AN ABSTRACT OF THE THESIS OF

Rachel B. Sanders for the degree of Master of Science in Oceanography presented on December 15, 2003.
Title: Studies on the Spatial Variability of Phytoplankton Physiology and Biomass ir the Oregon Upwelling System

Abstract approved:

*Redacted for Privacy*

Mark R. Abbott

The Oregon upwelling system is a region of high biomass and primary productivity as well as strong mesoscale variability. In order to examine the interaction of physical forcing and ecosystem dynamics, four 3-week sampling cruises were conducted in the Oregon upwelling system as part of the Northeast Pacific Global Ocean Ecosystem Dynamics (NEP GLOBEC). During each of the four cruises, which took place in June and August of 2000 and 2002, a series of cross-shelf transects was completed in the region between 41.5° N to 45° N and -124° W to -126.5° W. Sea surface temperature, salinity, phytoplankton fluorescence, and $F_v/F_m$, the theoretical maximum quantum yield of photosynthesis, were measured continuously from an underway flow-through system with an intake at 5 m depth. During all four cruises, temperature increased offshore, and salinity was high nearshore and low offshore, corresponding to upwelling conditions. Overall trends in

$F_v/F_m$ were similar to patterns defined by temperature and salinity. $F_v/F_m$ was high near the coast and decreased further offshore, suggesting that phytoplankton were healthiest in recently upwelled water. Closer examination of individual transects revealed additional, small-scale variability in all parameters. Decorrelation analysis of 25-km transect sections indicated that this variability occurred over 3 km on average. However, the scales of variability of $F_v/F_m$ were slightly shorter than those of temperature, salinity, or phytoplankton fluorescence. Overall, there were no trends relating the short scale variability of $F_v/F_m$ to that of any other parameter within a given transect, suggesting that short-scale variability in Fv/Fm is not driven by temperature, salinity, or phytoplankton biomass, but by some other parameter or combination of parameters. Additional comparisons between phytoplankton fluorescence and $F_v/F_m$ show high $F_v/F_m$ associated with high phytoplankton biomass and variable $F_v/F_m$ when phytoplankton biomass is low. This pattern is also reflected in comparisons between nutrient levels and $F_v/F_m$, with $F_v/F_m$ high when levels of available nitrogen, phosphorus, and silica are high, and variable when nutrient levels are low, supporting the theory that nutrient limitation affects $F_v/F_m$. These results suggest that both ecosystem dynamics and physical forcing drive variability in biomass distribution and primary productivity in the Oregon upwelling system. However, they do not provide the means to determine which forcing mechanism is dominant.

# Studies on the Spatial Variability of Phytoplankton Physiology and Biomass in the Oregon Upwelling System

by
Rachel B. Sanders

A THESIS

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Master of Science

Presented December 15, 2003
Commencement June 2004

Master of Science thesis of Rachel B. Sanders presented on December 15, 2003.

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Rachel B. Sanders, Author

ACKNOWLEDGEMENTS

I would like to thank my major and minor advisors, Mark Abbott and Ricardo Letelier for their support and guidance throughout this project. Mark provided a framework for this thesis, and helped me to step back and think about the implications of my project on some of the big ecological questions. Ricardo gave me continual feedback on everything from data analysis to interpretation, and his help was essential to the completion of this thesis. The many discussions with him over the past three years have greatly expanded the way I think about oceanic ecosystems, and I am very grateful to him for the time and effort he gave to helping me.

I do not know how to thank Kerry Browne, Corinne Manogue, and Sam Laney for the effort they put into helping me both finish my thesis and grow as a person and a scientist. Kerry's love, encouragement, and belief in me throughout the process were invaluable in that they enabled me to believe in myself. Corinne's sound advice and timely anecdotes, combined with plenty of hugs, helped me to deal with the big problems I encountered and taught me to write my thesis one small goal at a time. Sam dedicated hours of his time to discussing the details of my thesis, helping me with outlines, and reading drafts. He has truly helped me not only to finish my thesis, but to helping me become a better writer overall. Kerry, Corinne, and Sam's support was above and beyond anything I could have asked for and I am glad to have this opportunity to let them know.

The effort involved in data collection and management for the NEP GLOBEC project was enormous. I would like to thank the Chief Scientists of the GLOBEC

cruises, Jack Barth and Tim Cowles. Many thanks to Chris Wingard and Russ Desiderio for management of the flow-through systems on all four cruises and collection and initial processing of the flow-through data. Amanda Ashe's exceptional organizational skills and dedication to collection of clean data, as well as the effort she expended on cruise prep and sample collection helped make this project a success. Finally, thanks to everyone who participated in the at-sea sampling: Amanda Ashe, Amanda Briggs, Megan Carney, Guido Corno, Cidney Howard, Ricardo Letelier, Roberto Venegas, and Angel White.

Finally, I would like to thank my family and friends who tolerated my erratic thesis-writing behavior and continually supported me with hugs, laughs, outdoor expeditions, and many a Monday night at Bombs. In alphabetical order: Cornelius Beilharz, Gwen Bury, Megan Carney, Larry O'Neill, Keeta Owens, Soo Potter, Ida Royer, Natacha Ryckelynck, Jean and Harold Sanders (Mom and Dad), Jane Thomas, Rhiannon Thomas, Emily Townsend, Till Ulbrich, Claire Varian, Hannah Weiss, Wolfgang Westje, and Christopher Wolfe.

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## 1 Introduction

A central question in biological oceanography is how physical forcing and ecological interactions influence the distribution of phytoplankton biomass in the ocean. Phytoplankton biomass distribution is often used to define areas of high primary productivity as well as to determine the processes involved in trophic transfer and carbon sequestration. Moreover, it is necessary to understand the relationship between physical forcing and biomass distribution. Some researchers maintain that distributions of plankton biomass are driven solely by ecological interactions, but others contend that they are controlled by physical forcing alone. These opposing views are well represented by the arguments of McGowan and Walker (1985) and Harris (1986). McGowan and Walker showed that the zooplankton community structure in the Central Pacific Gyre did not appear to respond to variability in the physical environment and concluded that the community structure was determined solely through biological interactions. Conversely, Harris argued that the stable, closed systems necessary for biological control to develop and dominate ecosystem structure are rare in nature and that most ecosystems are structured by the interactions between individual species and the variable physical environment. In reality, the extremes represented by these views are likely the endpoints of a continuum where

both environmental and biological interactions control biomass distribution (Cullen et al., 2002).

However, if an ultimate goal in understanding biomass distribution is to assess trophic transfer and carbon sequestration in the ocean, it becomes necessary to understand rates of biological processes, not just biomass distribution. For example, phytoplankton primary productivity (PP) can be defined as a function of phytoplankton biomass and growth rate. This relationship is often expanded to include a relative biomass term, such as chlorophyll concentration, and parameters relating to growth rate. A typical expression for primary productivity is

$$PP = E \cdot [chl\text{-}a] \cdot a^* \cdot \varphi p \qquad [1]$$

where E is the light intensity, [chl-a] is the concentration of chlorophyll a, a* is the specific absorption coefficient of chlorophyll a, and $\phi p$ is the quantum yield of photosynthesis. This quantum yield is the proportion of moles of photosynthetic product stored to the number of photons absorbed by the photosystem. Under light saturating conditions, if $a^*$ is assumed constant, the distribution of primary productivity is driven only by the phytoplankton biomass and the quantum yield of photosynthesis. Consequently, when calculating primary productivity, it may be important to account for the variability in physiological rates as well as the biomass distribution, especially when physiological rates vary independently of biomass.

It is relatively easy to measure variability in phytoplankton biomass using chlorophyll fluorescence as a proxy. Fluorescence in phytoplankton is strongly correlated with biomass and can be measured at high temporal and spatial resolutions both *in situ* using active fluorescence and remotely using sensors aboard the current generation of satellites such as the Moderate Resolution Imaging Spectroradiometer (MODIS) that measure passive, sun-stimulated fluorescence. However, it remains very difficult to measure variability in physiological parameters, particularly those associated with primary productivity. Physiological parameters can vary much more rapidly than does biomass, on the order of seconds to days rather than days to months (Reynolds, 2002). Consequently, to characterize this variability, these parameters must be measured at higher temporal and spatial resolutions. In addition, phytoplankton physiology is influenced by many physical variables such as nutrients, light, temperature, and nutrient and light history. Each of these factors may result in different physiological responses, complicating the choice of physiological parameter to measure. Thus, in order to measure the variability in phytoplankton physiology accurately and on the required scales, it is necessary to determine which physiological parameters contain the most useful information. It is also necessary to assess methods for measuring those parameters quickly and easily at high spatial and temporal resolution. Only after these physiological variables are appropriately quantified can their interaction with biomass distribution and physical forcing be examined.

Tools for examining how biomass distribution correlates with physical forcing are well developed for oceanographic studies. A powerful technique for such comparisons is an analysis and comparison of the variability in both the physical and biological systems. This technique was pioneered by Denman and Platt in the 1970's using spectral analysis to compare the frequency or wave number spectrum of the biomass distribution with a parameter representing the physical forcing such as temperature or salinity (Platt, 1972; Denman and Platt, 1975; Fasham and Pugh, 1976). These comparisons showed strong correlations in frequency and wave number spectra between biomass and temperature over many temporal and spatial scales suggesting a strong physical influence on biomass distribution. However, small differences between the spectra suggest that some element of biological forcing also contributes to phytoplankton biomass distribution (Denman, 1976). More recently decorrelation analysis and similar statistical methods have been used to evaluate the temporal and spatial variability in oceanic biomass distribution (Mackas, 1984; Denman and Abbott, 1988). While spectral analysis gives a distribution, decorrelation analysis quantifies the spatial or temporal scales over which a parameter is self-coherent. Mackas (1984) uses correlation length scales to compare the length scales over which community composition and biomass of zooplankton and phytoplankton remain constant off the coast of British Columbia. In this study, alongshore structure tended to remain coherent over longer spatial extents than cross-shore structure. Furthermore, community composition remained coherent over longer spatial scales than did biomass. Denman and Abbott (1988) calculated lagged

squared coherence estimates of coastal zone color scanner (CZCS) chlorophyll images from off Vancouver Island, Canada to determine the length of time over which chlorophyll structure lost coherence. This approach, similar to a lagged autocorrelation, revealed that offshore patterns in phytoplankton chlorophyll remained coherent over longer spatial scales than those in coastal regions. Such methods, developed to compare physical forcing and biomass distribution, can also be used to assess the spatial variability of physiological parameters and to compare them with physical forcing and biomass distribution. These comparisons depend on the development of reliable, high-resolution tools to measure phytoplankton physiology.

While it is difficult to measure phytoplankton physiology accurately and with high resolution, a number of studies show that it does vary at high temporal and spatial scales. Abbott et al., (1982) compared fluctuations in active fluorescence with those in the ambient light intensity. Strong correlations observed between fluorescence and light level indicated that phytoplankton physiology can respond rapidly, on the order of seconds to minutes, to environmental variability. However, the authors suggest that this rapid response would not change the photosynthetic rate, which should vary over a longer time scale. More recently, variations in passive fluorescence and the ratio of fluorescence per unit chlorophyll (F/Chl) have been used as proxies for the phytoplankton photosynthetic response. The ratio of F/Chl provides an estimate of the average quantum yield of photosynthesis times the chlorophyll specific absorption, ($a^* \cdot \phi p$ in Equation [1]) (Kiefer et al., 1989). F/Chl has been used as an indication of phytoplankton stress level to explain some

mechanisms for bloom development and decline along the Antarctic Polar Front (Abbott et al., 2000; Abbott et al., 2001). Abbott and Letelier (1998) used decorrelation scales to define the characteristic time scales over which F/C varies in the California Current and to compare this variability with that of temperature and chlorophyll concentration. This study suggested that phytoplankton physiological parameters can vary on shorter time scales than biomass distribution or physical forcing, especially in more turbulent areas such as coastal upwelling regions. These short time scales for F/C indicate that high-resolution sampling of physiological parameters is necessary to measure physiological variability. While F/C might possibly be used to assess physiological changes at the appropriate scales, it is limited in that this property can only be measured during the day. Also, F/C does not directly measure the quantum yield of photosynthesis, which is fundamental to understanding variability in primary productivity.

A promising new tool for examining photosynthetic variability in the ocean is Fast Repetition Rate fluorometry (FRRf). FRRf uses measurements of chlorophyll fluorescence to calculate the maximum change in variable fluorescence ($F_v/F_m$) which can be equivalent to the maximum change in the quantum yield of fluorescence ($\Delta\phi_m$), an indicator of the chlorophyll-specific photosynthetic rate (Falkowski and Kolber, 1993; Kolber and Falkowski, 1993). Although FRRf has frequently been used as a method of determining photosynthetic rates *in situ*, not many researchers have used its fundamental output to examine coupling between physical forcing, phytoplankton biomass distribution, and photosynthetic variability. One notable

exception is a study by Strutton et al., (1997), who used spectral analysis to compare variability in salinity and biomass distribution with average values of $\Delta\phi_m$ in the Southern Ocean. There, $\Delta\phi_m$ and the total variability in the biomass distribution were well correlated. Additionally, higher $\Delta\phi_m$ was associated with stronger decoupling between the biomass and salinity distributions. However, both correlations were somewhat weaker at spatial scales less than 10 km, suggesting that smaller scale processes might have different interactions between physical forcing and biological response. While this work compares variability in physical forcing and phytoplankton biomass distribution, it does not take advantage of the high-resolution sampling available using FRRf to consider the variability in phytoplankton physiology. Future work should look at the variability in phytoplankton physiology as well as focus on smaller spatial scales.

The Oregon coast offers us the opportunity to examine the spatial variability of physics, biomass distribution and ($F_v/F_m$) over small temporal and spatial scales. This upwelling region is dominated by strong mesoscale variability associated with upwelling fronts, but also contains jets, eddies, and the low salinity Columbia River plume. The inshore region tends to have cold, nutrient-rich water during upwelling events, with warmer, more nutrient-limited regions further offshore. This mesoscale variability produces strong variability in biomass distribution (Abbott and Zion, 1987; Hood et al., 1990; Thomas and Strub, 2001). Thus, this area provides a good location to assess how well the FRRf parameters can be used to quantify the interactions between physical forcing, biomass distribution, and physiological variability.

