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Hierarchical and dynamic seascapes: A quantitative framework for scaling pelagic biogeochemistry and ecology

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ABSTRACT

Comparative analyses of oceanic ecosystems require an objective framework to define coherent study regions and scale the patterns and processes observed within them. We applied the hierarchical patch mosaic paradigm of landscape ecology to the study of the seasonal variability of the North Pacific to facilitate comparative analysis between pelagic ecosystems and provide spatiotemporal context for Eulerian time-series studies. Using 13-year climatologies of sea surface temperature (SST), photosynthetically active radiation (PAR), and chlorophyll a (chl-a), we classified seascapes in environmental space that were monthly-resolved, dynamic and nested in space and time. To test the assumption that seascapes represent coherent regions with unique biogeochemical function and to determine the hierarchical scale that best characterized variance in biogeochemical parameters, independent data sets were analyzed across seascapes using analysis of variance (ANOVA), nested-ANOVA and multiple linear regression (MLR) analyses. We also compared the classification efficiency (as defined by the ANOVA F-statistic) of resultant dynamic seascapes to a commonly-used static classification system. Variance of nutrients and net primary productivity (NPP) were well characterized in the first two levels of hierarchy of eight seascapes nested within three superseascapes ($R^2 = 0.5–0.7$). Dynamic boundaries at this level resulted in a nearly 2-fold increase in classification efficiency over static boundaries. MLR analyses revealed differential forcing on $p\mathrm{CO}_2$ across seascapes and hierarchical levels and a 33% reduction in mean model error with increased partitioning (from 18.5 µatm to 12.0 µatm $p\mathrm{CO}_2$). Importantly, the empirical influence of seasonality was minor across seascapes at all hierarchical levels, suggesting that seascape partitioning minimizes the effect of non-hydrographic variables. As part of the emerging field of pelagic seascape ecology, this effort provides an improved means of monitoring and comparing oceanographic biophysical dynamics and an objective, quantitative basis by which to scale data from local experiments and observations to regional and global biogeochemical cycles.

1. Introduction

1.1. The necessity of a formal pelagic seascape concept

The pelagic ocean is a complex system in which organism distributions are affected by and provide feedbacks to physical and biogeochemical processes on multiple scales of spatial, temporal, and biological organization (Lubchenco and Petes, 2010; Doney et al., 2012). Non-linearities are common in biogeochemical (e.g. Gruber, 2011; Hales et al., 2012), biophysical (e.g. Hsieh et al., 2005) and trophic (Litzow and Ciannelli, 2007, Brander, 2010) interactions. Furthermore, spatial heterogeneity is ubiquitous and occurs at all scales observed (Steele, 1991; Levin and Whitfield, 1994; Mitchell et al., 2008). Understanding and modeling pelagic ecosystem responses and feedbacks to environmental perturbation is therefore hampered by the lack of an objective framework to (1) scale local processes to ocean basins (2) define how temporal and spatial scaling of habitats may change regionally, and (3) place the 'snapshots' of data collected in a typical oceanographic research expedition into a regional context.

To address issues of scale, change and context, terrestrial ecologists have looked toward the field of landscape ecology

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(Turner et al., 2001; Turner, 2005). Terrestrial ecosystems are parsed into landscapes, defined in space by the main complex causal (Troll, 1950) or reciprocal (Turner, 2005) relationships between the environment and the distributional patterns of organisms. Likewise, in the marine environment, physiological and ecological responses are closely coupled to the scale of physical forcing (Steele, 1989). Thus, the global ocean may be viewed as a mosaic of distinct seascapes, composed of unique combinations of physicochemical forcing and biological responses and/or feedbacks.

The characterization of distinct ocean ecosystems based on ocean color can be traced as far back as Somerville (1853); however, the most comprehensive approach combining geography, ocean color, and biogeochemistry can arguably be attributed to Longhurst (1998, 2007). The Longhurst classification used chlorophyll a (chl-a) from the Coastal Zone Color Scanner, ship-based climatologies of nutrients, euphotic depth and several physical variables describing water column stratification. Although the classified provinces are static, rectilinear, and subjectively chosen, the resultant framework has been instrumental in understanding changes in fishery and zooplankton distributions (Beaugrand et al., 2000) and optimizing biogeochemical models, particularly satellite primary productivity algorithms (Siegel et al., 2001). More recent efforts have used the maturing satellite data record to classify regions of biophysical coherence for coastal (Saraceno et al., 2006; Devred et al., 2007; Hales et al., 2012) and open ocean regions (Oliver and Irwin, 2008). The majority of these efforts have been temporally static (but see Devred et al., 2009; Irwin and Oliver, 2009) and at a single scale. Importantly, few have verified their classifications with rigorous post hoc statistical analyses using independent data sets at multiple scales (but see Vichi et al., 2011).

