurring summer anticyclone in the California Current. *Journal of Geophysical Research*, **97**, 12,557-12,568.
- Lande, R., and M. R. Lewis (1989) Models of photoadaptation and photosynthesis by algal cells in a turbulent mixed layer. *Deep-Sea Research*, **36**, 1161-1175.
- Lawson, L. M., Y. H. Spitz, E. E. Hofmann and R. B. Long (1995) A data assimilation technique applied to a predator-prey model. *Bulletin of Mathematical Biology*, **57**, 593-617.
- Lawson, L. M., E. E. Hofmann and Y. H. Spitz (1996) Time series sampling and data assimilation in a simple marine ecosystem model. *Deep-Sea Research*, **43**, 625-651.
- Legendre, L., S. Demers and D. LeFaivre (1986) Biological production at marine ergoclines. In: *Marine Interfaces and Ecohydrodynamics*, J. C. J. Nihoul, editor, Elsevier, Amsterdam, pp. 1-54.
- MacIsaac, J. J., R. C. Dugdale, R. T. Barber, D. Blasco and T. T. Packard (1985) Primary production cycles in a coastal upwelling regime. *Deep-Sea Research*, **32**, 503-529.

- Margalef, R. (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, **1**, 493-509.
- Mariano, A. J., and O. B. Brown (1992) Efficient objective analysis of dynamically heterogeneous and nonstationary fields via the parameter matrix. *Deep-Sea Research*, **39**, 1255-1271.
- McGowan, J. A. (1974) The nature of oceanic ecosystems. In: *The Biology of the Oceanic Pacific*, C. B. Miller, editor, Oregon State University Press, Corvallis, pp. 9-28.
- McGowan, J. A., and P. W. Walker (1985) Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs*, **55**, 103-118.
- McLean, S., B. Schofield, G. Zibordi, M. Lewis, S. Hooker and A. Weidemann (1996) Field evaluation of anti-biofouling compounds on optical instrumentation. *Proceedings of the Society of Photo-Optical Instrumentation Engineers, Ocean Optics XIII*, **2963**, 708-713.
- Michaelsen, J., X. Zhang and R. C. Smith (1989) Variability of pigment biomass in the California Current system as determined by satellite imagery, 2. Temporal variability. *Journal of Geophysical Research*, **93**, 10,883-10,896.
- Mitchell, B. G., and O. Holm-Hansen (1991) Bio-optical properties of Antarctic Peninsula waters: differentiation from temperate ocean models. *Deep-Sea Research*, **38**, 1009-1028.
- Mohanty, N., and H. Y. Yamamoto (1995) Mechanism of non-photochemical chlorophyll fluorescence quenching. I. The role of de-epoxidised xanthophylls and sequestered thylakoid membrane protons as probed by dibucaine. *Australian Journal of Plant Physiology*, **22**, 231-238.
- Nelson, N. B., B. B. Prézelin and R. R. Bidigare (1993) Phytoplankton light absorption and the package effect in California coastal waters. *Marine Ecology Progress Series*, **94**, 214-224.
- Paduan, J. D., and P. P. Niiler (1990) A Lagrangian description of motion in northern California coastal transition filaments. *Journal of Geophysical Research*, **95**, 18,095-18,110.
- Peláez, J., and J. A. McGowan (1986) Phytoplankton pigment patterns in the California Current as determined by satellite. *Limnology and Oceanography*, **31**, 927-950.
- Platt, T., W. G. Harrison, M. R. Lewis, W. K. W. Li, S. Sathyendranath, R. E. Smith and A. F. Vezina (1989) Biological production of the oceans: The case for a consensus. *Marine Ecology Progress Series*, **52**, 77-88.
- Powell, T. M., et al. (1974) Spatial scales of current speed and phytoplankton biomass fluctuations in Lake Tahoe. *Science*, **189**, 1088-1090.
- Siegel, D. A., and A. F. Michaels (1996) Quantification of non-algal light attenuation in the Sargasso Sea: Implications for biogeochemistry and remote sensing. *Deep-Sea Research*, **43**, 321-345.
- Simpson, J. J., C. J. Koblinsky, J. Peláez, L. R. Haury and D. Wiesenhahn (1986) Temperature-plant pigment-optical relations in a recurrent offshore mesoscale eddy near Point conception, California. *Journal of Geophysical Research*, **91**, 12,919-12,936.
- Smith, R. C., and K. S. Baker (1981) Optical properties of the clearest natural waters. *Limnology and Oceanography*, **23**, 260-267.
- Smith, R. C., X. Zhang and J. Michaelsen (1989) Variability of pigment biomass in the California Current system as determined by satellite imagery, 2. Spatial variability. *Journal of Geophysical Research*, **93**, 10,683-10,882.
- Strub, P. T., P. M. Kosro, A. Huyer and CTZ Collaborators (1991) The nature of the cold filaments in the California Current system. *Journal of Geophysical Research*, **96**, 14,743-14,768.
- Swenson, M. S., P. P. Niiler, K. H. Brink and M. R. Abbott (1992) Drifter observations of a cold filament off Point Arena, California, in July 1988. *Journal of Geophysical Research*, **97**, 3593-3610.
- Venrick, E. L. (1982) Phytoplankton in an oligotrophic ocean: observations and questions. *Ecological Monographs*, **52**, 129-154.
- Winant, C. D., R. C. Beardsley and R. E. Davis (1987) Moored wind, temperature, and current observations made during Coastal Ocean Dynamics Experiments 1 and 2 over the northern California continental shelf and

upper slope. *Journal of Geophysical Research*, **92**, 1569-1604.