In order to compare the scales of variability of physical forcing, phytoplankton biomass, and photosynthetic rates, cross-shelf transects were sampled at multiple latitudes along the Oregon coast as part of the Northeast Pacific Global Ocean Ecosystem Dynamics (NEP GLOBEC) program during June and August of 2000 and 2002. A flow-through system sampled 5 m depth surface water every minute in 2000 and every second in 2002 for temperature, salinity, and phytoplankton fluorescence (as a proxy for biomass), and sampled the ratio of variable fluorescence to maximal fluorescence ($F_v/F_m$) (as a proxy for the photosynthetic rate) every minute in 2000 and every 7 seconds in 2002. The scales of variability of temperature, biomass, and $F_v/F_m$ were determined for each transect using decorrelation analysis. While there was no difference between the scales of variability for each parameter in the very nearshore region, further offshore the physiological proxy varied over shorter scales than temperature or phytoplankton biomass. These results suggest that $F_v/F_m$ does not vary on the same spatial scales as temperature, salinity, or phytoplankton biomass in some regions.

# 2 Methods

## 2.1 Data Acquisition

The data for the present study were collected during four Northeast Pacific (NEP) GLOBEC mesoscale cruises during the spring and summer of 2000 and 2002. Each cruise lasted approximately 3 weeks, and surveyed the region off the Oregon coast ranging from approximately 41.5° N to 45° N and from -124° W to -126.5° W. Each survey consisted of a mesoscale sampling grid of latitudinal transects with approximately 30 km between each transect, followed by finer sampling grids in the north and south of the survey region with approximately 15 km between each transect.

Temperature, salinity, phytoplankton fluorescence, and physiological parameters were sampled continually during each survey cruise from the ships flow-through system, located at approximately 5 m depth. May and August 2000 cruises were conducted on the R/V Wecoma. Temperature, salinity, and fluorescence were measured by a ship-based Turner Designs 10-AU Fluorometer and a SeaBird 25 CTD and binned into 1-minute averages. Physiological parameters were measured by a Chelsea Instruments Fast Repetition Rate Fluorometer (FRRf) every minute. The data were merged using nearest neighbor interpolation based on the GPS time for location, temperature, and fluorescence, and the internal clock time of the FRRf. The May 2002 cruise took place on the R/V Thomas G. Thompson and the August cruise

on the R/V Roger Revelle. During the 2002 cruises, location, temperature, salinity, and fluorescence were recorded by a GPS, a SeaBird 25 CTD and a Wet Labs WetStar fluorometer every second. Physiological parameters were measured approximately every 7 seconds by the FRRf. Timestamps from all instruments were recorded as one data file to allow direct comparisons of sample times. The data were merged using nearest neighbor interpolation based on the recorded timestamps. Thus, the final data sets for the 2000 cruises had a sampling rate of one sample per minute, while the 2002 data sets were more finely sampled at a rate of one sample every 7 seconds. Based on the average underway ship speeds of 13.5 km/hr in 2000 and 13.1 km/hr in 2002, these sampling rates translate into 4.25 samples / km in 2000 and 34.75 samples / km in 2002.

Nutrient samples were taken every hour during underway sampling. These 60-ml samples were collected in acid-washed bottles and frozen for analysis onshore. They were analyzed for phosphate ($PO_4^{3-}$), silica ($SiO_2$), nitrate ($NO_2^-$), nitrite ($NO_3^-$), and ammonium ($NH_4^+$).

## 2.2 Fast Repetition Rate Fluorometry Techniques

The FRRf measures physiological parameters by emitting a series of rapid, sub-saturating flashes of light to a phytoplankton sample and measuring the resulting fluorescence. The initial fluorescence, $F_0$, is assumed to be the fluorescence when all of the phytoplankton's photosystem II (PSII) reaction centers are open. Each consecutive flashlet closes more of the PSII reaction centers, thus increasing the

fluorescence, until all of the reaction centers are closed and a maximum fluorescence ($F_m$) is reached. The rapid rate of the flashes does not allow a significant portion of the reaction centers to relax during the measurement, keeping the measurement to a single turnover of each PSII reaction center (Falkowski and Kolber, 1993). The variable fluorescence ($F_v$) is defined as the maximum fluorescence minus the initial fluorescence ($F_m - F_0$).

The ratio of the variable fluorescence to the maximum fluorescence ($F_v/F_m$) can be used to describe the maximum quantum yield of photosynthesis. When a phytoplankton absorbs light, there are three pathways it can follow within photosystem II. It can be used for photosynthesis, (photochemical quenching), it can be dissipated as heat, (non-photochemical quenching), or finally it can be fluoresced. When we measure phytoplankton fluorescence, we measure the portion of the absorbed light that goes into fluorescence:

$$F = \frac{k_f}{k_f + k_h + k_p A} \qquad [2]$$

where F is the measured fluorescence, $k_f$, $k_h$, and $k_p$ are the rate constants of fluorescence, heat dissipation, and photosynthesis, and A is the fraction of PSII reaction centers that are open. If A = 1, all of the PSII reaction centers are open and the fluorescence is minimal ($F = F_0$) and if A = 0, the reaction centers are closed and fluorescence is maximal ($F = F_m$). Hence,

$$F_0 = \frac{k_f}{k_f + k_h + k_p} \qquad [3]$$

and

$$F_m = \frac{k_f}{k_f + k_h} \qquad [4]$$

Thus, it can be shown that:

$$\frac{(F_m - F_0)}{F_m} = \frac{F_v}{F_m} = \frac{k_p}{k_f + k_h + k_p A} \text{ where } A = 1. \qquad [5]$$

This is the quantum yield of photosynthesis, and since all of the reaction centers must be open, it becomes the maximum quantum yield of photosynthesis. The ratio of $F_v/F_m$ is therefore mathematically a useful measure of the fraction of open PSII reaction centers, or how much light a phytoplankton is able to use for photosynthesis. Physiologically, the limiting photosynthetic step is the oxidation of the Qa pool, and thus the ratio of $F_v/F_m$ reflects the size of the Qa pool, with a larger Qa pool allowing a faster photosynthetic rate and indicating a healthier cell.

## 2.3 Data Selection and Analysis

The data set used in this analysis was comprised of the nighttime portions of the latitudinal (cross-shelf) transects from each of the four NEP GLOBEC cruises. The entire data set was filtered using a 3 standard deviation filter that removed data points falling more than three standard deviations from the mean for the entire data set. This filtering removed major outliers and samples recorded while instruments were flushed with fresh water for washing. Nighttime portions of transects were selected to avoid changes in $F_v/F_m$ in response to light. $F_v/F_m$ has been shown to decrease as a result of photoinhibition and if measured when phytoplankton are not dark-adapted (Falkowski and Kolber, 1993). Within this data set, daytime $F_v/F_m$

decreased dramatically, but remained high and stable at night (Figure 1). The nighttime intervals were selected visually from this figure as 2000 to 0500 local time. Eliminating daytime samples from the analysis removed the effects of diel variability in $F_v/F_m$, allowing a focus on spatial variability.

After removing longitudinal and nighttime portions of the data set, the remaining transects were filtered again individually using a three standard deviation filter to remove outliers. Additionally, loops in the ship track and pauses for CTD stations were individually removed from each transect. Linear interpolation of each line to equidistant points in longitude corrected for small differences in ship speed within each line but did not dramatically change values of any of the parameters measured.

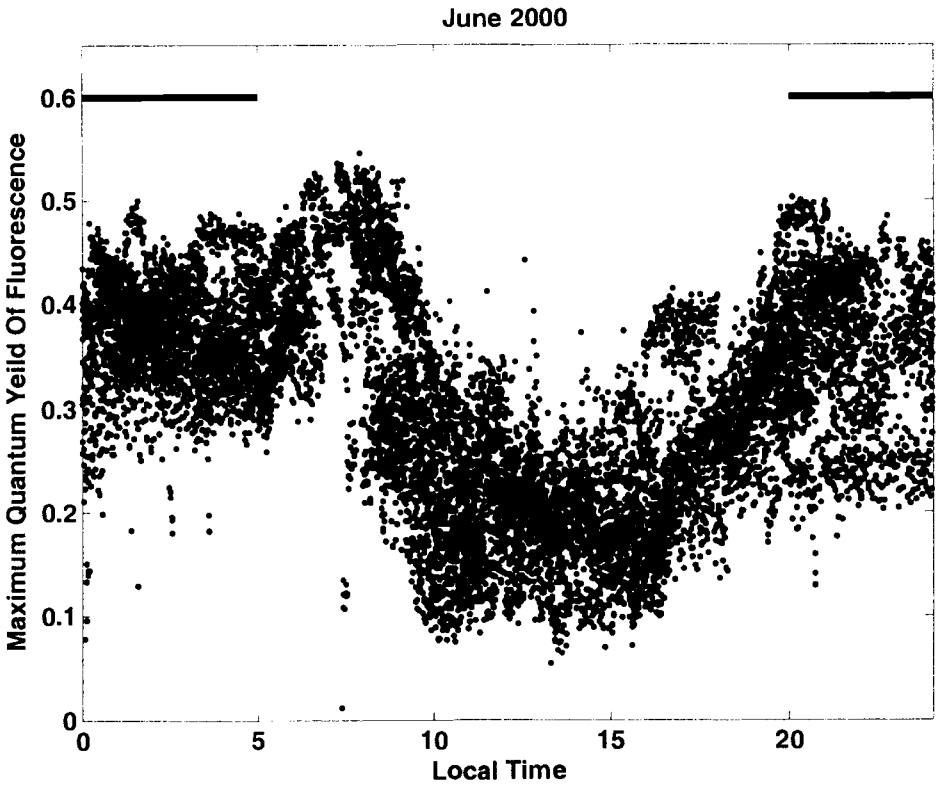



Figure 1: An example of the changes in $F_v/F_m$ with the time of day from the June 2000 GLOBEC cruise. $F_v/F_m$ decreases during the day as a result of photoadaptation and therefore does not provide a consistent measurement of cell physiology when it is light out. Only night time measurements, identified by the black lines, are used in this analysis.

In order to assess the small-scale variability in cross-shelf transects using decorrelation analysis, the influences of sharp, cross-frontal changes and large-scale gradients in temperature, salinity, phytoplankton fluorescence, and $F_v/F_m$ must be removed. Such large-scale features can dominate decorrelation scales and limit the information obtained about small-scale variability. Influences of cross-frontal changes were removed by dividing the study area into two regions, those inshore and

those offshore of the 13°C isotherm. The regions were divided at the 13°C isotherm because this boundary appeared to track the strongest temperature gradients in all four years. The exact location of the upwelling front as determined by a strong gradient in dynamic height (Barth et al., in prep.) was not available at the time of this analysis. Within each of these regions, 25-km sections of transects were selected for further analysis. Sections inshore of the 13° C began as close to shore as possible, and those offshore of the isotherm began as far offshore as possible. The transect locations are show in Figure 2. Large-scale gradients within each section were modeled using simple linear regressions that were then subtracted, along with the mean, from the transect data.

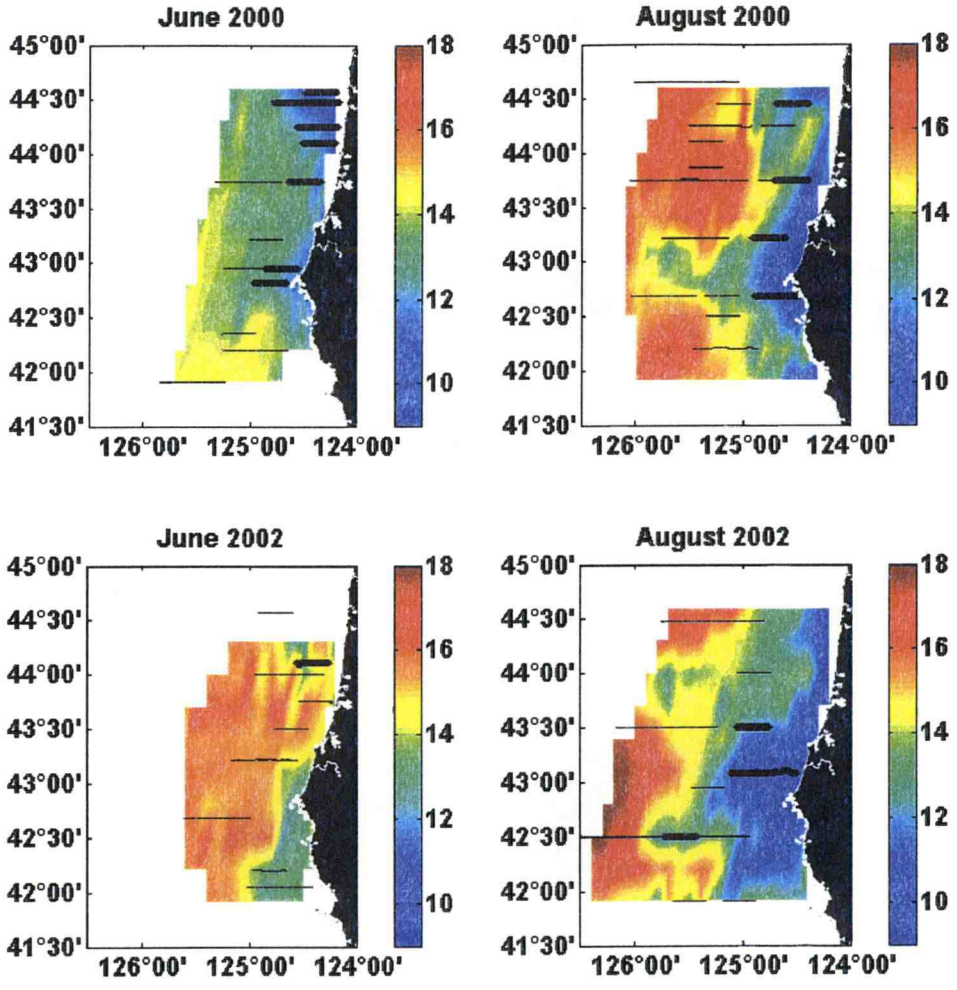



Figure 2: Locations of the transects used in this analysis displayed over temperature contours for all four cruises. Temperature contours are created from day and night surface data for horizontal transects during each cruise. Heavy lines show transects from inshore of the 13°C isotherm while thin lines show transects from offshore of the 13°C isotherm. Overlap between inshore and offshore transects occurs when large shifts in temperature changed the location of the isotherm over the course of the cruise. These shifts mean that a region may have been on one side of the isotherm early in the cruise and on the other when resampled later in the cruise. Longer transect have been divided into 25-km sections for analysis.

For each 25-km transect section, the decorrelation scale was calculated for temperature, salinity, phytoplankton fluorescence, and $F_v/F_m$. The decorrelation scale is defined as the point at which the lagged autocorrelation function first crosses the 95% confidence interval (Abbott and Letelier, 1998) (Figure 3). Decorrelation scales are compared between these four parameters for each cruise in the regions inshore and offshore of the 13°C isotherm.

