AN ABSTRACT OF THE DISSERTATION OF

Julie Eileen Keister for the degree of Doctor of Philosophy in Oceanography presented on February 21, 2008.

Title: Variability in Mesoscale Circulation and its Effects on Zooplankton Distribution in the Northern California Current.

Abstract approved:

Timothy J. Cowles, William T. Peterson

In eastern boundary current upwelling ecosystems, mesoscale circulation features such as eddies and upwelling filaments play a prominent role in the transfer of water and the associated plankton from the productive nearshore to the oligotrophic deep sea. The relationship between mesoscale circulation, zooplankton distributions, and the across-shelf transport of coastal taxa and biomass in the California Current System was studied using data collected as part of the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) Northeast Pacific Program. Sea surface height from >13 years of satellite altimeter data was used to characterize the spatial and temporal variability in mesoscale circulation in the northern California Current (35°N-49°N) and explore mechanisms of variability. High spatial and temporal variation in mesoscale energy occurred. Energy was not strongly linked to upwelling winds, but did correspond to climate indices, indicating that basin-scale processes play a role in controlling the circulation. CTD casts, zooplankton net tows, and Acoustic Doppler Current Profiler (ADCP) velocities collected during a research cruise conducted in summer 2000 off Oregon and northern California were used to describe the effects of mesoscale circulation on distributions of zooplankton. During the cruise, a filament of the coastal upwelling jet extended seaward of Cape Blanco (42.8°N) resulting in the displacement of coastal zooplankton to >100 km off the continental shelf. Velocities and standing stocks of zooplankton were used to estimate seaward transport of 0.5 Sv in the upper 100 m of the filament, in which zooplankton biomass averaged ~ 20 mg carbon/m³. That offshore transport equated to >900 metric tons of carbon each day, and $4-5 \times 10^4$

tons over the 6-8 week lifetime of the circulation feature. Although the flux represented a small portion (<2%) of the shelf zooplankton biomass, the transport resulted in an offshore "hot-spot" in which biomass was 3-4X higher than in the surrounding ocean. Distributions of early life history stages of euphausiids indicated that retention of coastal populations may be strongly affected by the offshore advection. Finally, satellite sea surface temperature (SST) and sampling conducted during five summers were used to explore variability in the relationship between mesoscale circulation features and distributions of zooplankton. Circulation patterns differed among cruises and were reflected in zooplankton distributions. Circulation features resulted in the occurrence of cold surface water and coastal taxa offshore, but species abundances and presence/absence of taxa at specific locations were not predictable from satellite SSTs. These results are relevant to studies of ecosystem dynamics and the global carbon cycle because mesoscale circulation plays an important role in the seaward transport of carbon, retention and loss of taxa from the continental shelf, and creation of offshore structure which may be exploited by upper trophic level organisms.

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Variability in Mesoscale Circulation and its Effects on Zooplankton Distribution in the Northern California Current

by Julie Eileen Keister

A DISSERTATION

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Doctor of Philosophy

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Variability in Mesoscale Circulation and its Effects on Zooplankton Distribution in the Northern California Current

Chapter 1. Introduction

The California Current System (CCS) is one of the most productive coastal boundary currents in the world in terms of primary production and fisheries yield (Barber and Smith, 1981). The system is characterized by temporally and spatially variable physical forcings, seasonal wind-driven upwelling in the northern CCS (NCC), and yearround upwelling in the southern CCS. The phytoplankton and zooplankton response to upwelling productivity supports high production of upper trophic level organisms. Mesoscale circulation features (features with scales of ~20-200 km) are an important component of the circulation in eastern boundary upwelling regions (Barton and Aristegui, 2004, Escribano and Hidalgo, 2000, Lutjeharms et al., 1991, Marchesiello et al., 2003, Strub and James, 2000, Waite et al., 2007). The energetic eddies, filaments, and meanders of the alongshore upwelling jet can persist for several days to months and are an important source of offshore transport (Huyer et al., 1998, Mackas et al., 1991).

Mesoscale-resolving surveys have been conducted to study the physical dynamics of mesoscale features in the CCS as part of the Coastal Ocean Dynamics Experiment (CODE, 1981-1982), Coastal Transition Zone program (CTZ, 1987-1988), Eastern Boundary Currents project (EBC, 1993), and U.S. Global Ocean Ecosystems Dynamics Northeast Pacific program (GLOBEC NEP, 2000 and 2002). From these research programs, numerous individual studies, and modeling efforts, it is thought that mesoscale circulation primarily derives its energy from baroclinic instabilities in the alongshoreflowing, coastal upwelling jet (Batteen, 1997, Haidvogel et al., 1991, Marchesiello et al., 2003, Narimousa and Maxworthy, 1989), that the energy propagates westward (seaward) on seasonal cycles (Marchesiello et al., 2003, Strub and James, 2000), plays an important role in ocean mixing and heat balance (Marchesiello *et al.*, 2003), and that features can transport coastal water to sea in volumes equal to, or exceeding that from, Ekman transport alone (Kosro and Huyer, 1986). The role of mesoscale circulation in zooplankton dynamics is less well understood. Several studies of individual mesoscale features demonstrated their potential for controlling species distributions by transporting coastal taxa offshore (e.g. Barth et al., 2002, Haury, 1984, Mackas et al., 1991). Eddies and upwelling filaments can be locations of elevated zooplankton biomass (Huntley et al., 1995, Mackas and Yelland, 1999) and secondary production (Smith and Lane, 1991) in otherwise oligotrophic open ocean habitats. Thus, though not as well studied as the physical dynamics, evidence of the importance of mesoscale circulation in biological dynamics in the CCS was accumulating, and was recognized by the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) Northeast Pacific (NEP) program as program goals were developed.

The overall goal of the GLOBEC NEP program was to understand the effects of climate variability and climate change on the distribution, abundance and production of marine animals in the eastern North Pacific (Strub et al., 2002). Two of the specific goals were 1) to examine the role of mesoscale variability in controlling zooplankton distribution, biomass, production, retention and loss from coastal areas, and 2) to determine how inter- and intra-annual variability in physical forcing affects ecosystem dynamics in the CCS. Because climate variability is associated with large-scale changes in winds and temperatures (*Bakun*, 1990; *Miller and Schneider*, 2000; *Schwing et al.*, 2002*a*; *Snyder et al.*, 2003), temporal variability in mesoscale circulation in the CCS is likely to vary with climate as well. Changes in circulation patterns and mesoscale activity are likely to be influenced by climate variability and change, and ultimately result in changes in zooplankton distributions and the transport of biomass seaward.

This dissertation examines variability in mesoscale circulation and the relationships between mesoscale features, zooplankton distributions, and cross-shelf transport of carbon as part of the U.S. GLOBEC NEP program. Understanding the links between mesoscale circulation and biological patterns requires quantitative measures of the variability of both the physics and the biology. Prior to this research, we lacked a quantitative evaluation of the inter-annual variability in mesoscale activity in the NEP, although many publications have described aspects of mesoscale circulation during specific cruises or years (e.g. Barth et al., 2005b, Chereskin et al., 2000, Kosro et al., 1991, Stegmann and Schwing, 2007, Strub and James, 2000, Strub et al., 1991). The first part of my research, described in Chapter 2, "Spatial and interannual variability in mesoscale circulation in the northern California Current System," expands upon those studies by explicitly examining interannual variability in circulation over >13 years (1992-2006). The strong 1997/1998 El Niño, and multi-year periods of 'warm' versus 'cold' ocean conditions occurred during the study, allowing me to examine the effects of climate on mesoscale circulation.

Significant spatial and interannual variation in mesoscale energy occurred over the region and years studied. The advective eddies and upwelling filaments associated with the coastal upwelling jet caused mesoscale energy to peak in summer and propagate offshore through fall. Energy was generally very low in winter and early spring. Energy was highest at ~38°N, decreasing to the north and south. North of Cape Blanco (41.9°N) energy was low except over the shelf. Zonally, mesoscale energy was highest between ~125°W and 129°W; very little energy occurred in the deep ocean west of 130°W. The primary climate signals were suppressed energy during La Niña and cold years and increased energy during El Niño events.

The cold upwelling filaments that are common in the NCC in summer caused large gradients in sea surface height that were reflected in the altimeter analysis as high mesoscale energy. In the 3rd chapter of this dissertation, "Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California Current," the effect of an upwelling filament on zooplankton distributions was studied during a cruise conducted in August 2000. Concurrent sampling of velocities, the hydrography, and zooplankton allowed a direct description of the effects of circulation on distributions and cross-shelf advection of zooplankton biomass. Offshore transport in the upper 100 m of the filament measured 0.5 Sv (1 Sv = 10^6 m³ s⁻¹) and resulted in displacement of >900 metric tons of carbon in the form of zooplankton biomass each day. More than 100 km offshore, the biomass within the filament was 3-4X higher than in surrounding ocean water and was comprised primarily of coastal taxa.

In the final chapter, "Variability in the relationship between mesoscale physical and biological patterns in the northern California Current," variability in the effects of mesoscale circulation features on zooplankton distributions was examined using satellite sea surface temperature (SST) and *in situ* data collected in six years of field sampling. This analysis extended previous investigations of the effects of strong circulation features on zooplankton distributions to include circulation features with weaker sea surface temperature expressions. As part of this study, the question of whether the physical variables that indicate advective mesoscale circulation (e.g. SST) can be used to infer biological distributions was investigated. The study revealed that zooplankton species which are characteristic of upwelling regions off Oregon, specifically the copepods *Calanus marshallae, Pseudocalanus mimus*, and *Acartia longiremis* (Keister and Peterson, 2003, Morgan et al., 2003, Peterson and Miller, 1977), were consistently found in elevated abundances in offshore expressions of cold mesoscale features compared to the surrounding oceanic water. In contrast, coastal species were not found offshore where mesoscale circulation features did not occur. However, the relative abundance of coastal versus oceanic taxa at any particular location was not predictable from sea surface temperatures, nor was the biomass or species abundance predictable at any location.

The dynamic nature of mesoscale circulation features makes them difficult to sample, but their importance in offshore transport of coastal water and the associated biomass is demonstrated by the results of this dissertation and previous studies (e.g. Kosro and Huyer, 1986, Mackas et al., 1991, Ramp et al., 1991). Future sampling effort should give careful thought to designing sampling strategies to capture the variability due to these features, which may otherwise be missed. Towards this goal, in Chapter 4, the complexities associated with sampling mesoscale features are described and the use of adaptive sampling strategies, in which the conditions present during sampling guides the selection of sampling locations, is argued for.

Finally, in Chapter 5, the main results and ecological implications of this dissertation research are summarized, some remaining research questions are posed, and ideas for future studies are given.

Chapter 2. Spatial and interannual variability in mesoscale circulation in the northern California Current System

Julie E. Keister and P. Ted Strub

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<u>Abstract</u>

We used wavelet analyses of sea surface height (SSH) from >13 years of satellite altimeter data to characterize the variability in mesoscale circulation in the northern California Current (35°N-49°N) and explore the mechanisms of variability. We defined 'mesoscale' circulation as features, such as eddies and filaments, which have 50-300 km length scales and 4-18 week temporal scales. Fluctuations in SSH caused by such features were reflected in wavelet analyses as power (energy). Spatial and inter-annual variation in mesoscale energy was high. Energy was highest at ~38°N, decreasing to the north and south. Between ~43-48°N, energy was low. Zonally, mesoscale energy was highest between ~125°W and 129°W at latitudes south of 44°N; very little power occurred in the deep ocean west of 130°W. Energy peaked during summer/fall in most years. The primary climate signals were suppressed energy during La Niña and cold years and increased energy during El Niño events. Energy was not strongly linked to upwelling winds, but did correspond to climate indices, indicating that basin-scale processes play a role in controlling mesoscale circulation. We hypothesize that climate affects mesoscale energy through changes in both potential and kinetic energy in the form of density gradients and coastal upwelling winds. The relationship between mesoscale circulation and climate was complex – no single climate, transport, or upwelling index explained the variability. These results are relevant to ecosystem dynamics and the global carbon cycle because mesoscale circulation features deliver nutrient-rich water and coastal organisms from productive upwelling areas to the deep sea.

Introduction

In coastal upwelling ecosystems, offshore advection is an important factor controlling populations of coastal organisms. Typically, wind-driven Ekman transport has been considered the dominant mechanism of cross-shelf flow during upwelling, but more recently circulation features such as 'squirts,' filaments, and eddies are recognized as being important contributors to such transport. One such feature may transport as much mass offshore as all of the Ekman transport forced by 10 m s⁻¹ (20 kt) winds along ~1000 km of coastline (Kosro and Huyer, 1986). Such features, particularly cold-core filaments, are common in some areas of the California Current System (CCS) and may persist several months, potentially delivering huge amounts of coastal water and the associated biology to the deep ocean (Brink et al., 2000, Huyer et al., 1998, Mackas et al., 1991).

In terms of primary production and fisheries yield, the California Current (CC) is one of the highly productive global Eastern Boundary Current (EBC) upwelling ecosystems (Barber and Smith, 1981). The system is characterized by temporally and spatially variable physical forcings, seasonal wind-driven upwelling in the northern CCS, and year-round upwelling in the southern CCS. The phytoplankton and zooplankton response to upwelling supports high production of upper trophic levels. The general circulation in the CCS includes energetic eddies, filaments, and meanders of the alongshore upwelling jet.

Many publications have described mesoscale circulation off the U.S. Pacific coast during specific cruises or over a few years. Eddy kinetic energy and individual circulation features in the CCS have been studied from shipboard observations (Barth et al., 2005b, Kosro et al., 1991, Kosro and Huyer, 1986), using satellite altimetry (Kelly et al., 1998, Strub and James, 2000, Strub and James, 2002a), moorings (Chereskin et al., 2000), satellite radiometers (Castelao et al., 2006, Legaard and Thomas, 2006), surface drifters (Brink et al., 2000), and subsurface floats (Collins et al., 2004). From the above studies we know that mesoscale variability peaks seasonally in late summer/fall, increases in areas of complex bottom topography (particularly in the vicinity of Cape Blanco, Cape Mendocino, and Pt. Arena) and that mesoscale features can carry energy and water mass from nearshore to offshore.

As part of the U.S. Global Ocean Ecosystems Dynamics Northeast Pacific program (GLOBEC NEP) we are studying how changing climate, through its impacts on local forcings (e.g. upwelling), affects variability in mesoscale circulation in the northern California Current System and how that variability cascades through the ecosystem. One of the goals of the GLOBEC NEP program is to examine the role of mesoscale variability in controlling zooplankton distribution and retention/loss from coastal areas. Mesoscale circulation in the northern CCS is believed to primarily derive its energy from baroclinic instabilities in the alongshore-flowing, surface-intensified, coastal upwelling jet (Batteen, 1997, Haidvogel et al., 1991, Marchesiello et al., 2003, Narimousa and Maxworthy, 1989). The upwelling jet draws its energy from alongshore, upwelling-favorable (equatorward) winds (Batteen, 1997) which are driven by basin-scale sea level pressure and temperature gradients (Batteen, 1997, Schwing et al., 2002a). Thus, because climate variability is associated with large-scale changes in winds and temperatures (Bakun, 1990, Miller and Schneider, 2000, Schwing et al., 2002a, Snyder et al., 2003), temporal variability in mesoscale circulation in the CCS is likely to be affected by climate. We hypothesize that interannual variability in the timing and intensity of mesoscale circulation is related to the timing of the transition to northerly, upwelling-favorable winds in spring, the cumulative intensity of northerly winds through the upwelling season, the southward transport into the CCS, and cross-shelf density gradients.

Changes in circulation patterns may impact the abundance and availability of prey to ecologically and commercially important fish populations and affect cross-shelf delivery of production to the deep sea. Understanding the links between climate, mesoscale circulation, and biological patterns will require quantitative measures of the variability of the physics and the biology. Several indices of climate relevant to the northeast Pacific have been developed—e.g. the Pacific Decadal Oscillation (PDO), the Multivariate ENSO Index (MEI), the Northern Oscillation Index (NOI), etc.—and have been shown to correlate with biological variability (Hooff and Peterson, 2006, Mantua et al., 1997, Schwing et al., 2002b). Changes in mesoscale circulation likely influence variability in primary production (Henson and Thomas, 2007b) and higher trophic levels. However, at present we lack a quantitative evaluation of the interannual variability in mesoscale activity in the NEP and its role in ecosystem dynamics.

We use satellite altimetry to study the spatial and temporal variability in mesoscale activity in the northern CCS as a step towards understanding how such variability may impact the productivity of the system on intra- and interannual timescales. This study expands upon previous studies of mesoscale activity in the CCS (Chereskin et al., 2000, Kelly et al., 1998, Strub and James, 2000) by explicitly examining interannual variability over >13 years (1992-2006). During this period, substantial variability in forcing, including a strong El Niño and La Niña occurred, which allows us to examine climate effects on mesoscale circulation.

Following a description of our study area (Section 2) and data (Section 3), we give a brief overview of our statistical method, wavelet transforms, in Section 4. We provide an overview of the spatial and temporal variability in the northern CCS using sea level observations and wavelet transforms of the data in Section 5, focusing on variability in mesoscale circulation. Therein, we include a detailed comparison of wavelet spectra from two locations as an introduction to the interpretation of wavelet results. In Section 6, we use observations of current transport, upwelling indices, and hydrographic data to address the question of how mesoscale activity responds to local forcings. Noting that interannual patterns of mesoscale energy do not closely match patterns of local forcings, we then investigate mechanisms through which basin-scale forcings may control mesoscale activity.

Study Area

Our study area is the northern California Current from 35°-49°N, 120°-132°W (Figure 2.1). The region encompasses an area in which the seasonal coastal upwelling jet closely follows the alongshore topography and mesoscale activity is low (north of ~43.5°N) and an area where the topography is complex and mesoscale activity is high (south of ~43.5°N) (Strub and James, 2000). The highest mesoscale activity in the California Current is reported to occur within our study area offshore and to the south of Cape Mendocino (Strub and James, 2000). The study area also includes the GLOBEC

NEP field-study region (42°-45°N) which surrounds Cape Blanco. We confine most of our analyses to within 3° offshore of the coast and focus on spring through fall, as that is the area and time most relevant to variability in primary and secondary production in the California Current System.

Data

We analyze the delayed time, 'updated,' v1rev4, gridded sea surface height (SSH) anomaly fields produced by Ssalto/Duacs and distributed by AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic,

http://www.aviso.oceanobs.com/). Tides have been removed and standard environmental corrections (e.g. inverted barometer, troposphere, ionosphere and electromagnetic bias) applied. The geoid was removed by removing a long-term temporal mean from each grid point. We use the weekly SSH anomaly fields that are gridded to a 0.25° x 0.25° Mercator grid. The interpolation technique is described in *Le Traon et al.*(2003). Each time-point incorporates six weeks of observations weighted to the central date and merged over multiple satellites to reduce spatial error. In the 'updated' version, the gridded products incorporate altimeter data from TOPEX/Poseidon (T/P), ERS-1, ERS-2, ENVISAT, Geosat Follow-On (GFO), and Jason-1 altimeters, as available, to improve mesoscale mapping resolution (Pascual et al., 2006). Seasonal cycles are not removed by AVISO. We calculate them by fitting the time series to annual and semi-annual harmonics and remove them only when presenting SSH Hovmöller (time-space) diagrams.

Methods

We examined the spatial and temporal variability in mesoscale activity from October 1992 - May 2006 using wavelet analyses of the SSH anomaly fields described above. Satellite-altimetry data has been used extensively to study mesoscale circulation in a variety of studies (Crawford et al., 2000, Holland and Mitchum, 2001, Strub and James, 2000, Wilkin et al., 2002). Wavelet analyses provide a method of statistically evaluating temporal changes in energy within specific scales of variability in a time series. The timeaveraged wavelet power spectrum is equivalent to the Fourier spectrum, but for analyzing non-stationary signals such as eddies, wavelet analyses have substantial advantages over Fourier analyses in that wavelets retain localized temporal information. This is particularly advantageous for geophysical time series, such as the sea level anomalies analyzed here, that have time-varying frequencies and amplitudes such as those due to local and distant winds, SST, and long-period climate forcings. When the wavelet power is calculated and averaged over a particular band of periods (as in "scale-averaging," discussed below), results are similar to an amplified (e.g. squared) band-pass filter.

The wavelet transform (*W*) is constructed by convolving a time series (x_n) with a scaled (i.e. stretched or compressed) and translated (i.e. moved along the time axis) wavelet (ψ), to produce a 2-D matrix of N data points by *s* scale factors:

$$W_{j,k} = \frac{1}{\sqrt{s_j}} \sum_{n=0}^{N-1} x_{(n\Delta t)} \psi * (\frac{n\Delta t - b_k}{s_j}) \Delta t$$

where N is the number of observations in the original time series and Δt is the sampling interval. The scales:

$$s_j = j \Delta t, j = 2, \ldots, J_{\max}$$

may run from the Nyquist $(2\Delta t)$ to $J_{\text{max}} \Delta t$, the largest scale of interest which must be $\langle N/2$. The translations (time-shifts) are:

$$b_k = k \Delta t, \ k = 0, \ldots, N-1$$

such that the transform is calculated with its center at each time location in the data series. The factor $1/\sqrt{s_j}$ normalizes the wavelet such that it has constant energy over all scales. The wavelet power is defined as the square of the absolute value of the amplitude of the convolution:

$$\left|W_{j,k}\right|^2.$$

The wavelet transform acts as a band-pass filter (Percival and Walden, 2000) with a width proportional to the scale (s_j) — the power spectrum can be thought of as a depiction of how the amplitude of features with a particular periodicity changes with time. The greater the similarity between the signal $(x_{j,k})$ and the wavelet function $(\Psi_{j,k})$, the greater the amplitude of the transform. It is important to note that the wavelet power does not

measure the absolute amplitude of signals, only the variance within the time window of the scaled wavelet. We give more description of the interpretation of wavelet analyses when discussing the results. We refer the reader to *Meyers et al.* (1993) for wavelet methods comparisons, to *Torrence and Compo* (1998) for the methods used here, and to *Percival and Walden* (2000) for a comprehensive review and mathematical derivation of wavelet analyses for time series applications.

The choice of a wavelet should largely be driven by the shape of the features of interest - preferably, the chosen wavelet is similar in shape to the phenomenon being analyzed. There are many wavelet functions to choose from in the literature, or wavelets can be designed for individual applications. Some wavelets (such as the simple Haar wavelet) are good for identifying sharp edges in a time series. Others, such as the "Mexican Hat" wavelet, are useful for finding individual dips or peaks. *Farge* (1992) describes several of the most common wavelets used in time series analyses. We chose the Morlet wavelet (with frequency parameter = 6) because its shape (a sine wave modified by a Gaussian, dampened to zero on either side of the central time) amplifies smoothly oscillating signals such as the sea level anomalies caused by circulation features. The multiple oscillations in the wavelet's shape integrate over many details of sea level variability that would otherwise complicate interpretation of our results. The Morlet wavelet has additional desirable properties in that it provides a balance between resolution in time and frequency and it's one of the most widely used wavelets in geophysical data analyses.

To evaluate the influence of choosing a particular wavelet function, we also evaluated two other common wavelets: the "Mexican Hat" and "Paul" wavelets (Farge, 1992, Torrence and Compo, 1998). All three are non-orthogonal; the Morlet and Paul wavelets are also complex whereas the Mexican Hat wavelet is real-valued, and hence does not preserve phase information. Analyses with the different wavelets all gave similar results though with different temporal and frequency resolution of signals. Due to its shape, the Mexican Hat wavelet returns sharp peaks in power from individual deviations in sea level, such as those produced by a propagating eddy. Hence, we used the Mexican Hat wavelet to locate the timing of significant peaks in energy more precisely than the Morlet wavelet allows. We also used the Mexican Hat wavelet to determine whether peaks in variance are due to high or low sea level features, which we determined from the sign of the wavelet amplitude before squaring. We used those results in combination with an examination of SSH maps and sea surface temperature (SST) images from the Advanced Very High Resolution Radiometer (AVHRR) or Geostationary (GOES) satellites to identify specific circulation features that resulted in high wavelet power. We describe a few of those features herein, but do not show the individual SSH and SST fields.

For each location A-H shown in Figure 2.1, we present full wavelet power spectra that are normalized by the variance of each time series. Such spectra provide a measure of the power in each time series with respect to white noise. However, because the variances among time series are not identical (ranging from 13 to 74 cm²) normalized power in one spectrum is not directly comparable to the normalized power from another time series. Since time series of sea level typically have red spectra (decreasing power over increasing frequency), we calculate 95% significance levels by comparing each wavelet power spectrum to a red noise background spectrum, modeled as univariate lag-1 autoregressive (AR-1) processes generated with variance equal to that of each time series (Torrence and Compo, 1998). Hence, significant power in one spectrum may be lower than non-significant power in another. The seasonal cycle is not removed from time series prior to wavelet analyses.

We refer to 'mesoscale energy' as the power in mesoscale periods, which we define as 4-18 weeks based on our observations of the development and propagation of features in our study area and previous study of dominant periodicities in the CCS (Kelly et al., 1998, Strub and James, 2000). To isolate variability in the mesoscale periods from the full wavelet power spectra, we calculate time series of the power averaged over only those periods. We use the methods of Torrence and Compo (1998) to calculate these "scaleaverages." Furthermore, we show results from both 4- to 12-week (hereafter "highfrequency mesoscale energy," or HFME) and 12- to 18-week (hereafter "low-frequency mesoscale energy," or LFME) period bands to distinguish relatively short from relatively longer duration signals. Unlike results showing the full power spectra, the power in these 'mesoscale energy' time series is not normalized by the variance, so the energy can be compared among times and locations. However, the 95% significance levels are derived as for the full spectra, so significant power in one time series may be lower than non-significant power in another.

Because we calculate wavelet energy at fixed point locations, the periodicity of a signal is determined by the local relationship between a feature's size and propagation velocity. Stationary features such as topographically-fixed upwelling filaments or eddies which persist for 4-18 weeks will be resolved in our mesoscale analyses. However, the smallest and largest propagating features may not exhibit energy in the mesoscale periods, depending on their velocities. For example, a small, 50 km diameter eddy must propagate between 0.4-1.75 km/d to be considered mesoscale, whereas a very large (300 km) eddy must propagate at >2.4 km/d. *Kelly et al.* (1998) found that the dominant eddies in the region 33° -40°N (the southern portion of our study area) had diameters of 100-200 km and westward velocities of ~2.5 cm/s, corresponding to periods of approximately 5-12 weeks.

