Contents lists available at ScienceDirect

### Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

## Seasonal, interannual and event scale variation in North Pacific ecosystems

Sinjae Yoo<sup>a,\*</sup>, Harold P. Batchelder<sup>b</sup>, William T. Peterson<sup>c</sup>, William J. Sydeman<sup>d,1</sup>

<sup>a</sup> Korea Ocean Research and Development Institute, Sa-dong 1270, Ansan, 425-170, South Korea

<sup>b</sup> Oregon State University, 104 COAS Admin Building, Corvallis, OR 97331-5503, USA

<sup>c</sup> NOAA Fisheries, Northwest Fisheries Science Center, Newport, OR 97365, USA

<sup>d</sup> Marine Ecology Division, PRBO Conservation Science, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA

#### ARTICLE INFO

Available online 4 April 2008

Keywords: North Pacific Phytoplankton Zooplankton biomass Seasonal cycle Interannual variation Event scale impacts

#### ABSTRACT

We synthesize information on changes in ecosystems of the North Pacific at seasonal, interannual, and event time scales. Three approaches are used to cope with inadequate temporal, spatial and trophic resolution in generating this synthesis. First, we use highly spatially and temporally resolved data on physical forcing and chlorophyll (SeaWiFS data from 1998 to 2005) to describe basin-wide spatial patterns and seasonal to interannual time scales. The second approach is to compare time series of zooplankton at selected spatial sites at which sampling resolution is sufficient to describe seasonal biomass/abundance patterns, and where multiple years of data exist to examine interannual variability. The third approach is to infer trophic relationships, and broaden the first two approaches to higher trophic levels, by examining the impacts of several event scale phenomena on many trophic levels, but only over a rather limited geographic region.

The 8 years of satellite chlorophyll data clearly show that interannually persistent seasonal patterns exist in most regions in the North Pacific, even in the tropical waters. From frequency analysis (Lomb periodograms), the annual cycle was the strongest in most regions, but in the tropics and eastern boundary current regions, periods greater than 1 year were significant. In mid- to high-latitude regions, periods of less than 1 year were also significant in addition to the annual period indicating double peaks with varying intervals. Seasonal progression of the timing of annual peak chlorophyll concentration in the North Pacific showed a different pattern compared with the Atlantic or Indian Ocean, largely due to the presence of the subarctic high nutrient-low chlorophyll (HNLC) and equatorial upwelling regions, which had later phytoplankton blooms than would have been predicted based on a simple equatorial to pole progression of bloom timing. Seasonal cycles in zooplankton were more or less synchronized (concomitant with or slightly lagged) with those of phytoplankton with a few exceptions. Exceptions occur in the Eastern Subarctic Gyre where annual peaks of chlorophyll occur in autumn, after the peak in zooplankton biomass. Interannual variation of annually averaged chlorophyll in 30 regions show three patterns, one positively related to El Niño, one negatively related to El Niño, and one with longer-scale variation, possibly related to climate regimes. Nine regions did not match any of the three patterns. Interannual variation in zooplankton abundance/biomass from selected regions indicates that El Niño may be the major source of interannual variability with its effects modulated by longer-scale variation, such as by the Pacific Decadal Oscillation. Two well-documented environmental events in the Northern California Current, in 2002 and 2005, exemplify how short-term disruption in atmospheric forcing causes changes in ocean hydrography and circulation that has significant impacts on primary production and ripple effects throughout multiple trophic levels of the ecosystem. We conclude that a closer look at the data often yields interesting results that might not necessarily be gained by considering the broad generalizations. Specifically, we observe that short-term disruptions of the ecosystem at the primary producer level may impact higher trophic levels in nonlinear ways that lead to unpredictable impacts when one considers the entire food chain. © 2008 Elsevier Ltd. All rights reserved.

#### 1. Introduction

As the sun moves seasonally across the equator, solstice to solstice, the upper mixed layer in the ocean shoals and deepens. The phytoplankton in the water experiences diverse conditions of light





<sup>\*</sup> Corresponding author.

E-mail address: sjyoo@kordi.re.kr (S. Yoo).

<sup>&</sup>lt;sup>1</sup> Present address: Farallon Institute for Advanced Ecosystem Research, P.O. Box 750756, Petaluma, CA 94975, USA.

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and nutrient accordingly and abundance of phytoplankton changes seasonally. Thus, seasonality in the abundance of phytoplankton cells in the sea is a prominent feature observed in mid- and high latitudes. Most of the subtropical and tropical regions show less seasonality. Of course, seasonality is not confined to producers; higher trophic components of food webs also show seasonality driven by bottom-up physical forcing and food resources influencing trophodynamics. Superimposed on the seasonal changes are both smaller-scale atmospheric conditions (e.g., position of jet stream; storm systems) and larger-scale atmospheric conditions and climate changes (like El Niño-Southern Oscillations; ENSOs) that impact ecosystem productivity and structure at correspondingly shorter and longer time scales, respectively. How the changes in physical forcing on various time scales are transferred from producers to higher trophic levels is fundamentally still not well understood. Substantial theories have been developed on this topic, including trophic cascades (Carpenter et al., 1985), bottomup and top-down forcing, wasp-waist impacts (Bakun, 2006), and the match-mismatch hypothesis (Cushing, 1990). Most marine food webs are comprised of populations that have ontogenetically complex life histories (a single species may be prey of another species at one life stage and predator upon that same other species at a later life stage), and which feed on multiple trophic levels, thereby introducing a complexity that inhibits simple modeling and understanding.

