Biogeography and phenology of satellite-measured phytoplankton seasonality in the California current

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A B S T R A C T

Thirteen years (1998–2010) of satellite-measured chlorophyll *a* are used to establish spatial patterns in climatological phytoplankton biomass seasonality across the California Current System (CCS) and its interannual variability. Multivariate clustering based on the shape of the local climatological seasonal cycle divides the study area into four groups: two with spring-summer maxima representing the northern and southern coastal upwelling zones, one with a summer minimum offshore in mid-latitudes and a fourth with very weak seasonality in between. Multivariate clustering on the seasonal cycles from all 13 years produces the same four seasonal cycle types and provides a view of the interannual variability in seasonal biogeography. Over the study period these seasonal cycles generally appear in similar locations as the climatological clusters. However, considerable interannual variability in the geography of the seasonal cycles is evident across the CCS, the most spatially extensive of which are associated with the 1997–1999 El Niño-Southern Oscillation (ENSO) signal and the 2005 delayed spring transition off the Oregon and northern and central California coasts. We quantify linear trends over the study period in the seasonal timing of the two seasonal cycles that represent the biologically productive coastal upwelling zones using four different metrics of phenology. In the northern upwelling region, the date of the spring maximum is delaying (1.34 days yr^{-1}) and the central tendency of the summer elevated chlorophyll period is advancing (0.63 days yr^{-1}). In the southern coastal upwelling region, both the initiation and cessation of the spring maximum are delaying (1.78 days yr^{-1} and 2.44 days yr^{-1}, respectively) and the peak is increasing in duration over the study period. Connections between observed interannual shifts in phytoplankton seasonality and physical forcing, expressed as either basin-scale climate signals or local forcing, show phytoplankton seasonality in the CCS to be influenced by changes in the seasonality of the wind mixing power offshore, coastal upwelling in the near-shore regions and basin-scale signals such as ENSO across the study area.

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1. Introduction

The California Current System (CCS) forms the relatively cold and biologically productive eastern boundary of the North Pacific Gyre. Seasonal shifts in atmospheric pressure systems over the CCS are characterized by the Aleutian Low driving winter storms into the CCS with accompanying mean poleward alongshore wind stress. In summer, the North Pacific High blocks storms from the region and, coupled with the summer North American continental low, drives equatorward, alongshore winds (Bakun and Nelson, 1991; Checkley and Barth, 2009). These seasonal equatorward winds drive the surface Ekman layer of the ocean offshore, upwelling cold, nutrient-rich, subsurface water near the coast

(Hill et al., 1998), and spurring elevated phytoplankton productivity that supports the highly productive marine ecosystem (Mann and Lazier, 2006). Latitudinal gradients in solar heating, light, and wind create a meridionally varying seasonal structure in both upwelling and phytoplankton concentrations (Hill et al., 1998; Thomas et al., 2001). Monthly mean winds are upwelling-favorable year-round south of ~33°N but become progressively more strongly seasonal and of increasing winter downwelling duration with increasing latitude (Bakun and Nelson, 1991). Superimposed on this seasonality is both strong interannual variability imposed by basin-scale, climate-related signals such as the El Niño-Southern Oscillation (ENSO) cycle (e.g. Kahru and Mitchell, 2000) and possible long-term trends such as increased upwelling from global warming (Bakun, 1990). While interannual anomalies (e.g. Thomas et al., 2003; Thomas and Brickley, 2006) and multi-year trends in phytoplankton biomass (e.g. Kahru et al., 2009; Thomas et al., 2013) are evident, the phytoplankton seasonal cycle itself remains less well understood in the CCS.

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Accounting for about 65% of the overall signal in the CCS (Vantrepotte and Mélin, 2009), phytoplankton seasonality causes higher trophic levels such as zooplankton (Richardson, 2008), shrimps (Koeller et al., 2009), larval fish (Brander et al., 2001) and birds (Sydeman et al., 2006) to time aspects of their own seasonality to favorable periods of food abundance. Temporal changes within the seasonality (phenology) of phytoplankton biomass can therefore have large impacts on the ecosystem by disrupting trophic connections (Barth et al., 2007; Ji et al., 2010). Moreover, phytoplankton may be sensitive indicators of climate change (Taylor et al., 2002) and may be responsible for non-linearities in connections between physical forcing and ecosystem productivity (Kirby and Beaugrand, 2009; Di Lorenzo and Ohman, 2012).

Satellite ocean color data provide the only viable way to consistently and synoptically quantify the dynamic structure of phytoplankton biomass over large spatial areas. Satellites provide systematic coverage of seasonality across highly dynamic areas (Vantrepotte and Mélin, 2009). Although measurement of potentially subtle phytoplankton temporal changes is ideally made from platforms with high temporal resolution (e.g. moorings or gliders), previous work has demonstrated the feasibility of measuring phytoplankton phenology with satellite data both regionally and globally (e.g. Henson and Thomas, 2007; Racault et al., 2012).

Here we use 13 years of satellite-measured ocean color data to view phytoplankton seasonal biogeography over the entire CCS, quantify its interannual variability and document changes in phenology. We proceed in three steps: (1) identify the most dominant seasonal cycle shapes in the climatology and map their spatial pattern (climatological biogeography), (2) identify the same seasonal cycles shapes within each year and present interannual variability in their biogeography (interannual biogeography), and (3) analyze shifts in the timing of specific aspects of the annual cycle within the regions characterized by the dominant seasonal cycle shapes (phenology). Lastly, we briefly compare specific features of observed interannual changes in biogeography and phenology to both local and basin-scale physical forcing.