To simplify discussion, we will refer to scale-averaged wavelet power as "low" if it is <3 standard deviations above the mean power in the full data set (where $\mu = 2.2 \text{ cm}^2$ and $1\sigma = 2.6 \text{ cm}^2$); "moderate" if the power is 3-5 σ above the mean; "moderately-high" if 5-7 σ above the mean; "high" if 7-8 σ above the mean; and "very high" if >8 σ above the mean. Those levels correspond to power of approximately 0-10, 10-15, 15-20, 20-25, and >25 cm², respectively.

With each weekly gridded sea level anomaly product, AVISO provides an assessment of the errors introduced into the estimates that result from interpolating the data to the full spatial and temporal domain. The error is expressed as the percent of the signal variance at each location. We used a temporal-average of these errors (Figure 2.2) to select specific locations for analyses, balancing low error with geographic spacing that permits regional comparisons. On average, lowest error occurs along groundtracks of the T/P and Jason altimeters because of their relatively short orbit periods (9.9 days). Highest errors occur between these tracks in regions with low signal variances. Temporally, mapping error was consistently lowest (<10% of total variance) along those groundtracks, was very high from January 1994 – March 1995 off those ground tracks (>50% error) when only the T/P altimeter was operational, and was low (<20% and mostly <10%)

throughout the study area from September 2002 – September 2005 when four altimeters were operational.

<u>Results</u>

Sea Surface Height Anomalies

We show Hovmöller (time-space) diagrams of SSH anomalies along several alongshore and zonal transects to illustrate patterns of variability in contrasting regions of our study area (Figures 2.3 and 2.4). Seasonal cycles are a dominant component of variability throughout the study area, although the amplitude and phase varies north to south and onshore to offshore. In the deep ocean (e.g. 2° and 3° offshore, Figure 2.3), seasonality is exhibited in the regular steric effects of seasonal heating and cooling, with warming leading to maxima in SSH anomalies in fall (~September-November) and cooling leading to minima in spring. Inshore, sea levels peak in December-February from coastal downwelling driven by poleward winds and flow of the Davidson Current. Upwelling causes negative anomalies nearshore in summer. North of latitude 44°N, the seasonal heating and cooling of the ocean is the primary sea level anomaly signal, exceeded only by El Niño/La Niña events (discussed below). Between ~38°-44°N, sea level is more temporally and spatially variable, with stronger gradients over shorter spatial scales, indicating higher mesoscale activity in that region. South of 38°N, SSH anomalies show less mesoscale variability inshore, but variability increases offshore.

Climate signals are apparent in the interannual variability in SSH. Most apparent are the extreme high anomalies inshore during the 1997/98 El Niño and the low sea level anomalies during the 1998-2000 La Niña and subsequent summers of 2001-2002. The 2002/2003 El Niño is manifested as weakly positive anomalies and possibly the positive anomalies evident west of 127°W at mid-latitudes (Figure 2.4). The influence of climate is more difficult to discern in areas of high mesoscale variability, such as along latitude 38.0°N (Figure 2.4), than in areas dominated by longer-period variability. Mesoscale features develop inshore and propagate westward, disrupting the annual cycle. In Figure

2.4, such features exhibit an upward inshore to offshore (right-to-left) slope over time as they propagate.

Wavelet Spectra

Wavelet analyses permit us to extract significant temporal components of SSH anomalies which are difficult to resolve from Figures 2.3 and 2.4 alone. We begin our analysis of the SSH variability by showing full wavelet transforms of time series extracted from eight locations (A-H in Figure 2.1), each location representing a 0.25° x 0.25° gridpoint of gridded data. We initially focus on two locations as examples of how to interpret the wavelet results. The eight locations were chosen for their low temporally-averaged mapping error and their geographic spacing, which facilitates inshore/offshore and north/south comparisons (Figure 2.2).

In Figures 2.5 and 2.6, we present the time series of SSH from each location above its wavelet power spectrum, calculated using the Morlet wavelet. In each spectrum, the yaxis is the Fourier period, running from the Nyquist (2 weeks) to $\langle N/2 \rangle$ (here, $\sim 5 \rangle$ years); the x-axis is time. The wavelet power is shown as multiples of the variance in each time series and as such, is a representation of the power with respect to white noise. The amplitude of the power is therefore not comparable among these spectra – a normalized spectrum provides an estimate of the magnitude of the variability relative to the variance at that location. Power above the 95% significance level is contoured in black. The "cone of influence" (Torrence and Compo, 1998) indicates areas beneath which edge effects may influence results.

To introduce the wavelet results, we compare the locations Figure 2.5A and 2.5D (48.5°N, 128.5°W and 44.8°N, 125.0°W). The time series of SSH at Location A shows a clear annual cycle overlaid with shorter-period variability. The resultant wavelet spectrum shows significant energy in the annual (52 week) period throughout the full time series and occasional significant shorter-period variability in periods ranging from ~2-30 weeks. In contrast, the SSH time series at Location D does not show a clear annual cycle – the variance appears to be contained primarily in short periods. Significant energy with mesoscale periods (4-18 weeks) occurs in most years, with a gap only in 1999-2000.

Positive SSH anomalies during the El Niño winters of 1997/1998 and 2002/2003 occur as significant energy with approximately semi-annual periods at both locations, especially D. Finally, note in Figure 2.5D that the El Niño/La Niña cycle caused SSH to slowly vary from anomalous highs to lows over 1997-2000. The wavelet transform captures this as significant power with periods of ~2-3 years, centered on winter 1997/1998. Thus, wavelet spectra extract and amplify the dominant periodic signals in our time series, only some of which are readily apparent to the eye.

With that brief introduction to the interpretation of wavelet spectra, we examine spectra from all eight locations (Figures 2.5 and 2.6) to explore general patterns of variability over the domain. There is significant power in a broad range of periods in our study area, with the mesoscale (4-18 week) and annual (52-week) period bands containing a large fraction of the significant power at most locations. Offshore, the annual period dominates the signal in the north where the seasonal steric effect is uninterrupted by mesoscale activity, but loses energy to the south where mesoscale activity is higher. In contrast, inshore, the annual period is not a significant component of the variability except at B, the shallowest and most northern location (Figure 2.1), where the seasonal summer upwelling/winter downwelling pattern (e.g. seasonal lows to seasonal highs) causes high energy in the annual band that is out-of-phase with that offshore. To the south, coastal winds are less seasonal and mesoscale features more frequently cause large deviations in SSH, both processes serving to diminish energy in the annual band.

Moving north to south, energy also shifts away from the very high-frequency variability seen in the north into longer-period mesoscale and intermediate-period variability, particularly offshore at Location G (Figure 2.6). Because the periodicity measured at fixed locations is an interaction between temporal and spatial scales, the shift to longer periods indicates that features have larger length scales and/or slower propagations speeds to the south and offshore. Globally, eddies tend to propagate with characteristic Rossby dynamics (Chelton et al., 2007), so a trend to slower propagation with decreasing latitude is unlikely. A tendency toward increasing spatial scales has been noted by *Ikeda and Emery* (1984) and *Marchesiello et al.* (2003) as filaments extend offshore and as eddies interact and merge as they move to the west. The change in

periodicity noted here may reflect those dynamics. Short-period variability at the northern inshore locations (Figures 2.5B and 2.5D) is likely due to coastal upwelling/downwelling dynamics and smaller-scale eddies that are generated over the shelf and slope.

Mesoscale Power Time Series

In time series of wavelet power that has been scale-averaged over 4-12 and 12-18 week periods at the eight locations (Figure 2.7), marked spatial and temporal variability in mesoscale energy emerges. The power in these time series is not normalized, so amplitudes may be compared among locations. Here, we note that the scale-averaged wavelet power is similar to results obtained using amplified (i.e. squared) and smoothed band-pass filtered data.

Offshore, the trend of increasing mesoscale energy with decreasing latitude is consistent with a progression from a more annually-dominated region north of Cape Blanco, to a more mesoscale-dominated region to the south. Interannual variability in mesoscale energy is high in the south, particularly at Location G, with energy episodically reaching $>7\sigma$ above average there. Circulation patterns are particularly complex offshore along this latitude. We found that strong signals from filaments and meanders of the upwelling jet, and strong cyclonic and anticyclonic eddies all contribute to significant mesoscale power there.

Inshore, patterns of variability are tightly related to the bathymetry and coastline topography. The northernmost location (B), lies at the mouth of the Strait of Juan de Fuca where mesoscale dynamics are driven by the topographically-fixed Juan de Fuca eddy (centered at ~48.4°N 125.4°W) (Hickey et al., 1991) which recurs in summer/fall, and by strongly positive winter anomalies in (typically) December/January that may be related to winter downwelling and freshwater outflow. Farther south, Location D is in the region of a nearly straight north-south coastline where SSH variability (Figure 2.3) and mesoscale energy is low, rarely exceeding 3σ above the mean. *Legaard and Thomas* (2007) found local minima in intra-seasonal variance of SST and chlorophyll in this same region. Moderately-high energy occurs in most summers SW of Cape Blanco (Location F), the hypothesized northernmost location at which the summer upwelling jet separates from the

coast and becomes an oceanic jet (Barth et al., 2000). In contrast, SE of Cape Blanco, Location H lies inshore of the meandering upwelling jet following its separation from the coast at Pt. Arena (Kosro and Huyer, 1986, Strub and James, 2000). There, energy is low, rarely exceeding 3σ above the mean.

Spatial and temporal variability

A map of temporally-averaged energy (Figure 2.8) gives the visual impression of energy spreading south and to sea, separating from the coastal zone south of Pt. Arena, and peaking almost 400 km offshore. The trend of increasing energy with decreasing latitude, noted at the individual locations above, does not extend to the far south of the domain (Figure 2.8). Energy in the deep ocean is highest, on average, in a broad area between 36°-43°N, 124°-130°W, in the vicinity and to the south of the coastal promontories. Overall, patterns of HFME and LFME are similar with a few notable exceptions. Within 1° of the coast, mesoscale energy is dominated by high-frequency variability whereas far offshore, longer-period energy dominates. (Note that the HFME at the mouth of the Strait of Juan de Fuca is anomalous, even compared to other coastal locations.)

In both frequency bands, energy is low along the coast south of Pt. Arena (~ 39° N). Using RAFOS float observations, *Collins et al.* (2004), also noted a relatively low-energy strip there where floats predominantly moved alongshore. The eastward curvature of the coastline and the separation and seaward movement of the upwelling jet may create this lee south of Cape Mendocino in which energy is low. On the other hand, modeling results predict highest eddy kinetic energy (EKE) nearshore (Marchesiello et al., 2003). The discrepancy may be due to shorter (< 4 week) period variability that is not resolved in this study.

The fan of energy that spreads southwest to sea has its northeast edge near Heceta Bank and Cape Blanco (Figure 2.8). The role that capes and promontories play in controlling spatial patterns of mesoscale energy in the northern CCS has been well-studied (Castelao and Barth, 2005, Haidvogel et al., 1991, Lagerloef, 1992, Marchesiello et al., 2003, Narimousa and Maxworthy, 1989, Strub and James, 2000). That variability has been shown to cascade into biological variability (Henson and Thomas, 2007a). North of
Heceta Bank (~44.2°N), there are no large promontories so the upwelling jet flows uninterrupted, tightly coupled to the regular alongshore bathymetry (Barth et al., 2005b, Narimousa and Maxworthy, 1989). There is some evidence from recent, unpublished studies of nearshore current structure using coastal high-frequency (HF) radar, that the upwelling jet may deviate from the coast around the Columbia River plume (M. Kosro, personal communication, 2007), but appears to turn back to the coast south of the plume without contributing to the generation of energetic offshore mesoscale circulation. We found higher energy in the area between Heceta Bank and Cape Blanco. Peak energy occurs just southwest of Cape Blanco and farther offshore downstream of Cape Mendocino.

LFME shows a strong preference for an offshore area (37-38°N, 127°-128°W) (Figure 2.8) that our study of SSH and SST images revealed as a location at which northwestward-turning, cold upwelling filaments generated between Pt. Arena and Pt. Reyes frequently interact with strong anticyclonic, SW propagating eddies. Historically, the cold filament had been noted in satellite SST images in many summers and was sampled during the Coastal Transition Zone (CTZ) Program in the 1980's (Strub et al., 1991). *Lagerloef* (1992) subsequently described the anticyclonic eddies as annuallyrecurring, topographically-controlled features that are dynamically coupled to the filaments. Thus, the time-averaged pattern of energy reflects the strong influence of topography on circulation, even hundreds of km to sea.

Extracting the temporally-integrated information along offshore transects (Figure 2.8) emphasizes the spatial patterns described above and, in combination with annual cycles of energy (Figure 2.9), indicates a seasonal SW progression of energy from nearshore generation in spring to peak levels offshore in summer/fall. Spatially-averaged, mesoscale energy peaks regularly in summer/fall (Figures 2.9 and 2.10) as has been previously reported (Collins et al., 2004, Strub and James, 2000). Energy tends to peak 1-1.5° farther south and 2-3 months later offshore compared to inshore. Energy at 1° offshore peaks in July, energy 2° offshore peaks in July/August, energy 3° offshore peaks in August, and 4° offshore, energy peaks in September/October. Both the SW propagation of many eddies and the separation and westward movement of the coastal upwelling jet

after separating from the coast at the capes are likely mechanisms for the apparent progression of energy. *Kelly et al* (1998) reported a westward movement of EKE between 125°W and 128°W that they ascribed to the seasonal offshore movement of the core of the CC south of 40°N.

Kelly et al. (1998), Strub and James (2000), Chereskin et al (2000), and Marchesiello et al. (2003) all reported an onshore to offshore decrease in EKE in the CCS. We find a general trend of lower energy at sea, particularly high-frequency energy (Figures 2.8 and 2.9), but between 2° and 4° offshore, the pattern is time-dependent (Figure 2.9). In spring and early summer, energy (particularly HFME) increases more quickly inshore than offshore. However, in fall and winter, as nearshore energy declines, energy is peaking offshore, causing higher levels of energy offshore at that time. Also note from Figure 2.10 that there is a great deal of interannual variability in both the relative timing of peak energy from nearshore to offshore, and the relative amplitude of peaks. That there is not a consistent pattern of lower amplitude peaks in energy occurring later in the year offshore indicates that there are important mechanisms of energy generation or intensification offshore. One such mechanism may be the interaction of oceanic expressions of features, as exemplified by the interaction between offshore expressions of eddies and upwelling filaments noted above. Others may be effects of submarine ridges (such as the Mendocino escarpment) (Narimousa and Maxworthy, 1989) or areas of intensified flow (Kelly et al., 1998).

We find significant wavelet power beyond 132°W at all latitudes (>800 km offshore of central California, not shown) although energy is strongly dampened that far to sea, and note that the signatures of upwelling filaments, cyclonic, and anticyclonic eddies are visible in sea level anomaly maps at least that far to sea. *Strub and James* (2000) also reported statistically-significant EKE calculated from sea surface height gradients as far as 130°W off central California (and as far as 135°W off Baja, California) and *Marchesiello et al.*(2003) modeled filaments and eddies that carried coastal water far to sea.

Discussion

Seasonal variability

Consistent with previous studies (Kelly et al., 1998, Marchesiello et al., 2003, Strub and James, 2000), we found that mesoscale circulation in the northern California Current typically peaks during summer and fall (Figure 2.9) when winds and alongshore transport are primarily equatorward. As the coastal upwelling jet migrates offshore through the summer (Strub and James, 2000), it pinches off eddies, both inshore in anticyclonic bends of meanders, and offshore at the tips of energetic, cyclonically and anticyclonically turning filaments. Those filaments and eddies that propagate westward to the deep ocean can transport large masses of water and coastal organisms to sea (Chereskin et al., 2000, Cornuelle et al., 2000, Mackas et al., 1991). Like others (Kelly et al., 1998, Marchesiello et al., 2003), we note a progressive movement of seasonal currents and energy offshore into the deep ocean on an annually-recurrent cycle. In winter, winds and currents in the northern CC are poleward and coastal downwelling dominates the inshore region. Consistent with model results which predict that poleward coastal jets generate less EKE than equatorward jets (Haidvogel et al., 1991) we found that mesoscale energy is at a minimum at this time, despite high coastal sea levels and strong winter winds.

Relationship to climate

Below, we explore the relationship between climate-variability and interannual variability in mesoscale circulation, and consider potential local and basin-scale forcing mechanisms. To examine temporal variability in mesoscale energy integrated over the northern California Current, we define an index of the total mesoscale variability in the region. The index consists of timeseries of wavelet power in the mesoscale period bands averaged between 1°-3° offshore, 36°-43°N (Figure 2.11, top panels). We refer to these spatially-averaged time series as the total mesoscale energy in the northern California Current. We restrict the index to within 3° of the coast because westward propagation of energy, which results in highest energy occurring offshore later in the year than inshore,

causes a smearing of the temporal signal if integrated far to sea. Because instabilities in the coastal upwelling jet and California Undercurrent are believed to be the primary sources of mesoscale circulation in the northern CCS (Chereskin et al., 2000, Marchesiello et al., 2003), restricting the index to within 3° of the coast, where the strongest alongshore currents reside, emphasizes temporal patterns in the generation of features and simplifies comparisons to indices of climate and local forcings.

The 1997/1998 El Niño

Visually, the clearest climate signal in our timeseries of total mesoscale energy is the suppressed energy in the middle of our study period (1998-2001) which coincides with the end of the 1997/1998 El Niño and the subsequent La Niña. On closer inspection, anomalous energy during the 1997/1998 and 2002/2003 El Niño events also stand out as a pattern of elevated energy during the winter followed by suppressed energy in the following spring/summer.

The physical effects of the 1997/1998 El Niño on the CCS are well described in the literature (Collins et al., 2002, Huyer et al., 2002, McPhaden, 1999, Strub and James, 2002b). The first definitive signal of the El Niño arrived off central California in June and off Oregon in July 1997 as elevated temperatures, high coastal sea levels, and anomalously poleward flow (Collins et al., 2002, Huyer et al., 2002, Kosro, 2002). In the northern CC, strongest sea level anomalies occurred in September 1997 through February 1998 with poleward flows off the shelf break exceeding 60 cm/s (>3X higher than average) in November (Kosro, 2002). The high coastal sea levels caused an offshore pressure gradient and resulted in eddies shedding off to sea. Atmospheric teleconnections in the form of anomalously strong winter winds and southwesterly storms (Figure 2.11, 3rd panel) further served to input energy into the system. Several other studies in the NEP have reported increased eddy-generation during El Niño events due to increased winds or flow (Melsom et al., 2003, Melsom et al., 1999, Zamudio et al., 2001).

In 1997, HFME increased in spring as usual, reaching a normalized peak of 0.6 in May/June (Figure 2.11, top panel). Because the first strong signs of El Niño did not reach central California until June 1997, that peak, although early, was probably a 'normal' summer peak in energy. However, the subsequent peak (of 0.8) in September/October

1997 was likely influenced by the El Niño as the amplitude was anomalously high and the timing corresponds with strong poleward transport and anomalous hydrography in the northern CC. Strong poleward advection persisted through February 1998 in the northern parts of the CCS (Strub and James, 2002b). Mesoscale energy declined more slowly than usual that winter, resulting in the highest winter HFME in our record, and did not drop to a minimum until June 1998, 3-4 months later than average. In fall 1998, a small increase in energy followed the return to near-normal temperatures, strong upwelling-favorable winds, and equatorward transport throughout the CCS (Figure 2.11).

The weaker 2002/2003 El Niño had a similar, though moderated, pattern of energy (Figure 2.11). Energy was anomalously high during winter when poleward winds were anomalously strong (Figure 2.11, 3rd panel) and stayed high until slightly later than normal before dropping to a minimum in late-March (HFME) or April (LFME). The largest difference in energy between the two El Niño events is that energy in summers 2002 and 2003 was not obviously influenced by the El Niño – the elevated energy was confined to winter. In 2002, sea level was not anomalously high until December (Figure 2.3) and transport was normal (Figure 2.11), which indicates that the increased winter energy may have primarily been due to atmospheric teleconnections in the form of anomalously strong winds.

Winds and transport

The generation and evolution of mesoscale circulation are ultimately controlled by the energy in the system. Locally, that energy may derive from winds, currents moving into the area, and density gradients. In a seasonal upwelling system, winds vary in both the timing of the "spring transition" (ST) from primarily downwelling-favorable to primarily upwelling-favorable winds and their intensity and duration through the season. Thus, we explore mechanisms of mesoscale variability by comparing the interannual variation in energy to the timing of the ST, the cumulative intensity of upwelling-favorable winds over the summer, and the strength (equatorward transport) of the CC, which varies independently of local wind-forcing (Strub and James, 2003), and to density gradients.

We used the methods of Pierce et al. (2006) to calculate the date of the ST at three latitudes (39°N, 42°N, and 45°N) using the Coastal Upwelling Indices (CUIs) produced and provided by the NOAA-Fisheries laboratory in Pacific Grove, CA (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices). Because winds and currents are highly variable during spring in the CC, it is not simple to determine a precise date of the spring transition, although many have endeavored to do so (Kosro et al., 2006, Pierce et al., 2006, Schwing et al., 2006) with often similar, but sometimes substantially different. results. The climatological date of the ST in the CC is generally earlier at decreasing latitudes (Schwing et al., 2006). In any particular year, however, a southern location may have delayed onset of upwelling whereas onset at northern locations may occur anomalously early, reversing the general pattern. Keeping those potential complications in mind, we present the annual Julian date of the ST and the daily CUIs from 42°N 125°W as a representation of the northern CCS wind-forcing (Figure 2.11, 3rd panel). In 1993-2005, the timing was always $ST_{39N} \leq ST_{42N} \leq ST_{45N}$. The only years in which the transition did not show a consistent decrease in timing with latitude were 1993 (ST_{39N}<<ST_{42N}=ST_{45N}), 2000 $(ST_{39N} < ST_{42N} < ST_{45N})$, and 2003 $(ST_{39N} < ST_{42N} = ST_{45N})$.

Also as in *Pierce et al.* (2006), we calculated an index of the integrated seasonal intensity of upwelling by accumulating the CUIs from the calculated date of the ST through October 1. Again, we present only those at 42°N 125°W (CU_{42N}) (Figure 2.11, 3rd panel). Interannual patterns of accumulated upwelling over the season were similar among the three locations despite some differences in the date of the ST.

Non-seasonal anomalies in the transport into the CC (Figure 2.11, 4th panel) were provided by *C. James* (Oregon State University). Transport anomalies were estimated geostrophically as in *Strub and James* (2003) from the east-west gradient in altimeter sea surface height averaged over the region 45°-53°N. Geostrophic transport of the CC may affect mesoscale energy by enhancing wind-driven equatorward currents in summer when transport is also equatorward (negative) or by diminishing wind-driven currents when transport anomalies are poleward (positive).

In several years, winds and transport anomalies appear to explain the annual level of mesoscale energy (Figure 2.11). For instance, total mesoscale energy was low in 1993

and 2005, years of very late STs, weak upwelling, and northward CC transport anomalies. Energy was high in 2001 and 2002, years of early STs, strong upwelling, and anomalously high equatorward transport. However, contrary to our expectations based on winds and transport, energy was at a minimum in 2000 when upwelling was moderate, the ST was slightly early, and alongshore transport was moderately equatorward. Furthermore, energy was at a maximum in 1994, a year of moderately early STs, southward transport, but relatively weak upwelling. (Note that results from 1994 should be interpreted with caution because only one altimeter was operational, so gridding-errors were high). The higher energy in summer 1996 compared to 2003 also counters our hypothesis—STs were late both years, transport was similar in spring/summer of both years, yet weak upwelling in 1996 compared to strong upwelling in 2003 resulted in opposite energy levels than predicted. Though Pierce et al. (2006) found a significant correlation between annuallyaccumulated upwelling indices and anomalies in available potential energy along 44.7°N, we do not find that upwelling translated directly to mesoscale energy in any obvious way. Overall, upwelling and transport indices did not consistently relate to the annual amplitude of mesoscale energy; controls on mesoscale energy are more complex than those few indices can explain.

The Pacific Decadal Oscillation, Climate, and Available Potential Energy

Because energy did not correspond closely to local forcings, we investigated the relationship between mesoscale energy and basin-scale indices of climate relevant to the NEP (e.g. the PDO, MEI, and NOI) for evidence of an influence by remote forcing. The MEI is positively related to high energy during fall/winter 1997 and winter 2002/2003, but otherwise does not predict energy levels well. HFME corresponded more strongly to the PDO than to the indices of wind and transport (Figure 2.11, 2nd panel) or the NOI (not shown). Energy was low in most years of negative PDO despite relatively strong winds, and moderate to high in most years of a positive PDO. Notable exceptions are 2001, an unusual year in which HFME was strongly decoupled from LFME indicating that different processes may have been important in the generation of mesoscale energy compared to other years, and 1994 (again with the caution that only one satellite was operational).

HFME lagged the PDO by 3 months and was correlated with r=0.31 (p-critical=0.30 with $N^*=44$).

The weakly significant correlation between the PDO and HFME indicates that basin-scale processes may affect mesoscale circulation. Weak density gradients and low available potential energy (APE) have been hypothesized to cause low mesoscale activity during El Niño events at low latitudes (Durazo and Baumgartner, 2002, Hormazabal et al., 2004b). Though we report an increase in energy during the peak of the El Niño due to intensified poleward winds and currents, mesoscale energy was strongly damped the following summer of 1998. That summer, ocean temperatures remained elevated at depth and hence cross-shelf density gradients were weaker than usual despite strong upwellingfavorable winds (Huyer et al., 2002).

