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Zooplankton Distribution and Transport in the California Current off Oregon

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Key words: Shelf · Coastal retention · Physical-biological coupling · Productivity

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ABSTRACT: The transport and retention of zooplankton biomass in the shelf and slope regions off Oregon were studied in June 2002. A towed undulating instrument package was used with 2 pairs of Conductivity–Temperature–Depth (CTD) sensors, a fluorometer and an Optical Plankton Counter (OPC) for high resolution measurements of temperature, salinity, depth, fluorescence and zooplankton abundance. The shipboard 153 kHz Acoustic Doppler Current Profiler (ADCP) was used for current measurements in water column. Two different analytical methods for the geostrophic current fields based on ADCP current measurements were employed based on minimizing current divergence. Results revealed high zooplankton biomass values in coastal upwelling areas on the shelf and exchanges between shelf waters with high zooplankton biomass and offshelf waters with low zooplankton biomass by crossing-isobath currents. In the shelf area of Heceta Bank off Newport, Oregon shallower than the 153 m isobaths bounded between 41º44´N and 44º37´N, the standing zooplankton biomass was approximately $4\times10^4$ ton C. The major flux of zooplankton biomass into the area occurred at the northern boundary at a rate of $1–2.5\times10^3$ ton C d$^{-1}$ or a specific rate of 0.03–0.06 day$^{-1}$ based on two different analytical methods; the flux at the southern boundary is one order of magnitude less than that of the northern boundary; and the significant flux out of the area occurred at the 153 m isobath at a rate of $0.8–3.7\times10^3$ ton C d$^{-1}$ or a specific rate of 0.02–0.09 day$^{-1}$. These rates are comparable with the zooplankton growth and mortality rates of approximately 0.1 day$^{-1}$ reported in literatures within this region. The offshelf transport of zooplankton contributes significantly to biomass losses in shelf ecosystems and in turn fuels offshelf ecosystems.
INTRODUCTION

High productivities and their association with mesoscale physical features in the California Current system off the Oregon and California coasts during spring and summer upwelling seasons have led to a number of scientific studies of physical, chemical and biological processes and the sustainability of fisheries associated with human activities. The Coastal Ocean Dynamics Experiment in the early 1980s revealed that the intensive offshore jets associated with cold filaments penetrated more than 100 m deep and transported coastal biota from the shelf to hundreds of kilometers off the shelf (Korso & Huyer 1986). The data from the Ocean Prediction Through Observations, Modeling, and Analysis Experiment in 1982–1986 showed that surface jets and eddies were more energetic in the summer than those in the winter (Rienecker & Mooers 1989; Strub et al. 1991). The Coastal Transition Zone Experiment in the late 1980s concluded that the cold filaments were originated from continuous, meandering jets which separated onshelf and offshelf waters (Strub et al. 1991), and deep phytoplankton layers in the offshelf water were originated from the subducted coastal cold water at the transition or converging zone (Brink & Cowles 1991). In the early 1990s, the Northern California Coastal Circulation Study discovered that the velocity variability on time scales from weeks to months was produced by mesoscale eddies impinging off the shelf (Magnell & Winant 1993). The Eastern Boundary Current Project was conducted in the early 1990s, focusing on mesoscale physical and biological fields. Results from this project indicated that maxima of zooplankton abundance and biomass coincided with mesoscale eddies (Huntley et al. 1995). Processes of zooplankton transport and population dynamics associated with these mesoscale eddies were further studied using the size-structured zooplankton model and objective interpolation method (Zhou & Huntley 1997; Zhou 2001). These results revealed that generation time scale of mesozooplankton and
macrozooplankton varies from 30 to 100 days (Huntley & Lopez 1992). Assuming the current of 10 cm s\(^{-1}\), the advective time scale over a mesoscale or topographic feature of 50–100 km is approximately 6–12 days which is much smaller than the generation time scales (Huntley & Lopez 1992; Zhou 2001). Thus, the effects of advection process on zooplankton distribution and productivity are expected to be on the first order.

