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Impacts on phytoplankton biomass and productivity in the Pacific Northwest during the warm ocean conditions of 2005

Raphael M. Kudela,[1] William P. Cochlan,[2] Tawnya D. Peterson,[3] and Charles G. Trick[4]

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[1] Delayed onset of the spring transition and upwelling-favorable winds in the Pacific Northwest during spring-summer 2005 resulted in a positive temperature anomaly and a pronounced negative anomaly in surface phytoplankton biomass (chlorophyll *a*) and primary productivity. Compared to time periods before and after the warm water event, total biomass was reduced by ca. 50% along a hydrographic line extending seaward from Grays Harbor, WA (47° N), with a concomitant decrease of ca. 40% in surface and depth-integrated primary productivity. Associated with these declines in biomass and productivity was a change in mean phytoplankton size, with >50% of the nearshore assemblage less than 5μm in size during the warm event, compared to <30% during more normal conditions. Unlike higher trophic levels, the phytoplankton rapidly recovered with the onset of upwelling, returning to more typical size structure, biomass, and productivity within one week of the onset of upwelling-favorable winds.

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1. Introduction

[2] The Pacific Northwest (PNW) region of the US west coast is characterized by a dynamic pelagic ecosystem that is strongly influenced by both seasonal and event-scale processes [*Hickey*, 1989; *Landry et al.*, 1989]. This area (from ca. 45° N) is rich in biological production from phytoplankton through fisheries [*Thomas and Strub*, 2001; *Ware and Thomson*, 2005]. Despite the recognized importance of these waters in terms of biological productivity, fisheries, and human activities, there have been relatively few measurements of primary productivity, with only one large-scale survey published in the last 20 years [*Perry et al.*, 1989]. Most reports have relied instead on remotely sensed data to infer productivity by examining standing stocks of chlorophyll or modeled carbon assimilation [*Carr*, 2002; *Thomas and Strub*, 2001; *Ware and Thomson*, 2005]. Using remote sensing methods, a general pattern of elevated biomass off the Washington coast (compared to Oregon) has emerged, driven seasonally by the annual pattern of wind forcing, which results in the upwelling of nutrient-rich, cold water to support enhanced phytoplankton standing stock [*Carr*, 2002; *Thomas and Strub*, 2001]. Superimposed on these seasonal patterns are changes caused by interannual variability, such as ENSO events [*Huyer et al.*, 2002] or basin-scale changes in water transport such as the 2002 invasion of cool, saline subarctic waters [*Freeland et al.*, 2003] that resulted in a strong positive chlorophyll anomaly off British Columbia, Washington, and Oregon in 2001–2002 [*Thomas et al.*, 2003; *Wheeler et al.*, 2003].

[3] In 2005, anomalously warm water in the PNW resulted in depressed chlorophyll biomass similar to an ENSO event. While strongest in the PNW, these anomalous conditions were evident throughout the California Current System [*Schwing et al.*, 2006]. This event captured the attention of the popular press, in large part because of the associated impacts on organisms at higher trophic levels such as birds, fish, and marine mammals. This temperature anomaly coincided with two major field programs in the PNW: the NOAA/NSF-sponsored ECOHAB Pacific Northwest project, with a focus on the ecophysiology and physical transport of toxigenic *Pseudo-nitzschia* species on the PNW coast, and the NSF-sponsored Coastal Ocean Processes (CoOP) program-River Influences on Shelf Ecosystems (RISE), aimed at studying the influence of the Columbia River on coastal oceanographic processes off the Oregon and Washington shelves. These two programs overlapped spatially in hydrographic and biological measurements along a transect line extending from Grays Harbor (GH), WA (Figure 1). As a result, we have excellent coverage of the GH hydrographic line from summer 2004 through fall 2005, including direct estimates of phytoplankton biomass (chlorophyll *a*) and primary productivity (^{14}C-bicarbonate uptake). Here we combine the data along the GH line to show the impact of this unusual climatological event on phytoplankton growth and standing stocks, and to document the rapid recovery following the delayed onset of springtime upwelling conditions.