2. Background

2.1. Biogeography

Biogeography attempts to simplify biological patterns by defining regions of similar characteristics. For biological ocean data, chronic under-sampling of the ocean provides another incentive to defining regions: a mechanism to extrapolate relatively few measurements to a larger area (Longhurst, 2007). The advent of satellite-measured ocean color data products provided the means to quantify aspects of surface phytoplankton biogeography with high spatial resolution over global scales. Platt et al. (1991) divided the North Atlantic into 12 regions to estimate primary production. Longhurst (1995) divided the global ocean into over 50 biogeographic provinces based in part on phytoplankton seasonal cycles.

A difficulty with oceanic biogeography is the contrast between the dynamic environment and the static nature of boundaries. Phytoplankton biomass is known to be patchy at a wide range of spatial and temporal scales (Haury et al., 1978), indicating that very few individual organisms experience 'average' conditions (Mackas et al., 1985), and constraining the effectiveness of oceanic biogeography. Appropriate spatial scales for averaging are also both time and space dependent in the ocean (Denman and Abbott, 1988), and might vary with the goals of the biogeographical analysis (Denman and Powell, 1984). Biogeographic boundaries of the ocean are typically based on climatological conditions (e.g. Longhurst, 1995; Oliver and Irwin, 2008; D'Ortenzio and

Ribera d'Alcalà, 2009; Vantrepotte and Mélin, 2009; Thomalla et al., 2011; D'Ortenzio et al., 2012) and thus do not necessarily reflect the environment at any single point in time. Fluid boundaries (e.g. Devred et al., 2007; Irwin and Oliver, 2009) alleviate this issue, though the timescales at which the maps should be redrawn raises other questions.

In the CCS (Fig. 1), biogeography has been widely used to simplify the highly dynamic environment. A survey of previous work suggests that the most common way of partitioning the CCS is latitudinally defined boundaries based on broad climatological hydrographic characteristics and obvious geographic features (e.g. Hickey, 1989). Studies defining three regions use borders at either Cape Blanco or Cape Mendocino and Point Conception (e.g. GLOBEC, 1991; Checkley and Barth, 2009; Kahru et al., 2009; Chenillat et al., 2012). Others use four regions, with divisions at the Oregon–California border or Oregon–Washington border, Cape Mendocino, Point Conception, and the U.S.–Mexico border or Punta Eugenia, (Longhurst, 1995; Kahru and Mitchell, 2001; Henson and Thomas, 2007). Ware and Thomson (2005) delineate five separate regions from Vancouver Island to Point Conception: Vancouver (47.5°N–50.5°N), Columbia (43°N–47.5°N), Eureka (40.5°N–43°N), Monterey (36°N–40.5°N) and Conception (32.5°N–36°N). Thomas and Strub (2001) use six regions, with boundaries at Juan de Fuca Strait, Cape Blanco, Cape Mendocino, Point Arenas, Point Conception, the U.S.–Mexico border, Punta Eugenia and Cabo San Lucas, leaving out the SCB and northern Baja California regions from their analysis. Henson and Thomas (2007) use multivariate clustering on satellite-measured phytoplankton pigment concentrations in the CCS to define alongshore-oriented biogeographical regions due to elevated levels in the coastal zone. Legaard and Thomas (2006) map the seasonal timing of the annual maxima and minima in satellite-measured phytoplankton pigment concentrations, showing similar alongshore oriented regions with a major discontinuity at Point Conception.

2.2. Phenology

Phenology is the study of the timing of periodic events in an organism's or population's seasonal cycle with respect to its environment. Phenology can reveal sensitive biological responses to climate change because temperature often cues the initiation and duration of life stages (Edwards and Richardson, 2004; Richardson, 2009). Warming temperatures cause many organisms to increase their metabolic rate, begin life history stages earlier, and progress through ontogeny more quickly (Walther et al., 2002; Parmesan, 2006; Yang and Rudolf, 2010). Some organisms respond more quickly than others to environmental cues (Ji et al., 2010), potentially creating temporal mismatches between trophic levels and severely impacting the ecosystem (Hjort, 1914; Cushing, 1990). As the base of the marine food web, phytoplankton biomass and the timing of events in its seasonal cycle are a critical control on the efficiency of carbon transfer to higher trophic levels, including economically important fisheries (Ware and Thomson, 2005; Platt and Sathyendranath, 2008).

Specific events that induced strong interannual variability in the CCS demonstrate how increased climate variability, a predicted outcome of global warming (IPCC, 2007), may influence this highly productive marine ecosystem (Schwing et al., 2006). There is evidence that many interannual events are linked to basin-scale climate signals. The El Niño event of 1997–1999 resulted in delayed and weak upwelling winds (Bograd et al., 2009) and an increased thickness of upper warm layers, reducing vertical nutrient flux and resulting in strong negative biomass anomalies (Kahru and Mitchell, 2000). The strong El Niño in 1983 brought similar hydrographic conditions (Thomas and Strub, 2001) as well as a decoupling of the spring arrival of upwelling winds and its