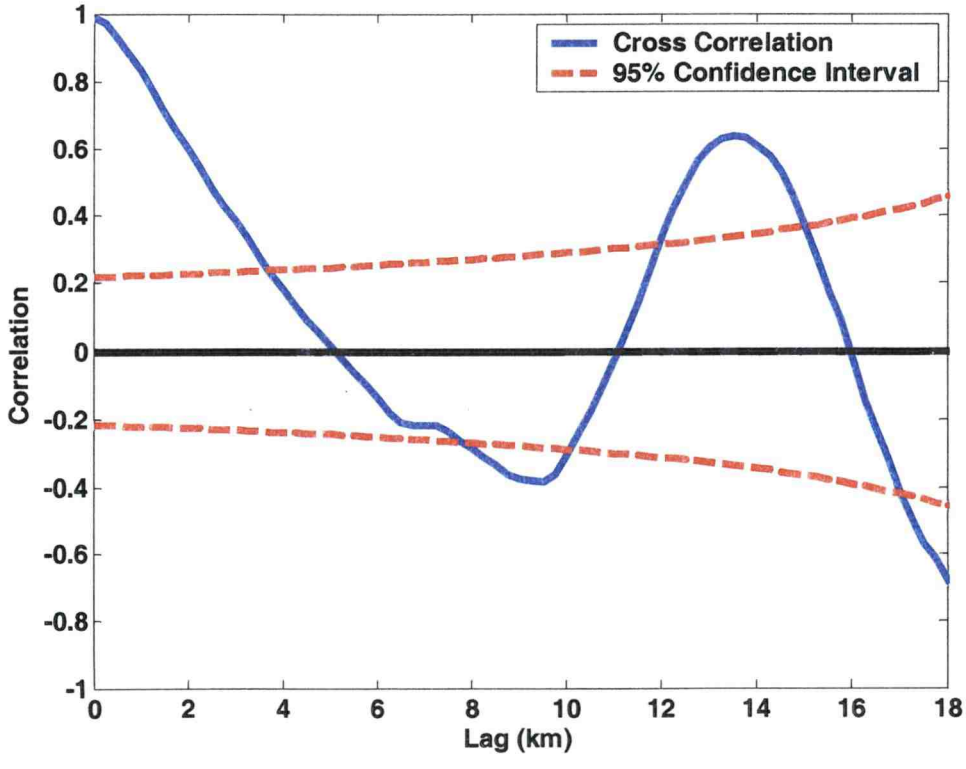



Figure 3: An example of decorrelation analysis using temperature data from a line in June 2000. The decorrelation scale is defined as the point at which the blue autocorrelation function first dips below the 95% confidence interval (dashed red line).

# 3 Results

## 3.1 Qualitative

The upwelling system was less developed in June than August in both years Barth et al. in prep.). June temperature profiles showed less cold upwelled water near the coast and lacked the meandering front characteristic of both August cruises (Figure 4). Additionally, neither June cruise showed the range of temperatures found in August. Overall, June 2000 was colder than June 2002, both in the nearshore upwelling band and the warmer region further offshore. June 2002 showed the beginnings of a temperature front in the region near Cape Blanco that was not seen in June 2000. The temperature ranges in August of both years were similar, with the 13°C isotherm farther offshore in August 2002. During all four cruises, upwelled water extended farthest offshore north of 44°30'N and south of 43°30'N, but tended to hug the coast in the regions around 44°N. In general, the salinity profiles were similar to the trends found in temperature, with high salinities associated with the cold, nearshore water (Figure 5). Intrusions of low-salinity water (salinity < 32.5 PSU) in the northeast of the survey region, especially apparent in June of both years are associated with the Columbia River plume (Huyer, 1983).

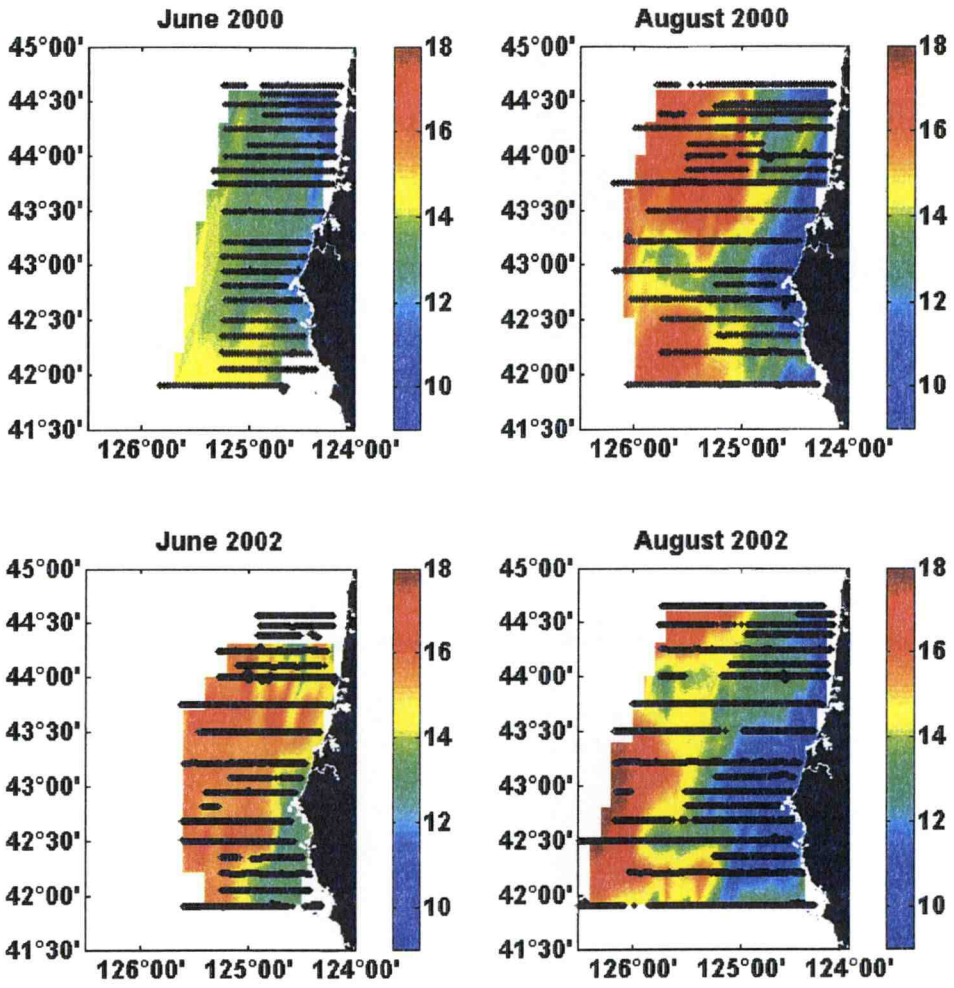



Figure 4: Sea surface temperature (°C) contours of each of the four cruises created from ship-based inline sampling. The black lines show the transects used in creating the figure and include data from both day and night sampling. Both August cruises show a much more developed upwelling front, with stronger meanders and sharper temperature gradients than in June. These same transects were used to create Figures 5 and 6.

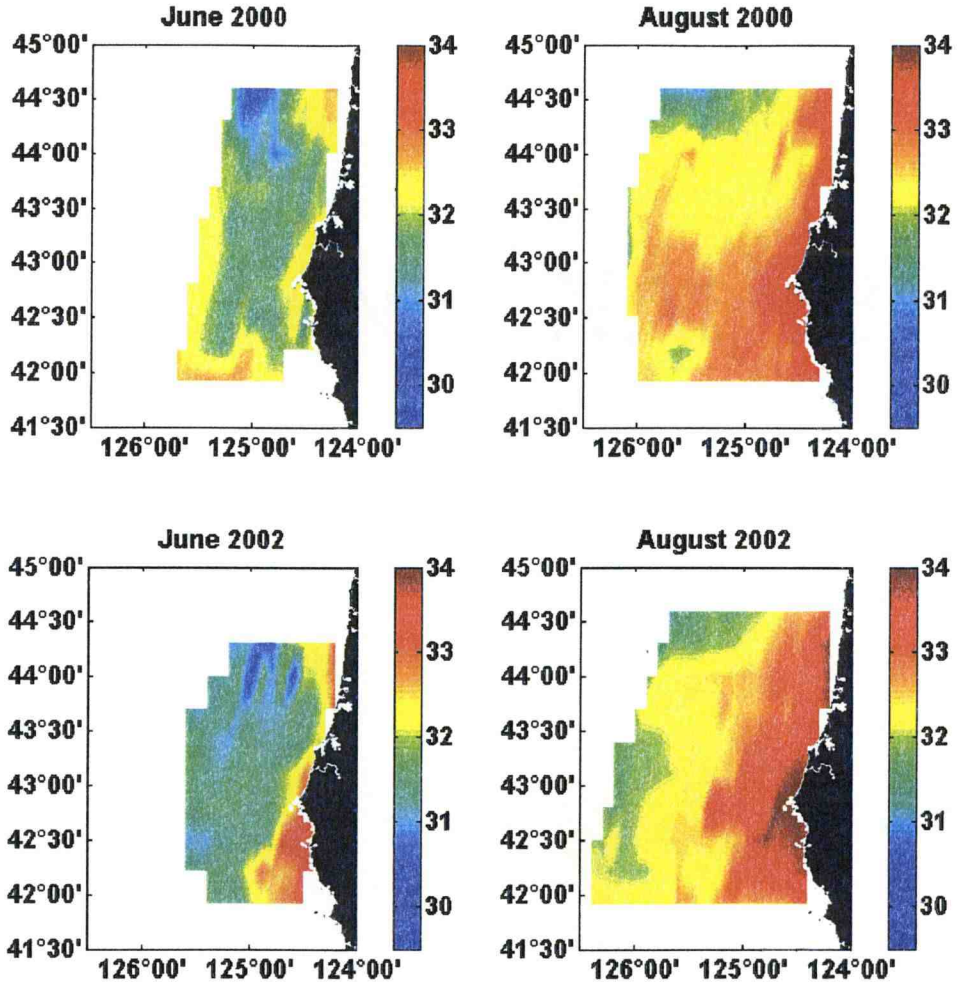



Figure 5: Sea surface salinity (PSU) contours of each of the four cruises created from ship-based inline sampling using both daytime and nighttime transects. Salinity gradients are associated with the upwelling front as well as with injections of the Columbia River plume. The Columbia River is identified by extremely low salinity (<31 PSU) in the north of the sampling region.

Phytoplankton fluorescence (Figure 6) is highest near the coast in June of both years, suggesting high surface concentrations of phytoplankton in this recently upwelled water. In August, the overall phytoplankton fluorescence was higher and extended further offshore. These patches of high offshore fluorescence are closely associated with cold temperature regions. Contrary to this trend, a region of very high phytoplankton fluorescence in August 2000 is seen in the far northwest corner of the survey area which does not have the low temperatures associated with the other major patches of high fluorescence. However, this patch does occur in a region dominated by mixing with Columbia River water.

The highest values of the maximum quantum yield of fluorescence ($F_v/F_m$) occur in the coastal regions associated with cold water and high phytoplankton fluorescence (Figure 7). In general, $F_v/F_m$ decreases with distance offshore. However, in August of 2002 the region of lowest $F_v/F_m$ occurs in the middle longitudes of the sampling region, around 125°W, with an area of higher $F_v/F_m$ offshore. Some reflection of this pattern is also seen in August of 2000. Neither of the June cruises sampled far enough offshore to determine if this pattern exists in both seasons.

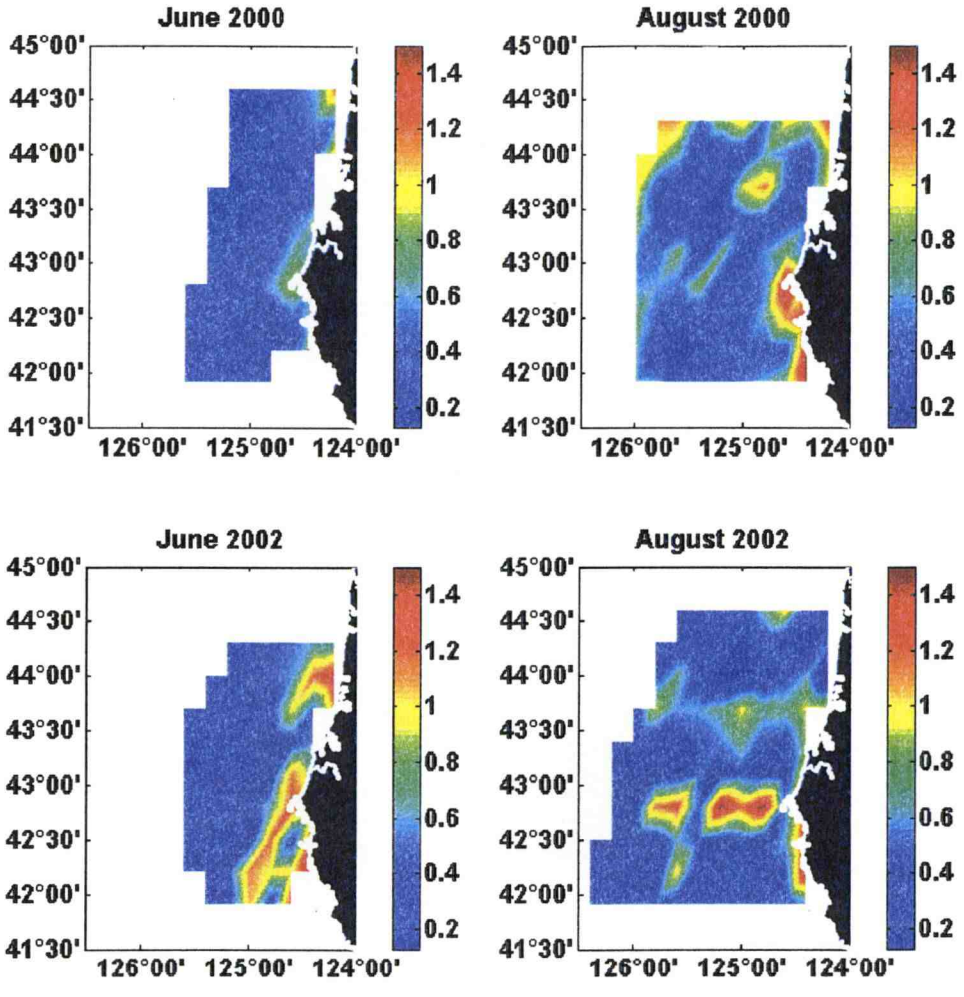



Figure 6: Sea surface fluorescence (V) contours of each of the four cruises created from ship-based inline sampling using both daytime and nighttime transects. To show increased spatial pattern, the maximum fluorescence is set at 1.5 V and all values higher than that are displayed as 1.5. The structure of the fluorescence signal does not match that of temperature or salinity.

