Submesoscale frontal dynamics enhances phytoplankton chlorophyll in the North Pacific Subtropical Gyre

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Key points:

1. A new statistical tool quantifies spatial heterogeneity from high-resolution satellite images.
2. Submesoscale dynamics is shown to enhance chlorophyll in the North Pacific Subtropical Gyre.
3. The impact of submesoscale physics on phytoplankton may modify the negative impact of warming.

ABSTRACT

Subtropical gyres contribute significantly to global ocean productivity. As the climate warms, the strength of these gyres as a biological carbon pump is predicted to diminish due to increased stratification and depleted surface nutrients. We present results suggesting that the impact of submesoscale physics on phytoplankton in the oligotrophic ocean is substantial and may either compensate or exacerbate future changes in carbon cycling. A new statistical tool was developed to quantify surface patchiness from sea surface temperatures. Chlorophyll concentrations in the North Pacific Subtropical Gyre were shown to be enhanced by submesoscale frontal dynamics with an average increase of 38% (max. 83%) during late winter. The magnitude of this enhancement is comparable to the observed decline in chlorophyll due to a warming of ~1.1°C. These results highlight the need for an improved understanding of fine-scale physical variability in order to predict the response of marine ecosystems to projected climate changes.

1. Introduction

The ocean and its biota are undergoing major changes as a result of natural and anthropogenic forcing. Over the past decades much has been learned with regard to alterations to large-scale (e.g. basin-wide) circulation in the ocean [*Vecchi et al.*, 2006], as well as the cascading effects on intermediate-scale dynamics such as eddies [*Davis and Di Lorenzo*, 2015]. The impact of these physical variations on nutrient distributions and ecosystem structures has been studied through long-term time-series programs, field campaigns, and a variety of numerical modeling experiments [e.g. *Corno et al.*, 2007; *Xiu and Chai*, 2012]. However, much less is known about the variations and impact of another class of ubiquitous features, submesoscale dynamics, due to their typical length (1-10 km) and time (one to several days) scales which make them difficult to observe and model [*Mahadevan and Tandon*, 2006]. These fine-scale features often arise through advective interactions with mesoscale frontal jets and eddy peripheries and are associated with sharp density gradients. These gradients create enhanced vertical velocities, promoting effective exchange between the ocean interior and surface layers [*Capet et al.*, 2008; *Klein and Lapeyre*, 2009; *Levy et al.*, 2010]. Sensors mounted on autonomous platforms, such as profiling floats and gliders, have captured enhanced, intermittent upwelling velocities into the euphotic zone that are hypothesized to result from submesoscale frontogenesis [*Johnson et al.*, 2010; *Niewiadomska et al.*, 2008]. However, both the net impact of fine-scale processes on large-scale ocean biogeochemistry and how these interactions might change in the future remain poorly understood.

Various mechanisms have been proposed regarding the potential impact of submesoscale physics on phytoplankton dynamics. In oligotrophic regions, the upward branches of the fronts may enhance phytoplankton growth and productivity by transporting nutrients into the euphotic zone [*Mahadevan and Archer*, 2000; *Johnson et al.*, 2010], while the downward components may facilitate export production by rapidly subducting biomass into the subsurface [*Niewiadomska et al.*, 2008; *Omand et al.*, 2015]. Using an idealized model, Levy et al. [2014] suggested that ~20% of new production in the oligotrophic subtropics could be explained by submesoscale dynamics. Conversely, in regimes where deep mixing frequently occurs and light is generally limiting, submesoscale instabilities may create a re-stratified sunlit layer that promotes productivity [*Mahadevan*, 2016]. It has also been argued that the downwelling side of the fronts subducts much of the phytoplankton biomass below the euphotic zone on short enough time-scales that the consumption of upwelled nutrients may be incomplete [*Levy et al.*, 2012]. As such, due to the complexity of mixed layer dynamics and light and nutrient availability, the net impact of submesoscale physics on phytoplankton has been difficult to determine. In this study, we focus on the impact of fine-scale bio-physical interactions in the nutrient-depleted (oligotrophic) regions, such as the subtropical gyres.

Subtropical gyres play a critical role in global ocean productivity and carbon cycling [*Karl et al.*, 1996; *Lomas et al.*, 2010]. As global temperatures continue to rise, the efficiency of carbon export within these gyres is predicted to decline due to increased stratification, reduced vertical nutrient exchange, and shifts in phytoplankton assemblages towards smaller size classes [*Hilligsoe et al.*, 2011; *Li et al.*, 2009]. In addition, some studies have detected decadal-scale increasing trends in the frequency of oceanic fronts and eddy kinetic energy in the oligotrophic ocean [*Matear et al.*, 2013; *Hogg et al.*, 2015]. These trends are hypothesized to be driven by climate and atmospheric instabilities. While direct predictions of future changes in submesoscale dynamics are lacking, these observed changes in large- and mesoscale processes may cause significant modifications to submesoscale dynamics.