2. Data and Methods

[4] The ECOHAB-PNW program conducted standard hydrographic surveys during September 8–28, 2004, July 6–27, 2005, and September 2–22, 2005, extending southward to ca. 47° N along the GH hydrographic line. The RISE program occupied the GH line as the northern extent of the sampling grid during July 9–26, 2004, May 30–June 19, 2005, and August 5–26, 2005. Thus, by combining these two data sets, we have coverage of this area prior to (July, September 2004), during (June, early July 2005), and

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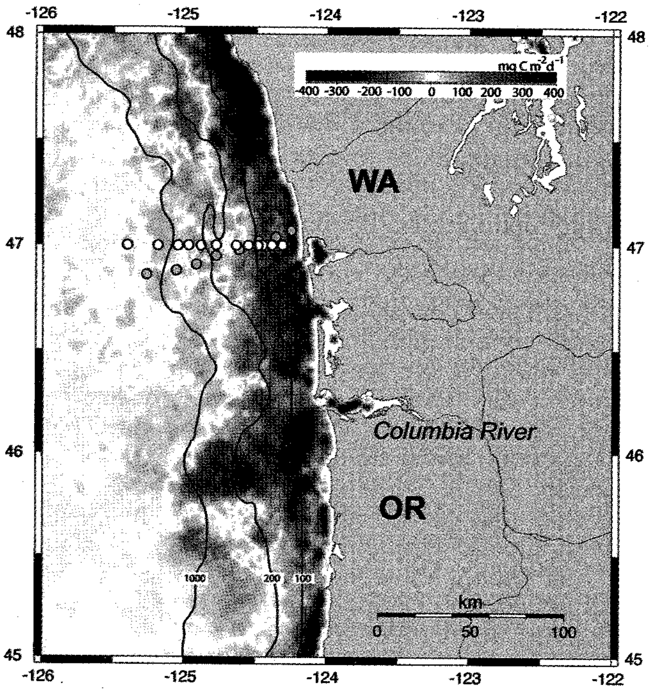

Figure 1. Pacific Northwest study area, showing bathymetry (100, 200, and 1000 m contours), station locations (open and grey circles denote the locations for the RISE and ECOHAB-PNW lines, respectively), and depth integrated primary production anomalies (mg C m^{-2} d^{-1}), calculated as June 2005–June 2004. "Inner shelf" refers to the innermost two stations for each line; "mid-shelf" refers to stations near the 100 m isobath; "offshore" stations are offshore of the 200 m isobath.

after (late July, September 2005) the anomalous warm conditions. Details of the physical forcing and timing of events can be found elsewhere in this volume.

[5] We focus on the spatial (onshore-offshore) and temporal trends in phytoplankton biomass and productivity. Chlorophyll *a* was determined using non-acidification, in vitro fluorometric analyses [*Welschmeyer*, 1994] after filtration onto Whatman GF/F filters (0.7-μm). Size-fractionated biomass was determined by filtration onto Poretics polycarbonate filters (5-μm). Samples were extracted in 90% acetone for ca. 24 hours (−20 to −80 °C) and fluorescence was measured with Turner Designs 10AU fluorometers calibrated at the beginning of each cruise with pure chlorophyll *a* (Sigma or Turner Designs). Phytoplankton carbon assimilation was determined using three methods. First, during the RISE program, productivity was routinely estimated for surface (ca. 2–5 m) samples by the addition of NaH^{14}CO$_3$ to 280-mL polycarbonate bottles and incubation for 24 hours using simulated in situ conditions followed by filtration (GF/F) and acidification. Second, at select stations, depth-integrated primary production was determined by conducting carbon rate measurements in a similar fashion, using water collected from depths corresponding to 100, 50, 30, 15, 5, and 1% surface irradiance and employing trapezoidal integration [*Kudela et al.*, 1997]. Finally, during both the ECOHAB-PNW and RISE programs, photosynthesis versus irradiance measurements (PE curves) were determined for samples collected from near-surface waters, using short-term (ca. 30–60 minute) incubations with white (halogen) light using 14–21 light levels between 0–1200 μmol photons m^{-2} s^{-1}, and ambient sea surface temperatures. Whole water samples were incubated in 25-mL glass vials and terminated by acidification of the entire volume, then radio-assayed using liquid scintillation counting. Data were fit to a PE model [*Webb et al.*, 1974] to determine maximum carbon fixation (P_{max}) and initial slope (α). Average depth-integrated primary production was also estimated using the VGPM (satellite) model [*Behrenfeld and Falkowski*, 1997], with daily 1-km resolution SeaWiFS data time-averaged for June 2004 and June 2005. A strong, linear relationship between VGPM and in situ productivity estimates for the GH line ($n = 9$, $r^2 = 0.67$, slope = 1.00, $p < 0.05$) was obtained after setting the P^B_{opt} term to the regional average of 5.81 mg C mg Chl^{-1} d^{-1}.