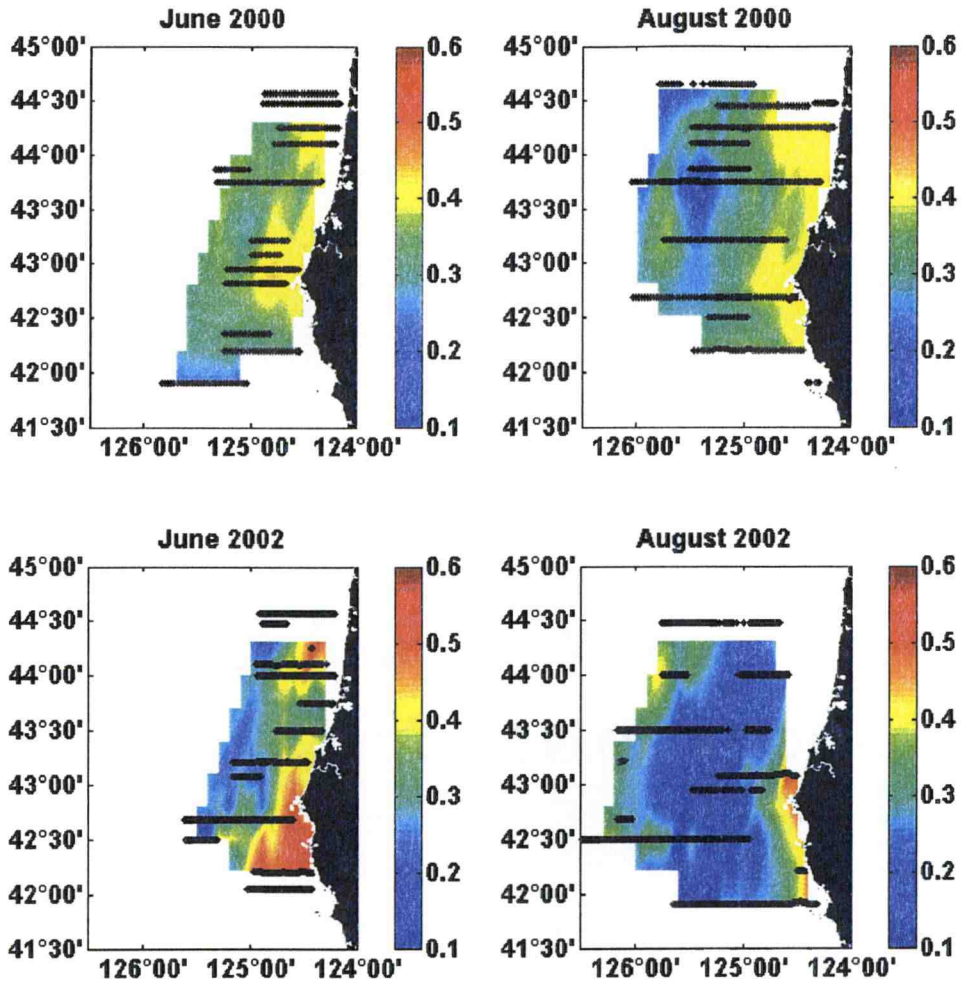
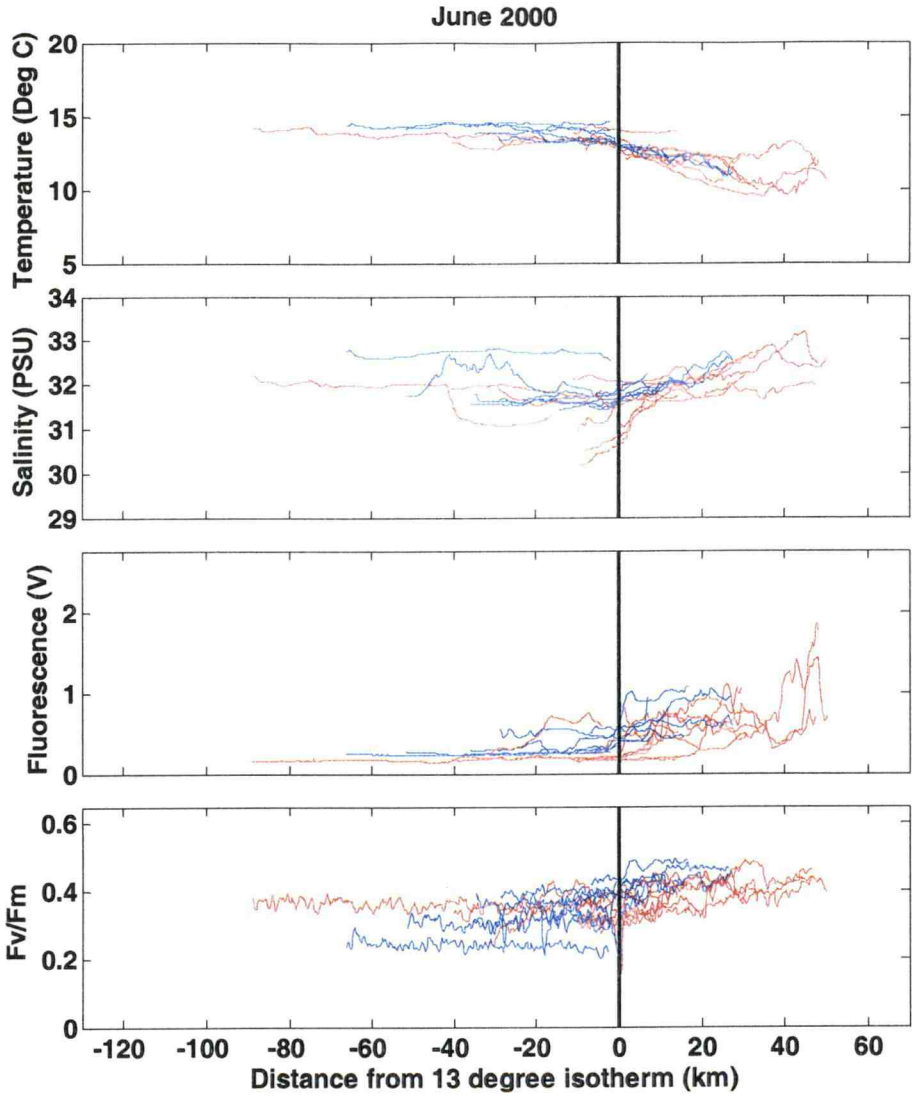
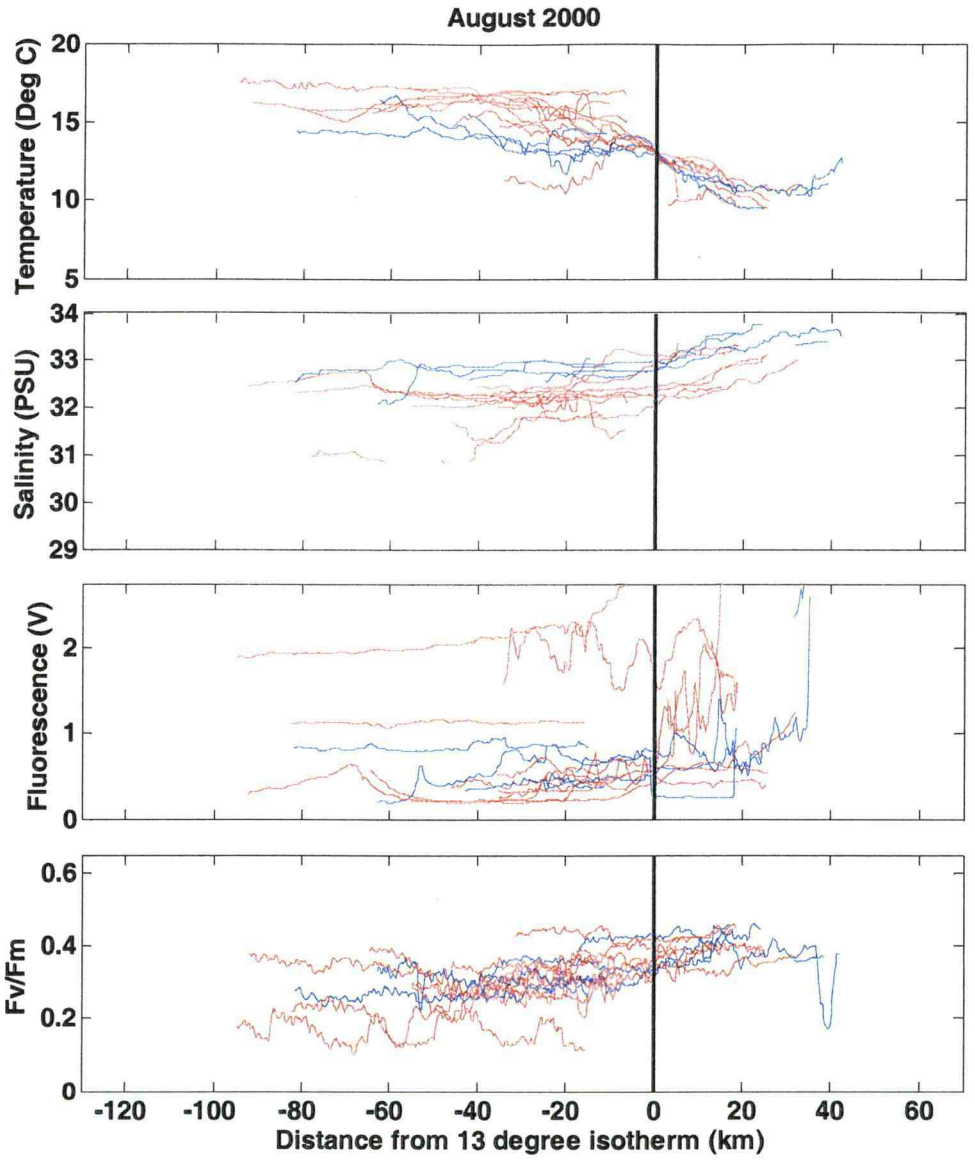
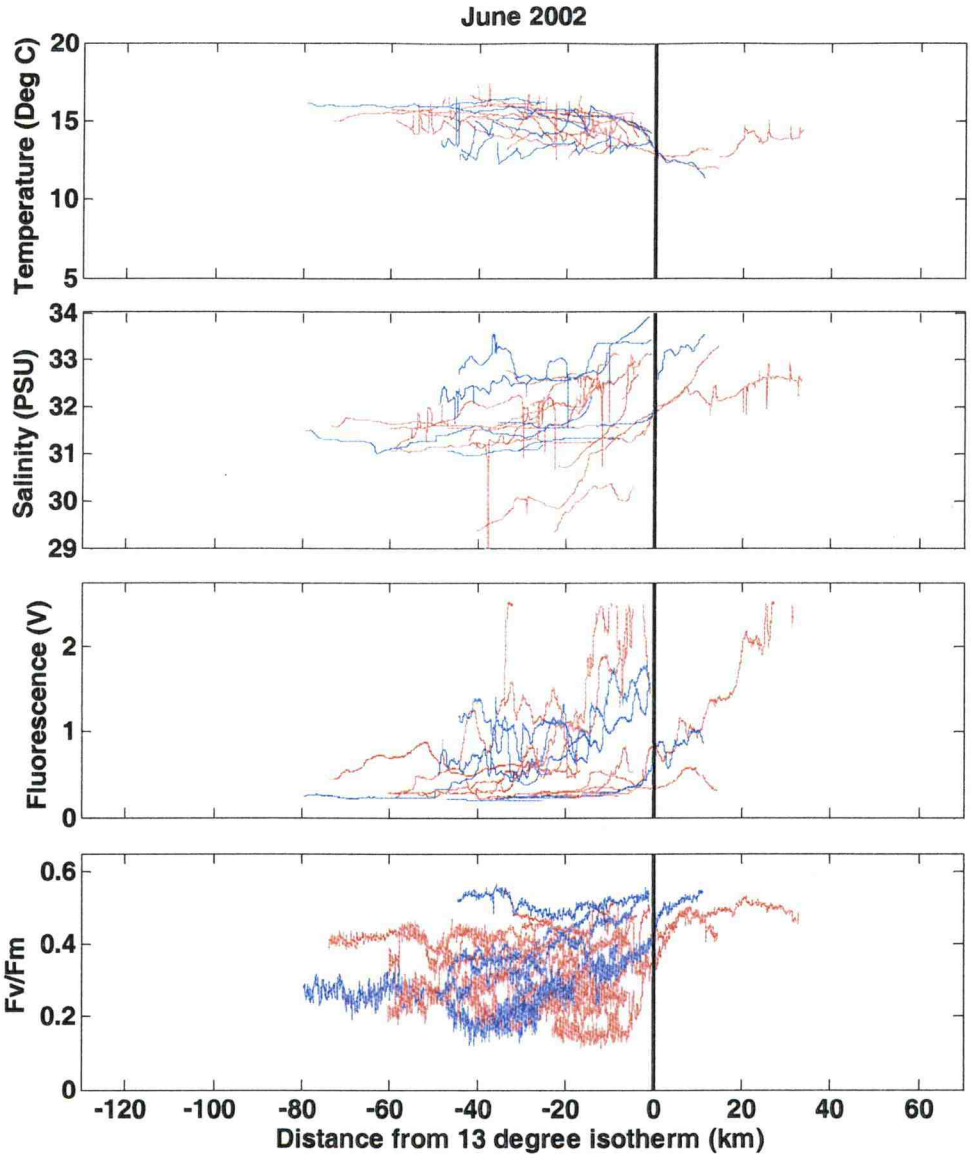



Figure 7: Sea surface $F_v/F_m$ contours of each of the four cruises created from ship-based inline sampling using only nighttime transects. The black lines show the nighttime transects used to create the contours for these plots.

A closer look at the individual transects (Figure 8) illustrates the variability on either side of the 13°C isotherm. The strong changes in temperature across this isotherm support its designation as the transition between the upwelled and offshore water masses. Salinity also appears well divided here, having generally higher salinities inshore of the 13°C isotherm, and lower salinities offshore. Fluorescence and $F_v/F_m$ both tend to be highest nearshore, but there are clearly some instances where this is not the case. In addition to these cross-frontal changes, all four parameters show variability on smaller scales. This is most evident in fluorescence and $F_v/F_m$ where the amplitude of this variability is sometimes higher than that of the cross frontal changes.