Therefore, we explored the hypothesis that the relationship between mesoscale energy and climate is through the system's APE. The APE can be determined by horizontal density gradients which in coastal upwelling systems are strongly affected by two factors: upwelling-favorable winds, and vertical density gradients. Winds provide the kinetic energy to upwell water from depth, generating upward-sloping isopycnals -the vertical density gradient determines the resultant horizontal gradient. The PDO is derived from the 1st principal component of North Pacific basin-scale SST (Mantua et al., 1997), hence CCS surface temperatures are strongly correlated with the PDO. The sea surface along the U.S. West Coast is anomalously cool during a negative PDO and anomalously warm during a positive PDO. But because the sign of the PDO does not connote a change in temperatures at depth, and temperatures at depth are lower than near-surface, stronger vertical upper-ocean temperature gradients may occur during some years of a positive PDO than during a negative PDO. Hence, largest cross-shelf gradients could occur in years of both a positive PDO (when surface temperatures are anomalously high) and strong upwelling-favorable winds and vice-versa. Evidence that long-term patterns in stratification are related to the PDO is found in Bograd and Lynn (2003) who reported that stratification in the California Bight increased following the 1976 'regime shift'— a climate shift which corresponded to a change from a mostly negative to a mostly positive PDO. We would not expect the trend to hold for each year of the time series, but Bograd

and Lynn's study provides a hint that variability in basin-scale stratification may be effecting circulation energy.

Although few long-term hydrographic studies have been conducted in our study area with which to test the link between mesoscale energy and APE, we examined hydrographic data collected by A. Huyer (Oregon State University) along a transect at 44.7°N each July of 1997-2005 as part of the GLOBEC NEP program. Horizontal gradients in steric height provide an estimate of gradients in the density of the underlying water column, thus, for each cruise we estimated the APE in the upwelling system as the gradient in steric height (geopotential anomaly) across the frontal upwelling jet between stations 9 km (Station "NH5") and 80 km ("NH45") from shore (Huyer et al., 2007) (Figure 2.11, bottom panel).

We found that the cross-shelf steric height gradient measured in July 1998 was the lowest in the 9-year record, and hence may help explain the low HFME that summer. Over all years, we found Pearson's r=0.60 (p=0.09) between the annual maximum in HFME and the July APE. When we either correlate the July APE with HMFE on August 1 (instead of the maximum amplitude, which varied in timing annually) or remove 1998 from the relation (the year of greatest temporal separation between the timing of maximum energy and the July occupation of the hydrographic transect), the correlation increases to r=0.70 or r=0.82 and the relationship is significant (p=0.05 or 0.02) even when using a reduced N*=7 to account for the low serial correlation in APE among years.

Our confidence in the link between APE and mesoscale energy is tempered by the few (nine) years in which we have measurements of APE and that the APE on a single occupation of a transect is in part influenced by recent wind conditions and not entirely by conditions integrated over the prior months. However, the significant correlation between APE and HFME indicates that a link exists between the two, thus demonstrating a relationship between basin-scale processes and regional mesoscale energy in the CCS. Modeling efforts and the increasing availability of *in situ* information may help resolve the relationship in the future.

Conclusions

The dynamics of cross-shelf transport of biological production have been a recurrent theme of study in upwelling systems. Large volumes of coastal water can be advected offshore in mesoscale circulation features (Kosro et al., 1991), so variability in the generation and energy in such features can have profound implications for biological processes. The transport by mesoscale features can effect populations of organisms in many ways — by redistributing coastal species into the deep ocean and oceanic species onto the shelf (Mackas and Coyle, 2005), redistributing nutrients available for production, preventing retention of species in critical nearshore habitat, creating offshore areas of localized production (Legaard and Thomas, 2006), and creating local "hot spots" of upper trophic activity (Palacios et al., 2006).

Mesoscale geostrophic features with spatial scales of >50 km are dominant circulation features in the CCS (Brink et al., 2000, Powell et al., 2006), contributing ~80% of the total variance in sea level (Marchesiello et al., 2003). Herein, we have presented a statistical analysis of the variability in mesoscale energy in the northern CCS that allows us to separate years and areas of high and low energy. Our results suggest that mesoscale circulation energy in the northern CCS is moderated by climate. We hypothesize that energy is proximally controlled by the APE in the system and that the APE is ultimately controlled by both local and basin-scale processes. Vertical density gradients (surface to ~150 m depth) may be controlled by basin-scale processes; gradients may be converted to tilted isopycnals and horizontal gradients by local upwelling winds. Our index of mesoscale variability will be useful to compare to other physical and biological parameters as a step toward understanding the mechanisms of variability in marine ecosystems.

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Figure 2.1 Study area showing bathymetry. Locations where data were extracted for analyses are shown as letters A-H, as alongshore lines at 1° , 2° , 3° , and 4° offshore and as the zonal transects.



Figure 2.2. Average error in sea level anomaly due to mapping, expressed as percent of total sea level variance. Estimates at each location were calculated by temporally-averaging the error estimates provided by AVISO over the full study period of October 1993 - May 2006. Analysis locations are shown as in Figure 2.1.



Figure 2.3. Time-latitude Hovmöller plots of sea surface height anomaly, with seasonal cycles removed, along lines at (left to right) 3°, 2°, and 1° offshore as shown in Figure 2.1, and (three small right panels) the seasonal (annual +semi-annual) cycle along each line.



Figure 2.4. Time-longitude Hovmöller plots of a) sea level anomaly, with seasonal (annual + semi-annual) cycle removed, along latitude 48.5° N, b) the removed seasonal cycle, c and d) as above but along 44.8° N, e and f) along 41.8° N, g and h) along 38.0° N.



Figure 2.5. Time series and results of wavelet analyses of sea surface height anomaly at the northern locations A) 48.5°N 128.3°W, B) 48.5°N 125.8°N, C) 44.8°N 127.8W, and D) 44.8°N 125.0°W. Top panels: individual time series. Lower panels: wavelet power spectra of the time series expressed as multiples of the variance in each time series. Power above the 95% significance level at each location is enclosed in black contours. Below the "cone of influence" are areas where edge effects are important. Horizontal dashed lines are at 4, 12, 18, and 52 week periods.



Figure 2.6. Time series and results of wavelet analyses on sea surface height anomaly at the southern locations E) 41.8°N 128.0°W, F) 41.8°N 125.3°W, G) 38.0°N 126.8°W, and H) 38.0°N 124.0°W. All else as in Figure 2.5.



Figure 2.7. Time series of the scale-averaged wavelet power in the 4-12 week period band (black line) and 12-18 week period band (gray line) from locations shown in Figures 2.5 and 2.6. The corresponding 95% significance levels are shown as horizontal dashed lines.



Figure 2.8. Temporally-averaged wavelet power over the study area in the (top) 12-18 week and (bottom) 4-12 week periods. White lines parallel to the coast indicate the 1°, 2°, 3° , and 4° offshore lines used in analyses. Power along those lines are extracted and shown to the right to clarify spatial patterns of variability.



Figure 2.9. Seasonal variability of mesoscale energy with (top) 4-12 week and (bottom) 12-18 week periods. Cycles were created by averaging all values in each month, along lines 1°, 2°, 3°, and 4° offshore between 36°-43°N.



Figure 2.10. Wavelet power in the (top) 4-12 week and (bottom) 12-18 week period bands averaged over Latitudes 36° - 43° N along lines at 1° , 2° , 3° , and 4° offshore, as shown in Figure 2.1.

Figure 2.11. Top panel: Normalized wavelet power in the 4-12 and 12-18 week mesoscale periods averaged over the area from 1-3° offshore between 36°-43°N, the area of highest mesoscale energy. Second panel: The normalized 4-12 week period power overlayed on the PDO, seasonal cycles removed from both. Third panel: The Coastal Upwelling Index at 42°N 125°W from NOAA PFEL (bars), the index accumulated annually from the date of the spring transition through Oct. 1 (points), and the annual Julian day of the spring transition in (). Fourth panel: Three-month averaged, non-seasonal anomalies of alongshore transport into the northern California Current calculated from sea level gradients between 45°N and 53°N within 250 km of the coast as in Strub and James (2003). Positive anomalies indicate poleward transport. Bottom panel: Gradient in steric height (in J/km) between stations 9 and 80 km offshore at 44.7°N during July cruises. A gradient of 1 J/kg is equivalent to a 10 cm change in layer thickness.



Figure 2.11.

Chapter 3. Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California Current

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<u>Abstract</u>

We conducted a research cruise in late summer (July-August) 2000 to study the effect of mesoscale circulation features on zooplankton distributions in the coastal upwelling ecosystem of the northern California Current. Our study area was in a region of complex coastline and bottom topography between Newport, OR (44.7°N) and Crescent City, CA (41.9°N). Winds were generally strong and equatorward for >6 weeks prior to the cruise resulting in the upwelling of cold, nutrient-rich water along the coast and an alongshore upwelling jet. In the northern part of the study area, the jet followed the bottom topography, creating a broad, retentive area near shore over a submarine shelf bank (Heceta Bank, 44°-44.4°N). In the south, a meander of the jet extended seaward off of Cape Blanco (42.8°N), resulting in the displacement of coastal water and the associated coastal taxa to >100 km off the continental shelf. Zooplankton biomass was high both over the submarine bank and offshore in the meander of the upwelling jet. We used velocities and standing stocks of plankton in the upper 100 m to estimate that 1×10^6 m³ of water, containing an average zooplankton biomass of $\sim 20 \text{ mg carbon/m}^3$, was transported seaward across the 2000 m isobath in the meandering jet each second. That flux equated to offshore transport of >900 metric tons of carbon each day, and $4-5 \times 10^4$ tons over the 6-8 week lifetime of the circulation feature. Thus, mesoscale circulation can create regions in which zooplankton populations are retained over the shelf and biomass can accumulate, and in which high biomass is advected offshore to the oligotrophic deep sea.

Introduction

Coastal upwelling brings nutrient-rich water to the sea surface and creates highly productive coastal ecosystems in which zooplankton thrive. However, advective transport during upwelling is a challenge that plankton must overcome to avoid local extinction. In relatively warm areas of the ocean, rapid growth and short generation times may off-set advective losses (Escribano and Hidalgo, 2000). In the northern California Current (NCC), where the cold temperature of upwelled water (generally <12°C) leads to longer development times, diel and/or ontogenetic vertical migrations by zooplankton to exploit vertical current shears have been proposed as the most likely compensation mechanisms (Peterson, 1998). However, studies which have provided careful calculations of the potential impact of vertical migration on retention (e.g. Batchelder et al., 2002b, Peterson, 1998, Wroblewski, 1982) have done so in areas where classical Ekman upwelling-cell circulation dominates. In areas of more complex 3-D alongshore and cross-shelf circulation, migration patterns which are effective in controlling population losses in closed-cell circulation schemes may no longer work, and losses to the deep ocean may be large.

Both coastline and bottom topography have profound influences on circulation patterns. Examples include vortices found over submarine canyons and seamounts (e.g. Hickey, 1997, Torres et al., 2004), island wakes (Caldeira et al., 2005), and oceanic filaments generated near coastal promontories (Haidvogel et al., 1991). Such features influence biological distributions, resulting in advection and redistribution of organisms (Mackas and Coyle, 2005, Mackas and Yelland, 1999). In addition to creating advective features, topography-current interactions can also generate retentive areas where advection is low relative to surrounding areas. Examples of this are upwelling 'shadows' (Graham and Largier, 1997, Wing et al., 1998), re-circulation over submarine banks (Ashjian et al., 2001), and stationary eddies (Nishimoto and Washburn, 2002). In these areas, where local growth may keep pace with or exceed advective losses, biomass may be considerably elevated above surrounding areas, creating localized 'hot-spots' important to population survival and the transfer of energy to upper trophic levels.

Several distinct regions of coastline and bottom topography occur in the northern California Current off Oregon and northern California. Off northern and central Oregon (north of ~44.5°N), the coastline and bottom topography vary slowly alongshore. Between 43.8°-44.5°N, a large, shallow submarine bank (Heceta Bank) extends > 100 km to sea. Farther to the south, Cape Blanco (42.8°N), Cape Mendocino (40°N), and Pt. Arena (39°N) are large coastal promontories which cause sharp deviations in the coastline. These topographic regions also differ in the complexity of alongshore and cross-shelf circulation patterns that occur during summer upwelling. In the north, the equatorward coastal upwelling jet flows along isobaths, roughly parallel to the coastline. The classic Ekmandriven 2-D upwelling cell dominates the zonal circulation. However, when the upwelling jet encounters Heceta Bank, it deviates around the bank, creating a wide area of upwelled water nearshore (Barth et al., 2005b, Gan and Allen, 2005). Circulation over the bank is not as tightly coupled to the wind as it is along the straighter topography to the north, resulting in an area of relatively low zonal velocities due to sluggish flow and recirculation (Castelao and Barth, 2005). The jet meanders strongly offshore of Cape Blanco (Barth et al., 2005b, Barth et al., 2000) causing high zonal flows. To the south of Cape Blanco and at each of the more southern promontories, cold filaments of the upwelling jet frequently extend far to sea, creating deep, strong cross-isobath flow with velocities and volume-transport that far exceed those in Ekman transport (Kosro and Huyer, 1986, Strub et al., 1991).

Evidence of the importance of mesoscale circulation patterns on the distribution of plankton in the NCC is accumulating from several studies of individual advective features, all of which have demonstrated offshore transport of coastal taxa and biomass (Barth et al., 2002, Haury, 1984, Hood et al., 1990, Huntley et al., 2000, Huntley et al., 1995, Mackas et al., 1991). Less attention has been paid to the biological impact of retentive areas (though see Largier et al., 2006, Roughan et al., 2006), even though such areas are potentially important to population growth and larval survival. Nearshore, mesoscale circulation may serve as a mechanism of either advective loss or retention of coastal populations, whereas advective features, such as upwelling filaments that cross the shelf break, may cause high transport of coastal organisms to the deep sea.

In late July-early August 2000 (hereafter August 2000), we investigated the role of mesoscale circulation on distributions of mesozooplankton in a study area between Newport, Oregon (44.7°N) and Crescent City, California (41.9°N), 2 to 145 km from shore. Concurrently, a fishing vessel conducted upper-ocean trawls for nekton and near-surface zooplankton (Reese and Brodeur, 2006, Reese et al., 2005) and gelatinous zooplankton (Suchman and Brodeur, 2005) while a third research vessel towed instrument packages to investigate the hydrography and circulation (Barth et al., 2005b), optical properties (Cowles, unpub. data), fish and zooplankton acoustic targets (Pierce et al., 2003, Ressler et al., 2005, Sutor et al., 2005), particle distributions (Zhou and Zhu, 2002), and study marine mammals and sea birds (Ainley et al., 2005, Tynan et al., 2005). The studies were part of the U.S. Global Ocean Ecosystems Dynamics Northeast Pacific Program (GLOBEC NEP) Mesoscale Processes study (Batchelder et al., 2002a).

In this paper, we use zooplankton collected with net tows and community analysis techniques to assess the relationship between circulation features and zooplankton community structure. Our goal is to describe the relationship between mesoscale circulation and patterns of coastal zooplankton taxa in our study area, examine differences in distributions among taxa, and use zooplankton distributions and concurrent velocity fields to estimate the impact of circulation features on the advection of biomass from nearshore to the deep sea.

Methods

Field Collections

We used conductivity-temperature-depth (CTD) profiles, vertical plankton tows, and a Multiple-Opening-Closing-Nets-and-Environmental Sensing System (MOCNESS) to study the physical and biological patterns from the R.V. New Horizon between 28 July-12 August, 2000. Our study area was between Newport Oregon (44.7°N) and Crescent City California (42°N), 2 to 145 km from shore (Figure 3.1). Cruise reports and data can be accessed through http://globec.coas.oregonstate.edu/.

At each station (Figure 3.1), zooplankton were collected with a 50 cm diameter, 202 µm mesh net towed vertically from near bottom (or 100 m depth in deep water) to the surface at a rate of 30 m/min. A TSK flowmeter was used to monitor the volume of water filtered. Samples were preserved in a 5% buffered formalin/seawater solution. In the laboratory, zooplankton samples were diluted to 5–10 times the settled volume and subsampled with a 1.1-ml stempel pipette. Two to four subsamples were counted. Copepods and euphausiids were identified by species and developmental stage. Other taxa were identified to genus when possible or larger taxonomic group otherwise. Euphausiid furcilia, chaetognaths, and the pteropod *Limacina helicina* were measured. The abundance of each taxonomic group (number of individuals m⁻³) was calculated. Species diversity was calculated both as the total number of taxa at a location and using H', the Shannon– Weiner diversity index (Macarthur and Macarthur, 1961, McCune and Grace, 2002),

$$H' = -\sum_{i}^{S} p_{i} \ln p_{i}$$

where p_i is the proportion of individuals from a sample unit belonging to species *i*. Biomass values were calculated from length-weight or stage-specific values found in the literature or generated in our laboratory (e.g. Chisholm and Roff, 1990, Peterson et al., 2002, Uye, 1982). With the exception of Doliolids, gelatinous forms were included in abundance data, but not biomass calculations. Each taxon was examined for differences between daytime and nighttime densities using all samples collected. Those which are known to perform diel migration below the depth of our 100 m net casts (euphausiids older than furcilia stage III, shrimp larvae, crab larvae, chaetognaths, and fish larvae) were excluded. No others showed significant differences, even those that can be strong migrators (e.g. the copepods *Calanus* spp., *Metridia pacifica*), so were retained in analyses. Other studies in our area have also shown little influence of diel migration on upper-100 m abundances (Peterson, 1972, Peterson and Keister, 2002, Shaw and Robinson, 1998).

In addition to vertical tows, a 1 m^2 mouth area MOCNESS equipped with 335µm mesh nets was used to collect depth-stratified samples at several stations. Of those stations, two in the offshore areas of the upwelling filament (Figure 3.1) were sorted for

several dominant coastal and offshore copepod species to determine whether horizontal patterns seen in upper-100 m distributions were representative of those at depth.

At each location where zooplankton were collected, we also performed a CTD cast to 5 m off the bottom or a maximum depth of 200 m in deep water using a Sea-Bird SBE 911 CTD. At most stations, water samples were taken from multiple depths for analyses for chlorophyll and nutrient (NO2, NO3, PO4) concentrations. Nutrients were analyzed by Oregon State University's Chemical Oceanography laboratory and analyzed following the protocols of Gordon et al. (1994). Water for chlorophyll analysis was filtered onto Whatman GF/F filters. Chlorophyll *a* was extracted with 90% acetone and analyzed using a Turner model 10AU fluorometer. All maps of water and biological properties (Figures 4, 5, 9, and 10) were generated by kriging the discrete data using Surfer 8.03 software (Golden Software Inc., 2002).

Satellite images:

Sea surface temperature data from the Advanced Very High Resolution Radiometer (AVHRR) were captured with 1 km resolution and processed by Ocean Imaging of Solana Beach, CA (<u>www.oceani.com</u>) for the U.S. GLOBEC program. All are single-pass images selected because they had the lowest cloud cover within the time period.

Velocity and transport estimates:

Shipboard ADCP velocity data were collected from the third research vessel, the R.V. Wecoma. We used an RD Instruments 153.6-kHz hull-mounted narrowband profiler, with 8 m vertical bins and 2.5 min ensemble averaging. The shallowest reliable data were from 17 m. Velocities were detided using the Erofeeva et al. (2003) tidal model. For other processing details, see Barth et al. (2005b). Volume transports are estimated from ADCP profiles by integrating the observed velocities down to 100 m. Velocities shallower than 17 m are estimated by extending the 17-m value to the surface, i.e. a "slab" model. Actual velocities at the surface are probably higher than the 17-m value, so the slab is a slightly conservative extrapolation method. Biomass transports are estimated by multiplying interpolated vertical net biomass data by the volume transport, point by point along the chosen boundary (eg. the 2000m isobath) and normal to the local boundary orientation.

Statistical Analyses:

We used non-parametric multivariate analyses to analyze zooplankton community structure (McCune and Grace, 2002). The original main "species" matrix had 82 stations X 64 taxa, with values in the matrix equal to the density (# m⁻³) of each taxon at each station. Prior to analyses, data were Log₁₀(Y+0.01)+2 transformed to normalize the variance while preserving distances among low values. Rare taxa (those present in <3 samples) were removed to prevent them from strongly influencing results. The final matrix consisted of 82 stations X 52 taxa. All multivariate analyses were conducted in PC-ORD for Windows 5.05 (McCune and Mefford, 2005).

We sought groupings based on zooplankton community structure using agglomerative hierarchical cluster analysis with a Euclidean distance measure and Ward's Linkage Method (McCune and Grace, 2002). For presentation, the cluster dendogram is scaled both by Wishart's (1969) objective function and by percentage of information remaining. Wishart's objective function is a measure of information loss as clustering proceeds, and is calculated as the sum of the error sum of squares from the centroid of each group to the items in that group. No rigorous criteria exist for deciding how many cluster groupings to retain, but we used multi-response permutation procedure (MRPP) (Mielke, 1984) and Indicator Species Analysis (ISA) (Dufrene and Legendre, 1997) to help decide the optimal number of groupings. The *A*-statistic from MRPP (Field et al., 1982) assesses within-group homogeneity, thus, when calculated for groups identified by varying numbers of clusters, can indicate the number of clusters at which within-group homogeneity peaks or plateaus. From ISA (described below), a maximum total number of significant indicator species and a minimum overall averaged p-value help determine the optimal number of clusters.

A separate cluster analysis was performed on stations in 'environmental space.' The clustering method was identical to the zooplankton community clustering described above except that groupings were based only on the hydrographic variables (temperature, salinity, density) measured at 3 m, 20 m, and 50 m depths. Results of this cluster analysis identified groups of stations with similar hydrographic characteristics. A comparison of how stations grouped "hydrographically" versus in "zooplankton community" structure helps elucidate the mechanisms of variability in community structure.

Following cluster analysis, ISA was used to investigate which taxa were driving the differences among the clusters identified in cluster analysis. The Indicator Value (IV) for a species in a group is calculated as the product of the relative abundance of the species in the group (the mean abundance in the group divided by the sum of the mean abundances in all groups) and the frequency of occurrence of the species in samples in the group. Indicator Values can range from 0 (no indication) to 100 (perfect indication, meaning the species was present in all samples in the group and was absent from all samples in other groups). The statistical significance of each species IV was determined by a Monte Carlo method, in which sample units were randomly reassigned 1000-times to test if the IV was higher than expected by chance (Dufrene and Legendre, 1997).

We used Non-metric Multi-Dimensional Scaling (NMDS) ordination using Sorensen's (Bray-Curtis) distance measure to examine similarities in zooplankton community composition among stations and to compare cluster groups to environmental gradients. NMDS was chosen for this analysis because it is considered one of the most robust ordination methods when dealing with zero-zero species density pairs (Field et al., 1982, Gray et al., 1988) as are common in our data. The final stress (a measure of the goodness-of-fit between the data and the final ordination) was examined in relation to the ordination dimensionality to help choose the fewest dimensions necessary to adequately describe the data. Dimensionality was increased if the addition of an axis reduced the stress by >5. Stress values approaching or exceeding 20 are considered high; a value of zero indicates perfect monotonicity (McCune and Grace, 2002). The coefficient of determination (r2) between distances in the ordination space and distances in the original space determines the proportion of variation represented by each axis. The Pearson correlation between each ordination axis and individual species and environmental parameters was used to measure the strength and direction (in relation to the axes) of relationships.

We correlated environmental variables with the NMDS ordination axes to examine which variables were important in the gradients along which community composition was aligned. The environmental variables we tested were hydrographic measurements at 3, 20 and 50 m depth (temperature, salinity, density), and chlorophyll and NO₃ measured from water collected between 1-2 m depth (hereafter, 'surface').

To identify potential outlier stations, we compared average community distances among stations. One of the 82 stations (FM11, 43.2°N, 126.2°W, Figure 3.1) had an average Sorenson distance of 4.1 standard deviations from the grand mean. Preliminary examination of the NMDS ordination showed that station FM11 resided on an edge of the ordination plot, separated from other stations. However, on examination of its taxonomic composition, we determined that no one or few taxa, or unusual total abundances, drove its outlying position. This was the most offshore station we sampled, and highest surface ocean temperature and lowest salinity occurred there. Therefore, we determined that its position as an outlier most likely reflects its position at the extreme of the environmental gradients we measured, and hence brings valuable information to the analyses. Experimental removal of the station from analyses did not noticeably change the ordination of the remaining stations, indicating that the axes were not strongly influenced by the taxonomic composition at that station. Therefore, station FM11 was retained in all multivariate analyses reported here.

<u>Results</u>

The Physical Setting

In the NCC, upwelling occurs seasonally in spring and summer. In 2000, the spring transition from poleward winds and downwelling to equatorward winds and upwelling occurred in mid-March though persistent upwelling did not begin until mid-May. Prior to our cruise in August, upwelling winds had been exceptionally strong for >6 weeks (Barth et al., 2005b) resulting in cold, upwelled water all along the coast (Figure 3.1).

Coastal upwelling results in an alongshore, equatorward-flowing upwelling jet. Through the upwelling season, the jet develops from a simple, alongshore-flowing current which closely follows isobaths to a complexly-meandering current which can only maintain connection with the bathymetry in regions of relatively simple coastline and bottom topography (Barth et al., 2005a, Gan and Allen, 2005). Where the jet is oriented along isobaths, it may act as a barrier to offshore transport (Castelao and Barth, 2005); where it deviates from the topography it can create strong across-isobath flow. Off northern and central Oregon, the jet flows primarily along isobaths in summer, but in southern Oregon it frequently deviates from the shelf into deep water in the vicinity of Cape Blanco. During our cruise, the meandering path of the jet caused expanded areas of cold, dense water over both the wide, shallow (<200m) Heceta Bank where the jet deviated westward to follow the bottom topography, and in a filament of water that extended seaward off of Cape Blanco (Figure 3.1). A time series of satellite sea surface temperature (SST) images from the AVHRR shows the development of upwelling over Heceta Bank area and the offshore filament (Figure 3.2). Between 11 July and 23 July, the area of upwelled water over Heceta Bank expanded to the 200 m isobath, where it remained until early September. Off Cape Blanco, an offshore deviation of the jet had developed by 11 July, and by 23 July had turned anticyclonically in which cold water was carried over the slope >100 km to sea, partially enclosing a warm pool.