[6] Using data from the RISE program for all years and all stations (including the GH line), we also found a good relationship between surface productivity estimates and depth-integrated estimates ($n = 42$, $r^2 = 0.65$, $p < 0.05$), similar to the results of *Perry et al.* [1989]. We therefore report surface productivity estimates, which increases our sample size, and assume that these values are representative of water column productivity.

3. Patterns of Phytoplankton Standing Stock and Production

[7] The GH hydrographic line is representative of the typical spatial patterns observed in the PNW (Figure 1). During summer, the oceanographic and biological state of this region is largely regulated by wind forcing (although the GH line is also influenced by the Juan de Fuca Eddy to the north [*MacFadyen et al.*, 2005], and the Columbia River to the south [*Hickey et al.*, 2005]). Upwelling brings cold, nutrient-rich waters to the surface nearshore, typically resulting in lower biomass and productivity at the innermost stations where surface waters have been diluted. Immediately offshore, the characteristically high biomass (and productivity) peaks at approximately mid-shelf (ca. 70–100 m bottom depth) and generally declines further offshore until reaching the relatively low biomass, low productivity waters of the open ocean (ca. 125.5° W). The spatial (longitudinal) extent of this characteristic gradient in biomass and productivity is controlled by the intensity and duration of upwelling-favorable winds. During periods of relaxation or downwelling, this general pattern persists, but is reduced in amplitude. For example, in August 2005, the GH line was occupied during a period of strong upwelling (August 6), and again three weeks later during a period when winds were upwelling-favorable, but considerably weaker (August 24). There was a shift in maximum biomass from inshore during weaker winds (Chl *a* = 12.89 mg m^{-3} at 124.289° W) to mid-shelf (Chl *a* = 17.42 mg m^{-3} at 124.489° W) during stronger upwelling-favorable winds. Further offshore, biomass converged as the coastal waters transitioned into oceanic waters (Chl *a* = ca. 0.40 mg m^{-3} offshore of 125° W). This general response to wind forcing is also evident from a time-series of Chl *a* at a single, mid-shelf station (Figure 2).

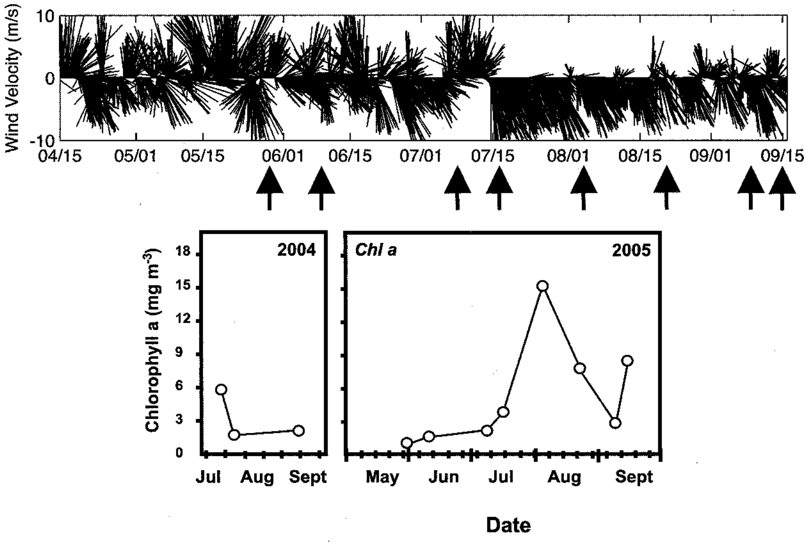

Figure 2. (top) Wind vectors for 15 April–15 September 2005 showing magnitude and direction (positive is towards the north) and (bottom) time series of near-surface chlorophyll *a* at mid-shelf (47°N, 124.6°W). The arrows in the top panel indicate the corresponding sampling times for the chlorophyll time series.