Over the past two decades, technological advances in remote sensing have provided synoptic surface views of the global ocean with improved temporal and spatial resolutions [*Gaultier et al.* 2014]. In this study, we investigated the impact of submesoscale physics on phytoplankton distributions using high-resolution satellite observations. Specifically, we developed a new metric (the Heterogeneity Index) that quantifies surface patchiness, and used it to identify signatures of fine-scale, frontal structures in the oligotrophic ocean from horizontal temperature gradients. We then established observational evidence for enhanced chlorophyll concentrations associated with submesoscale frontal dynamics in the North Pacific Subtropical Gyre (NPSG), with an average increase of up to 38% (maximum of 83%) during the later winter. These results have significant implications for understanding the impact of submesoscale physics on primary and export production in the oligotrophic ocean.

2. Methods and Data

2.1. Heterogeneity Index

Traditional approaches for quantifying patchiness in a resource field have primarily focused on data variance [e.g. *Doney et al.*, 2003], which only represents the average gradient in the field. Given the nonlinearity in biological responses to environmental conditions, the high degree of resource (e.g. nutrient) patchiness created by submesoscale dynamics is expected to produce a greater impact than the average gradient does. Cayula and Cornillon [1992] developed a method that uses SST histogram distributions to search for bimodality in resource distributions. This method was adapted to identify sea-surface fronts in various regions such as the California Current [*Kahru et al.*, 2012]. Here we combine these two approaches using measures of both variance and bimodality to quantify patchiness in SST. In addition, we add a third term that quantifies the skewness of the distribution. This additional term allows us to capture patchiness created by thin filaments, which often cause unimodal, skewed SST distributions. Our new metric of spatial patchiness, the Heterogeneity Index (HI), is defined as:

$$HI = a\left(b|\gamma| + c\frac{\sigma}{\sqrt{n}} + dP\right) \qquad \text{eq. (1)}$$

where γ is the skewness of the distribution, σ is the standard deviation, and n is the sample size. P describes the difference in area between the best 5th order polynomial fit to the data x [$p(x)$ in eq. (2)] and a Gaussian distribution with the same sample mean (μ) and σ [$g(\mu,\sigma)$ in eq. (2)]:

$$P = \int_{\min(x)}^{\max(x)} \frac{|p(x) - g(\mu,\sigma)|}{g(\mu,\sigma)} dx \qquad \text{eq. (2)}$$

Coefficients *b*, *c*, and *d* (for the NPSG: b = 1.07, c = 1.81, d = 1.11) scale each component between 0 and 1 such that equal weight is placed on each component, and *a* (a = 0.30) scales HI such that HI = 0 describes a homogenous system, and HI = 1 describes a maximally heterogeneous system. Coefficients *a*-*d* are region specific and must be retuned before HI can be applied to different regions (see Supporting Information *S1* and *S2* for details regarding HI formulation and normalization coefficients for other subtropical oceans).

HI is spatial-scale dependent and designed to identify physical processes occurring at the sub-domain scale. For example, elevated HI for a domain of 10 km × 10 km (HI_{10}) can be caused by the inclusion of a feature smaller than 10 km in length (e.g. a submesoscale filamentous front), or a fraction of a feature equal to or larger than 10 km (e.g. part of a mesoscale front or the edge of an eddy). Figure 1 shows an example of a SST image in which such frontal features result in skewed, high variance, and bimodal distributions and, therefore, elevated HI_{10} values at the fine-scale. While HI equally weights features with different underlying physical mechanisms, it highlights sharp horizontal density gradients occurring on the scale of a few kilometers (i.e. the submesoscale) that are typically associated with enhanced vertical velocities. As a simplification, hereafter we refer to all fine-scale frontal signatures as submesoscale structures due to the length scale of the gradients.

For this analysis, we apply HI to the oligotrophic NPSG. As density gradients are typically coincident with temperature gradients in this region, HI allows us to identify submesoscale structures in the NPSG from satellite-retrieved SST fields. However, caution is needed when applying HI to other oceanographic regimes where this underlying assumption may need to be revisited. For example, temperature may not be an appropriate indicator of water mass differences in high-latitude and coastal upwelling regions. Detection of patchiness in these regions using the HI metric may require the use of remotely sensed altimetry data (which currently precludes submesoscale analyses due to the spatial resolution of the data).