The California Current is generally southward close and parallel to the coast north of Newport, Oregon (Barth et al. 2000, 2005). It is topographically influenced forming mesoscale eddies or meanders over Heceta Bank entrapping the upwelled cold water near the coast. Frequently mesoscale eddies and filaments spin off from the coast and translate westward. The California Current separates from Cape Blanco and flows southwestward (Kosro et al. 1991; Barth et al. 2000). A subsurface northward undercurrent of 5 cm s\(^{-1}\) was observed between 35°N and 50°N along the shelf break in the depth range from 125 and 325 m (Pierce et al. 2000). In the upper 200 m, the vertical integrated volume transports of the southward California Current and the northward undercurrent are approximately 3 and 0.8 Sv, respectively (Barth et al. 2000; Pierce et al. 2000). The dynamics of these mesoscale features are associated with baroclinic instability of the California Current (Pierce et al. 1991), topographic features (Haidvogel et al. 1991), and wind stress (McCreary et al. 1991). Biological processes are coupled with mesoscale physical processes in the California Current (Huntley et al. 1995; Zhou & Huntley 1997; Barth et al. 2002). Phytoplankton and zooplankton biomasses enhanced by upwelling in coastal areas will be either transported by the California Current, or retained by eddies and meanders.

To understand the fate of zooplankton in eddies and jets requires resolving zooplankton distributions and processes at the scales of eddies and jets. Significant efforts have been made in the last 2 decades using towed optical and acoustic devices to resolve both physical and
biological fields at the same location and time. For example, in the California Current system, studies were conducted on correlations between zooplankton maxima, jets and eddies (Huntley et al. 1995; Zhou 2001; Barth et al. 2002); in the Georges Bank region, studies focused on the zooplankton recruitment and their cross-front transport mechanisms (Wiebe et al. 2001; Benfield et al. 2003; Ullman et al. 2003); and in northern Norwegian shelf areas, studies centered on onshore intrusions of zooplankton and their impacts on local productivity (Fossheim et al. 2005; Zhou et al. 2009; Zhu et al. 2009). Though results from these early studies elucidated qualitative relationships between physical and biological fields, quantitative estimates of transport and retention of zooplankton biomass and zooplankton process rates were rarely found. Without resolving the physical processes of advection and retention, population dynamic processes of zooplankton will not be resolved.

A cruise was conducted between June 1 and 17 2002, as a part of the United States (US) Global Ocean Ecosystems Dynamics Program (GLOBEC) Northeast Pacific Study (NEP) for surveying physical and biological fields using towed and shipboard physical–biological sensors (Barth et al. 2005). These integrated physical and biological data allowed us to make quantitative estimates of transport, retention and process rates, potential errors based on different analytical methods, and limits of survey and analytical methods. These results then allow us to access local food web dynamics.

**DATA AND METHODS**

**Data**

The study area was designed from 44°37′N off Newport, Oregon to 41°44′N off Crescent City, California and from the coast to approximately 100 km offshore (Fig. 1). The mesoscale survey was conducted in a period of 5 days with 12 cross–shelf transects approximately
0.25° apart in the latitude. Two fine–scale surveys were then conducted in the Heceta Bank and Cape Blanco regions with a latitudinal interval of approximately 0.05–0.15°. A towed SeaSoar instrument package was employed during the survey including 2 pairs of SBE 911 plus conductivity, temperature and depth sensors (CTD; Sea–Bird Electronics, Inc.) for the hydrographic data, a fluorometer (Wet Lab) for relative fluorescence and an Optical Plankton Counter (OPC; Focal Technologies) for zooplankton between 0.25 and 2.4 cm in Equivalent Spherical Diameter (ESD). The SeaSoar undulated from the surface to approximately 10 m above the bottom in coastal areas, or a maximum depth of approximately 200 m in offshore areas at a ship speed of 7–8 knots. The SeaSoar undulating cycle varied from 1.5 min on the shelf to 16 min off the shelf which led to horizontal resolutions of 350 m and 4 km on and off the shelf, respectively. The highest vertical resolutions of physical and biological data were determined by the SeaSoar undulation speed and sampling rates of CTD at 24 Hz, and both Fluorometer and OPC at 2 Hz. Due to the OPC failure, there were no OPC data collected on transects 8–12 of the mesoscale survey.