Measured ADCP velocities revealed a complex field of mesoscale circulation which included areas of retention and offshore advection (Figure 3.3). Velocity vectors show strong flow, particularly along the offshore edge of the warm, anticyclonic water (~43.5°N 125.5°W) where it is nearly enclosed by the upwelling filament: depth-averaged (0-100 m) velocities reached >50 cm/s and 25 m velocities reached >70 cm/s there (not shown). Strong westward flow occurred offshore of the northern and central edge of Heceta Bank (44.5°N 125.2°W), in the northwest-turning filament off Cape Blanco (43.25°N 125.3°N), and in the small filament present along the southwestern edge of our study area (41.8°N 125.6°W). Velocities were very low over Heceta Bank and at the inshore edge of our two southernmost transects. Velocities inshore of the 200 m isobath were nearly uniformly equatorward or shoreward north of Cape Blanco, but less so south of the Cape. The 250 m velocity field revealed a poleward undercurrent that hugged the seaward edge of the 200 m isobath (Figure 3.3B). Temperatures mapped using the CTD data (Figure 3.4A) agree well with satellite SST though the features were not as well defined using discrete observations. Both the expanded area of upwelled water over Heceta Bank and off Cape Blanco were evident to >50 m depth (Figure 3.4C). Near the surface of the filament (Figure 3.4A,B), the gradients in temperature and density between the oceanic and upwelled water were stronger and occurred farther offshore than at depth (Figure 3.4 C,D) indicating deep mixing of the upwelled and oceanic water. Station groups identified by hydrographic cluster analysis (using temperature, salinity, and density at three depths) (Figure 3.4B) indicate that stations along the outer edge of the Heceta Bank complex, in the center of Heceta Bank, and off Cape Blanco from the nearshore out toward the edge of the filament (Group B) had similar hydrography that differed from the offshore oceanic water (Group A). The region that Group B occupied in the center of Heceta Bank had elevated temperatures and lower density values than surrounding stations indicating the influence of offshore water. That influence was not apparent at 50 m depth.

Distributions

Zooplankton biomass was high in the cold, coastal water shoreward of the core of the upwelling jet all along the coast and offshore of Cape Blanco (Figure 3.5). Biomass was low in the warm offshore water. Biomass was negatively correlated with near-surface temperature (Pearson's r = -0.59, p<0.008), but was most strongly correlated with water density at 50 m depth (Figure 3.6) indicating integrity of the biomass with water masses (r = 0.77, p=0.0001 using log transformed data and a reduced N of 18 to account for autocorrelation in the data) (Figure 3.6). Zooplankton biomass was moderately correlated with surface chlorophyll (r=0.67, p=0.002). Chlorophyll was particularly high over Heceta Bank and south of the tip of Cape Blanco, but was also elevated in the offshore filament compared to other areas of the deep ocean. Nitrate showed a strong relationship to the hydrography. Note the relationship between chlorophyll and nitrate (Figure 3.5) – in areas of highest chlorophyll, especially over Heceta Bank and along the coast just south of the tip of Cape Blanco, nitrate is low compared to surrounding regions, suggesting draw-down of nutrients by the phytoplankton.

On average, copepods comprised 92% of the total biomass when excluding strong migrators and medusae. Copepods comprised <70% of the total biomass at only seven stations - four were dominated by doliolids and salps whereas the other three had very high euphausiid egg or calyptopis abundances. Including the migrators (late stage euphausiids, chaetognaths, etc.) but not medusae, copepods averaged 85% of the biomass.

Zooplankton communities

Cluster and ordination analyses revealed differences in zooplankton communities among stations. We chose to break the cluster dendogram at five cluster groups when guided by MRPP and ISA (Figure 3.7). These cluster groups separated along the ordination axes (Figure 3.8). A 3-dimensional ordination was selected based on the final, moderately low, stress value of 14.2. The final instability was <0.0001 indicating excellent stability of the final solution. The ordination cumulatively represented 85.4% of the community variance. After rigidly rotating the axes to express the environmental variable with the highest correlation (water density at 50 m depth) such that it was expressed entirely along the 1st axis (i.e. zero correlation with Axes 2 and 3), Axis 1 accounted for most of the variance (61.2%) in zooplankton community composition. Axes 2 and 3 explained 10.6% and 13.7% of the remaining variance, respectively.

Of the environmental variables we measured, density, salinity and temperature at all depths were strongly correlated with Axis 1 of the ordination (Table 1, Figure 3.8). The density at 50 m was most strongly related to the axis (r = 0.87) though near-surface and 20 m temperatures were also strongly negatively correlated (r=-0.80, r=-0.82 respectively). Those hydrographic variables were more strongly correlated with Axis 1 than either longitude (r=0.74), distance from shore (r=-0.76), or bottom depth (r=-0.67) indicating that the hydrographic variables were more important controls on zooplankton community composition than location relative to the shelf or shore. Latitude was very weakly correlated with Axis 1 (r=0.22), but was the strongest variable correlated with Axis 3 (r=-0.58). Other than latitude, no variable correlated with either Axis 2 or Axis 3 with $R^2>0.2$.

Cluster groups were clearly associated with particular locations and hydrography (Figure 3.4 symbols). Group 1 (\bullet) was present only offshore where surface water was warm. Group 2 (\bullet), which clustered closely with Group 1, occurred in slightly cooler water
just off the shelf in the north, and in the offshore expression of the upwelling filament off Cape Blanco. Group 3 (\diamond) occupied the shelf region around the tip of Cape Blanco and extended off the shelf in the cold, dense filament. Group 4 (\Box) dominated the zooplankton community over the Heceta Bank complex although a few expressions of this community occurred nearshore farther south. Group 5 (X) was distinct compared to the other coldwater groups based on the level at which it grouped in the dendogram and its location in the ordinations (Figure 3.8). Group 5 occurred only very nearshore all along the coast (Figure 3.4).

Although clustering based on zooplankton taxonomic composition did not consider hydrography in the analysis, hydrographic variables showed strong differences among cluster groups (Table 2) which are also revealed through the correlations between environmental variables and the ordination axes (Table 2, Figure 3.8). In general, temperatures decreased and salinity and density increased across groups, with warmest temperatures, lowest salinities, and lowest density occurring in Group 1 and the opposite in Group 5. Locations where Groups 1 and 2 occurred were several degrees warmer at 3 m depth than where other groups occurred. The hydrography where Groups 3 and 4 occurred (around Cape Blanco vs. over Heceta Bank) differed only slightly and is reflected in their lack of separation along Axis 1. The groups separated along Axis 3 of the ordination (Figure 3.8), indicating a stronger correlation with latitude than hydrography (Table 1).

Of the 52 taxa examined, 29 showed strong patterns along hydrographic variables and among cluster groups (Table 2, Figures 3.9 and 3.10). Several of the most abundant species (e.g. *Pseudocalanus mimus, Acartia longiremis, Calanus marshallae*, and *Centropages abdominalis*) showed gradations in abundance from Group 5 through Group 1: abundances were highest in the nearshore cluster (Group 5), high over Heceta Bank (Group 4), and decreased steadily from the nearshore portion of the upwelling filament to the offshore tip, to the warm, deep ocean (Group 3 to Group 2 to Group 1). All of these taxa were strongly positively correlated with Axis 1 of the ordination (Table 3.3) indicating that their abundances generally increased from left to right across the axis. Because Axis 1 represents low-to-high temperature and high-to-low salinity and density gradients, positive species correlations along that axis indicate increasing abundances from the warm, fresh offshore water to the cold, dense nearshore water. Several taxa (e.g. *Calanus pacificus, Clausocalanus arcuicornis*, and *Oncaea* spp.) showed the reverse pattern - they were most abundant in Group 1, least abundant or absent in Group 5, and were negatively correlated with Axis 1.

The offshore, warm-water group (Group 1) had the highest number of taxa, highest Shannon's diversity indices, and had the highest number of significant indicator species (Table 2). Taxa that were strongly associated with the offshore group were *Ctenocalanus vanus*, *Calanus pacificus*, *Paracalanus parvus*, *Mesocalanus tenuicornis*, all of the *Clausocalanus* species, Siphonphores, and Larvaceans (Figures 3.9 and 3.10). Acartia danae and Calocalanus styliremis were found almost exclusively in Group 1.

The Heceta Bank group (Group 4) had uniquely high numbers of euphausiid eggs and nauplii (Table 2, Figure 3.10). Those taxa and the small cyclopoid copepod, *Oithona similis*, were the only taxa with correlations with Axis 3 >0.6. The euphausiid eggs and nauplii were negatively correlated with the axis; *O. similis* was positively correlated. Their correlations with Axis 3, along which Groups 3 and 4 separated, and their contrasting distributions in relation to Heceta Bank suggest that those taxa drove the separation of the two cluster groups.

Discussion

In late summer 2000, the meandering path of the equatorward upwelling jet created local areas of onshore retention and offshore advection. Where the jet deviated from the coastline to flow around Heceta Bank, it left an inshore area where current velocities were low and thus retention times were high. South of Heceta Bank, AVHRR images (Figure 3.2) indicate that a meander of the jet developed off of Cape Blanco, extended >100 km offshore and broke down over an approximately eight week period. Seaward ADCP velocities were high in the filament, indicating large offshore transport of water to the deep sea. The effects on the zooplankton distributions can easily be seen from zooplankton distributions: copepod biomass was high nearshore, over the wide Heceta Bank area, and in the cool water advected offshore in the upwelling filament, but was low in the warm water.

Distributions of individual taxa and the zooplankton community patterns identified by cluster analysis were strongly related to the hydrography. Warm-water, oceanic taxa which are found throughout the area during winter (Keister and Peterson, 2003) were held offshore by the upwelling system in late summer. These taxa include the copepods *Clausocalanus* spp., *Paracalanus parvus*, and *Calanus pacificus* – they were in high numbers only well offshore and in the warm eddy off Cape Blanco (Figure 3.9). Coldwater taxa which are the typical nearshore dominants during summer upwelling (Keister and Peterson, 2003) were abundant on the shelf, in the retentive area over Heceta Bank, and offshore in the advective filament off Cape Blanco.

We separate the study area into four dynamic bio-geographic regions based on the zooplankton communities identified by cluster analysis. The very nearshore (Cluster 5) and offshore (Clusters 1 and 2) communities were the most dissimilar. Several taxa were good indicators of those contrasting communities (Table 3.2), indicating that those taxa were found most consistently in highest abundances at the locations that made up the clusters. Mid-shelf communities north (over Heceta Bank, Cluster 4) and south (off Cape Blanco, Cluster 3) separated from each other, but examination of the densities of animals in those clusters (Table 3.2) reveals few differences: euphausiid eggs and nauplii were in higher abundance over Heceta Bank (in Cluster 4) whereas euphausiid calyptopes and *Oithona similis* were in highest abundance to the south (in Cluster 3), but other densities were similar.

Heceta Bank retentive area

Heceta Bank is known as a 'hot spot' where high standing stocks of chlorophyll, nekton, and upper trophic levels occur (e.g. Ainley et al., 2005, Reese and Brodeur, 2006, Ressler et al., 2005, Tynan et al., 2005). Low velocities over the bank have been noted in several previous studies (Barth et al., 2005a, Castelao and Barth, 2005, Kosro, 2005). Modeling and observations during a 2001 study of Heceta Bank indicated that low velocities over the bank result from the offshore movement of the upwelling jet where the shelf widens, leaving a lee inshore of the jet (Barth et al., 2005a, Gan and Allen, 2005, Kosro, 2005). In 2000, the water in this lee was retained long enough to warm (Barth et al., 2005a, Barth et al., 2005b) and for primary production to draw down the ambient nutrients. Similar processes were noted in a 1995 study by van Geen et al. (2000) who reported biological drawdown of pCO_2 over Heceta Bank that did not occur south of Cape Blanco. The different advective regimes – active circulation in the south versus sluggish circulation over the bank - were implicated in the biological response.

The high abundance of euphausiid eggs on Heceta Bank reflects the location of spawning adults. Ressler et al. (2005) used acoustics and MOCNESS tows to study adult euphausiid distributions during this cruise. They report high abundances over Heceta Bank and directly offshore of Cape Blanco in cold chlorophyll-rich areas. Abundances elsewhere were very low. Gomez-Gutierrez et al. (2007) reported euphausiid fecundity from this cruise: only females collected from the Heceta Bank region produced large broods - females collected elsewhere produced small broods or did not spawn. From the distributions of spawning adults, eggs, and early life stages of euphausiids, it seems plausible that Heceta Bank was a primary spawning ground in August, from which larval euphausiids were advected south and offshore. Based on velocities measured where egg abundances were highest ($\leq 1 \text{ km/d}$ to the south, Figure 3.3), eggs would not have been advected off the Bank before hatching into nauplii ~40 hrs after spawning. We estimate the path length between peak naupliar abundance and peak calyptopis abundance as ~200 km (Figure 3.10), along which velocities of 17 ± 7 cm/s occurred, thus the journey would take \sim 8-20 days to complete. Because euphausiid nauplii develop to calyptopes in \sim 6-18 days (Feinberg et al., 2006), the distributions of the different euphausiid life stages supports the hypothesis that the calyptopes found offshore were spawned over Heceta Bank. The distributions also indicate near-continuous spawning over the bank: only a small region between the stations where nauplii and calyptopes were abundant was devoid of larval euphausiids. If spawning was synchronized and infrequent, we likely would not have sampled all of the early life stages during the few (\sim 6) days required to sample the study area. Furthermore, we returned to the transect at 44.3°N one week later where we again sampled equally high abundances of euphausiid eggs (not shown) indicating frequent high spawning over Heceta Bank that was not noted elsewhere.

The low velocities and high chlorophyll biomass over the Bank also provided suitable habitat for early life stages of other zooplankton. *Calanus marshallae* nauplii (the

only copepod nauplii we quantitatively sampled) were abundant over the Bank area (Figure 3.10). They were less abundant south of Cape Blanco and off the shelf, even south of the tip of Cape Blanco where chlorophyll was high (Figures 3.5B and 3.10). Heceta Bank region seems to be an example of an 'ocean triad' (Bakun, 1996) where zooplankton are concentrated (through high spawning and circulation), retained, and enriched (via upwelling and high chlorophyll biomass), thus making it a 'hot spot' of upper trophic activity (Reese and Brodeur, 2006).

Advective upwelling filament

In strong contrast to the retentive area over Heceta Bank, the seaward meander of the jet off Cape Blanco created a region of offshore, cross-isobath advection. Offshore advection of zooplankton is indicated by the distributions of several neritic taxa (Figures 3.9 and 3.10), community composition (Figure 3.4A) and the strong relationship between zooplankton biomass and water density (Figure 3.6). All previous studies of the impact of mesoscale circulation features on biological distributions in the NCC have reported transport of coastal species large distances off the shelf. Haury (1984) described coastal copepod species in an eddy located >400 km to sea off Pt. Conception, CA. Mackas et al. (1991) and Smith and Lane (1991) found high biomass of reproductively active coastal zooplankton in an upwelling filament >250 km off Pt. Arena, CA. Eddies surveyed offshore of Pt. Arena contained coastal zooplankton species (Huntley et al., 2000, 1995) and high biomass of chlorophyll (Barth et al., 2002) that had originated nearshore.

Our results appear to indicate a gradient in the effects of the offshore advection on neritic copepod distributions from the smallest taxa (*Oithona similis*, 1 µg C/female) (Figure 3.10) through moderately sized taxa (e.g. *Pseudocalanus mimus*, 14 µg C/female, and Acartia longiremis, 6 µg C/female) (Figure 3.9) to the largest taxa (*Calanus marshallae*, ~85 µg C per female) (Figure 3.9). Smaller taxa were much more strongly associated with the bounds of the circulation patterns. For example, *O. similis* were found offshore in nearly as high abundance as on the shelf whereas, relative to nearshore abundances, *Calanus marshallae* were found offshore in very low abundances. Possibly, the larger taxa that weren't found offshore in the upper layers of the filament exhibited behaviors that lead them to migrate below the depth of our nets (>100 m) when they

sensed increasing water temperatures or decreased chlorophyll offshore. Alternatively, because larger taxa may have higher food requirements (Vidal, 1980) or be subject to higher predation by visual predators (Luo et al., 1996), those taxa may have experienced higher mortality off the shelf than smaller taxa. This species-specific response to offshore advection has been noted in previous studies in this region (Peterson and Keister, 2002) and in eddies off British Columbia (Mackas and Galbraith, 2002). Because larger taxa are likely important prey items for visual predators, the mechanisms generating the patterns are of ecological interest.

We considered the role that vertical distributions may have played in the apparent 'loss' of large coastal taxa from the offshore filament by examining the depth distributions of several copepods at two offshore locations in the upwelling filament using MOCNESS collections to 350 m depth. Because the MOCNESS mesh size (335 µm) was too large to collect *Oithona similis*, we do not have vertical distribution data for that species. Depth-distributions varied by species (Figure 3.11). The smaller, neritic copepods *Acartia longiremis* and *Pseudocalanus mimus* were primarily restricted to the upper 100 m, as has been noted at other locations (Lamb and Peterson, 2005, Mackas and Galbraith, 2002) whereas the larger copepods, *Calanus marshallae* and *Calanus pacificus* (75 µg C/female), were distributed deeper. There were not apparent differences in vertical distributions due to the day/night sampling difference between the stations.

Interestingly, *Calanus marshallae* were found almost exclusively in the deepest layers sampled whereas *C. pacificus* were collected primarily from the upper 100 m. This contrast likely resulted from the different habitat preferences of the two species: *C. pacificus* is a warm-water species which usually inhabits the oligotrophic offshore waters whereas *C. marshallae* is a boreal, neritic species which thrives in cold, productive areas (Keister and Peterson, 2003). *C. marshallae*'s occurrence at depth may indicate that they descended to avoid the warm upper layers when carried off the shelf. However, the cues for such migration are not clear, and the low numbers even at depth (<20 m⁻³) compared to nearshore prevent us from ruling out other explanations (i.e. predation or starvation) for their low numbers in the surface layer.

Transport estimates

Upwelling filaments can transport considerable volumes of water offshore, and often persist for several weeks through fluctuating wind conditions. We assessed the offshore transport of zooplankton biomass in the filament surveyed during this cruise using ADCP velocities and zooplankton biomass interpolated to points along the 2000 m isobath (black vectors in Figure 3.3). Integrating upper 100 m velocities along the entire 2000 m isobath between 41.9° - 44.6° N gave a net offshore volume transport of 1.0 Sv (1 Sv= 10^{6} m^{3} /s) and a flux of 1200 metric tons carbon/day in zooplankton biomass moving seaward. Transport across the isobath within the filament itself (defined here as 42.5°-43.2°N based on satellite SST), though occupying only $\sim 1/4$ of the full latitudinal range, was about 1/2 of the total offshore transport (0.5 Sv seaward) and 3/4 of the biomass flux (900 tons C/d). During the 6-8 week lifetime of the filament, $4-5 \times 10^4$ tons of C may have been delivered in the form of zooplankton biomass to the deep ocean. Even recognizing the difficulty in estimating fluxes from biomass estimates in a dynamic system and hence the errors they include (e.g. errors introduced by temporal changes in biomass and flow fields and by integrating across discrete observations), the transport is significant and resulted in localized, elevated biomass offshore. Even >100 km off the shelf, biomass was 3-4 times higher within the filament than in surrounding oceanic water (Figure 3.5).

After accounting for the flux of ~700 tons C/d that moved into the study area along our northernmost and southernmost transects (Figure 3.3) and the 'instantaneous' standing stock of zooplankton inside the 2000 m isobath during the cruise ($\sim 3.2 \times 10^4$ tons C), a net seaward transport of ~2% of the biomass occurred per day in the upper 100 m. This is a conservative estimate because we have not accounted for velocity shear across the upper 17 m or transport that occurred below 100 m depth, both potentially large fractions of the total. Considering that crustacean zooplankton (the dominant taxa in our samples) grow at ~0.1/d (Peterson et al., 2002), advective losses were 15-20% of growth. This estimated flux is a larger portion of the inshore production than measured by Mackas and Yelland (<10%) (1999) in filaments off Vancouver Island, B.C., but their estimates included phytoplankton. In both regions, the offshore flux removed a small enough portion of the

total that populations could have increased (depending on other losses such as predation) even while high advective losses occurred.

Transport pathways

Retention or return to the nearshore is ecologically necessary for maintenance of nearshore populations, thus many coastal zooplankton have life history strategies that slow advective losses from the shelf to allow life cycle closure in upwelling ecosystems. These strategies can include ontogenetic and diel vertical migrations (Peterson, 1998) or high population growth rates (Escribano and Hidalgo, 2000). On Heceta Bank, low velocities indicate retention and low advective losses that allowed for high population growth and hence the high biomass we sampled there. Alternatively, those coastal populations may be continuously replenished from productive "upstream" regions not surveyed in this study.

The fate of plankton advected offshore in upwelling filaments is unknown. Because velocities in the filament did not tend to strongly change direction with depth in the upper 300 m (not shown), migrations within the depths of most zooplankton's diel range (<100 m) would not substantially slow their rate of offshore transport. However, one potential path of return from the offshore filament to nearshore is notable from hydrographic and zooplankton data collected during the August 2000 U.S. GLOBEC study period: Barth et al. (2005b) noted that surface drifters did not closely track the deeper circulation during our study period – one moved shoreward from the offshore tip of the upwelling filament. A drifter released over Heceta Bank traveled south alongshore, seaward and to the northwest tip of the offshore filament, then completed an anticyclonic path when it was entrained into the eastward moving jet on the southern, outer edge of Heceta Bank at ~44°N 125.25°W (Barth et al., 2005b). Though the drifter did not return all the way onto the shelf, it traveled >100 km shoreward from the deep ocean in <1 week. That near-surface drifter may have been subject to Ekman flow not reflected in the ADCP measurements and may indicate a mechanism for near-surface plankton to return from far offshore. A second drifter released at a similar location traveled offshore and separated from the first when it turned southwest in the offshore filament instead of northwest. That drifter did not return nearer shore – its path indicates permanent loss from the shelf.

The disconnect between the surface circulation indicated by drifter paths and deeper circulation indicated by the ADCP-measured velocities could serve as a mechanism of return to the nearshore from the otherwise deep unidirectional flow in the filament. Distributions of the small copepod, Oithona similis (Figure 3.10), seem to illustrate this pathway – abundances at the southern offshore edge of Heceta Bank were more similar to abundances in the northern offshore tip of the filament than to other locations within the bank region. It seems likely that the relatively high abundances at the edge of the Bank reflect a delivery of high numbers of individuals in near-surface circulation from offshore. Many of the dominant copepods in our study area reside just below the 10-20 m thick surface Ekman layer (Lamb and Peterson, 2005), possibly as a mechanism of avoiding surface transport or due to high mortality near surface. Those taxa may not have been able to exploit this return path. However, O. similis typically occupies the upper 20 m of the water column in our area (Lamb and Peterson, unpublished data) and so were probably within the Ekman layer experienced by the drifters and may have moved shoreward during a short-term wind reversal. Mackas and Galbraith (2002) also noted the importance of vertical position in the retention and loss of zooplankton from offshore features. Strong winds over the surface of eddies periodically move surface waters relative to the underlying geostrophic flow. Hence, taxa residing near-surface could be lost from the feature more easily than those beneath the Ekman layer.

Studies of individual upwelling filaments in the CCS indicate that circulation dynamics within the features differ spatially and temporally. Filaments can attain longer east-west spatial scales and higher volume transports than those measured here (Barth et al., 2000, Kosro and Huyer, 1986). Because mesoscale circulation varies spatially and temporally (Keister and Strub, 2008) and wind-forcing was about average in 2000 (Pierce et al., 2006), the impact of mesoscale circulation on abundances and distributions could easily be stronger in other years and at other locations.

Trophic interactions

Biological relationships among the chlorophyll, zooplankton, and hydrography noted in this study corresponded to patterns exhibited by organisms in higher trophic levels. Reese and Brodeur (2006) identified Heceta Bank and the nearshore area around the tip of Cape Blanco as 'hotspots' of nekton biomass and species diversity. Abundances of juvenile coho and chinook salmon (Brodeur et al., 2004) and seabirds (Ainley et al., 2005) were also elevated in those regions. Many of the seabirds, particularly Shearwaters and Cassin's Auklets, were strongly related to frontal areas and locations of high chlorophyll biomass during this cruise. Tynan et al. (2005) noted a strong association between humpback whales and harbor porpoises with areas of high chlorophyll biomass whereas Dall's porpoises were found far offshore in the upwelling filament.

The substantial elevation of zooplankton biomass within mesoscale features over that found in the surrounding open ocean, and the aggregations of upper trophics within them, indicates the ecological importance of the features in offshore areas. Their potential for transporting substantial portions of shelf populations offshore is indicated by the distributions of early life stages of euphausiids (Figure 3.10). It is not known whether the animals that are advected offshore in filaments and eddies in the NCC contribute to production in the offshore regions to which they have been moved. They may be subject to high mortality by predators over the continental slope and in the deep ocean where zooplanktivorous euphausiids and fish reside. However, copepod egg production measurements made in upwelling filaments off California (Smith and Lane, 1991) and in the Canary Current (Hernandez-Leon et al., 2002, Yebra et al., 2004) indicate that zooplankton may actively feed and reproduce in offshore expressions of features. In coastally-generated eddies off Vancouver, Canada, coastal taxa are found offshore >15 months after separating from the shelf (Mackas and Galbraith, 2002). Hence, advected coastal populations may continue to contribute to offshore production for substantial lengths of time.

Conclusions

Mesoscale circulation features can advect huge volumes of coastal water offshore (Hormazabal et al., 2004b, Kosro and Huyer, 1986, Mackas and Yelland, 1999). A single filament may advect as much water offshore as all of the Ekman transport along 1000 km of coastline (Kosro and Huyer, 1986). Several filaments simultaneously occur along the Oregon and California coast each summer. Their net offshore transport in coastal upwelling systems is clearly indicated by the dominance of neritic taxa within them (e.g. Haury, 1984, Mackas et al., 1991, Rodriguez et al., 1999). Here, we measured offshore transport in a meander of the upwelling jet as ~0.5 Sv, and a biomass flux of >900 tons of carbon per day in zooplankton alone. Both the timing and intensity of mesoscale circulation (Keister and Strub, 2008) and peak nearshore zooplankton biomass (Peterson and Keister, 2002, Peterson and Miller, 1975) vary spatially and interannually, so the biomass delivered to the deep sea, and hence the productivity of the ecosystem as a whole, are also likely to vary. Eastern boundary currents are highly productive in terms of primary and secondary production, so variability in the transfer of water and the associated planktonic communities between the shelf and deep ocean may have dramatic consequences for ecosystem dynamics and global carbon cycling, survival of oceanic zooplanktivores (e.g. Logerwell et al., 2001, Yen et al., 2006), and upper trophic level organisms (Palacios et al., 2006).