Wirick, C. D. (1994) Exchange of phytoplankton across the continental shelf-slope boundary of the Middle Atlantic Bight during spring 1988. *Deep-Sea Research*, **10**, 221-231.

<i>Drifter ID</i>	<i>Launch Date</i>	<i>Launch Position</i>	<i>Last Transmission Date</i>	<i>Comments</i>
20133	5/5/93	39.5°N, 125.5°W	8/8/93	
20134	7/8/93	37.7°N, 126.1°W	7/9/93	Failed after 1 day
20135	6/8/93	39.5°N, 125°W	9/11/93	
20136	6/8/93	39.5°N, 126.5°W	9/8/93	
20137	8/17/93	39°N, 124.2°W	9/26/93	
20138	6/8/93	39.5°N, 128°W	9/11/93	
20139	7/8/93	37.8°N, 126.2°W	10/21/93	
20140	8/1/94	39.5°N, 125°W	2/17/95	
20141	7/8/93	37.5°N, 126.1°W	7/9/93	Failed after 1 day
20142	7/8/93	37.9°N, 126.1°W	10/25/93	
20143	7/8/93	37.4°N, 126°W	9/10/93	
20144	8/1/94	39.5°N, 125.5°W	3/20/95	
20145	8/17/93	39°, 124.5°W	12/8/93	
20146	2/23/94	39.5°, 125°W	6/14/94	
20147	2/23/94	39.5°N, 125.5°W	6/21/94	
20148	7/8/93	38°N, 126°W	10/20/93	
20149	9/18/93	37.7°N, 124.7°W	3/9/94	
20150	9/18/93	37.6°N, 124.6°W	never transmitted	
20151	9/18/93	37.6°N, 124.7°W	9/24/93	Failed after 6 days
20152	5/16/94	39.5°N, 125°W	2/28/95	
20153	5/16/94	39.5°N, 125.5°W	1/14/95	
20154	5/16/94	39.5°N, 126°W	2/12/95	
20155	8/1/94	39.5°N, 126°W	6/16/95	
22622	8/1/94	39.5°N, 126.5°W	1/9/95	

**Table 1.** Drifter deployment information for the 24 bio-optical drifters released in the California Current. Note that only 20 returned usable data.

## Figures

Figure 1. Schematic of the bio-optical drifters that were deployed in the California Current. From Abbott and Letelier (1997).

Figure 2. Tracks of all 20 drifters that transmitted their positions for at least two weeks. All of the drifters were deployed in 1993-1994, although some continued to work into 1995. From Abbott and Letelier (1996).

Figure 3. Time series of the ratio of upwelling radiance at 683 nm to upwelling radiance at 555 nm from a typical bio-optical drifter record. Note the increase in the value of this ratio as well as the increase in variability in early August. This was taken as evidence of the onset of bio-fouling.

Figure 4. Plot of the ratio of upwelling radiance at 443 nm to 555 nm (which is inversely proportional to chlorophyll concentration) versus the ratio of upwelling radiance at 412 nm to 443 nm (which is inversely proportional to the ratio of CDOM to chlorophyll). Data are from all of the drifters.

Figure 5. An example of the temporal autocorrelation function of SST and chlorophyll. From Abbott and Letelier (1996).

Figure 6. (Top) Track of drifter 22622 that traveled around an anticyclonic eddy. (Bottom) Cross-correlation function of SST and chlorophyll. Negative lags correspond to changes in SST leading changes in chlorophyll. Adapted from Abbott and Letelier (1996).

Figure 7. Same as Fig. 6 except that data are from drifter 20139 that traveled around a cyclonic eddy. Adapted from Abbott and Letelier (1996).

Figure 8. Track of drifter 20135. This drifter traveled around an anticyclone in the north, and then traveled around a cyclone/anticyclone pair in the south.

Figure 9. (Top) Distance between drifters 20140 and 22622. Both drifters eventually sampled the same eddy beginning around day 240. (Middle) SST time series from both drifters. (Bottom) Same except time series is for chlorophyll. Adapted from Abbott and Letelier (1996).

Figure 10. Average decorrelation scales for SST, chlorophyll, fluorescence/chlorophyll, and drifter speed. Data are plotted as a function of the average distance offshore of the drifter tracks. The error bars represent  $\pm 1$  standard deviation. Adapted from Abbott and Letelier (1996).