[8] In the year preceding the anomalous warm water event (July 2004), biomass along the GH line approached 8 mg m^{-3} Chl *a* at the inshore stations, with >50% of the biomass larger than 5 μm, indicative of diatoms and other large phytoplankton (confirmed by microscopy, E. Lessard, personal communication, 2005). The relative contribution of the larger class (>5 μm) declined with the overall decrease in biomass moving offshore, accounting for <50% of the total biomass at the outer stations (Figure 3). In contrast, the warm water anomaly was associated with a reversal of this pattern in June 2005. Total biomass was substantially depressed, with a greater fraction of large cells offshore, and a predominance of small cells inshore; this was accompanied by a decrease in productivity over the shelf and a corresponding increase off-shelf (ca. 200–1000 m depth) for June 2005 compared to June 2004 (Figure 4). This decline in total biomass was also evident at mid shelf and offshore on July 9, 2005. However, by July 17, phytoplankton biomass made a dramatic reversal to more typical conditions, with an increase in total standing stock (maximum Chl *a* of 8.57 mg m^{-3} on July 17, 2005) and a shift to >60% of the total biomass larger than 5 μm. August 2005 was similar, while September 2005 showed a seasonal decline in total biomass. Size-fractionated data also suggest that during the warm anomaly (June 2005), small cells were increasingly dominant inshore, although this is clearly modulated by the presence/absence and strength of upwelling; by July 9, 2005 the pattern of large cells inshore and small cells offshore is evident, despite the depressed biomass. Using the most directly comparable data (July 2004 and late July 2005 versus June and early July 2005), the GH line exhibited a substantial decrease in total biomass across the entire transect (t-test, $p < 0.01$), with an average decline of 50% during the warm water anomaly. Spatially, this varied from inshore (25% decline) to mid-shelf (75% decline), with the outer stations showing either no decrease or an enhancement (0–100% increase); note that the outer stations had very low biomass regardless of the cruise, so

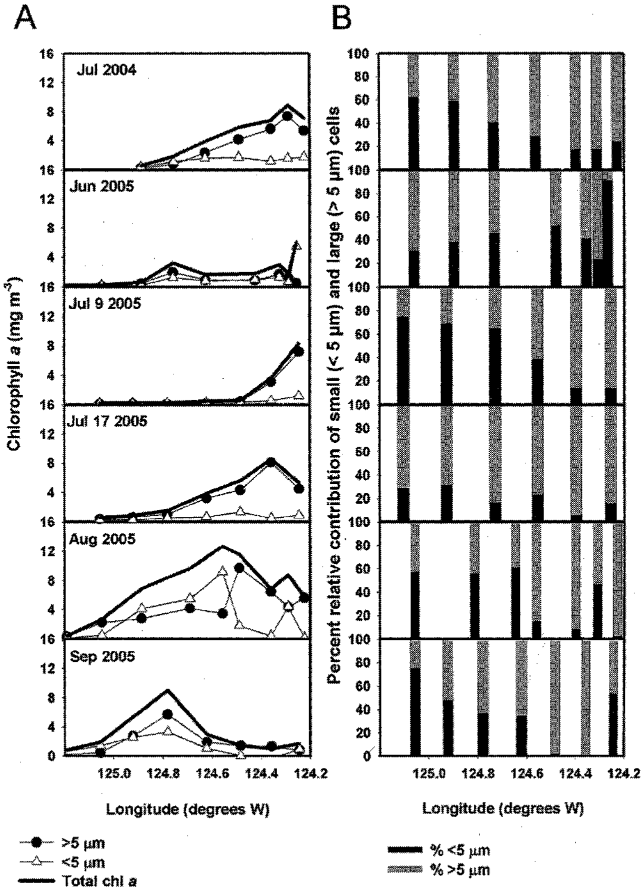

Figure 3. Seasonal change in (a) total chlorophyll *a* and (b) size-fractionated chlorophyll *a* from near-surface samples along the GH line during 2004 and 2005. The relative contribution of larger (>5 μm: grey) and smaller (<5 μm: black) phytoplankton is shown as a percentage of total chlorophyll *a* (thicker line) in panel A.