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Figure 3.1. Sea surface temperature image from the AVHRR on August 1, 2000 with locations of vertical net tows and CTD casts overlayed. Day (\circ) versus night (\bullet) sampling is indicated by the symbols. The two stations analyzed for depth-distributions from MOCNESS sampling are labeled as ZZ-3 and ZZ-7 and circled and the location of the statistical outlier station, FM11, is shown. The seaward location of the 13.5°C (yellow) isotherm roughly indicates the position of the core of the equatorward jet as defined in Barth et al. [2005b]. The black dashed line is the 200 m isobath.







Figure 3.3. Velocity vectors from the shipboard ADCP (left) depth-averaged over the upper 100 m and (right) at 250 m depth. The core of the upwelling jet, as defined in Barth et. al [2005b], is indicated by the solid line. In the left panel, 0-100 m velocities interpolated along the 2000 m isobath and along the northern and southernmost transects are darker. Isobaths are at 50, 100, 200, and 2000 m.



Figure 3.4. A-D) Temperature and density at 3 m and 50 m depths from CTD data. The 200 m isobath is shown. Symbols in A, C, and D represent zooplankton community cluster groupings identified by cluster analysis. Letters in B represent cluster groups defined by the hydrography rather than by the zooplankton community composition.



Figure 3.5. A: Zooplankton biomass integrated over the upper 100 m from vertical net tows. Strong migrators (see text) and medusae have been excluded. Symbols code for day (\circ) or night (\bullet) sampling. B: Total chlorophyll from near-surface bottle samples. C: NO₃ from near-surface bottle samples. The 150m isobath is the gray dashed line in each plot.



Figure 3.6. Total zooplankton biomass, excluding strong migrators and medusae, integrated over the upper 100 m in relation to density at 50 m depth. The Pearson correlation and significance level calculated using log transformed data are given. Data are coded by whether they were from on the continental shelf in <200 m water depth, or offshelf in >200 m water depth.



Figure 3.7. Zooplankton community dendogram of stations clustered in species space. Symbols are same as in Figure 3.4.



Figure 3.8. Non-metric Multidimensional Scaling (NMS) ordination of stations based on species composition. 3-dimensional results shown as **Top:** Axis 1 vs. Axis 2, **Bottom:** Axis 1 vs. Axis 3. Stations are coded by their cluster grouping as identified in cluster analyses (Figure 3.7 above). The environmental gradients that correlated with the axes $R^2 > 0.6$ are shown; the direction of the correlation is indicated by arrows; the magnitudes of the correlations are given in Table 1.



Figure 3.9. Abundance per m^3 of zooplankton (gray shading) which have strong correlations with Axis 1 of the NMDS ordination. Contour lines are from density at 50 m depth from CTD casts (Figure 3.4) to show the relationship between the hydrography and distributions. Contour intervals are shown at each 0.25 from 25 to 26 kg/m³. The 200 m isobath is shown as a dashed line.



Figure 3.10. Abundance per m^3 of zooplankton (gray shading) which have strong correlations with Axis 2 or 3 of the NMDS ordination, and *Calanus* nauplii. Contour lines are from density at 50 m depth from CTD casts (Figure 3.4) to show the relationship between the hydrography and distributions. Contour intervals are shown at each 0.25 from 25 to 26 kg/m³. The 200 m isobath is shown as a dashed line.



Figure 3.11. Depth distributions of copepods at stations ZZ-3 (left) and ZZ-7 (right) from MOCNESS tows expressed as the fraction of the species total upper 350 m abundance found in each depth interval. Station ZZ3 was sampled at night, ZZ7 during day. Total abundance m-2 in upper 350 m is given for each species/station combination. The upper and lower depths of each sampling strata are shown as the values on the y-axes.

Table 3.1. Pearson correlations between environmental variables and NMS ordination axes. D/N code is time of day, coded as day or night. On/Off code is station depth coded as >200 m or <200 m. Distance is distance from shore.

	Axis 1		Ax	is 2	Axis 3	
	r	\mathbf{r}^2	r	\mathbf{r}^2	r	r^2
Latitude	0.22	0.05	-0.09	0.01	-0.58	0.33
Longitude	0.74	0.55	-0.21	0.04	-0.10	0.01
Depth	-0.67	0.45	0.29	0.08	0.09	0.01
Distance	-0.76	0.58	0.17	0.03	-0.15	0.02
On/Off Code	0.75	0.56	-0.14	0.02	-0.22	0.05
D/N Code	-0.11	0.01	0.33	0.11	-0.01	0.00
3m Temperature	-0.80	0.64	0.21	0.05	-0.11	0.01
3m Salinity	0.70	0.50	0.07	0.01	0.30	0.09
3m σθ	0.81	0.65	-0.08	0.01	0.22	0.05
20m Temperature	-0.82	0.67	0.18	0.03	0.05	0.00
20m Salinity	0.75	0.56	0.13	0.02	0.24	0.06
20m σθ	0.85	0.72	-0.02	0.00	0.12	0.02
50m Temperature	-0.75	0.56	0.06	0.00	0.40	0.16
50m Salinity	0.79	0.62	0.04	0.00	0.09	0.01
50m σθ	0.87	0.76	0.01	0.00	0.00	0.00
1m Chla	0.58	0.33	0.13	0.02	-0.09	0.01

Table 3.2. Characteristics of five station groupings identified by cluster analysis. Mean values with standard errors in (). Only taxa that showed pattern across hydrographic variables or were significant indicators of a cluster group are shown. A * designates the group for which a taxon's indicator value was significant.

Cluster group	1	2	3	4	5
Number of samples	14	12	23	23	10
Average number of taxa	23.5	18.2	14.8	13.7	15.7
Shannon's diversity Index	3.13	2.87	2.62	2.57	2.73
Hydrographic characteristics					
Depth (m)	1557 (1064)	1920 (1144)	599 (780)	182 (292)	62 (24)
Temp at 3 m (°C)	16.1 (1.2)	14.6 (1.7)	11.6 (1.1)	11.6 (1.5)	11.2 (1.3)
Salinity at 3 m	32.4 (0.5)	32.5 (0.5)	33.1 (0.4)	32.9 (0.5)	33.6 (0.1)
σ_{θ} at 3 m	23.7 (0.6)	24.1 (0.7)	25.2 (0.5)	25.0 (0.6)	25.6 (0.3)
Temp at 50 m (°C)	9.8 (0.7)	9.3 (0.6)	8.9 (0.4)	8.0 (0.3)	8.2 (0.5)
Salinity at 50 m	33.0 (0.3)	33.1 (0.3)	33.6 (0.2)	33.6 (0.3)	33.9 (0.1)
σ_{θ} at 50 m	25.5 (0.3)	25.6 (0.2)	26.0 (0.2)	26.2 (0.3)	26.4 (0.1)
Chlorophyll at 1 m (µg/ml)	0.5 (0.4)	0.7 (0.5)	1.9 (1.2)	4.7 (3.1)	8.8 (5.9)
Zooplankton biomass (g C m ⁻³)	6.7 (3.1)	11.8 (6.5)	17.9 (10.2)	25.9 (17.7)	63.2 (31.4)
Species abundances (# m ⁻³)					
Copepods					
Acartia danae	3 (5)*	0 (1)	0 (0)	0 (0)	0 (0)
A. hudsonica	0 (0)	0 (0)	19 (37)	6 (12)	803 (1795)*
A. longiremis	88 (79)	133 (74)	412 (280)	480 (297)	1084 (706)*
A. tonsa	0 (1)	0 (0)	0 (1)	0 (1)	1 (4)
Calanus marshallae	5 (7)	8 (11)	79 (78)	91 (80)	232 (235) *
Calocalanus styliremis	9 (10) *	0 (1)	0 (0.6)	1 (3)	0 (0)
Calanus pacificus	4 (6)*	3 (4)	1 (3)	0(1)	0 (0)
Centropages abdominalis	1 (1.8)	$\frac{1}{2}$ (10)	9 (15)	20 (27)	290 (495) *
Clausocalanus arcuicornis	$1/(13)^*$	/ (16)	0(1)	0 (0)	0 (0)
C. parapergens	$3(3)^{*}$	$ \begin{array}{c} 0 & (0) \\ 1 & (2) \end{array} $	1(5)	$ \begin{array}{c} 0 & (0) \\ 1 & (2) \end{array} $	0 (0)
C. pergens	$12(1/)^{*}$	1 (2) 4 (10) *	4(11)	1(2) 0(0)	0 (0) 0 (0)
Corycaeus spp.	0(1) 20(15)*	4(10)	0(0) 16(38)	$0 (0) \\ 1 (4)$	0(0)
Eucolanus vanus	$20(13)^{-1}$	7(0)	10(38)	$1 (4) \\ 0 (0)$	3(3.3)
Eucaianus spp. Masocalanus tonuicornis	1(1) 12(8)*	$1 (1) \\ 2 (2)$	$ \begin{array}{c} 0 & (0) \\ 1 & (2) \end{array} $	$0 (0) \\ 1 (4)$	0(0)
Metridia pacifica	13(0) 13(7)	$\frac{2}{16}$ (12) *	20(15)	4 (5)	2(8)
Oithona similis	679(393)	742 (455)	835 (378)	404 (198)	1237 (690) *
Oncaea	11 (8) *	2(3)	3 (5)	0(1)	0(0)
Paracalanus parvus	159 (158) *	61 (50)	4 (8)	17 (20)	8 (10)
Pseudocalanus mimus	760 (664)	1157 (1063)	2319 (1083)	2412 (2091)	6827 (4073)
Scolecithricella minor	2 (3)	0 (1)	4 (5)	3 (4)	2 (4)
Other taxa					
Euphausiid calyptopes	109 (140)	147 (190)	11 (22)	35 (78)	174 (397)
Euphausiid eggs	3 (3)	5 (10)	6 (12)	239 (285) *	125 (343)
Euphausiid furcilia I-III	7 (9)	7 (6) *	4 (9)	2 (4)	48 (50)
Euphausiid nauplii	1 (2)	1 (2)	4 (12)	107 (166)*	129 (211)
Evadne spp.	0 (0)	0 (0)	1 (2)	3 (11)	242 (455) *
Gastropods	2 (5)	1 (2)	1 (5)	1 (2)	14 (22) *
Medusae	0 (0)	0 (0)	0 (0)	1 (3)	13 (34)
Larvaceans	130 (85) *	52 (69)	4 (13)	49 (67)	32 (27)
Podon spp.	$ \begin{array}{c} 0 & (0) \\ 1 & (2) \end{array} $	0 (0)	1(2)	0(2)	242 (267) *
Polychaetes	1 (2)	1 (1)	U (1)	3 (12)	66 (200)
Radiolarians	12 (13)	14 (13) *	3 (5)	0 (2)	0 (0)
Siphonophores	20 (18) *	16 (21)	0 (1)	0 (0)	0 (0)
Amphipods	0 (0)	0 (0)	1 (3)	0 (0)	6 (9)
Bivalves	0 (0)	0 (1)	2 (5)	2 (10)	288 (526) *
Doliolids	3 (7)	24 (49) *	0 (1)	0 (0)	0 (0)

Table 3.3. Pearson correlations between taxa and NMS ordination axes. The highest correlation with any axis is in bold. Only taxa that were significant indicators of a cluster group are shown.

	Axis 1		Axis 2		Axis 3	
	r	r2	r	r2	r	r2
Acartia danae	-0.55	0.31	0.11	0.01	-0.02	0.00
Acartia hudsonica	0.68	0.46	0.39	0.15	0.20	0.04
Acartia longiremis	0.73	0.53	-0.02	0.00	0.16	0.03
Bivalve larvae	0.42	0.18	0.40	0.16	0.03	0.00
Calanus marshallae	0.83	0.68	-0.09	0.01	0.21	0.04
Calocalanus styliremis	-0.56	0.32	0.12	0.01	0.02	0.00
Calanus pacificus	-0.48	0.23	0.27	0.07	0.17	0.03
Centropages abdominalis	0.58	0.34	0.20	0.04	0.01	0.00
Clausocalnus arcuicornis	-0.73	0.53	0.20	0.04	0.08	0.01
C. parapergens	-0.41	0.17	0.03	0.00	0.09	0.01
C. Pergens	-0.47	0.22	-0.05	0.00	0.06	0.00
Corycaeus sp.	-0.29	0.08	0.02	0.03	-0.05	0.00
Ctenocalanus vanus	-0.70	0.49	0.19	0.04	0.33	0.11
Doliolids	-0.51	0.26	0.26	0.07	-0.33	0.11
Euphausiid eggs	0.19	0.04	-0.27	0.07	-0.60	0.36
Euphausiid furcilia I-III	-0.01	0.00	0.59	0.35	-0.01	0.00
Euphausiid nauplii	0.44	0.19	0.03	0.00	-0.61	0.37
Evadne spp.	0.48	0.23	0.33	0.11	-0.07	0.01
Gastropod larvae	0.05	0.00	0.45	0.20	-0.01	0.00
Larvaceans	-0.34	0.11	0.59	0.35	-0.44	0.20
Mesocalanus tenuicornis	-0.62	0.39	0.21	0.05	0.18	0.03
Metridia pacifica	-0.55	0.30	-0.33	0.11	0.26	0.07
Oithona similis	0.15	0.02	0.29	0.08	0.61	0.38
Oncaea spp.	-0.55	0.31	0.08	0.01	0.33	0.11
Paracalanus parvus	-0.55	0.30	0.22	0.05	-0.44	0.19
Podon sp.	0.50	0.25	0.48	0.23	0.12	0.02
Pseudocalanus mimus	0.70	0.49	0.06	0.00	0.35	0.12
Radiolarians	-0.70	0.48	0.28	0.08	0.19	0.04
Scolecithricella minor	-0.10	0.01	-0.46	0.21	0.19	0.04
Siphonophores	-0.69	0.48	0.19	0.04	0.09	0.01

Chapter 4. Variability in the relationship between mesoscale physical and biological patterns in the northern California Current

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Introduction

It is a common goal of ecological studies to understand and predict patterns in the environment. In the ocean, biological patterns of biomass or abundance often are the consequence of underlying physical processes, but can be overlaid with patterns generated by biological processes such as migrations, predation, and reproduction. In areas where bottom-up control dominates (e.g. upwelling ecosystems, extreme environments), there is temptation to infer biological patterns from observed physical patterns. However, the multiple mechanisms that control biological patterns make it difficult to predict them from one or a few measures of the mechanistic or correlative physical variables. The degree to which biological patterns may be predicted from the physics is generally low, both because our understanding of the underlying mechanisms is always less than perfect, and because most biological patterns are only moderately correlated with physical parameters, even where physical controls are strong.

The spatial and temporal scales over which observations of correlative patterns are made influence our ability to predict biological distributions from physical patterns in the ocean. Large, broad scale biological distributions are generally more predictable than smaller scale patterns. For example, basin-scale circulation (oceanic gyres) controls global distributions of many species (e.g. Bieri, 1959, Brinton, 1962, Fleminger, 1964) which are patchy on small-to-coarse (<50 km) scales (Mackas, 1984). On scales of 100's to a few thousand km, patterns in biomass may be created by differences in productivity (e.g. coastal zones compared to the deep sea, coastal upwelling, tidal mixing), freshwater input, or circulation that may vary on annual timescales. The gradient and range of the physical variables over which changes in biomass and abundance are predicted is also important – larger differences in abundance may be expected across large physical gradients, and more predictable changes across broader physical ranges. Temporally, scales of physical control must be short compared to biological controls for predictions based on the physics to be possible, but must be long enough to establish pattern and allow sampling to occur.

Mesoscale circulation features (e.g. eddies, jets, and filaments) and their effects on physical and biological patterns have been well-studied world wide (e.g. . Over the past few decades, satellite observations have documented the frequent occurrence of mesoscale features, prompting investigation into their influences on ocean dynamics in many ecosystems. Mesoscale features are typically bounded by oceanographic fronts, across which larger-than-average gradients in water properties occur. These features may influence biological patterns by aggregating plankton (Aristegui et al., 1997), increasing local production through nutrient fluxes (Crawford et al., 2000, McGillicuddy et al., 2007), or transporting biomass and taxa to hydrographically different locations (Keister et al., In review, Mackas and Galbraith, 2002). But mesoscale features do not result in differences in biomass or abundance everywhere they are observed. For example, large, but shortlived phytoplankton blooms can occur in cyclonic eddies, resulting in elevated biomass at some times, but not others (McGillicuddy et al., 2007). Thus, patterns in the hydrography do not necessarily confer predictable patterns in the biology.

Mesoscale features are seasonally important components of the circulation in all of the eastern boundary upwelling regions (Barton and Aristegui, 2004, Escribano and Hidalgo, 2000, Lutjeharms et al., 1991, Marchesiello et al., 2003, Strub and James, 2000, Waite et al., 2007). In the California Current, several studies of individual mesoscale circulation features have demonstrated their potential for controlling patterns of species distributions by transporting coastal taxa from the nearshore upwelling area to the deep sea (e.g. Barth et al., 2002, Haury, 1984, Mackas et al., 1991). Mesoscale activity varies spatially, seasonally, and inter-annually in the northern California Current (Keister and Strub, 2008), as do biological fields (Huyer et al., 2005, Keister and Peterson, 2003). Thus, the effects of the circulation on biological patterns are also likely to vary. In this study, we add to ongoing investigations of how mesoscale physical variability impacts biological patterns by describing the physical and biological patterns during several research cruises and using the descriptions to examine the predictability of the link between physical and biological variability in the upwelling ecosystem of the NCC. We use examples of the physical and biological patterns obtained during five years of sampling in the California Current. In most years, mesoscale circulation features (dominated by eddies and upwelling filaments) were evident from satellite sea surface temperature (SST) images obtained before or during our cruises.

We conducted zooplankton sampling off southern Oregon and northern California in 1994, 1996, 1999, 2002 and 2006 as part of several different research programs. Most cruises were part of monitoring programs in which regular sampling locations were occupied without regard to the conditions at the time of the cruise. During the 2002 and 2006 cruises, we conducted adaptive sampling in which we targeted offshore expressions of mesoscale circulation features using satellite SST images to determine sampling locations. Here we use selected transects from these cruises to investigate the relationship between patterns in the hydrography and patterns in zooplankton distributions, the degree to which zooplankton distributions are qualitatively predictable from a characterization of the physical environment, and the ability of monitoring programs which employ preplanned sampling transects to capture mesoscale patterns of variability.

Methods

In situ sampling

In situ hydrographic and zooplankton data come from six cruises conducted as part of three different research programs during the summer upwelling season off Oregon and northern California. Cruises in 1994 and 1996 were conducted by R. Emmett (NOAA, Newport, OR) as anchovy and sardine egg and larvae surveys. Cruises in 1999 and 2002 were conducted as part of the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) Program. July 1999 and July 2002 cruises were part of the GLOBEC Long-Term Observations Program (LTOP) led by A. Huyer (Oregon State University); the August 2002 cruise was part of the GLOBEC Mesoscale Processes Studies led by T. Cowles (Oregon State University). In July 2006, data were collected opportunistically during part of a Layered Organization of the Coastal Ocean (LOCO) cruise led by T. Cowles. Additional zooplankton data collected from a coastal station over several days of a GLOBEC cruise in June 2002 were used to calculate confidence intervals on abundance and biomass estimates.

Zooplankton sampling protocols differed among cruises. In 1994 and 1996, vertical net tows were conducted at each station shown in Figures 4.1D and F using the

CALCOFI (California Cooperative Oceanic Fisheries Investigations) protocol (Smith et al., 1985). Tows were made from 5 m off the bottom, or from a maximum of 70 m, to the surface with a 150 µm mesh, 25 cm diameter CalVET net. In all other years (1999, 2002, 2006), zooplankton were collected at each station with a 50 cm diameter, 202 µm mesh net towed vertically from near bottom, or from a maximum of 100 m, to the surface. For all collections, a TSK flowmeter was used to monitor the volume of water filtered. Samples were preserved in a 5% buffered formalin/seawater solution. In the laboratory, zooplankton samples were diluted to 5-10 times the settled volume and subsampled with a 1.1-ml stempel pipette. Two to four subsamples were counted. Zooplankton were identified to species and developmental stage. The abundance of each species (number of individuals m⁻³) was calculated as total number of copepodite and adults (i.e. eggs and nauplii are excluded). Copepods from the genus Clausocalanus were identified to species in all but the 1994 and 1996 samples. All of the species of Clausocalanus that occur off the Oregon coast have warm-water affinities and tend to show similar distributions in relation to hydrographic variables (Keister and Peterson, 2003, Peterson and Keister, 2002). Therefore, we combined the *Clausocalanus* species for these analyses, though such grouping could result in some smearing of signals if distributions varied among species.

Biomass values were calculated from stage-specific values found in the literature (e.g. Chisholm and Roff, 1990, Uye, 1982). None of the copepod species we focus on in this study (described below) are known to perform diel migration below the depth of our net casts, even those that can be strong migrators (e.g. the copepods *Calanus* spp.), so day/night differences were not considered. Other studies in our area have shown little influence of diel migration on upper-100 m biomass or abundances (Peterson, 1972, Peterson and Keister, 2002, Shaw and Robinson, 1998).

At each location where zooplankton were collected, we also performed a CTD cast for temperature, density, and salinity profiles. On some cruises, more stations were sampled for hydrography than zooplankton – those locations are not indicated in Figure 4.1, but are shown in the hydrographic profiles (Figures 4.2, 4.4, 4.6, 4.8, 4.10, 4.12, 4.14). As with zooplankton collections, the depth to which we performed CTD casts varied among cruises. Maximum sampling depth was 70 m during 1994 and 1996, 200 m during the August 2002 and July 2006 cruises, and 1000 m during the July 1999 and 2002 cruises.

SST data from the Advanced Very High Resolution Radiometer (AVHRR) were captured with 1 km resolution and processed by Ocean Imaging of Solana Beach, CA (<u>www.oceani.com</u>) for the U.S. GLOBEC program. All are single-pass images which were either the images used to determine sampling locations during adaptive sampling (August 2002 and July 2006) or were the clearest images available within 1 day of sampling, retrieved after sampling had occurred.

Zooplankton Confidence Intervals

We do not have true replicate samples with which to evaluate our confidence in biomass and abundance estimates, so we used samples collected from a single location over several days to estimate confidence intervals. Samples were collected from a coastal station (60 m water depth) during daylight once per day for five sequential days in June 2002. From those collections, we estimate 95% confidence intervals (C.I.s) for total copepod biomass and abundances were \sim 38-41% of the mean (Table 4.1). Confidence intervals around abundances of individual taxa were much more variable, ranging from 130% to 620% of the mean. However, at this coastal station, lower variability occurred in abundances of coastal, cold-water species (C.I.s ranging from 130-185% of the mean) than abundance of the only oceanic species, which occurred in a single sample (*Paracalanus* parvus, C.I.=620% of the mean). The magnitude of the uncertainties are consistent with other estimates from net collections of mesozooplankton (Wiebe, 1971, Wiebe and Holland, 1968). These uncertainties combine the effects of unresolved horizontal patchiness of zooplankton and errors introduced by collection and sub-sampling techniques in the laboratory. To objectively assess the strength of patterns in this study, we will adopt a constant C.I. of 2/3 of the mean (i.e. two observations must differ by a factor of 5 to be significantly different) and will discuss 'strong' patterns as those across which significant differences of biomass or abundance occurred.

Physical-biological patterns

To investigate the relationship between patterns in SST and zooplankton distributions, and the degree to which we could qualitatively predict such relationships, we took the following four steps. 1) We used satellite SST images to select sampling transects for each cruise along which we predicted that zooplankton distributions would reflect the inferred circulation patterns (i.e. transects which crossed cold upwelling filaments or eddies that occurred off the continental shelf). 2) We identified specific sampling locations along those transects where we hypothesized (based on satellite SST patterns) that coastal taxa would occur in relatively high abundance off the shelf (i.e. in the cold features) compared to surrounding warm-water locations. 3) We selected transects across which no mesoscale features were visible in satellite SST images to contrast with transects along which patterns in SST did occur. 4) Along each selected transect, we examined the *in situ* hydrography (temperature, salinity, density) from CTD profiles and distributions of 'indicator species' (described below) to assess whether the predicted patterns occurred.

Because many zooplankton taxa in our study area are either highly patchy or always in low abundance, we selected seven indicator species on which to focus our analysis and discussion. These taxa are ones we expected, based on prior studies (Keister and Peterson, 2003, Keister et al., in review, Morgan et al., 2003), to have the most predictable relationship to temperature. All tend to be in moderate to high abundance during the summer and have exhibited affinities to either warm, oceanic water or cold, upwelled water off Oregon. Warm-water taxa include the copepods *Ctenocalanus vanus*, *Paracalanus parvus*, *Calanus pacificus*, and several species of *Clausocalanus*. These taxa are found throughout the study area in winter, but are only found in warm, oceanic water during summer. Cold-water taxa include the copepods *Calanus marshallae*, *Acartia longiremis*, and *Pseudocalanus mimus*. These taxa are boreal, neritic taxa that are indicative of summer upwelling off Oregon and are absent in winter.

Transects occupied in July 2006, 1999, 1994, and August 2002 crossed offshore expressions of cold mesoscale circulation features that we hypothesized, based on our accumulated understanding of nearshore circulation in the California Current, were

advective features in which nearshore water was transported off the shelf (Figure 4.1A,B,C,D). We anticipated that those transects would show patterns of zooplankton species distributions that reflected the hydrography. Specifically, our expectation was that the nearshore-to-offshore pattern of species distributions along those transects would show high abundances of coastal taxa nearshore, lower abundances off the continental shelf where warmer water occurred, then a region of elevated coastal abundances offshore where the satellite images showed cold surface temperatures indicative of an advective circulation feature. We expected the opposite pattern in abundances of warm-water, oceanic taxa.