2.2. Satellite data and analyses

Level-2 daily images of MODIS/Aqua SST (daytime) and chlorophyll-*a* concentration (Chl) at approximately 1 km resolution were retrieved from the NASA OB.DAAC for a region in the NPSG (10-30°N, 160°E-160°W) during a 13-year period (July 2002 - June 2015). The latest version (R20140) of the reprocessed data was used. A subset of images were selected using a filtering grid with a fixed window size of 100 km × 100 km to ensure maximal spatial coverage (75% for SST and 70% for Chl) and optimal data quality (*S1*). For each of the 32,222 selected images of 100 km × 100 km, an average HI_{10} was calculated for each individual pixel. Specifically, a grid with a cell size of 10 × 10 pixels was applied to the SST data and HI_{10} was computed for each grid cell. The grid was then shifted eastward or southward at increments of one pixel at a time, and a new HI_{10} was calculated for each cell at the new grid location. Pixel-level HI_{10} was then estimated as the averaged HI_{10} from all possible grid locations.

To identify the fractional area impacted by submesoscale structures, heterogeneity maps of HI_{10} (1 km resolution) were examined at weekly intervals. For a single week, the background field was defined as those pixels with a HI_{10} within 2σ from the mode of all HI_{10} values for the week, and the region impacted by submesoscale structures was defined as pixels with a HI_{10} at least 4σ greater than the mode (*S3*). Several different threshold values were tested and the results were not sensitive to the choice of 4σ. Weekly climatologies of SST and Chl in the impacted regions were then compared with those in the background field.

3. Results

Seasonal climatologies of SST and HI_{10} over the 13-year period showed an inverse relationship between fine-scale heterogeneity (HI_{10}) and SST, with winter dynamics resulting in increased mixed layer depths, reduced SST, and elevated HI_{10} (Fig. 2; *S6*). Overall, a positive relationship was observed between the seasonality of HI_{10} and Chl, with elevated values in the winter and spring and reduced values in the summer. Chl peaked in early February, coincident with an increasing HI_{10}, and then steadily declined while HI_{10} remained elevated. The fractional area impacted by submesoscale structures (indicated by elevated HI_{10}) was greatest during the winter-spring period, and lowest in the late summer and early autumn, with an annual mean of 5.2% (Fig. 3a). This is in agreement with a previous remote sensing study that suggests that 4–10% of the California Current System is covered by fronts [*Woodson and Litvin*, 2015].

Regions with submesoscale structures were also associated with lower SST and elevated Chl. The greatest change in SST relative to the background field was seen in late

February with a weekly average difference of up to 1.7°C (Fig. 3b). This is consistent with results from current profilers that showed an increase in the strength of submesoscale features during the winter (Jan-Mar) due to more frequent larger-scale features [*Callies et al.* 2015]. Chl within submesoscale structures showed the greatest enhancement relative to the surrounding regions during the wintertime, with an average increase of 38% and a maximum increase of 83% (Fig. 3c). The average impact of submesoscale fronts was negligible in the summer and early autumn, during which period the fractional area impacted by submesoscale structures was also at its lowest. We hypothesize that the decreased impact during the summertime was driven by a deepening of the nutricline coupled with increased stratification thereby limiting the ability of submesoscale features to access deep nutrients (see *Discussion* and *S7*).

Ocean eddies play an important role in facilitating submesoscale activities due to baroclinic instabilities that frequently occur in their vicinity [*Klein and Lapeyre*, 2009]. A remote sensing based analysis of eddy location and age [*Chelton et al.*, 2011] suggests that mesoscale eddies are more frequent during the winter-spring period in the NPSG, and that summertime eddies are on average older and so theoretically less energetic (*S8*). This, combined with the seasonality in HI_{10}, suggests a coupling between both the frequency and intensity of mesoscale and submesoscale features in the region. As the average radius of eddies in the NPSG is estimated to be ~100 km [*Gaube et al.*, 2015], HI_{10} allows us to separate the impact of eddy-associated submesoscale features from that of upwelling in eddy interiors. Thus, the enhancement associated with elevated HI_{10} is primarily due to submesoscale dynamics and is in addition to the enhancement that occurs within mesoscale eddies.