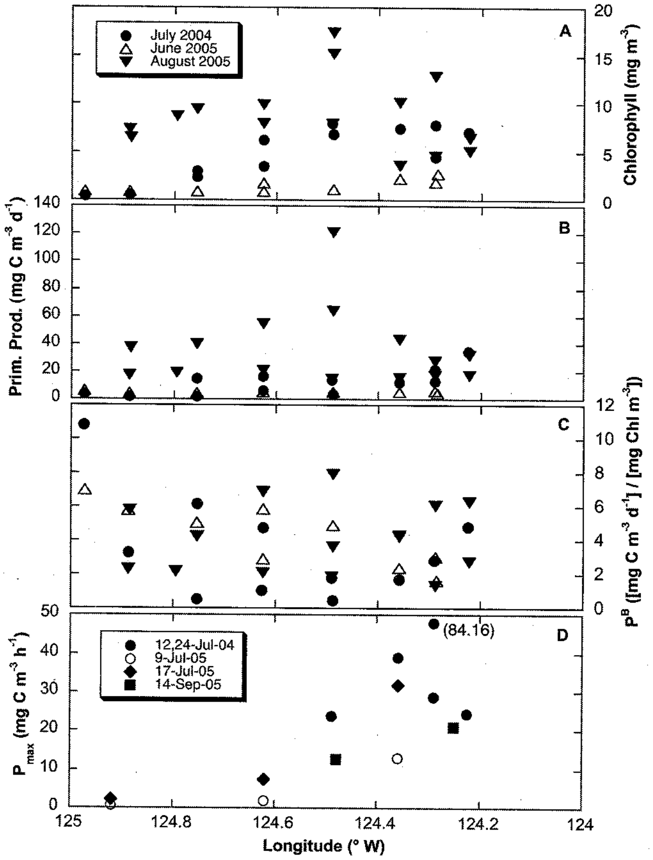

Figure 4. (a) Phytoplankton biomass as chlorophyll *a*, (b) primary productivity (Prim. Prod.), (c) chlorophyll-specific primary productivity (P^B), and (d) the maximum rate of photosynthesis (P_{max}) from short-term PE curves along the GH Line for July 2004, June 2005, and August 2005 (upper 3 panels) and July 12 and 24, 2004, July 9 and 17, 2005, and September 14, 2005 (Figure 4d). The open symbols in each panel represent the warm anomaly. One point in Figure 4d (84.16 mg C m^{-3} h^{-1}) is greater than the y-axis scale.

the observed enhancements are statistically not significant (ANOVA, $p > 0.05$).

[9] Unlike most previous studies, we report direct estimates of primary productivity (as carbon fixation) to accompany our estimates of phytoplankton biomass. The most striking difference between cruises was the range of productivity values: June 2004 (1.55–34.36 mg C m^{-3} d^{-1}), June 2005 (1.40–5.74 mg C m^{-3} d^{-1}), and August 2005 (0.90–121.50 mg C m^{-3} d^{-1}). As expected, based on the Chl *a* patterns, the productivity values during "normal" (July 2004, August 2005) versus anomalous (June 2005) periods converged offshore at a low value (ca. 1 mg C m^{-3} d^{-1}). Although biomass declined from ca. 25–75% moving from inshore towards mid-shelf, declines in productivity were more uniform cross-shelf, averaging ca. 40% (Figure 4). This is also evident from the satellite data (Figure 1). For the region 45–48°N, 122–126°W, median productivity declined from 150 to 75 mg C m^{-2} d^{-1}, or a 50% decrease. Thus, the anomalous warm conditions resulted in a substantial decline in both shelf biomass and productivity, concomitant with a shift in phytoplankton size. Although we focus on the GH line, *Thomas and Brickley* [2006] report negative chlorophyll anomalies for April–June northward of ca. 40°N out to 100 km from the coast; using that region, estimated productivity declined from a median value of 264 to 222 mg C m^{-2} d^{-1}, or ca. 16% (data not shown), consistent with the warm anomaly being greatest in the PNW [*Schwing et al.*, 2006; *Thomas and Brickley*, 2006].