We classified satellite-derived seascapes in a spatially and temporally specific fashion and explicitly test the hypothesis that coherent regions as identified with satellite data represent distinct regions of ecosystem functioning (Platt and Sathyendranath, 1999). We extend the methods presented by Saraceno et al. (2006) and Hales et al. (2012) to resolve the intra-annual evolution of seascapes in the open North Pacific based on a 13-year climatology of satellite observations. Furthermore, we explicitly apply the concept of patch hierarchy (Kotliar and Wiens, 1990; O'Neill et al., 1992; Wu and Loucks, 1995). Borrowed from landscape ecology, the hierarchical patch mosaic paradigm views the system as a nested and partially ordered set, where system dynamics are defined by the composite of interacting, but distinct patches within the system. In our analysis, individual seascapes comprise the patches which aggregate (or split) to form superseascapes (subseascapes) at larger (finer) spatiotemporal scales. This application allowed us to classify basin-scale and gyre scale dynamics with the same domain and test hypotheses regarding resolution requirements for characterizing variability of different biogeochemical processes. First, we describe the general patterns of seasonal seascape variability across hierarchical levels. Then, we test the assumption that seascapes represent areas of distinct biogeochemical function by evaluating differences between seascapes using independent *in situ* distributions of nutrients, net primary productivity (NPP) and the partial pressure of carbon dioxide ($p\mathrm{CO_2}$) in the surface ocean. On a subset of these data, we compare the efficiency of classification between seasonally dynamic seascapes and a commonly utilized static framework (Longhurst, 1998, 2007). Finally, we demonstrate the utility of the dynamic seascape framework in reducing model error and illuminating regional variability of biophysical forcing of important biogeochemical processes and patterns.

2. Methods

2.1. Study area

The North Pacific includes the oligotrophic and subarctic gyres that are separated by the broad North Pacific current, NPC (Fig. 1). In the western basin, the strong Kuroshio (~3 km $\mathrm{h^{-1}}$) and Oyashio currents generate sharp physical and biochemical gradients. In the east, the NPC broadens and slows (~0.5 km $\mathrm{h^{-1}}$), bifurcating off the coast of British Columbia coast to form the Alaska and California Currents and contribute to the boundary circulation of the subarctic and subtropical gyres. The subarctic–subtropical transition zone from the Kuroshio extension into the eastern subarctic gyre is the largest sink region for atmospheric carbon dioxide in the North Pacific (Takahashi et al., 2009). Here, while biological uptake of dissolved inorganic carbon (DIC) tends to counteract the warming effect in the summer, the bulk of the $\mathrm{CO_2}$ drawdown coincides with winter cooling and the resultant increase in solubility of $\mathrm{CO_2}$ in seawater (Takahashi et al., 2002).

Superimposed on the physical boundaries described above, seasonal and latitudinal changes in surface temperature (SST) and photosynthetically active radiation (PAR) contribute to defining the seascapes in which ecological assemblages develop and persist. In this study, we have selected to restrict the domain to 120–240°W, 15–65°N in order to highlight open ocean variability by minimizing the influence of extreme values associated with ice-edge responses in the northern latitudes and tropical instability waves that pulse along the equator in the southern portion of the North Pacific subtropical gyre (Evans et al., 2009).

2.2. Satellite data and processing

As a first step, we classified seascapes using remote sensing data that was related to phytoplankton dynamics, namely chl-a, PAR and SST. We used archived monthly averages and 8-day composites of the latest processing of satellite data provided by the Ocean Productivity Group (www.science.oregonstate.edu/ocean.productivity), as used in their primary productivity algorithms. These data have been cloud-filled which results in reduced variability at seascape boundaries that would otherwise have been associated with patchy cloud cover (Kavanaugh unpubl. data). We downloaded Level 3, 18 km binned, 8-day composites and monthly averages of SeaWiFS (R2010) chl-a, PAR, and Advanced Very High

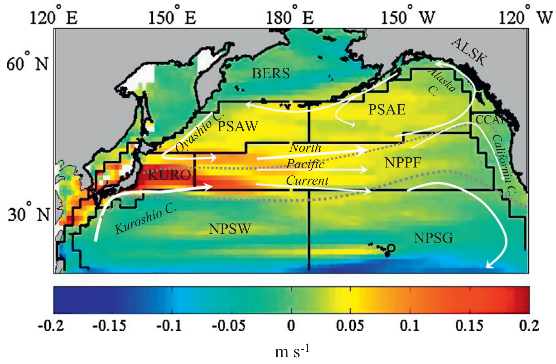

Fig. 1. Mean annual meridional surface velocities of the North Pacific (1998–2010). Current velocities are modeled from satellite altimetry (Ocean Surface Current model, OSCAR; Bonjean F. and G.S.E. Lagerloef, 2002). Overlain are general locations of major currents (white lines, italics), classic static province divisions (black lines; Longhurst, 1997, 2008) and seasonal range of the transition zone chlorophyll front, TZCF (grey dashed, Polovina and others, 2001). See text for further description of natural features (Introduction 2.2) and comparisons between Longhurst provinces (Methods 3.6) and dynamic seascapes (this study).