A vessel mounted 153 kHz Narrow Band (NB) Acoustic Doppler Current Profiler (ADCP; RD Instruments) was used for current measurements with the bin length of 8 m and ensemble average of 5 min. The error in 5–minute averaged velocities was 0.04 m s⁻¹ and 0.02 m s⁻¹ using navigation and bottom track, respectively (Barth et al. 2005). Wind measurements were obtained from NOAA National Data Center buoy 46050 located at 44°37´N, 124°30´W, approximately 37 km offshore of Newport, Oregon (www.ndbc.noaa.gov). For zooplankton taxonomic information, live samples were collected on May 31 2002 over Heceta Bank (Fig. 1) by using a 0.5 m² ring net with 202 μm mesh towed in the upper 100 m at 1 knot (Courtesy of W. Peterson, NOAA NW Fisheries Science Center).
Data processing

The OPC provides plankton counts in 3494 digital sizes corresponding to a size range between 0.25 and 24 mm in ESD (Herman 1992). For using the carbon unit, the ESD of a zooplankter was converted to its body carbon based on the equation of Rodriguez and Mullin (1986) developed specially for California Current system by assuming the length to width aspect ratio of 1.61 for copepods (Huntley et al. 2002), i.e.,

\[
\log_{10}(\mu gC) = 2.23 \log_{10} (\text{ESD in } \mu m) - 5.58.
\]  

(1)

To increase the statistics of measurements in a given size interval, 3494 body carbon sizes were integrated into 50 body carbon size intervals on an equal log\(_{10}\) basis. Within each size interval, accumulative biomass (\(\mu g\) C) of zooplankton was computed for every 0.5 s, and then normalized by the water volume filtered (m\(^3\)) and size interval (\(\mu g\)C) that leads to a normalized biomass spectrum in the unit of m\(^{-3}\) following Platt and Denman (1978) and Zhou and Huntley (1997) (referred to hereafter as biomass spectrum). All OPC data were processed along the undulating paths for the mesoscale and fine-scale surveys. It should be kept in mind that the uncertainty of OPC in estimating zooplankton biomass due to different optical properties of zooplankton species and spatial variation of taxonomic compositions may significantly affect zooplankton biomass estimates though this manuscript focuses on effects of physical processes on process rate estimates (Herman 1992; Huntley et al. 1995).

To compute coupled physical and biological data and variables, all CTD, fluorometer and OPC data were further processed into 8 m vertical bins to match the ADCP data. Because the first depth bin of ADCP measurements started from 25 m, all CTD, fluorometer and OPC data in the upper 25 m were averaged. Then at each depth bin, all data were interpolated into 50×50 horizontal grids by using the Objective Interpolation method within the survey area bounded by
The spatial decorrelation scales and covariance functions were determined from the autocorrelations of temperature data from CTD in the zonal and meridional directions based on Legendre (1983). The zonal correlations were computed at individual longitudinal transects, and then the mean zonal correlation was obtained by taking a latitudinal average. For the mean meridional correlation, we first binned the data into 0.15° longitudinal bins along each transect, computed the meridional correlation at a given longitude, and then averaged meridional correlations longitudinally. The minimum scale of physical and biological features in the latitude was determined by the distance between two transects approximately 0.25°. The results indicated an anisotropic field with the decorrelation scales of 33 km and 88 km in the zonal and meridional directions, respectively (Fig. 2), both of which are much larger than the spatial resolutions in the datasets. The decorrelation scales were consistent with that estimated from the time series of current data off Oregon (Kundu & Allen 1976). An appropriate covariance function \((1 - r)e^{-r} \) was selected to fit autocorrelation data where \( r \) is equal to \( \sqrt{(\Delta x/l_x)^2 + (\Delta y/l_y)^2} \), and \( l_x \) and \( l_y \) are the decorrelation scales in the zonal and meridional directions, and \( \Delta x \) and \( \Delta y \) are the distances between two locations in the longitude and latitude.