[10] This decrease in productivity was also confirmed through comparison of maximum photosynthetic rates (P_{max}, mg C m^{-3} h^{-1}) obtained from PE curves in July 2004, July 2005 (before and after upwelling winds), and September 2005 along the GH line. PE curves remove some of the variability associated with simulated in situ incubations and provide a standardized metric for comparison of distinct phytoplankton assemblages. The general pattern of the PE data follows that for biomass and productivity, with higher values inshore to mid-shelf, decreasing offshore (Figure 4 and Table 1). Again, maximum photosynthetic values converge offshore, with relatively greater differences at mid-shelf and inshore stations (Table 1). Productivity

Table 1. Summary of Phytoplankton Photosynthetic Parameters and Biomass From All Stations Along the GH Hydrographic Line[a]

Date	Latitude, °N	Longitude, °W	P_{max}, mg C m^{-3} h^{-1}	α^{chl}, mg C mg Chl^{-1} h^{-1} μmol photons m^{-2} s^{-1}	R^2	Chl *a*, mg m^{-3}
12-Jul-04	47	124.29	84.16	0.051	0.96	7.43
12-Jul-04	47	124.49	23.91	0.040	0.77	2.56
24-Jul-04	47	124.22	24.49	0.018	0.88	7.11
24-Jul-04	47	124.29	28.61	0.031	0.62	4.52
24-Jul-04	47	124.36	38.87	0.021	0.98	6.72
9-Jul-05	47.04	124.36	12.87	0.008	0.94	4.43
9-Jul-05	46.98	124.63	1.81	0.017	0.82	0.44
9-Jul-05	46.91	124.92	0.70	0.110	0.41	0.15
17-Jul-05	47.04	124.36	31.81	0.042	0.98	6.69
17-Jul-05	46.98	124.62	7.43	0.018	0.96	3.12
17-Jul-05	46.91	124.92	2.27	0.019	0.97	0.79
14-Sep-05	47.07	124.25	20.95	0.019	0.97	10.46
14-Sep-05	47.02	124.48	12.83	0.029	0.97	5.18

[a] The 9 July data are from the warm anomaly. Note that there were no PE data available for the GH line during the other sampling periods.

estimates are often normalized to chlorophyll concentration in order to more directly relate these rates to intrinsic growth rates; the PE curves thus provide the normalized maximum, or light-saturated, carbon fixation rate (P^B_{max}; mg C mg Chl^{-1} h^{-1}), and the light-limited rate or initial slope (α^{chl}; mg C mg Chl^{-1} h^{-1} [μmol photons^{-1} m^{-2} s^{-1}]). The simulated in situ rate measurements can also be used to determine P^B_{opt}, the maximum biomass normalized productivity (mg C mg Chl^{-1} m^{-3} d^{-1}) from the water column, functionally equivalent to P^B_{max} [*Behrenfeld and Falkowski*, 1997].

[11] Using either of these normalized rates (P^B_{max} or P^B_{opt}), it is apparent that there was very little difference in the underlying physiology of the phytoplankton assemblages among cruises or time periods (ANOVA, $p > 0.1$), with an average P^B_{opt} value for all stations and cruises of 5.81 (±4.34) mg C mg Chl^{-1} d^{-1} (n = 42), and an average P^B_{max} value of 4.81 (±2.81) mg C mg Chl^{-1} h^{-1} (Figure 4). Although P^B_{max} and P^B_{opt} are not identical measurements, changes in P^B_{opt} are largely driven by corresponding changes in P^B_{max} [cf. *Behrenfeld and Falkowski*, 1997], such that patterns, but not absolute values, can be compared. This suggests that there were no substantial differences in photophysiological competence of the phytoplankton communities during the anomalous warm period compared to other times.