As the climate warms, changes in physical dynamics across many different scales may alter nutrient distributions in the oligotrophic ocean, with the interactions between these impacts being complex and difficult to predict. For example, temperatures in the upper ocean are anticipated to rise, which will enhance stratification and reduce vertical nutrient exchange. However, the frequency and amplitude of submesoscale processes are also likely to be modified, though the sign and magnitude of these changes remain unknown. To understand the interactions between these processes and their net impact on phytoplankton dynamics over a large domain, we analyzed the relationship between SST_{100}, Chl_{100}, and HI_{100}^{10}, which are defined as the average SST, Chl, and HI_{10} over a 100 km × 100 km region (Fig. 4). To isolate the impact of submesoscale dynamics and remove the strong relationship between SST and Chl in the NPSG, the correlation between HI_{100}^{10} and Chl_{100} was examined at each SST_{100} level.

We found significant positive correlations between HI_{100}^{10} and Chl_{100} for all SST_{100} levels and all seasons, with the exception of 29.2°C during the summertime potentially due to limited data. In addition, these results suggest that changes in SST_{100} and HI_{100}^{10} have opposite impacts on Chl_{100} of approximately the same magnitude. For example, a moderate change of HI_{100}^{10} from 0.242 to 0.266 (indicating intensified submesoscale dynamics and enhanced nutrients fluxes) in the winter at 22.14°C results in an increase in Chl_{100} of 0.015 mg m^{-3}. This change is similar to the decline in Chl_{100} due to a warming of 2.41°C (indicating enhanced stratification and reduced nutrients fluxes) with HI_{100}^{10} remaining at 0.242. Similarly, a moderate decline in submesoscale activity (reduced HI_{100}^{10}) combined with an increase in SST_{100} significantly enhanced the negative impact of warming on chlorophyll concentrations. These findings suggest that the impact of submesoscale dynamics has the potential to either compensate or exacerbate nutrient depletion caused by increased stratification of the oligotrophic ocean.

4. Discussions and Implications

Vertical exchange of nutrients between the ocean interior and upper layers is critical to phytoplankton growth and productivity. However, global estimates of new production exceed estimates of nutrients fluxes from large-scale circulations, winter convection, and mesoscale eddies [*McGillicuddy et al.*, 1998, 2003; *Klein and Lapeyre*, 2009]. The impact of submesoscale physics has been proposed as one of the missing physical mechanisms behind this imbalance as these features are associated with strong vertical velocities that are more than an order of magnitude greater than that associated with large-scale circulation and the interior of eddies [*Thomas et al.*, 2008]. High-resolution surveys have found efficient vertical exchange of water properties in the vicinity of fronts and eddies where submesoscale features are prevalent [*Lima et al.*, 2002; *Omand et al.*, 2015]. In the oligotrophic ocean where the discrepancy between nutrient requirements and replenishment is large [*McGillicuddy et al.*, 1998], it is of particular importance to understand the role of submesoscale physics in driving additional vertical nutrient supply and, therefore, enhanced productivity. The Heterogeneity Index (HI) provides a means of quantifying the impact of fine-scale frontal structures such as thin filaments, mesoscale frontal jets, and the peripheries of eddies on primary production in this important region.

Our results demonstrate that submesoscale dynamics enhanced the overall concentration of Chl in the oligotrophic NPSG through most of the year. These findings suggest both that submesoscale features increased nutrient supply to the surface ocean and that the timescales of these fluxes exceeded the doubling time of phytoplankton cells. However, the impact of submesoscale processes on Chl varied seasonally with diminished impact during the summer (Fig. 3c). This may be due to decreases in the effectiveness of submesoscale processes in supplying nutrients to the surface ocean caused by both a deepening of the nutricline and a strengthening of the stratification in the upper ocean [*Mahadevan*, 2016]. Specifically, we hypothesize that enhanced winds (maximum during March, Fig. *S9*) and weakened stratification during the late winter strengthened the vertical motions associated with submesoscale features and facilitated the access of deep nutrients thereby increasing the response of phytoplankton to these dynamics. Conversely, solar heating stratified the upper ocean during the summer and nutrients were depleted to a greater depth resulting in a strong pycnocline lying above the nutricline. We hypothesize that during summertime a significant fraction of submesoscale structures could not access the nutricline and thus had a minimal impact on nutrient transport and phytoplankton growth. Further *in situ* observations, such as vertical measurements of density and nutrients made directly within submesoscale structures, are needed in order to understand causative mechanisms behind the differential impact of submesoscale features in the winter-spring relative to the summer.