To remove barotropic tidal current components from ADCP current measurements is challenging because errors can be introduced by measurements, predicted tidal currents from a tidal model and interpolation method used for gridding. The predicted tidal currents from a tidal model were extracted based on the location and time along the ship track (Erofeeva et al. 2003), and the detided currents were obtained by subtracting the predicted tidal currents from the ADCP current measurements. Because there is no streamfunction for tidal currents, fitting a
streamfunction to detided currents during interpolation will further remove tidal and ageostrophic components. We used two objective interpolation methods developed by Barnes (1964) and Bretherton et al. (1976) (Referred to hereafter as Barnes and BDF interpolations, respectively). Barnes interpolation is a successive correction method by minimizing differences between passes under defined decorrelation scales. The streamfunction was then calculated based on Hawkins and Rosenthal (1965). BDF interpolation is based on statistics and defined decorrelation scales, and the streamfunction is obtained by minimizing divergences (Bretherton et al. 1976; Dorland & Zhou 2007). Although these two mathematical interpolations are all valid and well tested, the differences in results between these two different methods will bring insight into the sensitivities and uncertainties for interpreting population dynamic processes.

We tested two spatial covariance functions for Barnes interpolation of which one is an isotropic covariance function with decorrelation scales of 50 km in both zonal and meridional directions to match previous studies (Huntley et al. 1995), and another is anisotropic covariance function with decorrelation scales of 33 km in the zonal direction and 88 km in the meridional direction which match the decorrelation scales computed from our data. Two passes were applied for both covariance functions and the velocity differences between two passes are less than 1 cm s\(^{-1}\). We found no significant differences in results between these two different covariance functions. For the consistency with previous studies the results from the isotropic 50 km Barnes interpolation are presented in this paper. Because BDF interpolation turns to maximize mesoscale features at the defined spatial scales, we used the anisotropic covariance function with scales of 33 km in the zonal direction and 88 km in the meridional direction. The numerical divergences of interpolated current fields are in the order of \(10^{-7}\) s\(^{-1}\) and \(10^{-18}\) s\(^{-1}\) for Barnes and BDF interpolations, respectively.
For zooplankton biomass \( b \), the local change is primarily determined by the convergence of biomass transport, and the bio–reaction related to the population dynamics processes, i.e.,

\[
\frac{\partial b}{\partial t} = R(b,t) - \left( \frac{\partial ub}{\partial x} + \frac{\partial vb}{\partial y} + \frac{\partial wb}{\partial z} \right),
\]

(2)

where \( t \) is the time, and \( u, v, \) and \( w \) are the zonal \((x)\), meridional \((y)\) and vertical \((z)\) velocity components, respectively. On the right side of Eq. (2), \( R(b, t) \) represents the bio–reaction, a net production, and the second term presents the advection or convergence of zooplankton transports. In order to examine the total biomass variation, we integrate Eq. (2) over the water column \( H \) assuming there is no flux crossing the surface and bottom, we will have

\[
\frac{\partial}{\partial t} \int_{H}^{0} b dz = \int_{H}^{0} R(b,t) dz - \left( \int_{H}^{0} \frac{\partial}{\partial x} ub dz + \int_{H}^{0} \frac{\partial}{\partial y} vb dz \right).
\]

(3)