In contrast to patterns along the above transects across which obvious mesoscale circulation features occurred, we show data collected over summers 1999-2003 in a region off Newport, Oregon at 44.6°N (historically referred to as the "NH Line", Huyer et al., 2007) where mesoscale circulation features do not occur, and along transects during two cruises (June 1996 and July 2002) (Figure 4.1F,G) with minimal offshore mesoscale structure. If the predicted relationships held, zooplankton distributions along those transects should have reflected a simple onshelf-offshelf gradient with little structure.

Results

Sea surface temperature images show highly variable circulation patterns during the summer surveys (Figure 4.1). In all years, we sampled transects that crossed regions of relatively cold/coastal and warm/oceanic water, but the complexity of circulation patterns varied among years. Here, we will begin by describing distributions of copepod biomass and coastal taxa collected along the NH Line to show the patterns that exist where mesoscale features do not occur. Then we describe results from cruises conducted in areas where mesoscale features are common, beginning with cruises in which the strongest relationships between SST and zooplankton patterns occurred (large gradients in SST accompanied by significant changes in zooplankton distribution), followed by weaker relationships, and ending with examples of the hydrographic and zooplankton patterns during cruises when no mesoscale circulation features were visible in satellite SST.

NH Line

Copepod biomass and abundances of coastal taxa along the NH Line were consistently, and often significantly, highest over the continental shelf and lowest offshore (Figure 4.2). Biomass varied among cruises, but within each cruise, was never significantly higher at any location offshore than at locations over the shelf. Coastal taxa were always absent, or nearly so, at the three most offshore stations.

July 2006

In July 2006 (Figure 4.1A), we targeted five stations that crossed over a cold upwelling filament off of Cape Mendocino, bracketing two stations in the core of the filament, where we predict relatively high abundance of coastal taxa (circled in Figure 4.1A), by stations in the warm water to the north and south where we predicted low abundances of coastal taxa and higher abundance of oceanic taxa. Along a 10 km stretch of the transect, SST dropped from >15.5°C outside the filament to <12.5°C inside the filament. Temperature, salinity, and density profiles from CTD casts (Figure 4.3) reflect the patterns seen in SST. Isotherms, isohalines, and isopycnals domed upward at the stations that were identified from satellite SST as within the cold filament (stations at 40.4°N and 40.5°N). The stations in the filament were colder, more saline, and denser throughout the water column as compared to the surrounding warm-water stations. Of the oceanic stations, the northernmost station at 41.0°N was slightly cooler, but less saline, than the two southernmost stations. Note that the spacing of our sampling likely did not resolve the actual hydrographic gradients across the filament boundaries.

Total copepod biomass and distributions of individual species were strongly related to the hydrographic patterns (Figure 4.4). Total biomass and abundances of the coastal, cold-water taxa, *Calanus marshallae*, *Acartia longiremis*, and *Pseudocalanus mimus*, were all elevated at the two stations within the upwelling filament relative to surrounding waters, whereas the oceanic, warm-water taxa (*Calanus pacificus*, *Clausocalanus* spp., *Ctenocalanus vanus*, and *Paracalanus parvus*) were all in lower numbers in the filament than in the warmer water to the north and south. Differences in coastal taxa and total biomass were significant assuming confidence intervals of 2/3 of the mean. Of the warmwater taxa, only *Paracalanus parvus* were significantly less abundant within the filament compared to oceanic water to the north.

1 August 2002

On 1 August 2002, satellite SST (Figure 4.1B) showed a cold, cyclonic feature centered at 42.8°N 125.6°W that appears from the SST image to be rooted in the upwelling region just north of Cape Blanco. SST dropped 2.6°C within the feature compared to SST on its shoreward side. We identified three stations along the transect that crossed the feature where we predicted elevated abundances of coastal, cold-water taxa (circled in Figure 4.1B). *In situ* salinity and density (Figure 4.5) match the inferred circulation pattern with upwardly-domed isohalines and isopycnals occurring between 125.4 and 125.8°W. Temperature patterns at depth were more complex. Near-surface temperatures matched the SST image, with <12°C water present at the surface between 125.4 and 125.8°W and warmer water both toward shore and offshore. Deeper temperatures show upwardly domed isotherms both where the surface expression of the feature occurred and more inshore at 125.2°W. Uplifted isoclines characteristic of strong coastal upwelling occurred nearshore. Shading in Figure 4.5 indicates the three stations sampled within the cold, offshore feature seen in the satellite SST image.

Copepod biomass and species distributions along 42.7°N again reflect the satellite SST and *in situ* salinity patterns (Figure 4.6). Total biomass was high in the upwelling area over the shelf (124.6-124.8°W), lower in the warmer, less saline water off the shelf, then significantly elevated in the cold, offshore feature. At the most offshore location (126.0°W), biomass was sharply lower than at the adjacent location within the feature. Abundances of the cold-water copepods *Calanus marshallae* and *Pseudocalanus mimus* were highest on the shelf and in the cold feature and low where warmer water occurred. The other coastal species, *Acartia longiremis*, was not found in high numbers on the shelf – it was only abundant at 125.8°W, the most seaward station of the feature, and was absent in the oceanic water offshore. All of the coastal taxa were significantly more abundant at one or more of the stations within the feature than at shoreward and seaward locations.

The warm-water, oceanic taxa *Calanus pacificus, Paracalanus parvus*, *Ctenocalanus vanus*, and *Clausocalanus* spp. were all significantly most abundant at the offshore station and in low abundances in the feature and nearshore. Slightly (though not significantly) elevated numbers of *C. pacificus*, *P. parvus*, and *C. vanus* occurred in the warmer, fresher water between the feature and the coast.

July 1999

In July 1999, satellite SST showed a cold upwelling filament extending seaward south of Cape Blanco (Figure 4.1C). A transect at 41.9°N crossed from the cold nearshore area, over a region of slightly warmer (~14°C SST) surface water, then into the cold (12.2°C SST) offshore filament. We predicted that the two offshore stations (circled in Figure 4.1C), particularly the most seaward station, would have higher abundances of coldwater taxa than the stations towards the continental shelf. Hydrographic profiles (Figure 4.7) showed up-tilted isoclines both over the shelf indicating coastal upwelling, and offshore where the cold filament was apparent in the SSTs.

Total copepod biomass (Figure 4.8A) was highest over the shelf and at two offshore stations, but no station was significantly different than others. Abundances of cold-water species (Figure 4.8B,C) were all elevated in the filament and over the shelf whereas abundances of warm-water taxa (Figure 4.8B,D) were highest in warmer water near the shelf break.

July 1994

In July 1994, SSTs were high throughout the region (Figure 4.1D). An upwelling filament extended offshore of Cape Blanco, but the low range of SSTs across the filament indicate that it was not as strong as features sampled in other years. A sampling transect along 43.1°N crossed over the offshore northern branch of the cool feature. SSTs were \sim 1.6°C lower at the coolest point of the filament than in the warmer water toward shore. From the SST image, we identified the 5th and (secondarily) 4th stations from the seaward edge as locations where we expected cold, coastal water and the associated taxa to occur (circled in Figure 4.1D), but those stations fell on either side of the location were coldest SST occurred. The *in situ* hydrography during the 1994 cruise (Figure 4.9) shows warm surface temperatures across the entire transect in 1994, but temperatures below 20 m depth were cool. Upwardly domed isohalines and isopycnals 100-130 km offshore (125.8-
126.2°W) demark the hydrographic feature seen in satellite SST as the tip of the upwelling filament. The feature appeared broader in temperature profiles - doming of isotherms occurred between 100-130 km offshore, but the sharpest temperature front occurred farther offshore between the 144 and 180 km stations. At the outer edge of the transect, high temperatures and low salinities characteristic of oceanic water occurred.

Copepod biomass in July 1994 was elevated at the most nearshore station and at the station 126 km offshore where we had predicted higher biomass and abundance of coastal species. However, biomass was not elevated at 108 km, where we had also predicted increased biomass. Biomass was high one station seaward of the predicted stations (at 144 km). None of the differences were significant.

Abundances of the cold-water taxa *Calanus marshallae* and *Acartia longiremis*, were significantly higher at one or more stations within the filament than at most of the surrounding locations (Figure 4.10 panels B, C), although abundance of *A. longiremis* was also very high at the 144 km station we had not identified as part of the filament. Abundances *Pseudocalanus mimus* (Figure 4.10C), showed only a slight trend toward higher numbers in the filament. All of the cold-water taxa were absent or in very low numbers in the oceanic water beyond 144 km and tended to be in lower abundance between the filament and nearshore stations.

Warm-water taxa tended to be less abundant in the filament and over the shelf than in warmer water (Figure 4.10B,D). However, the patterns were variable. *Calanus pacificus* and *Paracalanus parvus* were abundant at the seaward (126 km) station of the filament. *Clausocalanus* spp. and *Ctenocalanus vanus* were most abundant at the offshore stations and uncommon in the cold filament. All of the warm-water taxa were more abundant inshore of the filament stations than at that station. None were abundant over the shelf.

6 August 2002

On 6 August, 2002, we sampled a southern transect at 41.9°N that extended through a broad area of coastal upwelling to warm, oceanic water offshore (Figure 4.1E). The pattern of i*n situ* temperatures (Figure 4.11) was similar to SST – temperatures were cooler between the coast and 125.2°W, beyond which higher temperatures occurred.

Salinity profiles showed more structure than did temperature profiles. Isopycnals and isohalines were upwardly-domed between ~125.0°W-125.3°W indicating a circulation feature that is not apparent in the satellite image except as a temperature front. Isopycnals indicate upwelling at the inner shelf stations and oceanic water offshore.

Along 41.9°N, copepod biomass was very high nearshore and quickly dropped to significantly lower values on the outer shelf and offshore (Figure 4.12). Biomass was uniformly low off the shelf. The coastal species were all most abundant at the most nearshore stations, decreasing in abundance off the shelf. All were absent, or nearly so, beyond 125.2°W. Warm-water taxa showed the opposite pattern – they were significantly more abundant at the two outermost, oceanic stations and less common inshore of 125.2°W (Figure 4.12). None were collected from the most coastal station.

June 1996

In 1996, an across-shelf gradient from cold nearshore upwelling to warm, offshore SSTs occurred (Figure 4.1F). No mesoscale circulation features occurred offshore. The *in situ* hydrography (Figure 4.13) shows broadly spaced up-tilted isohalines and isopycnals nearshore, indicating the broad region of coastal upwelling visible in SSTs. Warm, low salinity (<31.5 psu) water characteristic of the Columbia River plume, which is advected offshore and south from 46.2°N during summer upwelling, was present in the surface layer seaward of 60 km offshore. The depth of the plume is typically between 10-30 m (Huyer et al., 2005), and was about 20 m at this location in 1996. Below the plume, cooler, denser oceanic water occurred. As in the SST image, no hydrographic structure occurred offshore that would indicate that a mesoscale circulation feature was present in 1996.

Zooplankton distributions in 1996 showed simple onshore-offshore patterns related to the hydrography (Figure 4.14). Total biomass (Figure 4.14A) and abundances of coldwater coastal taxa (Figure 4.14B,C) were significantly elevated within the broad nearshore upwelling zone. Warm-water taxa (Figure 4.14B,D) were most abundant and fairly evenly distributed across the transect seaward of the upwelling region. As expected from the hydrography and satellite images (Figures 4.1F and 4.13), no offshore stations showed strongly elevated numbers of coastal species or depressed numbers of oceanic taxa that would indicate an advective circulation feature.

July 2002

As in June 1996, no feature occurred offshore along the transect in July 2002 (Figure 4.1G) – the SST image indicated warm water immediately adjacent to the coast, separated from warm offshore oceanic water by a band of cold coastal upwelling. Hydrographic profiles also indicated coastal upwelling (Figure 4.15). Progressively deepening isoclines seaward of the shelf break indicated a coastal-to-oceanic pattern uninterrupted by advective circulation features. The small, nearshore region of warm surface water seen in the satellite SST was also seen in the CTD profiles. Salinity profiles did not show fresher water there, indicating that localized warming rather than input of terrestrial or oceanic water may have been responsible for the elevated temperatures.

Copepod biomass was high over the shelf and low offshore (Figure 4.16A). Coldwater taxa (Figure 4.16B,C) were most abundant over the continental shelf whereas warmwater taxa (Figure 4.16 B,D) which were in low abundances everywhere, were most abundant offshore and generally decreased in abundance toward the shelf. Moderate numbers of the warm-water species, *Ctenocalanus vanus* (Figure 4.16D), occurred at the warm, nearshore station. No other warm-water species occurred there.

Discussion

In all cruises, patterns in zooplankton distributions were related to patterns in satellite SST, but the strength of the relationships varied greatly among cruises. The features across which largest gradients in SST occurred were related to the largest changes in zooplankton biomass and abundances, whereas weaker SST features resulted in weaker and less predictable biological patterns. The two transects along which mesoscale features resulted in the largest SST gradients (>3°C across the filament in July 2006; 2.5°C across the feature in August 2002) showed significant differences in zooplankton biomass and abundance inside versus outside of the features (Figures 4.4, 4.6). Along transects that crossed smaller, weaker features (2.3°C range in July 1999; 1.6°C in 1994), coastal taxa tended to be more abundant where cold water occurred than in surrounding warmer water, but the magnitude of the differences were not as large (Figures 4.8, 4.10). All contrasted

with patterns along transects on the NH Line and those which did not cross mesoscale circulation features (June 1996, 41.9°N in August 2002, July 2002). Along those transects, coastal taxa were only abundant over the shelf in the upwelling region and were absent or in low abundance in oceanic water.

Deviations from expected patterns

Although SST patterns tended to be reflected in biological patterns, particularly where SST gradients were large, relative abundances of taxa at any particular station were not predictable. There are several possible mechanisms that could have caused deviations from expected patterns. One of the largest potential factors leading to variability in relative biomass and abundances is the temporal and spatial variability of species abundances in the coastal source waters of circulation features. Temporally, coastal zooplankton biomass and abundances of individual taxa vary on intra-seasonal, seasonal, and interannual scales. The variability is such that taxa may be absent from locations where, at other times, they dominate. In our study region, alongshore currents reverse from poleward in winter to equatorward in summer, resulting in seasonal shifts in zooplankton communities (Keister and Peterson, 2003, Peterson and Miller, 1977). Interannually, large climate-related shifts in abundances of individual species occur (Peterson and Keister, 2003).

Spatial patchiness can be just as extreme. Zooplankton distributions in July 1999 (Figure 4.8) illustrate the potential coarse-scale (5-20 km) spatial patchiness that occurs on the shelf. Total copepod biomass and abundances of coastal species varied by >3X at stations on the shelf where abundances of coastal taxa are generally considered 'high.' Even in the absence of a strong hydrographic gradient, *Pseudocalanus mimus* and *Acartia longiremis* were, respectively, 3X and 40X less abundant at 124.3°W than <10 km away at 124.4°W. Such patchiness also occurs alongshore on the shelf (Keister et al., in review) and may result in higher or lower than expected abundances in circulation features. For example, distributions along the northern transect in August 2002 (Figure 4.6) illustrate the potential effect of alongshore variability on offshore distributions - abundances of coastal taxa were higher in the circulation feature than on the shelf. The timescales of advection

within these features (on the order of 1-3 weeks) were shorter than would allow growth to significantly influence the biomass or population structure. The elevated offshore abundances likely reflect higher abundances over the shelf in the source waters to the north compared to on the shelf at the latitude sampled. Abundances of zooplankton are frequently higher north of Cape Blanco than south (Huyer et al., 2005, Keister et al., in review and unpub. data), so abundances in the feature probably reflect their transport pathway from the shelf to the feature. Notably, biomass and abundances of neritic taxa were highest at the most seaward location in the feature at 125.8°N and declined coastward, perhaps as mixing with oceanic water occurred. Several neritic taxa not shown also occurred in relatively high abundance in the feature. Barnacle nauplii and the copepods, *Centropages abdominalis* and *Acartia hudsonica*, all of which tend to occur only very nearshore in our study area in the absence of mesoscale circulation, were found in the feature but not in surrounding oceanic water. Those occurrences suggest that the circulation was rooted very close to shore, within a few km of the coastline.

While an absence of species from locations where they were expected may have been due to temporal variability or patchiness in source waters, the occurrence of species where we did not predict their occurrence from SST patterns was most likely due to mixing or the vertical shear of water masses. Oceanic boundaries are biologically 'leaky' (Mackas and Coyle, 2005), and mixing of water masses in advective environments is high, resulting in mixed zooplankton communities. Shear of water types via surface layer Ekman transport or vertically-sheared circulation leads to stratified water columns containing multiple community types, across which vertical-net tows integrate. In July 1994 (Figure 4.10), the weak SST gradients relative to those across other features, and the mix of cold and warm-water species we observed at stations in the filament may have resulted from shearing and mixing along the boundaries of the feature.

Other mechanisms that may affect the relationship between the physical and biological patterns are predation, behavior, and alternative mechanisms of physical variability that generate similar patterns. For example, oceanic Ekman pumping, rather than horizontal transport, may cause localized areas of cold surface water that appear similar to mesoscale circulation features. Such processes may result in increased production and biomass in the deep ocean, but not abundances of coastal taxa. Biological patterns cannot be easily predicted from the hydrography where temporal and spatial variability occurs in the coastal 'source' waters, or the mechanisms behind the observed physical patterns are not correctly inferred.

Ecological impacts

Distinct patterns of elevated biomass and abundances of coastal taxa within offshore expressions of mesoscale features demonstrates the ecological consequences of the circulation. These circulation features act as a mechanism to transfer a portion of the high shelf production offshore to the deep California Current. The ecological impacts of individual upwelling filaments and eddies have been documented in several studies. The circulation features result in locally elevated plankton biomass (Keister et al., in review, Mackas et al., 1991) and production (Smith and Lane, 1991, Yebra et al., 2004) and may result in significant losses to some shelf populations (Keister et al., in review). Upper trophic level organisms utilize the fronts created by the features (Tynan et al., 2005) implying that their piscine prey are also more abundant there.

One effect of the offshore-directed circulation features seen in this study is that they appear to result in biomass that is spread more broadly between the coastal and ocean zone than when circulation features are absent. Biomass along transects when mesoscale features were present ranged ~3-4X across the transects (Figures 4.6, 4.8, 4.10) whereas biomass ranged >10X along transects where no features occurred (Figures 4.12, 4.14, 4.16), with highest biomass occurring over the shelf and lowest offshore. Biomass was significantly higher over the shelf than at offshore locations in all cruises where mesoscale features did not occur offshore but was never significantly higher over the shelf along transects which did cross offshore features. Because some populations which prey upon zooplankton mainly occur over the shelf whereas others primarily occur over the slope and offshore (e.g. fish larvae, Auth and Brodeur, 2006), the large temporal and spatial variability that occurred as a result of the circulation patterns may have had very different consequences for the success of different planktivorous populations. Previous studies in the Northeast Pacific (Keister et al., in review, Mackas and Yelland, 1999) have found that mesoscale circulation features result in seaward displacement of only a small portion of the coastal biomass. However, species patterns in several of the cruises here and found in eddies off Vancouver Island (Mackas and Galbraith, 2002) indicate that at some times and locations, abundances can be as high or higher offshore in the features than over the shelf. These patterns demonstrate that circulation features can constitute an important mechanism for transporting water and coastal material to sea and they should be sampled as part of monitoring programs that aim to capture changes in such fluxes.

Field sampling design

Dynamic circulation features which result in localized hot-spots of production and biomass may substantially contribute to the overall production of systems in which they occur (Michaels, 2007). Our results demonstrate that it is difficult to sample these features reliably using the widely-spaced, pre-determined sampling transects used in many monitoring programs, so much of that production could be missed by standard sampling strategies. In this study, we show selected cruises during which sampling of offshore circulation features occurred. Using similar sampling designs, we also conducted numerous cruises not shown here during which mesoscale circulation features were present, but were not sampled on the appropriate spatial scale.

The dynamic nature of mesoscale circulation features makes them difficult to sample. Sampling must either occur with high enough spatial resolution to assure sampling features when/where they occur, or must incorporate adaptive sampling in which stations are chosen based on a recent view of the hydrography. Sampling strategies based on occupation of pre-determined, widely-spaced sampling locations are not sufficient to capture the variability. In the California Current, mesoscale circulation features can have spatial scales of >200 km, making them easy to sample with pre-planned transects, but the smaller mesoscale features we measured may have spatial scales of <50 km along one zonal or meridional direction. Such features require sampling every 15-20 km to resolve the spatial patterns.

Adaptive sampling requires knowledge of the spatial pattern in hydrography at the time of sampling. We've shown that satellite SST images can be used to guide sampling in regions where circulation features result in visible surface temperature gradients (e.g. Figure 4.1). But up-to-date images cannot always be obtained while at sea or in areas prone to cloud-cover. In those cases, an understanding of the dynamics and temporal scales of the local circulation is needed to make decisions based on 'old' images. This 'intuition-guided' sampling should be supported by shipboard under-way data for real-time assessment of the ship's position relative to observed hydrographic features or by conducting an ADCP section before selecting sampling stations to help sample as close to the center of features as possible.

Our August 2002 sampling illustrates the need for up-to-date hydrographic data. Winds prior to the cruise had been strongly equatorward for >8 days, resulting in the circulation patterns observed in the 1 August image (Figure 4.1B) which we used to guide our sampling locations over the next week. We occupied the northern (42.7°N) and southern (41.9°N) transects on 4 and 6 August, respectively, without updated satellite images. Winds remained equatorward through 4 August, but between sampling the northern line and the southern line, winds relaxed and reversed, causing a relaxation of coastal upwelling and a shoreward push of surface water. An SST image from 6 August (Figure 4.1E) shows that the filament that had been a dominant feature along the southern transect on 1 August (Figure 4.1B) was no longer clearly defined and the upwelling front had collapsed coastward. The 6 August SST image more closely matches the in situ hydrography (Figure 4.7) and species distributions (Figure 4.8) we measured along the southern transect, which were different than we expected based on the earlier SST image. The significant hydrographic changes that occurred over a few days at sea provide a clear example of the problem associated with using recent, but out-dated, satellite images to drive sampling decisions.

Conclusions

Because zooplankton play a critical role in marine ecosystems as the link between primary and upper trophic level production, advancing our ability to study mechanisms of their variability would substantially further our understanding of ecosystem processes. Currently, the rate at which scientists are able to gather species information is hindered by the time commitment required for taxonomic identification. Although rapid taxonomic identification is advancing through optical, visual, and genomic techniques, identification of most organisms remains time-consuming and labor-intensive. On the other hand, the relative ease and rapidity of obtaining physical measurements allows us to observe the physical environment in near-real time and over large spatial scales. Therefore, developing the ability to predict biological patterns from physical patterns, and determining when such predictions are feasible, would be a big step towards improving our understanding of biological variability. The key to gaining such predictive power lies in understanding the temporal evolution of physical-biological relationships and the mechanisms behind them.

In the California Current, as in other boundary current ecosystems, circulation is a dominant force structuring distributions of zooplankton, particularly during summer upwelling. In this study, we used our knowledge of underlying physical mechanisms to explore the degree to which we can use observed physical patterns to predict biological patterns. We found that the strength of the relationship between the circulation patterns (here inferred from SST) and the zooplankton distributions largely depended upon the strength of the physical patterns. Using examples from six research cruises in five summers, we found that we can predict that elevated zooplankton biomass and abundances of coastal organisms will occur offshore when advective circulation features are present and will not occur offshore in the absence of such features. We were not able to predict with accuracy the abundances of taxa at any location or the presence/absence of specific taxa at specific locations. The predictive ability arose from our fundamental understanding of the mechanism behind the relationships – i.e. dynamics of offshore advection of coastal water masses and the associated plankton in mesoscale circulation features. The predictive ability ended with generalization of 'relative abundance' patterns because patchy

abundances, interannual variability in populations, biologically-driven processes, and mixing of water masses added uncertainty.

Adequately sampling patterns in the environment such that the important ecosystem processes are captured is a continuous challenge in ecology, particularly in pelagic ecology where the environment itself is not just changing in time, but is moving in space over fixed locations. Designing sampling strategies to quantitatively assess patterns is difficult – the balance between temporal and spatial resolution prevents synoptic observations over large scales. A strength of long-term observations programs is that 'baselines' can be developed against which we can evaluate changes. After >10 years of sampling within the U.S. GLOBEC program, we can now use the conceptual model we've developed of the dynamics in our study area to quickly identify unusual patterns and occurrences. However, many monitoring programs, including ours, sample at coarse temporal and spatial resolution and thus miss much of the natural variability. Future studies must give careful thought to sampling strategies to capture patterns on the mesoscale.

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Figure 4.1. Sea surface temperature maps from satellite AVHRR data during each cruise. Locations of zooplankton net tows are marked and those occurring at cold, offshore locations are circled. Note that cloud masks are not applied except in the July 1999 and 2002 images. Images are labeled by the local date and time of the satellite pass. CB=Cape Blanco, CM=Cape Mendocino.



Figure 4.2. Distribution of copepod biomass and abundances of cold-water copepods during summer along the NH line (44.7°N). Symbols represent the month/year of each cruise. Dashed vertical lines indicate the 200 m shelf break.

July 2006 Temperature Depth (m) 12 14 Salinity - 33 Depth (m) 33.5 Density 25.5 Depth (m) 25.5 200 <u>↓</u> 41.0 40.5 40.4 39.8 39.6 Latitude (°N)

Figure 4.3. Temperature, salinity, and density profiles from CTD casts during the July 2006 cruise off Cape Mendocino. Stations occupied are indicated by vertical lines and latitude labels. Gray highlighting at 40.4°N and 40.5°N indicates stations in the cold filament identified in Figure 4.1A. Dashed horizontal line at 100 m depth shows the maximum depth of zooplankton net tows. Color map is satellite SST image from Figure 4.1A.



Figure 4.4. Total copepod biomass and abundances of taxa collected during the July 2006 cruise off Cape Mendocino. Taxa are designated as cold-water (C) or warm-water (W) type. Note that abundances of *A. longiremis* and *P. parvus* are on the right axes. Gray highlighting indicates stations within the cold filament. Color map is satellite SST image from Figure 4.1A.