June 2000
Temperature (Deg C)
20
15
10
5
Salinity (PSU)
34
33
32
31
30
29
Fluorescence (V)
2
1
0
Fv/Fm
0.6
0.4
0.2
0
-120
-100
-80
-60
-40
-20
0
20
40
60
Distance from 13 degree isotherm (km)


August 2000
Temperature (Deg C)
20
15
10
5
Salinity (PSU)
34
33
32
31
30
29
Fluorescence (V)
2
1
0
Fv/Fm
0.6
0.4
0.2
0
-120
-100
-80
-60
-40
-20
0
20
40
60
Distance from 13 degree isotherm (km)


June 2002
Temperature (Deg C)
20
15
10
5
Salinity (PSU)
34
33
32
31
30
29
Fluorescence (V)
2
1
0
Fv/Fm
0.6
0.4
0.2
0
-120
-100
-80
-60
-40
-20
0
20
40
60
Distance from 13 degree isotherm (km)

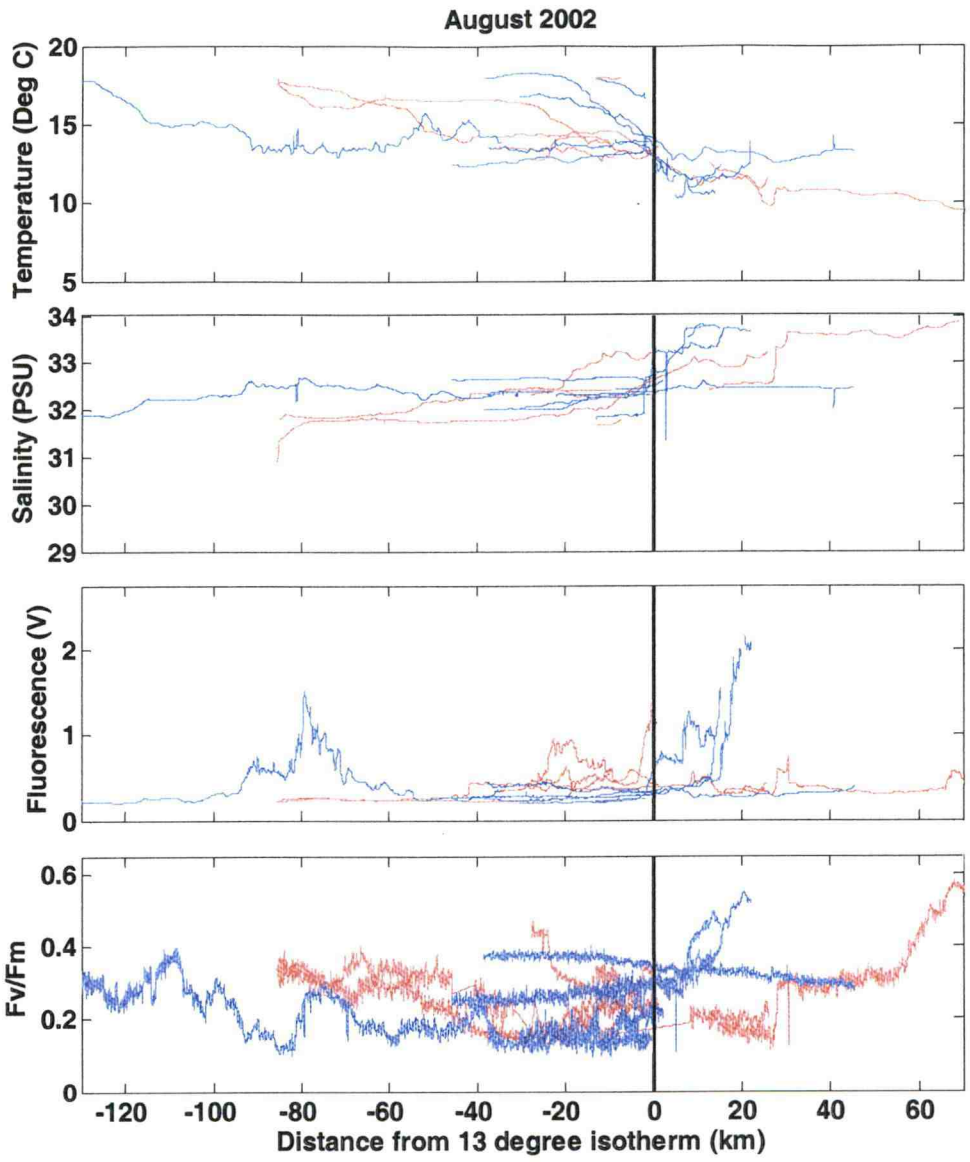



Figure 8: Cross frontal trends within each parameter on all four NEP GLOBEC cruises. Transects are plotted with respect to distance from the 13°C isotherm to show cross frontal trends as well as variability within each transect. Red lines are located within the northern half of the sampling region, at latitudes > 43°N. Blue lines are in the southern half.

## 3.2 Quantitative

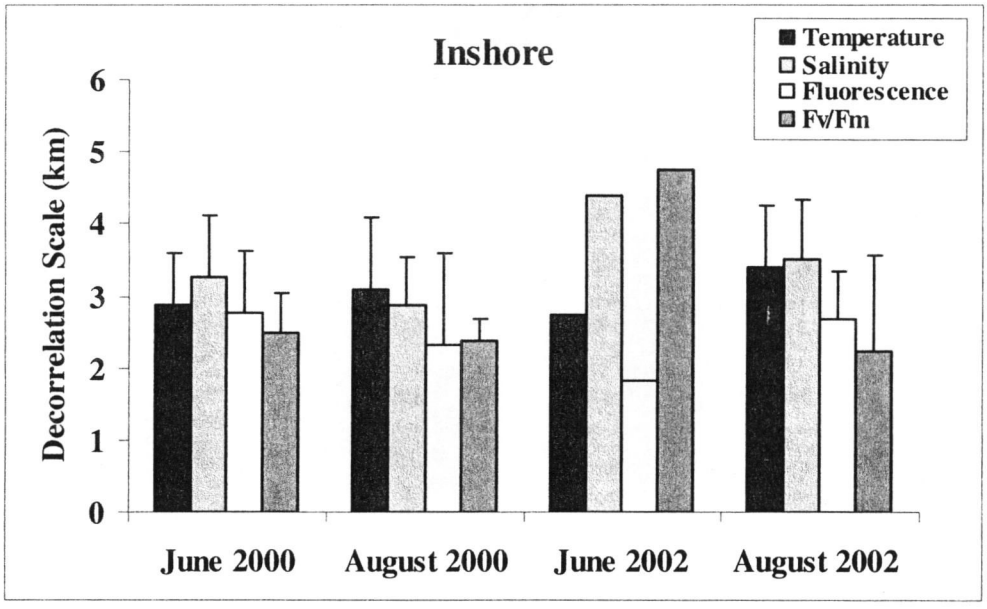
In order to determine the distances over which the short spatial scale, high-amplitude variations occurred, decorrelation scales were calculated for 81 25-km transects. Eighteen transect sections were selected for decorrelation analysis in the nearshore (< 13°C) region and 63 sections from the offshore (> 13°C) region (Figure 2). Sections from the June and August 2000 cruises averaged 107 ± 7 data points per 25-km or approximately 4.25 points per km. Sections from the 2002 cruises averaged 839 ± 93 points per 25-km or 34.75 points per km. Under-sampling of the nearshore region resulted because there was frequently only a narrow band of cold upwelled water inshore of the 13°C isotherm, and many of the transects within this regions were not 25 km long. Compounding this problem, high numbers of crab pots in the nearshore regions made it difficult to sample there at night, limiting the number of nearshore transects appropriate for this study.

Visual assessment of the decorrelation analysis suggested that the decorrelation scales did not accurately represent the variability in two of the transects from the offshore region of August, 2002. Rather, the decorrelation scales in these transects appeared to resolve only the noise in measurements of $F_v/F_m$, and they were removed from further analysis. Of the 79 remaining 25-km transects segments, the decorrelation scales range from 0.1 km to 6.4 km with averages of approximately 3 km (Table 1). In the nearshore region there are no significant differences between the decorrelation scales of temperature, phytoplankton fluorescence, and $F_v/F_m$ ($p >> 0.05$, Kruskal-Wallis Rank test, Sokal and Rohlf, 1981). However, in the offshore

region, significant differences between these three parameters occur in June and August, 2000 ($p < 0.01$, Figure 9). No post hoc analysis was performed, but a visual inspection reveals a lower decorrelation scale in $F_v/F_m$ than in either temperature or fluorescence.

Table 1: Mean decorrelation scales in km ±1 standard deviation of the 25-km transects selected for each cruise. Transects were divided into inshore and offshore based on their location with respect to the 13°C isotherm. Those to the east, or inshore, of the 13°C isotherm are "Inshore" while those to the west are "Offshore".

| Year | Region | Temperature | Salinity | Fluorescence | $F_v/F_m$ | N |
|---|---|---|---|---|---|---|
| June 2000 | Inshore | 2.9 ± 0.7 | 3.3 ± 0.9 | 2.8 ± 0.9 | 2.5 ± 0.5 | 8 |
| | Offshore | 2.8 ± 0.7 | 3.4 ± 0.8 | 3.0 ± 1.1 | 1.0 ± 0.6 | 10 |
| August 2000 | Inshore | 3.1 ± 1.0 | 2.9 ± 0.7 | 2.3 ±1.3 | 2.4 ± 0.3 | 5 |
| | Offshore | 3.3 ± 0.9 | 3.4 ± 1.0 | 3.1 ± 0.9 | 2.3 ± 0.9 | 23 |
| June 2002 | Inshore | 2.7 | 4.4 | 1.8 | 4.8 | 1 |
| | Offshore | 2.7 ± 1.0 | 2.6 ± 1.2 | 2.7 ± 0.7 | 2.1 ± 1.1 | 15 |
| August 2002 | Inshore | 3.4 ± 0.8 | 3.5 ± 0.8 | 2.7 ± 0.6 | 2.2 ± 1.3 | 4 |
| | Offshore | 3.5 ± 1.0 | 3.4 ± 1.1 | 3.4 ± 1.0 | 2.1 ±1.4 | 13 |



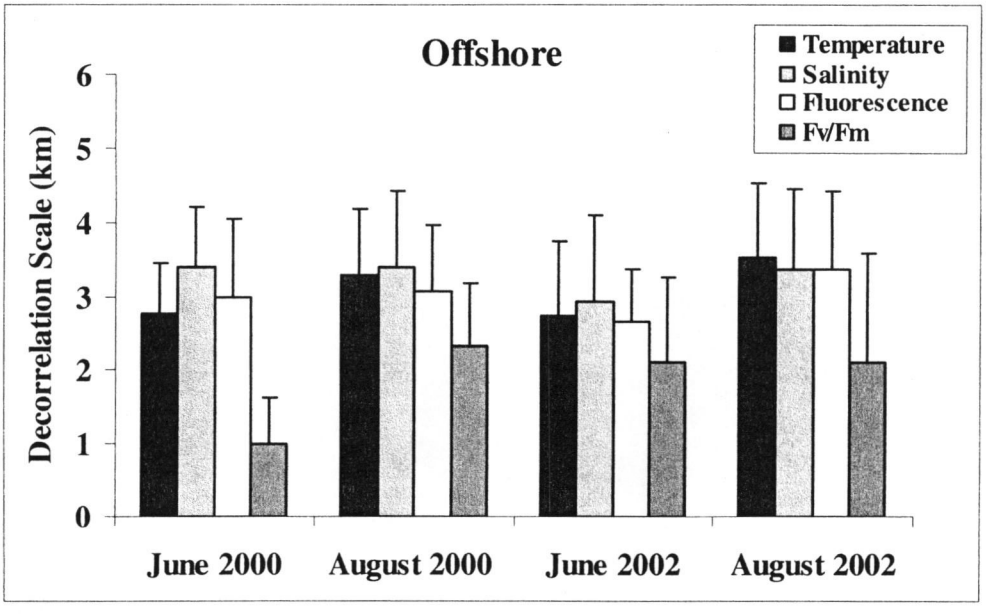




Figure 9: Decorrelation scales of temperature, phytoplankton fluorescence, and $F_v/F_m$ off the Oregon coast during the NEP GLOBEC cruises. Nearshore regions are those inshore of the 13°C isotherm, offshore regions are those outside of the 13°C isotherm. Significant differences exist between $F_v/F_m$ and the other parameters in June and August, 2000. Error bars show 1 standard deviation.

# 4 Discussion

## 4.1 Limitations of Methods

Any study will have errors inherent in its sampling methods and analytical techniques. A careful examination of these biases and the limitations they impose on further interpretation of results is key to avoiding incorrect conclusions. The choice and timing of transects used in this field experiment, the hydrodynamics of the ships' flow-through systems, and FRRf measurement noise present potential biases or limitations in the present analysis. There is a substantial spatial bias in the data sampled, as sampling in the nearshore region was generally confined to the daytime, when the crabpots could be spotted and potential entanglement of the towed Sea Soar vehicle could be avoided. Consequently, the data for this study were more often collected in the offshore region. This bias is especially prevalent during the 2002 cruises, when more care was taken to avoid nearshore regions at night. Additionally, the east-west heading of the ship on these transects is a potential source of error because upwelling surface currents on the Oregon coast tend to move offshore and southwards. Thus, data collected on a westward transect will correspond to shorter distances traveled over water than over land, causing the transect to appear slightly stretched. In the same way, data collected on eastward transects will appear slightly compressed. These distortions have the potential to affect the decorrelation scales, such that decorrelation scales of westward transects would appear shorter and eastward transects longer than if all data were collected on a stationary surface.

However, this expansion or compression would affect all parameters within each transect equally. Thus, while the decorrelation scales may be somewhat biased by current direction, relative comparisons within the study should not be compromised. Correction of this distortion may be possible using Acoustic Doppler Current Profile (ADCP) data collected during the GLOBEC cruises, but is beyond the scope of this study.

The hydrodynamics of the ships' flow-through systems potentially affects the FRRf variable fluorescence data in several ways. Exposing the phytoplankton sample to light within the flow-through system, mixing within the system, and changes in temperature between the intake and instruments may lead to systematic measurement errors. Exposing the sample to light within the flow-through system in the labs may close PSII reaction centers and therefore bias measurements of $F_v/F_m$. All hoses and plumbing connections were covered with insulation to block light from reaching the phytoplankton during their transit through the instruments. Mixing and homogenization within the flow-through systems could not be controlled, and any mixing will reduce the minimum spatial scale we can resolve. However, mixing within the system should affect temperature, salinity, phytoplankton fluorescence, and $F_v/F_m$ in the same way. Thus, this mixing should not change the relationship between the decorrelation scales of these four parameters.