Using high resolution satellite data (1 km, daily snapshots), we identified signatures of submesoscale structures as heterogeneity "hotspots" and demonstrated that, in the oligotrophic subtropical gyre, increased patchiness in SST resulted in increased Chl concentrations. However, in order to understand the implications of submesoscale dynamics on phytoplankton productivity and carbon cycling, we rely on the assumption that remotely sensed Chl is a good proxy for phytoplankton biomass. Although we believe that this assumption holds true as a first-order approximation over large-scales, changes in environmental conditions can trigger rapid physiological responses in phytoplankton, such as modified intracellular Chl:C ratios, which may introduce some uncertainty into our results. Specifically, phytoplankton cells typically exhibit significant increases in Chl:C ratio with reduced light levels and/or increased nutrient input [*Behrenfeld et al.*, 2015; *Halsey et al.*, 2015]. In the subtropical gyres where growth is primarily nutrient limited, the input of new nutrients may result in an increase in cellular Chl:C and therefore an increase in Chl concentration without necessarily a corresponding increase in biomass. While increases in Chl:C ratio are typically associated with concurrent increases in photosynthesis and growth rates [*Graziano et al.*, 1996; *Moore et al.*, 2008; *Li et al.*, 2015], such variations in phytoplankton Chl:C ratio may contribute significantly to the observed increase in Chl and cloud our interpretation of changes in phytoplankton biomass and productivity associated with submesoscale features. Additional work is needed to better understand how changes in nutrient stoichiometry, photo-acclimation, and community composition impact variability in Chl:C ratio [*Behrenfeld et al.*, 2015]. Furthermore, satellite records only capture changes in the surface ocean and are not fully indicative of water column properties. As such, a necessary next step is to merge satellite observations that resolve surface properties with *in situ* (e.g. gliders and floats) profiles that diagnose vertical dynamics in order to fully understand the role of fine-scale processes in determining depth-integrated primary and export production.

The submesoscale has been largely ignored by the current generation of global climate models. While these models are powerful tools for exploring the impacts of large-scale climate-driven processes on marine biota, they are typically run at coarse resolutions (1-3°) due to computational constraints and thus only represent the mean fields of a resource environment which, in reality, includes a great deal of spatial and temporal heterogeneity over much finer scales. Our findings provide observational evidence that fine-scale processes may play a significant role in modulating phytoplankton growth and biomass distributions in the oligotrophic ocean, and that the magnitude of the biological response is comparable to that of a warmer, more stratified ocean. These results provide a first-order estimate of fine-scale bio-physical interactions that have been previously under-determined by *in situ* observations. While this study has exclusively focused on the subtropical gyres, expanding this analysis to other oceanographic regimes may provide a means for parameterizing coarse resolution global climate models for the impact of fine-scale bio-physical interactions, ultimately improving our understanding of the response of marine ecosystems to future climate changes.

Acknowledgments

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Figure Captions

Figure 1. Feature identification using the Heterogeneity Index. An example of MODIS-Aqua SST image from 04/04/2003 is shown. Sub-regions (10 km × 10 km) associated with submesoscale structures are identified by high HI_{10} values while the background field is characterized by low HI_{10}.

Figure 2. Weekly climatologies of SST, Chl, and submesoscale heterogeneity (HI_{10}) averaged over the study region (July 2002 to June 2015). Error bars represent ±0.25σ from the mean.

Figure 3. Impact of submesoscale heterogeneity (HI_{10}) on SST and Chl. Panel a) shows the fractional area impacted by submesoscale features (high HI_{10}). Panels b) and c) show the difference in SST and Chl between the background field and the feature-impacted regions. In all panels, the central mark of each box plot is the median, edges of the box are the 25th and 75th percentiles, and whiskers extend to the most extreme data points excluding outliers which are denoted by red +. The solid and dashed lines are generated using a 3-point moving average filter. Note the changes in y-axis scales for panels a) and c).

Figure 4. Impact of SST and submesoscale heterogeneity (HI_{10}) on Chl. SST_{100}, Chl_{100}, and HI_{100}^{10} are defined as the average SST, Chl, and HI_{10} over 100 km × 100 km regions. Results are presented by season with bins colored by Chl_{100}. Chl_{100} increases with decreasing SST_{100} (horizontal axis) and increasing HI_{100}^{10} (vertical axis). The significance of the positive relationship between HI_{100}^{10} and Chl_{100} for each SST_{100} bin is shown on top of each column with $p < 0.01$ denoted by two stars (**) and $p < 0.05$ denoted by one star (*). White bins indicate conditions where less than 15 images (100 km × 100 km with good spatial coverage) were available. The arrows demonstrate the comparable, and compensating, change in Chl_{100} (0.015 mg m^{-3}) that would result from a moderate increase in HI_{100}^{10} from 0.242 to 0.266 (solid arrow) versus a warming of the same waters by 2.41°C (dashed arrow).

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