Figure 4.5. Temperature, salinity, and density profiles from CTD casts during August 2002 along the transect at 42.7°N. Stations occupied are indicated by vertical lines. Gray shading indicates stations in the cold feature identified in Figure 4.1B. Dashed horizontal line at 100 m depth shows the maximum depth of net tows. Color map is satellite SST image from Figure 4.1B.



Figure 4.6. Abundances of taxa collected during August 2002 along the transect at 42.7°N. Taxa are designated as cold-water (C) or warm-water (W) type. Gray highlighting indicates stations within the cold feature identified in Figure 4.1B; the vertical dashed line shows the location of the 13°C SST isotherm to indicate the upwelling front. Color map is satellite SST image from Figure 4.1B.



Figure 4.7. Temperature, salinity, and density profiles from CTD casts during July 1999 along a transect at 41.9°N. Stations sampled for zooplankton are labeled with longitudes along the bottom axis, locations of CTD profiles are indicated by vertical lines in each panel. Gray shading indicates stations in the cold offshore filament, identified from Figure 4.1C. Horizontal dashed line shows the depth of net tows. Color map is satellite SST image from Figure 4.1C.



Figure 4.8. Copepod Biomass and abundances of zooplankton collected during July 1999. Gray highlighting shows stations in the cold filament, identified from Figure 4.1C; the vertical dashed line is the location of the 13°C SST isotherm to indicate the upwelling front. Stations occupied are indicated by distance and latitude labels in top and bottom panels. Note that *Acartia longiremis* abundance is on the 2nd axis. Taxa are designated as cold-water (C) or warm-water (W) type. Color map is satellite SST image from Figure 4.1C.

July 1994 Temperature (°C) 0 Depth (m) 20 40 60 80 180 162 72 63 54 45 36 27 18 9 144 126 108 90 Station Locations (km) Salinity 0 Depth (m) 20 40 60 ŝ 80 Density (kg m⁻³) 0 Depth (m) 20 127 126 125 124 25 40 60 80 126.8 126.4 126.0 125.6 125.2 124.8 124.4 Longitude (°W)

Figure 4.9. Temperature, salinity, and density profiles from CTD casts during July 1994. Zooplankton were not collected at every station – stations sampled for zooplankton are labeled with distances in the top panel, and locations of CTD profiles are indicated by vertical lines. Gray shading indicates stations in the cold offshore filament, identified from Figure 4.1D. Color map is satellite SST image from Figure 4.1D.



Figure 4.10. Total copepod biomass and abundances of individual species collected during July 1994. Gray highlighting shows stations within the cold filament, identified from Figure 4.1D; the vertical dashed line is the location of the 16°C SST isotherm to indicate the upwelling front. Stations occupied are indicated by distance labels. Note that abundances labels for *C. marshallae* (panel B), *A. longiremis* (panel C) and *P. parvus* (panel D) are on the right axes. Taxa are designated as cold-water (C) or warm-water (W) type. Color map is satellite SST image from Figure 4.1D.



Figure 4.11. Temperature, salinity, and density profiles from CTD casts during August 2002 along the transect at 41.9°N. Stations occupied are indicated by vertical lines. Horizontal dashed lines at 100 m depth shows the maximum depth of zooplankton net tows. Zooplankton were not collected at every station – latitude labels on the lower axis shows locations of zooplankton net tows. Color map is satellite SST image from Figure 4.1E.



Figure 4.12. Abundances of taxa collected during August 2002 along the transect at 41.9°N. Taxa are designated as cold-water (C) or warm-water (W) type. Stations where zooplankton were collected are indicated by latitude labels along the x-axis. The vertical dashed line is the location of the 13°C SST isotherm to indicate the upwelling front. Color map is satellite SST image from Figure 4.1E.



Figure 4.13. Temperature, salinity, and density profiles from CTD casts during June 1996 Zooplankton were not collected at every station – stations sampled for zooplankton are labeled with distances in top panel; vertical lines indicate locations of CTD profiles. Color map is satellite SST image from Figure 4.1F.



Figure 4.14. Total copepod biomass and abundances of individual species collected during June 1996. Stations occupied are indicated by distance labels. Note that abundances labels for *A. longiremis* (panel C) and *P. parvus* (panel D) are on the right axes. Taxa are designated as cold-water (C) or warm-water (W) type. The vertical dashed line shows the location of the 13°C SST isotherm to indicate the upwelling front. Color map is satellite SST image from Figure 4.1F.



Figure 4.15. Temperature, salinity, and density profiles from CTD casts during July 2002 along 41.9°N. Stations sampled for zooplankton are labeled with longitudes along the bottom axis, locations of CTD profiles are indicated by vertical lines in each panel. Color map is satellite SST image from Figure 4.1G.



Figure 4.16. Total copepod biomass and abundances of individual species collected during July 2002. Stations occupied are indicated by longitude labels in bottom panels. The vertical dashed line shows the location of the 13°C SST isotherm to indicate the upwelling front. Note that *Acartia longiremis* abundance is on the 2nd axis. Taxa are designated as cold-water (C) or warm-water (W) type. Note that the station at 126.0°W is not spaced to scale. Color map is satellite SST image from Figure 4.1G.

Table 4.1. Estimate of 95% confidence interval on copepod biomass and abundance using collections from a coastal station ("NH5"), 44.65°N 124.18°W, 60 m water depth.

Collection date	Collection time	Total Biomass	Total Abundance
4 June 2002	19:25	20.8	3261
5 June 2002	17:50	25.5	4577
6 June 2002	10:40	16.9	2414
7 June 2002	08:30	35.0	5766
8 June 2002	11:50	19.1	3474
Mean		23.5	3898
Std. Error		3.2	580
95% C.I.		± 8.9	± 1610
C.I. % Of Mean		38%	41%

Chapter 5. Conclusions

In this dissertation, the links between mesoscale physical variability and zooplankton distributions were examined from three perspectives. Observations of sea surface height from satellite altimetry were used to analyze spatial and temporal variability in the energy in mesoscale circulation in the northern California Current (Chapter 2). It was then demonstrated that individual advective features influence distributions of coastal and oceanic zooplankton species (Chapter 3). Lastly, satellite images of sea surface temperature and *in situ* collections of zooplankton were used to examine variability in the relationship between physical patterns and zooplankton distributions (Chapter 4). These studies extend our understanding of the role of mesoscale circulation in transporting water, biomass, and coastal taxa from the continental shelf to the oligotrophic deep sea. Collectively, they further our understanding of the variability in the physical-biological processes that control zooplankton distributions and cross-shelf exchange. In this concluding chapter, the results of the preceding chapters are synthesized to show the role of one of the dominant factors (mesoscale energy) controlling cross-shelf distributions of plankton in the northern California Current. The physical and ecological implications of the findings are discussed and compared to those from other Eastern Boundary Current systems. Finally, questions that both remain from, and were brought to light by, this research are posed.

In Chapter 2, "Spatial and interannual variability in mesoscale circulation in the northern California Current System," variability in mesoscale circulation was investigated using satellite altimetry from 1992-2006. The variability in sea surface height (expressed as variance, or 'energy') that occurs on 4-18 week, 'mesoscale,' periods was characterized. The alongshore and zonal variability in the energy was described - regions of high and low energy, which were related to coastline and bottom topography, were found. Temporally, the seasonal peak in energy occurred on average in August, the month when the climatological peak in zooplankton biomass also occurs over the shelf (Peterson and Miller, 1977, Peterson unpublished data). Because the amplitude and seasonal timing of

both peak mesoscale activity and peak zooplankton biomass vary interannually, changes in the relative timing of the two could lead to substantial changes in cross-shelf biomass flux.

To explore mechanisms of variability in the circulation, a 1993-2006 time series of the energy averaged over the region 36°N-43°N, between 1-3° offshore (the most energetic region of the NCC) was developed, which serves as an index of mesoscale circulation in the NCC. Such a quantification of the interannual variability in mesoscale activity had not before been attempted, but was a necessary step toward advancing our understanding of the potential mechanisms of variability. The index was then compared to time series of potential forcings, including winds, alongshore transport, and stratification, but no single mechanism or combination of mechanisms satisfactorily explained the variability in the energy.

Elevated energy in winter during El Niño events, dampened energy the following summers, and low energy during some years of a negative Pacific Decadal Oscillation lead to a working hypothesis that the annual amplitude of mesoscale energy in the NCC is controlled by both wind and stratification. An exploration of the interannual variability in available potential energy using field data from July GLOBEC cruises provided preliminary evidence for the hypothesis. Stratification has been previously suggested as a control on mesoscale activity (Durazo and Baumgartner, 2002, Hormazabal et al., 2004b), with weaker stratification leading to lower mesoscale energy. But the small amount of field data, and the unexpected lack of direct correspondence to upwelling winds, leaves the hypothesis open for future exploration. Future modeling efforts may help resolve the mechanisms of variability.

In Chapter 3, "Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California Current," the role that mesoscale circulation features play in structuring zooplankton distributions was investigated using a cruise conducted in August 2000. During that cruise, circulation patterns created both retentive and advective regions. Inshore of where the coastal upwelling jet deviated around Heceta Bank, low flow velocities resulted in the retention of upwelled water, and chlorophyll and zooplankton biomass were high. Spawning female euphausiids and large numbers of euphausiid eggs, as well as euphausiid and *Calanus*

nauplii, were collected over the Heceta Bank region. To the south of Heceta Bank, the upwelling jet meandered offshore of Cape Blanco creating an upwelling filament in which high zonal velocities resulted in the offshore advection of large volumes of coastal water and the associated taxa. Concurrent observations of sea birds and mammals (Ainley et al., 2005, Tynan et al., 2005) demonstrated the ecological importance of the mesoscale feature to upper trophic level organisms. Yet, the fate of the zooplankton that were advected offshore, and their role in population dynamics and secondary production, remains uncertain. Although it was estimated that a small fraction of the total shelf zooplankton biomass was advected seaward in the filament, and therefore that losses to shelf populations may be negligible, distributions of early life stages of euphausiids indicated that a substantial portion euphausiid production may have been advected offshore during the cruise. Therefore, a better understanding of potential paths by which organisms may return to the shelf would advance our understanding of population dynamics of coastal species in this region.

Certainly, many individuals which are lost from the shelf in mesoscale features suffer mortality due to predation, temperatures that exceed physiological tolerances, or food depletion, but it is also possible that some may return to the shelf. In the upper 50-100 m where most zooplankton reside, mechanisms of return exist primarily through episodic reversals of upwelling winds, which result in shoreward Ekman surface flow and dissipation of the smaller mesoscale features. During the August 2000 cruise, this potential pathway was illustrated by a near-surface (15 m) drogued drifter that returned to the slope from the northern offshore tip of the upwelling filament (Barth et al., 2005b), a distance of ~ 100 km. On longer time scales, drifter paths indicate that organisms that move offshore late in the upwelling season (August/September), remain near surface, and survive through fall, may return to the shelf a month or more following the seasonal shift to downwelling (Barth et al., 2000). It seems unlikely that a substantial portion of the zooplankton that are advected offshore may survive in upper 20 m of the oligotrophic ocean long enough to return to the shelf in winter, but some lipid-bearing species such as Eucalanus spp. (Smith and Lane, 1991) and Calanus spp. (Peterson, 1980) may be able to do so. Deeper in the water column, return circulation may occur on shorter time scales in

the poleward, shelf-break undercurrent (Pierce et al., 2000) or on the equatorward side of upwelling filaments (Brink *et al.*, 1991), though only organisms that reside at depths of >100 m will be able to exploit those currents.

Though a fairly small fraction of shelf biomass was displaced seaward during the August 2000 cruise, the concentration relative to the offshore biomass concentration was significant. The flux resulted in 3-4 fold increase in biomass within the bounds of the filament compared to the surrounding ocean. More than 900 metric tons of carbon in the form of zooplankton was transported seaward each day in the circulation feature. The flux would be substantially higher if phytoplankton, migratory zooplankton (e.g. adult euphausiids, amphipods, and shrimp), and ichthyoplankton were considered. To put the transport into an ecological perspective, it was estimated that the biomass advected over the 2000 m isobath each day was equivalent (in weight, but not composition) to the energy required to sustain >1800 humpback whales (which eat ≤ 0.5 tons of carbon as krill and fish per day) should the whales be able to exploit this windfall. However, because this quantification of the flux relative to shelf biomass is rare in the literature, more studies of offshore losses due to mesoscale advection are necessary to constrain the estimates. Large variability in the volume transport of features and interannual variability in zooplankton biomass will lead to high variance.

To extend the above analyses to include circulation features of varying structure, zooplankton distributions along transects selected from six research cruises during five summers of sampling off Oregon and northern California were examined. The goal of the research in Chapter 4, "Variability in the relationship between mesoscale physical and biological patterns in the northern California Current," was to examine the variability in the relationship between circulation patterns as inferred from satellite sea surface temperature (SST) and zooplankton distributions. Four of the selected transects crossed offshore expressions of cold mesoscale circulation features. Those were contrasted with transects which were occupied when no advective mesoscale circulation features occurred. Distributions of coastal and oceanic zooplankton reflected the circulation patterns. Coastal taxa tended to occur in significantly higher abundances offshore where mesoscale circulation features were noted in SST images, whereas oceanic taxa were most abundant in warm, oceanic waters offshore and when warm water occurred between the nearshore upwelling zone and cold offshore features. However, relative abundances of cold versus warm water taxa varied among circulation features, and biomass and species abundances varied substantially by location.

The primary characteristics of the circulation of the four major Eastern Boundary Currents (California Current, Benguela Current, Canary Current, and Humboldt Current) are comparable (Relvas et al., 2007). In all four systems, broad, offshore equatorward flow forms the main body of the current and is punctuated by seasonal or year-round coastal upwelling generated by equatorward winds. During upwelling, alongshore-flowing upwelling jets develop, the meanders of which lead to the formation of eddies and upwelling filaments which can transport cold, nutrient rich water offshore. Topographic features such as capes are important influences on alongshore variations in upwelling intensity and the generation of meanders of the upwelling jets.

Although there have been few studies of mesoscale variability in the Benguela Current System, several large research programs in the Canary Current (especially the Canary Islands Azores Gibraltar Observations, CANIGO) and Humboldt Current Systems (FONDAP - Fondo de Investigacion Avanzado en Areas Prioritarias) have increased our understanding of the role mesoscale features play in structuring biological distributions and carbon fluxes in those regions. As in the California Current System, eddies and upwelling filaments are common during summer and result in elevated abundances of coastal phytoplankton and zooplankton taxa in oceanic areas (Escribano and Hidalgo, 2000, Hernandez-Leon et al., 2007, Mackas et al., 1991, Morales et al., 2007) and can be sites of elevated numbers of coastal fish larvae (Hormazabal et al., 2004a, Rodriguez et al., 1999).

The relative importance of filaments and eddies in the offshore advection of coastal production among the Eastern Boundary Currents ecosystems is difficult to assess both because few direct measures of the biomass transport within mesoscale features have been made, and because values in the literature are not measured or reported on comparable temporal and spatial scales. Marin et al. (2003) used SeaWiFs images of 'squirts' off Chile to estimate a maximum offshore advection of 1.6×10^3 metric tons of carbon per day in the form of chlorophyll, resulting in a net export of ~12% of the net coastal carbon production.

However, Morales et al. (2007) suggested that Marin et al.'s study underestimated the impact – Morales et al. adapted *in situ* measurements by Grunewald et al. (2002) to estimate that as much as 50% of the coastal production off Chile could be exported in upwelling filaments. Those biomass fluxes are on the order of those reported here (Chapter 3) - we estimated that the filament studied in the CCS transported 1.2×10^3 metric tons carbon/day in the form of zooplankton biomass. We estimate that phytoplankton biomass was somewhat higher than zooplankton biomass within the filament (assuming a chlorophyll:carbon weight conversion of 1:50), resulting in higher biomass flux than those reported elsewhere. While we did not estimate the loss of shelf primary production, we estimated that $\sim 2\%$ of the zooplankton production was advected offshore in the filament.

Upwelling filaments in the Canary Current system are believed to be shallower and lower velocity than those in the California and Humboldt Current systems (Hernandez-Leon et al., 2007). Reported volume transports in Canary Current filaments range from 0.9 to 1.5 Sv (Barton et al., 2004) whereas in the California Current, volume transport of up to 3 Sv has been measured (Barth et al., 2000). In both the Humboldt Current (Leth and Shaffer, 2001) and California Current (Ramp et al., 1991), filaments and eddies with depths of >300 m occur, as compared to <100 m in the Canary Current (Hernandez-Leon et al., 2007), so seaward carbon flux may also be expected to be higher.

In the Iberian upwelling system in the northern extreme of the Canary Current, upwelling filaments are also dominant features in SST images, but a Lagrangian study of a decaying filament in August 1998 revealed relatively weak (<30 cm/s), shallow offshore surface flow in the filament. Nutrients (Joint et al., 2001), chlorophyll, and copepod biomass (Halvorsen et al., 2001) were all low compared to those measured during our August 2000 cruise in the NCC. The Iberian study indicated that the filament significantly contributed to offshore export of dissolved organic matter (Alvarez-Salgado et al., 2001) but model simulations (Slagstad and Wassmann, 2001) suggest that particulate organic matter export was low compared to export in filaments off California and Peru/Chile.

Mesoscale circulation features in upwelling systems can advect huge volumes of coastal water offshore. In the Northern California Current, both the timing and intensity of

mesoscale circulation and peak zooplankton biomass vary spatially and interannually, so the biomass delivered to the deep sea, and hence the productivity of the ecosystem as a whole, are also likely to vary. Eastern boundary currents are highly productive in terms of primary and secondary production, so variability in the transfer of water and the associated planktonic communities between the shelf and deep ocean may have dramatic consequences for ecosystem dynamics and global carbon cycling, survival of oceanic zooplanktivores (e.g. Logerwell et al., 2001, Yen et al., 2006), and upper trophic level organisms (Palacios et al., 2006).

Future field and modeling efforts are needed to help resolve remaining questions of the role of mesoscale features in ecosystems dynamics. To better understand the mechanisms of mesoscale variability including the relative contribution of winds and stratification to the development of features, ocean models with <20 km resolution and realistic, interannually-varying forcing will be needed. Individual-based biological models which include vertical migration of organisms and couple to realistic circulation models could explore the role of features in the retention and loss of coastal organisms, paths of return from the open ocean, and potential strategies of life-cycle closure. Because of the high variability in both biological abundances within and the physical structure of individual features, more high-resolution field studies will be necessary to constrain estimates of volume transport, species distributions, coastal population losses, and carbon flux that are due to the circulation. Together, future field and modeling studies could progress our understanding of the role of mesoscale circulation in structuring coastal population abundances and distributions and their contribution to across-shelf flux and the global carbon cycle.

Bibliography

- Ainley, D. G., Spear, L. B., Tynan, C. T., Barth, J. A., Pierce, S. D., Ford, R. G., and Cowles, T. J., 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep-Sea Research II 52, 123-143.
- Alvarez-Salgado, X. A., Doval, M. D., Borges, A. V., Joint, I., Frankignoulle, M., Woodward, E. M. S., and Figueiras, F. G., 2001. Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian Upwelling System. Progress in Oceanography 51, 321-337.
- Aristegui, J., Tett, P., HernandezGuerra, A., Basterretxea, G., Montero, M. F., Wild, K., Sangra, P., HernandezLeon, S., Canton, M., GarciaBraun, J. A., Pacheco, M., and Barton, E. D., 1997. The influence of island-generated eddies on chlorophyll distribution: A study of mesoscale variation around Gran Canaria. Deep-Sea Research I 44, 71-96.
- Ashjian, C. J., Davis, C. S., Gallager, S. M., and Alatalo, P., 2001. Distribution of plankton, particles, and hydrographic features across Georges Bank described using the Video Plankton Recorder. Deep-Sea Research II 48, 245-282.
- Auth, T. D., and Brodeur, R. D., 2006. Distribution and community structure of ichthyoplankton off the coast of Oregon, USA, in 2000 and 2002. Marine Ecology-Progress Series 319, 199-213.
- Bakun, A., 1990. Global climate change and intensification of coastal ocean upwelling. Science 247, 198-201.
- ---, 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. California Sea Grant College System, La Jolla, CA, 323 pp.
- Barber, R. T., and Smith, R. L., 1981. Coastal upwelling ecosystems. In: A. R. Longhurst, (ed, Analysis of Marine Ecosystems, Academic Press, New York, 31–68.
- Barth, J. A., Cowles, T. J., Kosro, P. M., Shearman, R. K., Huyer, A., and Smith, R. L., 2002. Injection of carbon from the shelf to offshore beneath the euphotic zone in the California Current. Journal of Geophysical Research 107, doi:10.1029/2001JC000956.
- Barth, J. A., Pierce, S. D., and Castelao, R. M., 2005a. Time-dependent, wind-driven flow over a shallow midshelf submarine bank. Journal of Geophysical Research-Oceans 110, doi:10.1029/2004JC002761.
- Barth, J. A., Pierce, S. D., and Cowles, T. J., 2005b. Mesoscale structure and its seasonal evolution in the northern California Current System. Deep Sea Research II 52, 5-28.

- Barth, J. A., Pierce, S. D., and Smith, R. L., 2000. A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. Deep Sea Research 47, 783-810.
- Barton, E. D., and Aristegui, J., 2004. The Canary Islands coastal transition zone upwelling, eddies and filaments. Progress in Oceanography 62, 67-69.
- Barton, E. D., Aristegui, J., Tett, P., and Perez, E. N., 2004. Variability in the Canary Islands area of filament-eddy exchanges. Progress in Oceanography 62, 71-94.
- Batchelder, H., Barth, J., Kosro, P., Strub, P., Brodeur, R., Peterson, W., Tynan, C.,
 Ohman, M., Botsford, L., Powell, T., Schwing, F., Ainley, D., Mackas, D., Hickey,
 B., and Ramp, S., 2002a. The GLOBEC Northeast Pacific California Current
 System Program. Oceanography 15, 36-47.
- Batchelder, H. P., Edwards, C. A., and Powell, T. M., 2002b. Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. Progress in Oceanography 53, 307-333.
- Batteen, M. L., 1997. Wind-forced modeling studies of currents, meanders, and eddies in the California Current system. Journal of Geophysical Research 102, 985-1010.
- Bieri, R., 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnology and Oceanography 4, 1-28.
- Bograd, S. J., and Lynn, R. J., 2003. Long-term variability in the Southern California Current System. Deep-Sea Research II 50, 2355-2370.
- Brink, K. H., Beardsley, R. C., Niiler, P. P., Abbott, M., Huyer, A., Ramp, S., Stanton, T., and Stuart, D., 1991. Statistical properties of near-surface flow in the California Coastal Transition Zone. Journal of Geophysical Research 96, 14,693-14,706.
- Brink, K. H., Beardsley, R. C., Paduan, J., Limeburner, R., Caruso, M., and Sires, J. G., 2000. A view of the 1993-1994 California Current based on surface drifters, floats, and remotely sensed data. Journal of Geophysical Research-Oceans 105, 8575-8604.
- Brinton, E., 1962. The distribution of Pacific euphausiids. Bulletin of the Scripps Institution of Oceanography of the University of California, La Jolla 8, 51-269.
- Brodeur, R. D., Fisher, J. P., Teel, D. J., Emmett, R. L., Casillas, E., and Miller, T. W., 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current. Fishery Bulletin 102, 25-46.
- Caldeira, R. M. A., Marchesiello, P., Nezlin, N. P., DiGiacomo, P. M., and McWilliams, J. C., 2005. Island wakes in the Southern California Bight. Journal of Geophysical Research-Oceans 110, doi:10.1029/2004JC002675.
- Castelao, R. M., and Barth, J. A., 2005. Coastal ocean response to summer upwelling favorable winds in a region of alongshore bottom topography variations off
Oregon. Journal of Geophysical Research-Oceans 110, doi:10.1029/2004JC002409.

- Castelao, R. M., Mavor, T. P., Barth, J. A., and Breaker, L. C., 2006. Sea surface temperature fronts in the California Current System from geostationary satellite observations. Journal of Geophysical Research 111, doi:10.1029/2006JC003541.
- Chelton, D. B., Schlax, M. G., Samelson, R. M., and de Szoeke, R. A., 2007. Global observations of large oceanic eddies. Geophysical Research Letters 34, doi:10.1029/2007GL030812.
- Chereskin, T. K., Morris, M. Y., Niiler, P. P., Kosro, P. M., Smith, R. L., Ramp, S. R., Collins, C. A., and Musgrave, D. L., 2000. Spatial and temporal characteristics of the mesoscale circulation of the California Current from eddy-resolving moored and shipboard measurements. Journal of Geophysical Research 105, 1245-1269.
- Chisholm, L. A., and Roff, J. C., 1990. Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. Marine Biology 106, 71-77.
- Collins, C. A., Castro, C. G., Asanuma, H., Rago, T. A., Han, S.-K., Durazo, R., and Chavez, F. P., 2002. Changes in the hydrography of Central California waters associated with the 1997-98 El Nino. Progress in Oceanography 54, 129-147.
- Collins, C. A., Ivanov, L. M., Melnichenko, O. V., and Garfield, N., 2004. California Undercurrent variability and eddy transport estimated from RAFOS float observations. Journal of Geophysical Research-Oceans 109, doi:10.1029/2003JC002191.
- Cornuelle, B. D., Chereskin, T. K., Niiler, P. P., Morris, M. Y., and Musgrave, D. L., 2000. Observations and modeling of a California undercurrent eddy. Journal of Geophysical Research-Oceans 105, 1227-1243.
- Crawford, W. R., Cherniawsky, J. Y., and Foreman, M. G. G., 2000. Multi-year meanders and eddies in the Alaskan Stream as observed by TOPEX/Poseidon altimeter. Geophysical Research Letters 27, 1025-1028.
- Dufrene, M., and Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345-366.
- Durazo, R., and Baumgartner, T. R., 2002. Evolution of oceanographic conditions off Baja California: 1997–1999. Progress in Oceanography 54, 7-31.
- Erofeeva, S. Y., Egbert, G. D., and Kosro, P. M., 2003. Tidal currents on the central Oregon shelf models, data and assimilation. Journal of Geophysical Research 108, doi:10.1029/2002JC001615.
- Escribano, R., and Hidalgo, P., 2000. Spatial distribution of copepods in the north of the Humboldt Current region off Chile during coastal upwelling. Journal of the Marine Biological Association of the United Kingdom 80, 283-290.
- Farge, M., 1992. Wavelet transforms and their applications to turbulence. Annual Review of Fluid Mechanics 24, 395-457.