In the North Pacific, there are different types of oceanic environments such as the equatorial zone, subtropical gyres, high-latitude and coastal regions, where different seasonality in forcing is present. Due to its immense expanse, longitudinal and latitudinal differences are much greater across the Pacific Ocean and adjustment to wind stress takes longer than other oceans (Longhurst, 1998). It is logical to assume that different seasonal forcing in different domains of the Pacific would in turn produce differences in seasonality in biological structure and productivity. Our goal is to provide a synthesis of ecosystem productivity and structural responses to physical forcing at several different time scales: seasonal, interannual, and event scale; three spatial scales: basinwide, regional and local; and several trophic scales: producers, primary grazers, and secondary consumers.

To achieve these objectives would require data sets covering all space and time scales for multiple trophic levels. Needed data to accomplish this are not yet available with existing observational technologies. Our knowledge of structure and behavior of marine ecosystems is severely limited by lack of observations. Therefore our synthesis will take a piecemeal approach as illustrated in the conceptual diagram of Fig. 1. Where spatially and temporally comprehensive data exist, we will use them. An example is satellite based measures of chlorophyll-a (a measure of phytoplankton biomass; Type A study of Fig. 1). This type of approach on the seasonality in phytoplankton in global oceans can be found in Yoder et al. (1993), Banse and English (1994), Longhurst (1995, 1998) and Obata et al. (1996) using CZCS (Coastal Zone Color Scanner) data and more recently in McClain et al. (2004), Dandonneau et al. (2004), and Wilson and Coles (2005) using SeaWiFS (Sea-viewing Wide Field-of-view Sensor) data. Satellite data, however, have their own limitations and are available for only a few variables (mostly surface physical measurements such as SST, and surface chlorophyll). Data for upper trophic levels like zooplankton, fish and marine birds cannot be collected with current remote sensing technologies. For these variables, we use a different approach, wherein we identify a few long-term time series of observations of zooplankton, for example, at a single or few stations, and use those data sets to examine temporal variability (Type B study of Fig. 1). Examples of such time series can be found in Rebstock and Kang (2003) and McKinnell and Mackas (2003). For the highest trophic levels, the best long-term data are time series of fish catch.



**Fig. 1.** Conceptual view of multidimensional ocean ecosystem. In this view, there are three dimensions: Time, Space and Trophic Level. The subregional polygons correspond to the types of data examined: Green (A) polygon shows multiple space and time, but single trophic level data set (e.g., SeaWiFS chlorophyll). Blue (B) polygon shows multiple time, but limited spatial information for a single trophic level (e.g., Station P zooplankton biomass). Red (C) polygon shows multiple trophic level information at a single time and single location (e.g., the 2002 event scale response in the Northern California Current).

These data are most commonly reported on an annual basis, thus are of no value for evaluating seasonal variability. Several recent papers provide analysis of patterns of covariability of fish populations and ocean variability (Ebbesmeyer et al., 1991; Hare and Mantua, 2000; Hollowed et al., 2001) in the eastern North Pacific. Spatial scales of covariability for marine and anadromous fish are documented in several publications (Myers et al., 1997; Peterman et al., 1998; Mueter et al., 2002; Pyper et al., 2005). The effects of one "interannual forcing", e.g., that of El Niño on fish stocks is well documented (see for example, Lehodey et al., 2006). Downton and Miller (1998) found significant interannual covariability between Alaska salmon catch and sea surface temperatures. There is no need to repeat those analyses here; instead, for the higher trophic levels (esp. fish and seabirds), we examine trophic and ecosystem responses to several specific events at a local or regional scale for which observations at multiple trophic levels are available (Type C study of Fig. 1). Our ultimate goal is to synthesize knowledge obtained from all three study types to develop ideas about general responses of ecosystem productivity and structure to interannual and higher frequency variation in physical forcing.

In this paper, we will analyze seasonal patterns of phytoplankton biomass (chlorophyll as a proxy) for the period 1998–2005. By this, we will limit our analysis to shorter-than-interdecadal variability. First, we will focus on timing and periodicity in seasonal cycles. Seasonality in phytoplankton is compared with that in zooplankton. The period from 1998 to 2005 includes one major El Niño, one moderate El Niño and one moderate La Niña, and provides an opportunity to study the responses in the primary producers to year-to-year variation in addition to ENSO-related variability. Then we will discuss interannual variation in zooplankton in the North Pacific ecosystems. In typical situations, how the change in the primary producer level is translated into upper trophic levels may not be clear. Sometimes, episodic events with dramatic consequences could reveal the linkages from physical forcing through higher trophic levels. We will discuss two examples that illustrate this.

#### 2. Data and methods

SeaWiFS chlorophyll-*a* data were obtained from the NASA Goddard Space Flight Center Distributed Active Archive Center

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