Understanding the effects of instrument noise as a source of variability is crucial when using decorrelation analysis. In our data, we observe a high-frequency, low-amplitude signal in measurements of $F_v/F_m$ that is not apparent in measurements

of temperature, salinity, or fluorescence (Figure 8). Theoretical and lab studies under optimal conditions show potential biases resulting from inherent instrument noise and from nonlinearities in FRRf analysis software (Laney, in press). Consequently, these or similar errors are probably affecting the *in situ* measurements of $F_v/F_m$ in this study, causing the observed high-frequency low-amplitude signal. Noise in a signal is not problematic in the context of decorrelation analyses, provided that the ratio of signal to noise is much larger than 1. When this ratio approaches or becomes less than one it becomes more difficult to distinguish between the signal and the noise. In the data for this study, the high-frequency, low-amplitude noise observed in $F_v/F_m$ would limit our ability to detect variability with amplitudes less than approximately 0.05 $F_v/F_m$ units. In certain transects, slowly varying changes in $F_v/F_m$ are much larger than those of this presumed FRRf noise, and consequently this decorrelation analysis is unaffected. In other transects, however, where the signal-to-noise ratio approaches 2, this noise causes rapid drops in correlation and thus decorrelation scales are decreased. In two cases, the signal-to-noise ratio was so close to 1 that the presumed physiological variability in $F_v/F_m$ was undetectable and the transects decorrelated in only 1–2 data points. These transects were identified before any statistical comparisons were made and therefore do not affect the results of this study. These results indicate the need for higher signal-to-noise ratios to better resolve any meaningful physiological variability represented by changes in $F_v/F_m$ less than 0.05 $F_v/F_m$ units. Although smoothing and filtering can decrease or remove the noise in

the $F_v/F_m$ measurements and minimize these biases, such averaging techniques would limit the frequencies over which a meaningful signal can be detected.

## 4.2 Variability in $F_v/F_m$

Continuous, in-line measurement of $F_v/F_m$ using variable fluorescence methods has only become possible in the past 10 years with the advent of FRR fluorometers. However, debate continues over what ecological factors determine its fluctuations *in situ*. One suggestion is that $F_v/F_m$ decreases in response to photoinhibition and nutrient limitation and therefore reflects the level of light or nutrient stress in a population (Falkowski and Kolber, 1993; Kolber and Falkowski, 1993). Photoinhibition is thought to damage the photosystem II reaction center, causing absorbed light to be dissipated as heat rather than fluoresced, decreasing the maximal fluorescence ($F_m$) and therefore decreasing $F_v/F_m$ (Han et al., 2000). Nutrient limitation inhibits nighttime repair of damaged reaction centers, maintaining a low $F_v/F_m$ (Han et al., 2000). This behavior has been empirically shown in several field and laboratory studies (Falkowski et al., 1991; Falkowski et al., 1992; Geider et al., 1992; Falkowski and Kolber, 1993; Kolber and Falkowski, 1993). However, some studies suggest that this model is too simplistic, only reflecting phytoplankton responses to changes in nutrient level, and is therefore not applicable in a stable environment. In experiments where continuous diatom cultures grown at different nutrient concentrations were exposed to sharp drops in nutrient availability for phytoplankton in steady state, $F_v/F_m$ is either maximal, indicating adaptation to the

available nutrient level, or minimal, with not enough nutrients to sustain the photosystem (Parkhill et al., 2001). Fluctuations in $F_v/F_m$ occur only when phytoplankton are removed from steady state, and the timing of these fluctuations is modulated by their original steady state nutrient levels (Parkhill et al., 2001). The implication of this research is that $F_v/F_m$ reflects the stability of phytoplankton populations rather than overall levels of nutrient stress. Consequently, although $F_v/F_m$ may not be a direct measure of nutrient stress, especially in stable environments, in variable environments such as the Oregon coast upwelling system, it may still be a strong indicator of a phytoplankton community's adaptation to its environment. Qualitative analysis of nutrient distributions collected during the GLOBEC cruises shows high nutrient levels inshore and decreasing levels offshore during all four cruises (Figure 10, Figure 11, and Figure 12). The value of $F_v/F_m$ also follows this pattern in many cases, suggesting that $F_v/F_m$ does reflect a physiological response to nutrient stress off the Oregon coast (Figure 7).

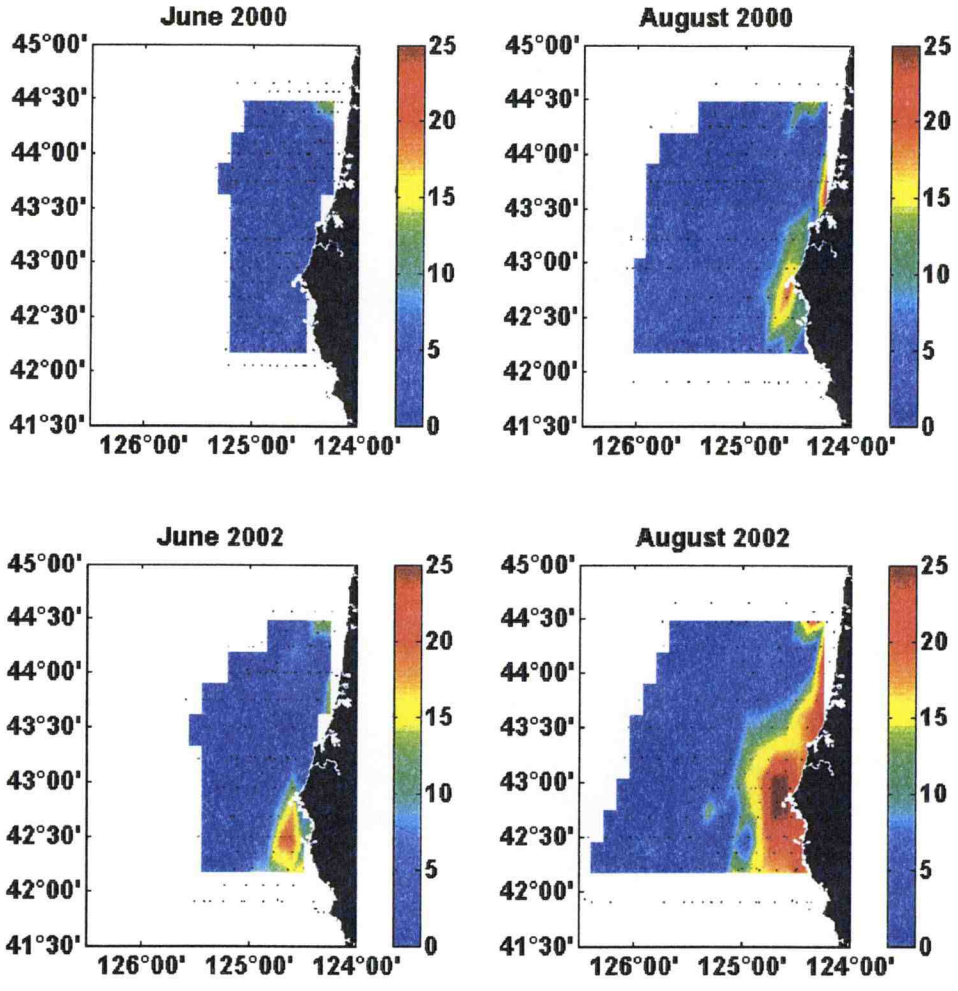



Figure 10: Distributions of nitrate ($NO_3^-$) + nitrite ($NO_2^-$) (μmol/L) during each of the four GLOBEC cruises. Locations of nutrient samples used to make this plot are indicated by black dots. These plots include data from both daytime and nighttime sampling along cross-shelf transects. There are some similarities between the distribution of nitrate + nitrite and that of $F_v/F_m$.

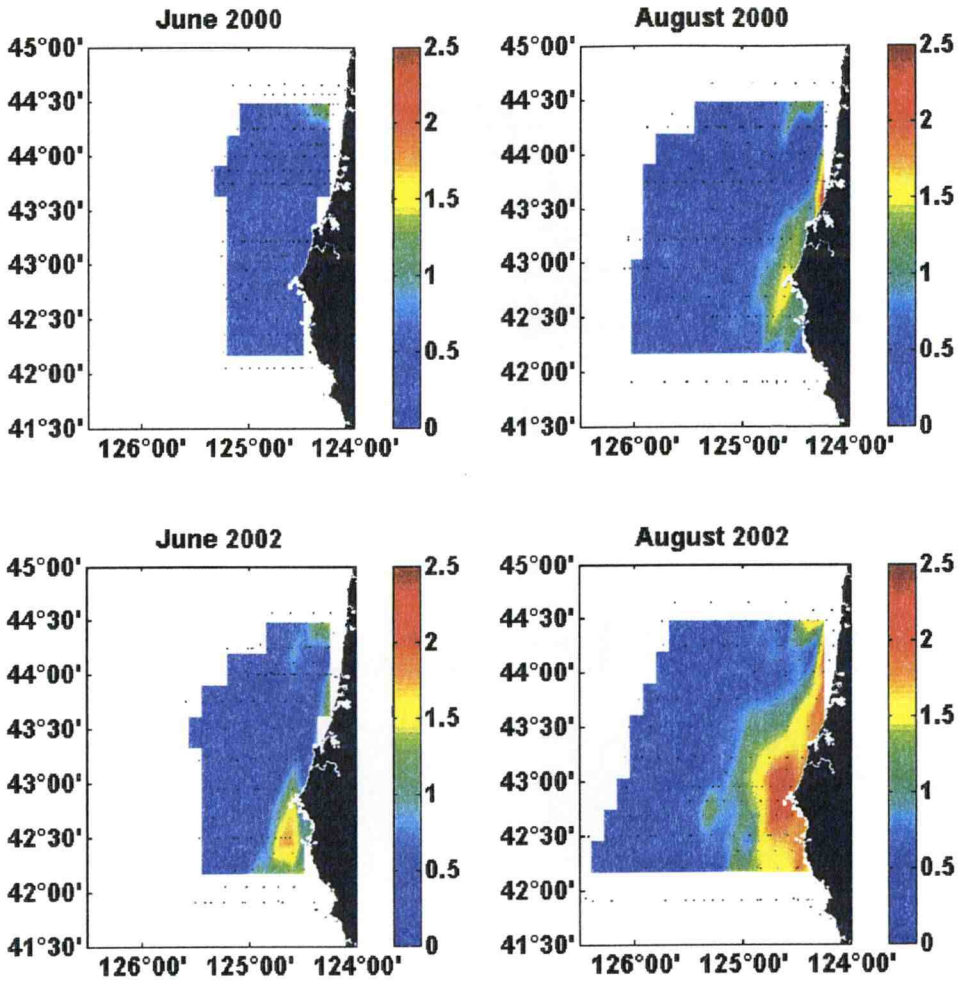



Figure 11: Distributions of phosphate ($PO_4^{3-}$) (μmol/L) during each of the four GLOBEC cruises. Locations of nutrient samples used to make this plot are indicated by black dots. These plots include data from both daytime and nighttime sampling along cross-shelf transects. There are some similarities between the distribution of phosphate and that of $F_v/F_m$.

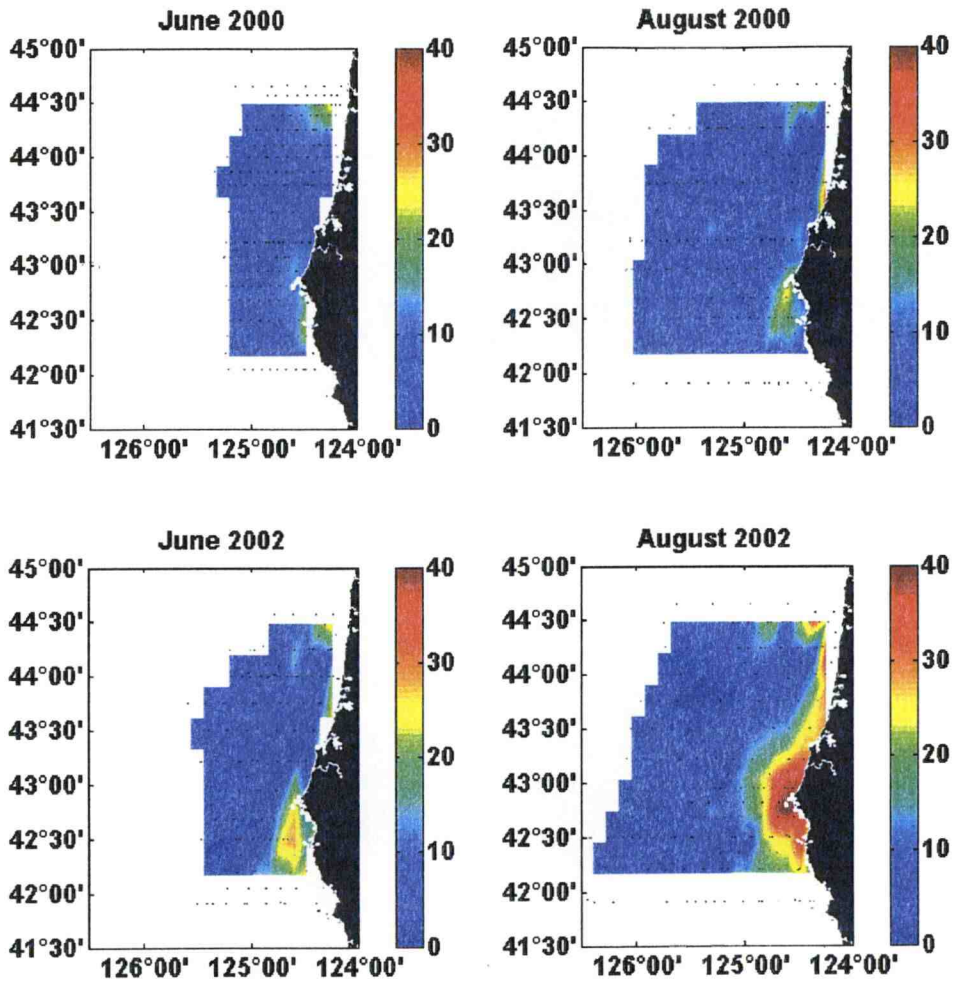



Figure 12: Distributions of silicate ($SiO_2$) (μmol/L) during each of the four GLOBEC cruises. Locations of nutrient samples used to make this plot are indicated by black dots. These plots include data from both daytime and nighttime sampling along cross-shelf transects. There are some similarities between the distribution of silicate and that of $F_v/F_m$.

Inspection of the spatial variability in $F_v/F_m$ within the individual inshore and offshore regions (Figure 8) shows changes in amplitude nearly as large as those associated with cross-shelf variability in some transects. The spatial decorrelation scales calculated in this study attempt to determine the distances over which these small-scale h'gh-amplitude changes occur. On average, the decorrelation scales of $F_v/F_m$ are shorter than those of temperature, salinity, and phytoplankton fluorescence during almost every cruise. These differences are significant in the offshore regions during June and August of 2000. Within individual transects, however, there are generally no fixed relationships between the variability of $F_v/F_m$ and that of any other parameter (Figure 8, Figure 13). While in some transects decorrelation scales between $F_v/F_m$ and another parameter may be similar, these patterns are not consistent between transects or parameters. For example, decorrelation scales of $F_v/F_m$ may be similar to those of temperature in one transect or region of a transect, but similar to salinity or phytoplankton fluorescence in another (Figure 13). Additionally, although decorrelation scales of $F_v/F_m$ were usually shorter than those of temperature, salinity, or phytoplankton fluorescence, they were occasionally longer than those of the other parameters. A core result of this study is that within the entire study area, there are no consistent relationships between the decorrelation scales of $F_v/F_m$ and that of temperature, salinity, or phytoplankton fluorescence.