- Feinberg, L. R., Shaw, C. T., and Peterson, W. T., 2006. Larval development of Euphausia pacifica in the laboratory: variability in developmental pathways. Marine Ecology Progress Series 316, 127-137.
- Field, J. G., Clarke, K. R., and Warwick, R. M., 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8, 37-52.
- Fleminger, A., 1964. Distributional atlas of calanoid copepods in the California Current region, Part I. California Cooperative Oceanic Fisheries Investigation, Atlas No. 2, 1-313.
- Gan, J. P., and Allen, J. S., 2005. Modeling upwelling circulation off the Oregon coast. Journal of Geophysical Research-Oceans 110.
- Gomez-Gutierrez, J., Feinberg, L. R., Shaw, C. T., and Peterson, W. T., 2007. Interannual and geographical variability of the brood size of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* along the Oregon coast (1999-2004). Deep-Sea Research I 54, 145-2169.
- Gordon, L. I., Jennings, J. J. C., Ross, A. A., and Krest, J. M., 1994. A suggested protocol for continuous flow analysis of seawater nutrients (phosphate, nitrate, nitrite, and silicic acid) in the WOCE Hydrographic Program and the Joint Global Ocean Fluxes Study. Woods Hole, MA, WOCE Hydrograph. Prog., np.
- Graham, W. M., and Largier, J. L., 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Continental Shelf Research 17, 509-532.
- Gray, J. S., Aschan, M., Carr, M. R., Clarke, D. R., Green, R. H., Pearson, T. H., Rosenberg, R., and Warwick, R. M., 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. Marine Ecology Progress Series 46, 151-165.
- Grunewald, A. C., Morales, C. E., Gonzalez, H. E., Sylvester, C., and Castro, L. R., 2002. Grazing impact of copepod assemblages and gravitational flux in coastal and oceanic waters off central Chile during two contrasting seasons. Journal of Plankton Research 24, 55-67.
- Haidvogel, D. B., Beckmann, A., and Hedstrom, K. S., 1991. Dynamical simulations of filament formation and evolution in the coastal transition zone. Journal of Geophysical Research 96, 15017-15040.
- Halvorsen, E., Pedersen, O. P., Slagstad, D., Tande, K. S., Fileman, E. S., and Batten, S. D., 2001. Microzooplankton and mesozooplankton in an upwelling filament off Galicia: modelling and sensitivity analysis of the linkages and their impact on the carbon dynamics. Progress in Oceanography 51, 499-513.
- Haury, L. R., 1984. An offshore eddy in the California Current System. Part IV: Plankton distributions. Prog. Oceanogr. 13, 95-111.
- Henson, S. A., and Thomas, A. C., 2007a. Interannual variability in timing of bloom initiation in the California Current System. Journal of Geophysical Research-Oceans 112, doi:10.1029/2006JC003960.

- —, 2007b. Phytoplankton scales of variability in the California Current System: 1. Interannual and cross-shelf variability. Journal of Geophysical Research-Oceans 112, doi:10.1029/2006JC004039.
- Hernandez-Leon, S., Almeida, C., Portillo-Hahnefeld, A., Gomez, M., Rodriguez, J. M., and Aristegui, J., 2002. Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off northwest Africa. Journal of Marine Research 60, 327-346.
- Hernandez-Leon, S., Gomez, M., and Aristegui, J., 2007. Mesozooplankton in the Canary Current System: The coastal-ocean transition zone. Progress in Oceanography 74, 397-421.
- Hickey, B. M., 1997. The response of a steep-sides, narrow canyon to time variable wind forcing. Journal of Physical Oceanography 27, 697–726.
- Hickey, B. M., Thomson, R. E., Yih, H., and LeBlond, P. H., 1991. Velocity and temperature fluctuations in a buoyancy-driven current off Vancouver Island. Journal of Geophysical Research 96, 10,507–10,538.
- Holland, C. L., and Mitchum, G. T., 2001. Propagation of Big Island eddies. Journal of Geophysical Research 106, 935-944.
- Hood, R. R., Abbott, M. R., Huyer, A., and Kosro, P. M., 1990. Surface patterns in temperature, flow, phytoplankton biomass, and species composition in the coastal transition zone off northern California. Journal of Geophysical Research 95, 18081-18094.
- Hooff, R. C., and Peterson, W. T., 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. Limnology and Oceanography 51, 2607-2620.
- Hormazabal, S., Núñez, S., Arcos, D., Espindola, F., and Yuras, G., 2004a. Mesoscale eddies and pelagic fisshery off central Chile (33-40°S). Gayana 68, 291-296.
- Hormazabal, S., Shaffer, G., and Leth, O., 2004b. Coastal transition zone off Chile. Journal of Geophysical Research 109, doi:10.1029/2003JC001956.
- Huntley, M. E., Gonzalez, A., Zhu, Y., Zhou, M., and Irigoien, X., 2000. Zooplankton dynamics in a mesoscale eddy-jet system off California. Marine Ecology-Progress Series 201, 165-178.
- Huntley, M. E., Zhou, M., and Nordhausen, W., 1995. Mesoscale distribution of zooplankton in the California Current in late spring, observed by optical plankton counter. Journal of Marine Research 53, 647-674.
- Huyer, A., Barth, J. A., Kosro, P. M., Shearman, R. K., and Smith, R. L., 1998. Upperocean water mass characteristics of the California current, Summer 1993. Deep Sea Research 45, 1411-1442.
- Huyer, A., Fleischbein, J. H., J.E. Keister, P. M. K., Perlin, N., Smith, R. L., and Wheeler, P. A., 2005. Two coastal upwelling domains in the Northern California Current System. Journal of Marine Research 63, 901-929.

- Huyer, A., Smith, R. L., and Fleischbein, J., 2002. The coastal ocean off Oregon and Northern California during the 1997-8 El Niño. Progress in Oceanography 54, 311-341.
- Huyer, A., Wheeler, P. A., Strub, P. T., Smith, R. L., Letelier, R., and Kosro, P. M., 2007. The Newport line off Oregon – Studies in the North East Pacific. Prog. Oceanogr. 75, 126-160.
- Ikeda, M., and Emery, W. J., 1984. Satellite observations and modeling of meanders in the California Current system. Journal of Physical Oceanography 14, 1434-1450.
- Joint, I., Rees, A. P., and Woodward, E. M. S., 2001. Primary production and nutrient assimilation in the Iberian upwelling in August 1998. Progress in Oceanography 51, 303-320.
- Keister, J. E., and Peterson, W. T., 2003. Zonal and seasonal variations in zooplankton community structure off the central Oregon coast, 1998-2000. Progress in Oceanography 57, 341-361.
- Keister, J. E., Peterson, W. T., and Pierce, S. D., In review. Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California Current. Deep-Sea Research I, In Review.
- Keister, J. E., and Strub, P. T., 2008. Spatial and interannual variability in mesoscale circulations in the northern California Current System. Journal of Geophysical Research, doi: 10.1029/2007JC004256.
- Kelly, K., Beardsley, R., Limeburner, R., Brink, K., Paduan, J., and Chereskin, T., 1998. Variability of the near-surface eddy kinetic energy in the California Current based on altimetric, drifter, and moored current data. Journal of Geophysical Research C. Oceans 103, 13,067-13,083.
- Kosro, P., Huyer, A., Ramp, S., Smith, R., Chavez, F., Cowles, T., Abbott, M., Strub, P., Barber, R., Jessen, P., and Small, L. F., 1991. The structure of the transition zone between coastal waters and the open ocean off northern California, winter and spring 1987. Journal of Geophysical Research C. Oceans 96, 4,707-4730.
- Kosro, P. M., 2002. A poleward jet and an equatorward undercurrent observed off Oregon and northern California during the 1997-98 El Niño. Progress in Oceanography 54, 343-360.
- —, 2005. On the spatial structure of coastal circulation off Newport, Oregon, during spring and summer 2001 in a region of varying shelf width. Journal of Geophysical Research-Oceans 110, doi:10.1029/2004JC002769.
- Kosro, P. M., and Huyer, A., 1986. CTD and velocity surveys of seaward jets off northern California, July 1981 and 1982. Journal of Geophysical Research 91, 7680-7690.
- Kosro, P. M., Peterson, W. T., Hickey, B. M., Shearman, R. K., and Pierce, S. D., 2006. Physical versus biological spring transition: 2005. Geophysical Research Letters 33, doi:10.1029/2006GL027072.

- Lagerloef, G. S. E., 1992. The Point Arena Eddy: A recurring summer anticyclone in the California Current. Journal of Geophysical Research 97, 12557-12568.
- Lamb, J. F., and Peterson, W. T., 2005. Ecological zonation of zooplankton in the COAST study region off central Oregon in June and August 2001 with consideration of retention mechanisms. Journal of Geophysical Research 110, doi:10.1029/2004JC002520.
- Largier, J. L., Lawrence, C. A., Roughan, M., Kaplan, D. M., Dever, E. P., Dorman, C. E., Kudela, R. M., Bollens, S. M., Wilkerson, F. P., Dugdale, R. C., Botsford, L. W., Garfieldg, N., Cervantes, B. K., and Koracin, D., 2006. WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. Deep-Sea Research II 53, 2833-2849.
- Le Traon, P. Y., Faugere, Y., Hernandez, F., Dorandeu, J., Mertz, F., and Ablain, M., 2003. Can we merge GEOSAT Follow-On with TOPEX/Poseidon and ERS-2 for an improved description of the ocean circulation? Journal of Atmospheric and Oceanic Technology 20, 889-895.
- Legaard, K. R., and Thomas, A. C., 2006. Spatial patterns in seasonal and interannual variability of chlorophyll and sea surface temperature in the California Current. Journal of Geophysical Research 111, doi:10.1029/2005JC003282.
- —, 2007. Spatial patterns of intraseasonal variability of chlorophyll and sea surface temperature in the California Current. Journal of Geophysical Research 112, doi:10.1029/2007JC004097.
- Leth, O., and Shaffer, G., 2001. A numerical study of the seasonal variability in the circulation off central Chile. Journal of Geophysical Research-Oceans 106, 22229-22248.
- Logerwell, E. A., Lavaniegos, B. E., and Smith, P. E., 2001. Spatially-explicit bioenergetics of Pacific sardine in the Southern California Bight: are mesoscale eddies areas of exceptional prerecruit production? Progress in Oceanography 49, 391-406.
- Luo, J., Brandt, S. B., and Klebasko, M. J., 1996. Virtual reality of planktivores: a fish's perspecive of prey size selection. Marine Ecology Progress Series 140, 271-283.
- Lutjeharms, R. E., Shillington, F. A., and Duncombe Rae, C. M., 1991. Observations of extreme upwelling filaments in the Southeast Atlantic Ocean. Science 253, 774-776.
- Macarthur, R. H., and Macarthur, J. W., 1961. On bird species diversity. Ecology 42, 594–598.
- Mackas, D. L., 1984. Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. Limnology and Oceanography 29, 451-471.
- Mackas, D. L., and Coyle, K. O., 2005. Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. Deep Sea Research II 52, 707-725.

- Mackas, D. L., and Galbraith, M. D., 2002. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: 1. Transport and loss of continental margin species. Journal of Oceanography 58, 725-738.
- Mackas, D. L., Washburn, L., and Smith, S. L., 1991. Zooplankton community pattern associated with a California Current cold filament. Journal of Geophysical Research 96, 14781-14797.
- Mackas, D. L., and Yelland, D. R., 1999. Horizontal flux of nutrients and plankton across and along the British Columbia continental margin. Deep-Sea Research II 46, 2941-2967.
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. BULLETIN OF THE AMERICAN METEOROLOGICAL SOCIETY 78, 1069-1079.
- Marchesiello, P., McWilliams, J. C., and Shchepetkin, A., 2003. Equilibrium Structure and Dynamics of the California Current System. Journal of Physical Oceanography 33, 755-783.
- Marin, V. C. H., Delgado, L. E., and Luna-Jorquera, G., 2003. S-chlorophyll squirts at 30 degrees S off the Chilean coast (eastern South Pacific): Feature-tracking analysis. Journal of Geophysical Research-Oceans 108.
- McCune, B., and Grace, J. B., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, 300 pp.
- McCune, B., and Mefford, M. J., 2005. PC-ORD, 5.0. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McGillicuddy, D. J., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C., Falkowski, P. G., Goldthwait, S. A., Hansell, D. A., Jenkins, W. J., Johnson, R., Kosnyrev, V. K., Ledwell, J. R., Li, Q. P., Siegel, D. A., and Steinberg, D. K., 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. Science 316, 1021-1026.
- McPhaden, M. J., 1999. Genesis and evolution of the 1997-98 El Niño. Science 283, 950-954.
- Melsom, A., Metzger, E. J., and Hurlburt, H. E., 2003. Impact of remote oceanic forcing on Gulf of Alaska sea levels and mesoscale circulation. Journal of Geophysical Research 108, doi:10.1029/2002JC001742.
- Melsom, A., Meyers, S. D., Hurlburt, H. E., Metzger, E. J., and O'Brien, J. J., 1999. ENSO effects on Gulf of Alaska eddies. Earth Interactions 3, (Available at <u>http://EarthInteractions.org)</u>.
- Meyers, S. D., Kelly, B. G., and O'Brien, J. J., 1993. An introduction to wavelet analysis in oceanography and meteorology: with application to the dispersion of Yanai Waves. Monthly Weather Review 121, 2858-2866.
- Michaels, A. F., 2007. Highly active eddies. Science 316, 992-993.

- Mielke, P. W. J., 1984. Meterological applications of permutation techniques based on distance functions. In: P. K. Sen, (ed, Handbook of statistics: Nonparametric methods, 4. Elsevier Science Publishers, Amsterdam, 813–830.
- Miller, A. J., and Schneider, N., 2000. Interdecadal climate regime dynamics in the North Pacific Ocean: theories, observations and ecosystem impacts. Progress in Oceanography 47, 355–379.
- Morales, C. E., Gonzalez, H. E., Hormazabal, S. E., Yuras, G., Letelier, J., and Castro, L. R., 2007. The distribution of chlorophyll-a and dominant planktonic components in the coastal transition zone off Concepcion, central Chile, during different oceanographic conditions. Progress in Oceanography 75, 452-469.
- Morgan, C. A., Peterson, W. T., and Emmett, R. L., 2003. Onshore-offshore variations in copepod community structure off the Oregon coast during the summer upwelling season. Marine Ecology Progress Series 249, 223-236.
- Narimousa, S., and Maxworthy, T., 1989. Application of a laboratory model to the interpretation of satellite and field observations of coastal upwelling. Dynamics of Atmospheres and Oceans 13, 1-146.
- Nishimoto, M. M., and Washburn, L., 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. Marine Ecology-Progress Series 241, 183-199.
- Palacios, D. M., Bograd, S. J., Foley, D. G., and Schwing, F. B., 2006. Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. Deep-Sea Research II 53, 250-269.
- Pascual, A., Faugere, Y., Larnicol, G., and Traon, P.-Y. L., 2006. Improved description of the ocean mesoscale variability by combining four satellite altimeters. Geophysical Research Letters 33, doi:10.1029/2005GL024633.
- Percival, D. B., and Walden, A. T., 2000. Wavelet methods for time series analysis. Cambridge University Press, Cambridge, New York, 594 pp.
- Peterson, W. K., 1972. Distribution of pelagic Copepoda off the coasts of Washington and Oregon during 1961 and 1962. In: D. L. Alverson, (ed, The Columbia River estuary and adjacent ocean waters, University of Washington Press, Seattle, 313-343.
- Peterson, W. T., 1980. Life history and ecology of *Calanus marshallae* Frost in the Oregon upwelling zone. Oregon State University, Corvallis, OR, 200 pp.
- —, 1998. Life cycle strategies of copepods in coastal upwelling zones. Journal of Marine Systems 15, 313-326.
- Peterson, W. T., Gomez-Gutierrez, J., and Morgan, C. A., 2002. Cross-shelf variation in calanoid copepod production during summer 1996 off the Oregon coast, USA. Marine Biology 141, 353-365.
- Peterson, W. T., and Keister, J. E., 2002. The effect of a large cape on distribution patterns of coastal and oceanic copepods off Oregon and northern California during the 1998/1999 El Niño/La Niña. Progress in Oceanography 53, 389-411.

- —, 2003. Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach. Deep-Sea Research II 50, 2499-2517.
- Peterson, W. T., and Miller, C. B., 1975. Year-to-year variations in the planktology of the Oregon upwelling zone. Fishery Bulletin 73, 642-653.
- ---, 1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fishery Bulletin 75, 717-724.
- Pierce, S. D., Barth, J. A., Peterson, W. T., and Cowles, T. J., 2003. Bioacoustic surveys in the northern California Current System: zooplankton retention mechanisms. EOS Transactions American Geophysical Union 84, Abstract OS21-B23.
- Pierce, S. D., Barth, J. A., Thomas, R. E., and Fleischer, G. W., 2006. Anomalously warm July 2005 in the northern California Current: Historical context and the significance of cumulative wind stress. Geophysical Research Letters 33, doi:10.1029/2006GL027149.
- Pierce, S. D., Smith, R. L., Kosro, P. M., Barth, J. A., and Wilson, C. D., 2000. Continuity of the poleward undercurrent along the eastern boundary of the mid-latitude North Pacific. Deep Sea Research 47, 5-6.
- Powell, T. M., Lewis, C. V. W., Curchitser, E. N., Haidvogel, D. B., Hermann, A. J., and Dobbins, E. L., 2006. Results from a three-dimensional, nested biological-physical model of the California Current System and comparisons with statistics from satellite imagery. Journal of Geophysical Research-Oceans 111, doi:10.1029/2004JC002506.
- Ramp, S. R., Jessen, P. F., Brink, K. H., Niiler, P. P., Daggett, F. L., and Best, J. S., 1991. The physical structure of cold filaments near Point Arena, California, during June 1987. Journal of Geophysical Research 96, 14,859-14,883.
- Reese, D. C., and Brodeur, R. D., 2006. Identifying and characterizing biological hotspots in the northern California Current. Deep-Sea Research II 53, 291-314.
- Reese, D. C., Miller, T. W., and Brodeur, R. D., 2005. Community structure of nearsurface zooplankton in the northern California Current in relation to oceanographic conditions. Deep-Sea Research II 52, 29-50.
- Relvas, P., Barton, E. D., Dubert, J., Oliveira, P. B., Peliz, A., da Silva, J. C. B., and Santos, A. M. P., 2007. Physical oceanography of the western Iberia ecosystem: Latest views and challenges. Progress in Oceanography 74, 149-173.
- Ressler, P. H., Brodeur, R. D., Peterson, W. T., Pierce, S. D., Vance, P. M., Rostad, A., and Barth, J. A., 2005. The spatial distribution of euphausiid aggregations in the Northern California Current during August 2000. Deep-Sea Research II 52, 89-108.
- Rodriguez, J. M., Hernandez-Leon, S., and Barton, E. D., 1999. Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. Deep-Sea Research I 46, 1969-1984.

- Roughan, M., Garfield, N., Largier, J., Dever, E., Dorman, C., Peterson, D., and Dorman, J., 2006. Transport and retention in an upwelling region: The role of across-shelf structure. Deep-Sea Research II 53, 2931-2955.
- Schwing, F. B., Bond, N. A., Bograd, S. J., Mitchell, T., Alexander, M. A., and Mantua., N., 2006. Delayed coastal upwelling along the U.S. West Coast in 2005: A historical perspective. Geophysical Research Letters 33, doi:10.1029/2006GL026911.
- Schwing, F. B., Murphree, T., deWitt, L., and Green, P. M., 2002a. The evolution of oceanic and atmospheric anomalies in the northeast Pacific during the El Niño and La Niña events of 1995–2001. Progress in Oceanography 54, 459-491.
- Schwing, F. B., Murphree, T., and Green, P. M., 2002b. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Progress in Oceanography 53, 115-139.
- Shaw, W., and Robinson, C. L. K., 1998. Night versus day abundance estimates of zooplankton at two coastal stations in British Columbia, Canada. Marine Ecology Progress Series 175, 143-153.
- Slagstad, D., and Wassmann, P., 2001. Modelling the 3-D carbon flux across the Iberian margin during the upwelling season in 1998. Progress in Oceanography 51, 467-497.
- Smith, P. E., Flerx, W., and Hewitt, R. P., 1985. The CalCOFI vertical egg two (CalVET) net. In: Lasker, (ed, An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). 36. U.S. Department of Commerce, NOAA Technical Report, National Marine Fisheries Service, Washington, D.C., 27-32.
- Smith, S. L., and Lane, P., 1991. The jet off Point Arena, California: Its role in aspects of secondary production in the copepod Eucalanus californicus Johnson. Journal of Geophysical Research 96, 14849-14858.
- Snyder, M. A., Sloan, L. C., Diffenbaugh, N. S., and Bell, J. L., 2003. Future climate change and upwelling in the California Current. Geophysical Research Letters, doi:10.1029/2003GL017647.
- Stegmann, P. M., and Schwing, F., 2007. Demographics of mesoscale eddies in the California Current. Geophysical Research Letters 34, doi: 10.1029/2007GL029504.
- Strub, P. T., Batchelder, H. P., and Weingartner, T., 2002. U.S. GLOBEC Northeast Pacific Program : Overview. Oceanography 15, 30-35.
- Strub, P. T., and James, C., 2000. Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. Deep-Sea Research II 47, 831-870.
- —, 2002a. Altimeter-derived surface circulation in the large-scale NE Pacific Gyres. Part 1. Seasonal variability. Progress in Oceanography 53, 163-183.

- —, 2002b. Altimeter-derived surface circulation in the large-scale NE Pacific Gyres. Part
 2: 1997-1998 El Niño anomalies. Progress in Oceanography 53, 185-214.
- —, 2003. Altimeter estimates of anomalous transports into the northern California Current during 2000-2002. Geophysical Research Letters 30, doi:10.1029/2003GL017513.
- Strub, P. T., Kosro, P. M., and Huyer, A., 1991. The nature of the cold filaments in the California Current System. Journal of Geophysical Research 96, 14,743-14,768.
- Suchman, C. L., and Brodeur, R. D., 2005. Abundance and distribution of large medusae in surface waters of the northern California Current. Deep-Sea Research II 52, 51-72.
- Sutor, M., Cowles, T. J., and Peterson, W. T., 2005. Acoustic observations of finescale zooplankton distributions in the Oregon upwelling region. Deep-Sea Research II 52, 109-121.
- Torrence, C., and Compo, G. P., 1998. A practical guide to wavelet analysis. Bulletin of the American Meteorological Society 79, 61-78.
- Torres, C. R., Mascarenhas, A. S., and Castillo, J. E., 2004. Three-dimensional stratified flow over Alarcon Seamount, Gulf of California entrance. Deep-Sea Research II 51, 647-657.
- Tynan, C. T., Ainley, D. G., Barth, J. A., Cowles, T. J., Pierce, S. D., and Spear, L. B., 2005. Cetacean distributions relative to ocean processes in the northern California Current System. Deep-Sea Research II 52, 145-167.
- Uye, S., 1982. Length-weight relationships of important zooplankton from the inland Sea of Japan. Journal of the Oceanographic Society of Japan 38, 149-158.
- van Geen, A., Takesue, R. K., Goddard, J., Takahashi, T., Barth, J. A., and Smith, R. L., 2000. Carbon and nutrient dynamics during coastal upwelling off Cape Blanco, Oregon. Deep-Sea Research II 47, 975-1002.
- Vidal, J., 1980. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Marine Biology 56, 111-134.
- Waite, A. M., Thompson, P. A., Pesant, S., Feng, M., Beckley, L. E., Domingues, C. M., Gaughan, D., Hanson, C. E., Holl, C. M., Koslow, T., Meuleners, M., Montoya, J. P., Moore, T., Muhling, B. A., Paterson, H., Rennie, S., Strzelecki, J., and Twomey, L., 2007. The Leeuwin Current and its eddies: An introductory overview. Deep-Sea Research Part Ii-Topical Studies in Oceanography 54, 789-796.
- Wiebe, P. H., 1971. A computer model study of zooplankton patchiness and its effects on sampling error. Limnology and Oceanography 16, 29-38.
- Wiebe, P. H., and Holland, R. H., 1968. Plankton patchiness: effects on repeated net tows. Limnology and Oceanography 13, 315-321.
- Wilkin, J. L., Bowen, M. M., and Emery, W. J., 2002. Mapping mesoscale currents by optimal interpolation of satellite radiometer and altimeter data. Ocean Dynamics 52, 95-103.

- Wing, S. R., Botsford, L. W., Ralston, S. V., and Largier, J. L., 1998. Meroplanktonic Distribution and Circulation in a Coastal Retention Zone of the Northern California Upwelling System. Limnology and Oceanography 43, 1710-1721.
- Wishart, D., 1969. An algorithm for hierarchical classifications. Biometrics 25, 165-170.
- Wroblewski, J. S., 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone a simulation. Deep Sea Research 29, 665-686.
- Yebra, L., Hernandez-Leon, S., Almeida, C., Becognee, P., and Rodriguez, J. M., 2004. The effect of upwelling filaments and island-induced eddies on indices of feeding, respiration and growth in copepods. Progress in Oceanography 62, 151-169.
- Yen, P. P. W., Sydeman, W. J., Bograd, S. J., and Hyrenbach, K. D., 2006. Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. Deep-Sea Research II 53, 399-418.
- Zamudio, L., Leonardi, A. P., Meyers, S. D., and O'Brien, J. J., 2001. ENSO and eddies on the southwest coast of Mexico. Geophysical Research Letters 28, 13-16.
- Zhou, M., and Zhu, Y., 2002. Mesoscale zooplankton distribution and its correlation with physical and fluorescence fields in the California Current in 2000. EOS Transactions American Geophysical Union 83, Abstract OS21N-04.