4. Comparison to Previous Anomalies

[12] The 2005 anomaly was characterized by a dramatic decline (ca. 50%) in total biomass, and a corresponding decline (ca. 16–50%) in primary productivity within the coastal waters of the region analyzed herein (ca. 45–48° N). Although warmer waters are often associated with enhanced P^B_{opt} [*Behrenfeld and Falkowski*, 1997] eastern boundary current systems generally exhibit an increase in P^B_{opt} with decreasing temperature [*Chavez et al.*, 2002] (these data, not shown) attributed to nutrient (nitrate) availability associated with cold, upwelled waters. Previous work has shown that the PNW is primarily limited by the availability of nitrate at this time of year [*Corwith and Wheeler*, 2002; *Hill and Wheeler*, 2002], which has been confirmed for both the ECOHAB-PNW and RISE programs (unpublished). Thus, the warm anomaly primarily impacted the phytoplankton community through nutrient limitation. This appears to have caused a shift in species composition, with a reversal of the normal pattern in which coastal waters are dominated by large (diatom) assemblages, and offshore waters are dominated by picoplankton. In 2001, which was similarly characterized by fairly warm water, picoplankton were also found in much higher abundance compared to the 2002 cool anomaly [*Sherr et al.*, 2005]. Although the lack of response in photophysiological parameters is at first surprising given the warm, nutrient-depleted conditions, the corresponding shift in phytoplankton assemblages to smaller size-classes presumably offset the physical changes, resulting in essentially constant photosynthetic parameters despite dramatically lower total biomass. This likely occurred because of both a positive increase in P^B_{opt} and P^B_{max} with increasing temperature [cf. *Behrenfeld and Falkowski*, 1997] and a decrease in nutrient stress with decreasing phytoplankton size.

[13] In the recent past, several other documented anomalous events have impacted this coastal region. The 1997–98 ENSO period resulted in a substantial decrease in phytoplankton standing stock off Oregon, with a ca. 67% decline in spring and ca. 25% decline in summer, attributed to nitrate limitation, with a corresponding shift from large to small phytoplankton compared to 1998–99 [*Corwith and Wheeler*, 2002]. Further south, *Chavez et al.* [2002] estimated that this ENSO event reduced phytoplankton standing stocks by 50–80% off central California, and was accompanied by a 68% decrease in new production relative to a long-term average (1989–99). At the opposite extreme, the anomalous cold event of 2001–2002 [*Freeland et al.*, 2003] enhanced nitrate availability, resulting in a 100% increase in algal standing stocks [*Wheeler et al.*, 2003], extending over the entire shelf region from 40–50° N and >200 km offshore of WA [*Thomas et al.*, 2003]. Within this context, the 2005 anomaly resulted in a decrease of phytoplankton productivity similar to an ENSO event. With the onset of upwelling-favorable conditions, however, the phytoplankton made a rapid recovery (within one week) in phytoplankton biomass, size, and primary productivity. Thus it appears that the phytoplankton can rapidly respond to large-scale forcing, with a resulting range of 25–75% decreases to 100% increases in biomass (and presumably production) over relatively short time scales.

[14] In contrast to primary producers, higher trophic levels cannot rapidly adjust to changes in the physical environment and prey (phytoplankton) availability due to the longer periods required for development. The 2005 warm anomaly was characterized by highly publicized declines in fisheries, bird mortalities, and changes in marine mammal behavior. Despite the rapid recovery of the phytoplankton community, other trophic levels responded more slowly, ranging from a few months [*Brodeur et al.*, 2006], or longer [*Sydeman et al.*, 2006; *Weise et al.*, 2006] suggesting that there is a critical time window for trophic transfer. The cold anomaly of 2001–2002, which enhanced phytoplankton growth, similarly did not result in enhanced trophic transfer. Rather, the enhanced standing stock of phytoplankton may have resulted in increased water column and benthic respiration, which in turn may have caused the reported low oxygen "dead zone" that occurred for two months off Oregon in 2002 [*Wheeler et al.*, 2003]. A similar dead zone appeared off Oregon in 2004 [*Service*, 2004], possibly related to large-scale changes in circulation caused by the "regime shift" associated with the Pacific Decadal Oscillation [*Chavez et al.*, 2003].

[15] It is unclear at this time how anomalies such as the Subarctic cool intrusion of 2002 and the warm event of 2005 relate to the large-scale changes in the Pacific Ocean, including the apparently anthropogenic warming of the oceans during the last several decades [*Field et al.*, 2006]. Despite these uncertainties, the 2005 anomaly suggests that warming or delayed onset of upwelling will have a direct negative impact on biomass, and productivity, with a decrease in the average size of the phytoplankton assemblage. Given the strong bottom-up control of the ecosystem in the PNW [*Ware and Thomson*, 2005], we highlight the importance of coordinated observational programs in studies of the coastal ocean aimed at understanding and predicting the impact of regional and large scale forcing on these

ecosystems, and underscore the critical importance of phytoplankton biomass and productivity to these systems.

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