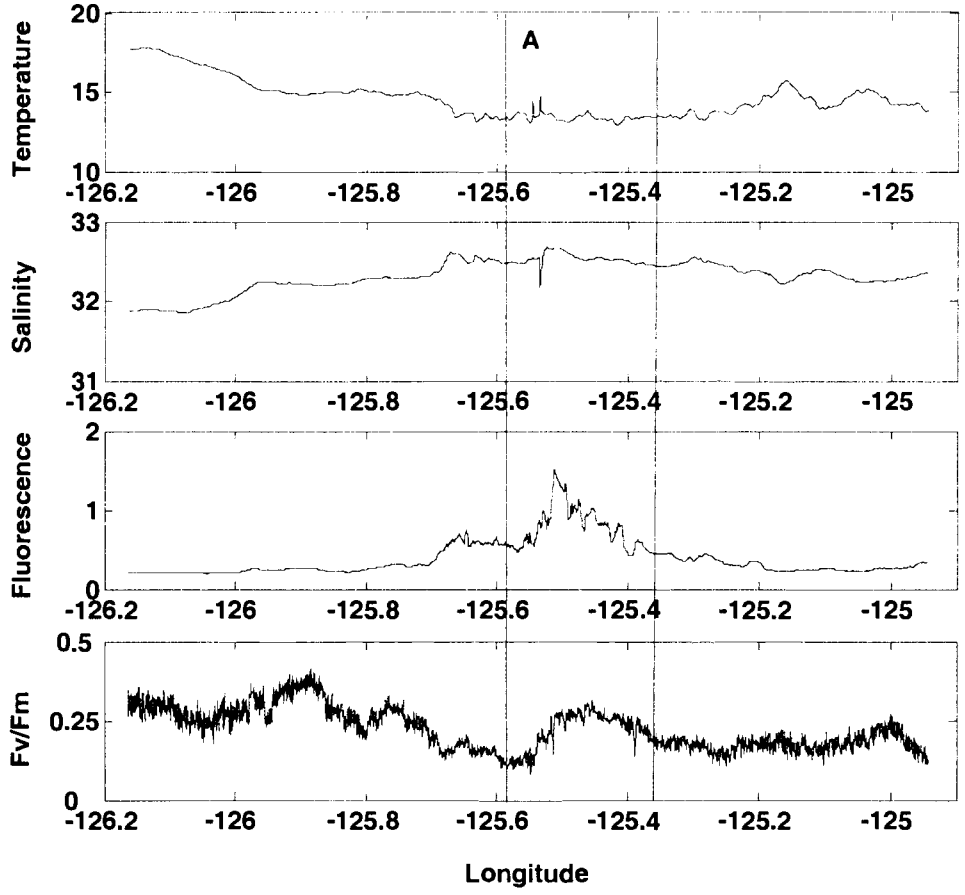



Figure 13: A cross-shelf transect of temperature, salinity, phytoplankton fluorescence, and $F_v/F_m$ from the southern region of the August, 2002 cruise. The peak in phytoplankton fluorescence in region A is accompanied by a similar rise in $F_v/F_m$, but there are no related changes in temperature and salinity. However, outside of region A there are many fluctuations in $F_v/F_m$ that do not correspond to variability in any other parameter.

The lack of any consistent overall relationship between the decorrelation scales of $F_v/F_m$ and those of temperature, salinity, or phytoplankton fluorescence within the study area may result from regional differences in physical and environmental forcing. In the Oregon coast upwelling system, the influence of the Columbia River in the north creates a different hydrographic setting than that in the southern region through the injection and subsequent mixing of the upwelled water with a warm, low salinity plume in the north. Consequently, patterns in $F_v/F_m$ may be more strongly influenced by salinity in the north than in the south, where upwelling driven circulation is more dominant. Furthermore, environmental forcing may differ between the inshore and offshore regions, because of increased heating and nutrient depletion of the upwelled water as it moves offshore. To examine this possibility, the study area was divided into four quadrants based on inshore or offshore location (divided at the 13°C isotherm) and north-south location (divided at 43°00'N). However, even within these quadrants, no consistent relationships between the decorrelation scales of $F_v/F_m$ and any other parameter were observed. Consequently, it is apparent that in this study region, $F_v/F_m$ has its own unique scales of variability, and in order to determine the variability of $F_v/F_m$, it must be measured separately. Temperature, salinity, and phytoplankton fluorescence cannot be used as reliable proxies for $F_v/F_m$ on the Oregon coast if resolving small-scale variability is important.

The character of variability in $F_v/F_m$ observed in these data may contribute to similar variability in primary productivity in this study region. While there are many models used to calculate primary productivity (Falkowski and Kolber, 1993; Kolber

and Falkowski, 1993; Falkowski and Kolber, 1995; Boyd et al., 1997; Suggett et al., 2001), most of them rely on a basic structure similar to that of Equation [1], in which primary productivity is a linear function of light, light absorption, number of light absorbers, and efficiency of light usage. Because $F_v/F_m$ can be interpreted as reflecting the fraction of functioning Photosystem II reaction centers (e.g., Kolber and Falkowski, 1993), $F_v/F_m$ is incorporated in productivity models as a proxy for the efficiency term, $\phi p$. When applied to the Oregon coast region, such models must capture the actual variability in $F_v/F_m$ to best reflect the actual variability in phytoplankton primary productivity. In order to determine this variability, it is important to include some measure of $F_v/F_m$.

Current productivity models that incorporate remote sensing parameters use temperature to assess maximum rates of productivity (Behrenfeld and Falkowski, 1997). The rationale is that temperature modifies rates of certain key enzymatic reactions in photosynthesis and in that way limits overall photosynthetic rates. This simple model may be adequate in regions where $F_v/F_m$ is stable with respect to temperature. However, in the coastal region examined in this study, changes in $F_v/F_m$ are often large and occur over shorter spatial scales than those of temperature. Consequently, models using temperature as a proxy for $F_v/F_m$ when calculating primary productivity will not be capable of resolving the variability in primary productivity in similarly dynamic populations. Within a single transect of this study, $F_v/F_m$ changed by 20% within its possible range of 0 to 0.65 (Falkowski and Kolber, 1993), while temperature remained effectively stable (Figure 13). Using models

similar to Equation [1], and substituting temperature for $F_v/F_m$, up to 20 % of the variability in primary productivity may have been lost. Because many of these satellite-based productivity models also use remote sensing data collected on resolutions of 4 km or greater, such models would miss the variability in this data set that occurs over smaller spatial scales. Thus, while these models may provide large-scale trends in primary productivity, they will be less robust when characterizing the variability in smaller regions such as the Oregon upwelling system.

## 4.3 Relationship of $F_v/F_m$ to Phytoplankton Biomass

Knowledge of the variability in important physiological measurements such as $F_v/F_m$ may provide insight into ecosystem processes such as photosynthesis and primary productivity. Determining the relationship between phytoplankton biomass and physiology may offer understanding of ecosystem function, defining the physiological status of different groups of phytoplankton. This relationship may be particularly useful in variable regions such as the Oregon coast in which many phytoplankton taxa coexist. Patterns in phytoplankton fluorescence and $F_v/F_m$ (Figure 14) were similar during all four GLOBEC cruises, in that regions with high biomass tended to have high $F_v/F_m$, while those with low biomass had either high or low $F_v/F_m$. These trends were especially pronounced in June of both years, while in August, they were somewhat obscured by additional variability. Consequently, it is likely that this analysis revealed a seasonal pattern in the relationship between phytoplankton fluorescence and $F_v/F_m$ off the Oregon coast.

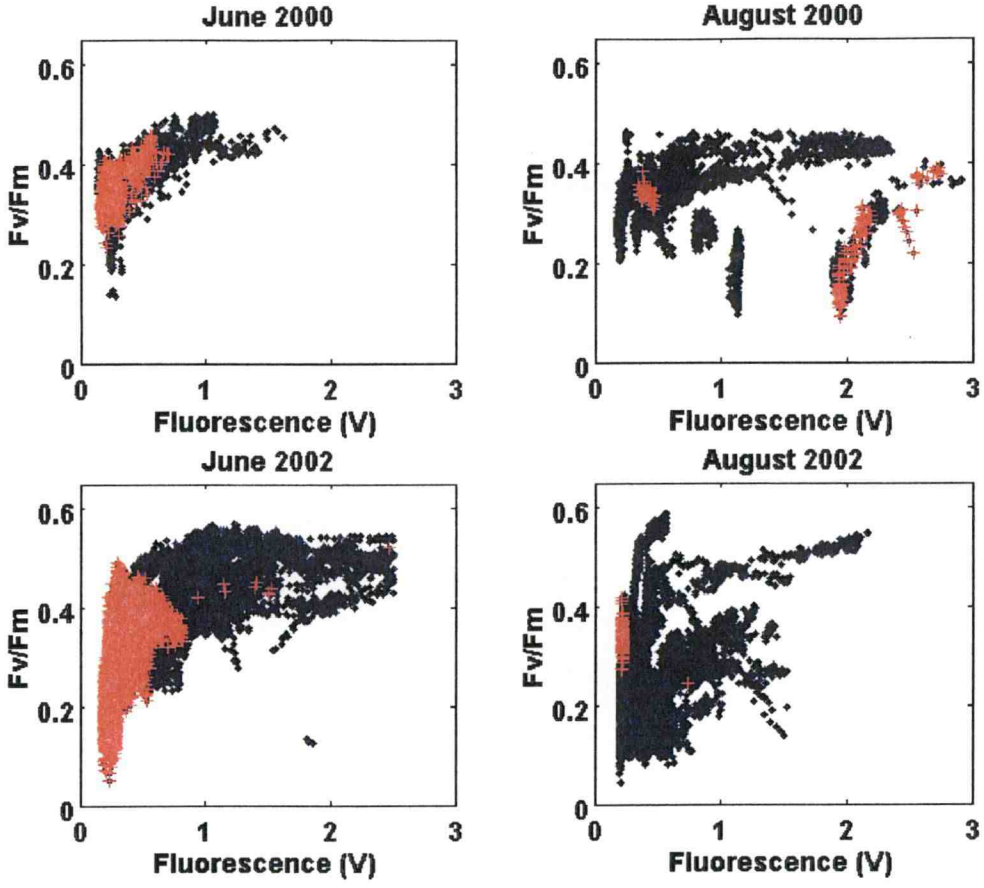



Figure 14: Relationship between phytoplankton fluorescence and $F_v/F_m$ during all four GLOBEC cruises. Red crosses show water with salinity < 31.6 PSU which is most likely associated with the Columbia River plume. The June data tend to fall within a well defined region. While the August data show a basic shape similar to that in June, the patterns are not as simple.

During both June cruises, the physical system off the Oregon coast exhibited constrained coastal upwelling but no strong frontal development, as suggested by the temperature distribution (Figure 4) (Barth et al., in prep).. In addition, an intrusion of low salinity water from the Columbia River was evident in the north of the sampling region (Figure 5). The relationship between phytoplankton fluorescence and $F_v/F_m$ follows a well defined pattern in June of both years, with high fluorescence associated with high $F_v/F_m$ (>0.4 $F_v/F_m$ units) and low fluorescence regions with large ranges in $F_v/F_m$ (< 0.1 to >0.5 $F_v/F_m$ units) (Figure 14). While the high fluorescence regions are dominated by cold, high-salinity water, those with low fluorescence are composed of both cold, high-salinity water and warmer, low-salinity water which is associated with the Columbia River plume. Parkhill et al., (2001) suggest that $F_v/F_m$ tends to be maximal during balanced growth, decreasing when conditions of steady state are lost. According to their model, the high fluorescence regions off the Oregon coast in June should be in steady state, while those with lower fluorescence frequently are not. In addition, changes in $F_v/F_m$ are closely related to nutrient stress (Parkhill et al., 2001). The relationship between $F_v/F_m$ and sources of nitrogen, phosphorus, and silica in this study has high $F_v/F_m$ associated with high nutrient levels and variable $F_v/F_m$ associated with low nutrient levels (Figure 15, Figure 16, and Figure 17) supporting the conclusions of Parkhill et al., (2001). However, it is surprising that there are no regions with high fluorescence and low $F_v/F_m$, because these dense populations would be expected to become nutrient limited, leading to decreased $F_v/F_m$.

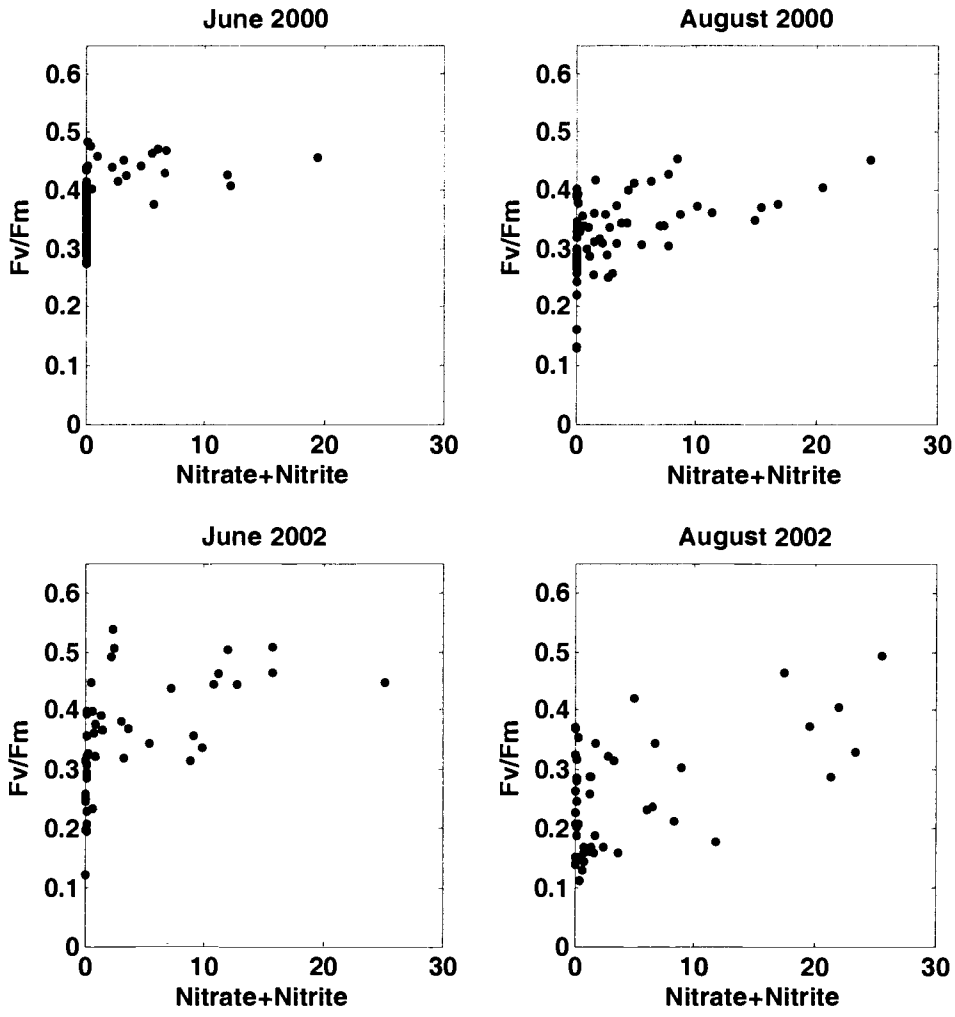



Figure 15: Relationship between $NO_3^- + NO_2^-$ (μmol/L) and $F_v/F_m$ for all four GLOBEC cruises. Only nighttime nutrient samples are included in this figure. High $NO_3^- + NO_2^-$ concentrations are almost always associated with high $F_v/F_m$, but at low $NO_3^- + NO_2^-$ there is a range of values of $F_v/F_m$. August 2002 is an exception to this pattern.

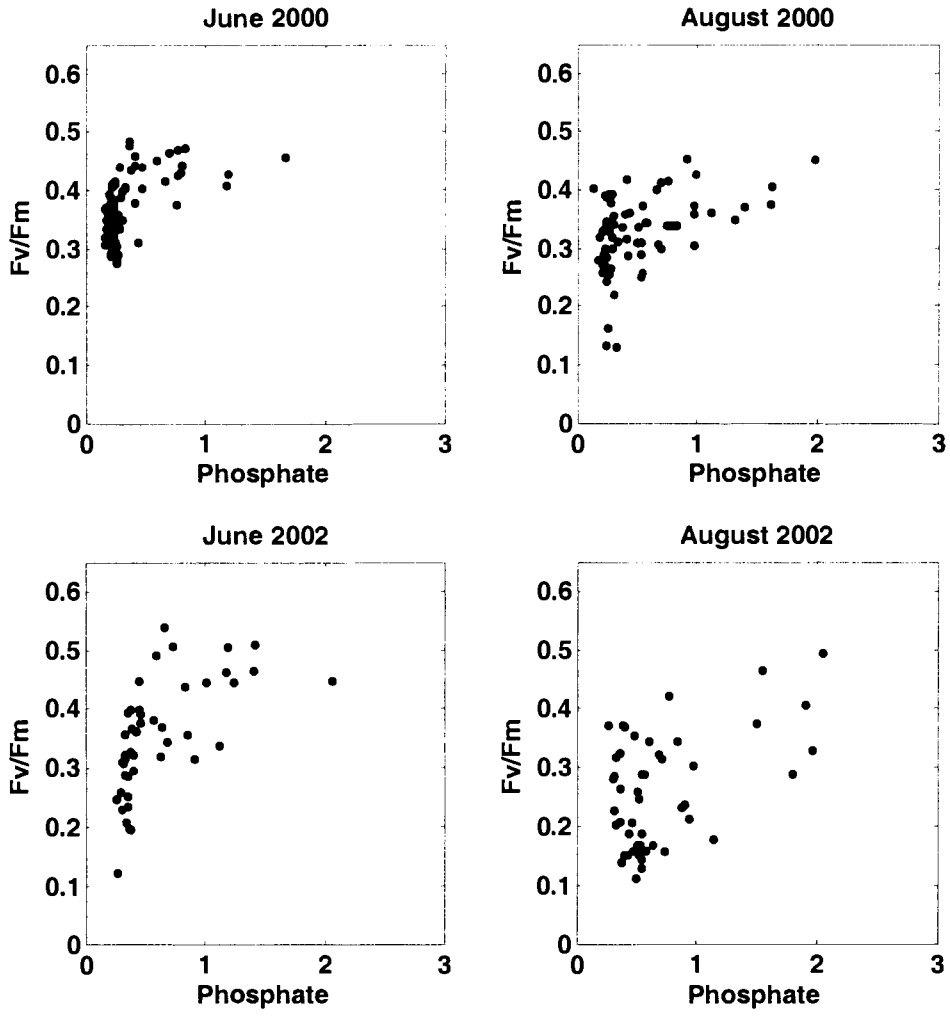



Figure 16: Relationship between $PO_4^{3-}$ (µmol/L) and $F_v/F_m$ for all four cruises. Only nighttime nutrient samples are included in this figure. High $PO_4^{3-}$ concentrations are almost always associated with high $F_v/F_m$, but at low $PO_4^{3-}$ there is a range of values of $F_v/F_m$. August 2002 is an exception to this pattern.

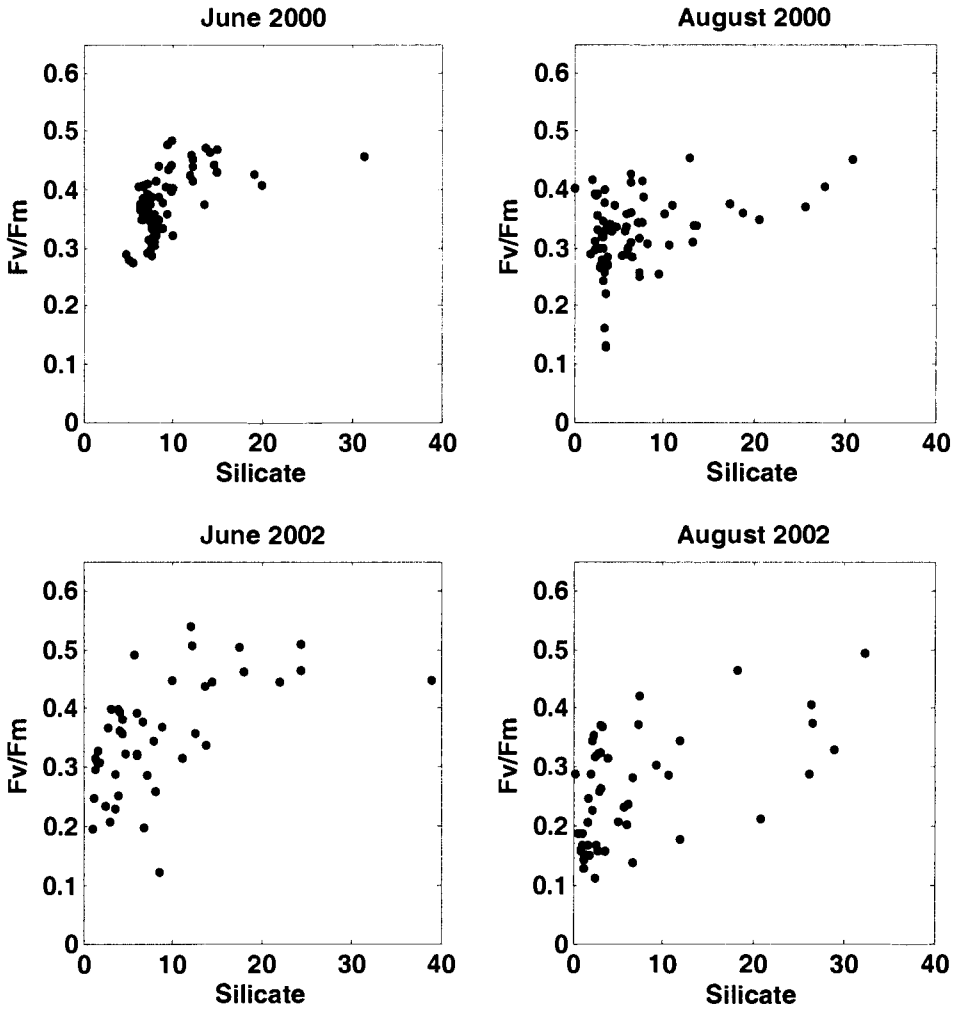



Figure 17: Relationship between $SiO_2$ (µmol/L) and $F_v/F_m$ for all four cruises. Only nighttime nutrient samples are included in this figure. High $SiO_2$ concentrations are almost always associated with high $F_v/F_m$, but at low $SiO_2$ there is a range of values of $F_v/F_m$. August 2002 is an exception to this pattern.

In contrast to the June cruises, the August cruises exhibited more complicated upwelling systems, characterized by larger temperature gradients, more strongly meandering fronts, and some eddy development (Figure 4) (Barth et al., in prep.). The relationship between fluorescence and $F_v/F_m$ in August is not as simple as that in June, although the basic June structure can be seen to some extent. In August, low-salinity, high-temperature water is still associated with low levels of phytoplankton fluorescence, although it is much less predominant than in June. However, in 2000 low-salinity water also corresponded to higher fluorescence levels, forming a separate region with a similar shape (Figure 14). It is likely this region corresponds to the offshore region of low salinity and high biomass in August 2000 (Figure 5, Figure 6), but it is unclear what causes this deviation from the usual pattern. Unlike the June cruises, the August cruises, especially August 2002, have regions of high biomass, high salinity, and low-temperature water that do not have maximal $F_v/F_m$. Additionally, there are regions of high nutrients but lower $F_v/F_m$. According to the results of Parkhill et al., (2001), these regions are not in balanced growth. They may result from changes in nutrient availability following bloom conditions. More detailed analysis of these structures and behaviors may provide a better understanding of the phytoplankton growth dynamics off the Oregon coast.

The results of this study suggest that the biomass distribution off the Oregon coast is driven by both physical and biological forcing mechanisms. However, it is beyond the scope of this study to determine the relative extent to which these mechanisms affect the biomass distribution. The large-scale patterns in temperature

and salinity match those of phytoplankton fluorescence and $F_v/F_m$, indicating a strong connection between the physical upwelling dynamics and the response in both phytoplankton biomass and physiology. This connection suggests that physical forcing plays a strong role in the ecosystem dynamics. However, decorrelation analysis indicates that variations in physiology occur on different scales than the variations associated with temperature and salinity, the indicators of physical forcing in this study. These differences between the scales of variability of physical and biological forcing parameters indicate that there is some amount of biological control over biomass distribution and primary productivity. The relationship between nutrient availability and $F_v/F_m$ implies that nutrients may play a role in this bottom-up biological control. While the trends in this study may suggest mechanisms of biological and physical control, they are far from conclusive. Determining levels of physical and biological control of biomass distribution and primary productivity continue to be major challenges in biological oceanography.

## 4.4 Future Research

The results presented in this study describe one of the first attempts to compare the spatial variability of temperature, salinity, and phytoplankton fluorescence with FRRf-derived $F_v/F_m$. While these results provide an overview of the relationship between the four parameters studied, there is ample room for future research to clarify the interaction between phytoplankton physiology and biomass distribution or primary productivity. Specifically, future research should be aimed at

determining what ecological changes are associated with variability in $F_v/F_m$ and which physical and biological mechanisms cause this variability in $F_v/F_m$. Additionally, studies need to examine the role of phytoplankton physiology in regulating biomass distribution and controlling variability in primary productivity. Further analysis of NEP GLOBEC data can begin to address the first of these questions. However, future field and laboratory studies are necessary to fully understand the other two questions and, ultimately, what controls variability in biological systems.

Within the GLOBEC data set, both High Performance Liquid Chromatography (HPLC) samples and Wet Labs 9 wavelength absorption and attenuation meter (AC-9) flow-through data can be used to associate ecological changes with variability in $F_v/F_m$. HPLC, while limited in resolution because it is discretely sampled, may reveal changes in species composition associated with high-amplitude changes in biomass or $F_v/F_m$. These coupled changes may indicate locations where physiological stress leads to species turnover, suggesting a level of physiological control of species composition within an ecosystem. Furthermore, high-resolution AC-9 data will allow comparisons between the variability of $F_v/F_m$ and the variability in optically derived parameters such as particle size distribution and, potentially, taxonomic group. Such comparisons may also illuminate connections between physiological and ecological changes. Overall, subjecting HPLC and AC-9 GLOBEC data to analyses similar to those described in this study

should shed light on the relationship between phytoplankton physiology and community ecology.

In addition to analysis of GLOBEC data, further studies are needed to develop a better understanding of what drives variability in Fv/Fm and how this variabilty affects biomass distribution and variability in primary productivity. Previous research (Falkowski et al., 1991; Falkowski et al., 1992; Geider et al., 1992; Falkowski and Kolber, 1993; Kolber and Falkowski, 1993, Parkhill et al., 2001) and the results of this study show strong connections between nutrients and $F_v/F_m$. High-resolution field measurements of both nutrients and physiological parameters such as $F_v/F_m$ may reveal strong correlations in the variability of nutrients and $F_v/F_m$, potentially identifying a major cause of variability in $F_v/F_m$. In that case, further studies should examine causes of *in situ* variability in nutrients, including biological feedbacks on nutrient availability.

Future field sampling, laboratory research, and high-resolution remote sensing are necessary to determine the role phytoplankton physiology plays in controlling biomass distribution and variability in primary productivity. Specifically, development of new proxies to represent physiological variability combined with accurate assessments of phytoplankton community structure and biomass distribution should contribute to an emerging picture of mechanisms for bottom-up control of phytoplankton biomass distribution. High-resolution measurements of temporal variability in physical forcing, biomass distribution, and phytoplankton physiology over broad spatial scales may help identify which mechanisms are most strongly

affecting changes in the phytoplankton community. These measurements may be possible through high-resolution hyper-spectral geosynchronous satellites. Eventually, through more detailed analysis of currently available data and development of new measurement techniques, a coherent picture of the ways in which physical forcing and ecological interactions control biomass distribution and variability in primary productivity should emerge. This knowledge will further understanding of the event-scale processes that drive the carbon cycle and eventually, help predict ecosystem response to climate change.

# 5 Conclusions

The research presented in this study used a simple analytic tool to determine the scales of variability of temperature, salinity, phytoplankton fluorescence, and $F_v/F_m$ off the Oregon coast. While the problems and limitations of the methods restrict the conclusions that can be drawn, it is clear that measuring the variability in phytoplankton physiology provides information critical to understanding the ecology of upwelling ecosystems. $F_v/F_m$ depicts the physiological status of phytoplankton and allows us to measure its variability on small scales. This knowledge provides a more thorough understanding of photosynthetic variability and primary productivity in the coastal ocean. Further knowledge of the variables affecting primary productivity will eventually lead to a better understanding of higher processes such as trophic transfer and carbon sequestration.

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