In Eq. (3), on the left side the term is the local change rate of vertically–integrated biomass in the water column, and on the right side the first and second terms are the bio–reaction and convergence of horizontal transport, respectively. The horizontal transport can be calculated directly from binned current and OPC data. The horizontal convergence of biomass can be further separated into two terms as,

\[
-\left( \int_{H}^{0} \frac{\partial}{\partial x} ub dz + \int_{H}^{0} \frac{\partial}{\partial y} vb dz \right) = -\int_{H}^{0} \left( u \frac{\partial b}{\partial x} + v \frac{\partial b}{\partial y} \right) dz - \int_{H}^{0} \left( \frac{\partial u}{\partial x} + \frac{\partial v}{\partial x} \right) dz.
\]

(4)

On the right side, the first term is the biomass convergence contributed by gradient advection, and the second term is the retention of \( b \) determined by current convergence. This current convergence term should be small because the flow field at the spatial scale of our interests is
nearly geostrophically balanced (Kosro & Huyer 1986; Pickett et al. 2003; Shearman et al. 2000). The current convergence estimates resulted from the Ekman pumping driven by wind stress curl and from the secondary circulation determined by the quasi–geostrophic dynamics are on the second order. Thus, in a heterogenic zooplankton field, the advection of zooplankton gradients should play the dominant role in concentrating or dissipating zooplankton.

The sign of the biomass gradient advection implies a high biomass or a low biomass center moving into an area. When a positive (negative) current advects a negative (positive) gradient, the higher biomass is moving in which we refer as a positive gradient advection. When a positive (negative) current advects a positive (negative) gradient, the lower biomass is moving in which we refer as a negative gradient advection.

To examine the productivity of a given region, a Eulerian control water volume ($V$) can be selected. For example, a control water volume of Oregon coastal region can be bounded by Transects 1 and 12 in the latitude, the coast and 153 m isobath in the longitude, and the surface and bottom in the vertical. Integrating Eq. (3) over an area ($S$) bounded by the boundary ($\delta S$) and water depth ($H$), and applying Stokes’ theory (Beyer 1987), we have

$$\frac{\partial}{\partial t} \int_S (bdz) dS = \int_S \left[ \int_0^H [R(b,t)dz] dS - \oint_{\partial S} \left( \int_0^H ubdz \right) dy + \left( \int_0^H vbdz \right) dx \right].$$  (5)

Eq. (5) again represents the balance between biomass change in a control region, local net production and transport fluxes.

The errors during estimating biomass transports are contributed from errors in both currents and zooplankton biomass estimates. Theoretically, the errors of those estimated streamfunctions and zooplankton distributions should be known because those interpolations are based on
statistics and given covariance functions (Bretherton et al. 1976; Barth et al. 2000). However, the detided ADCP current measurements include unknown errors in ship movements, modeled tidal currents and ageostrophic currents. Zooplankton measurements include unknown errors due to zooplankton patchiness, migration behavior and avoidance. Though these errors could be small as indicated, we do not know them quantitatively and their statistical characteristics, and cannot resolve these errors in our datasets and progresses of these errors in Eq. (5).

RESULTS

Wind condition

The wind during the survey period (June 2–15 2002) was predominately southward, upwelling–favorable with a maximum wind speed of approximately 10 m s$^{-1}$ (Fig. 3). There were two northward wind events on June 4 and 13 2002. The first event approximately 2 days occurred in the second half of the mesoscale survey, and the second event less than 2 days occurred in the southern fine–scale survey. The predominated upwelling favorable wind, short–term relaxation and downwelling favorable wind led upwelling and downwelling.

Horizontal distributions of temperature, currents, chlorophyll, and zooplankton

The results from the autocorrelation analysis of CTD data indicate an anisotropic field (Fig. 2). In the zonal direction, the autocorrelation decreases quickly within 18 km, becomes flat between 18 and 27 km, and has the first zero–crossing at 33 km, which implies there were multiple scales. In the meridional direction, the autocorrelation decreases monotonically crossing the zero at 88 km. The fits using different theoretical functions were tested. The covariance function of $\exp(-r)$ was the best–fit and chosen for the interpolations of temperature, chlorophyll, zooplankton abundance and biomass, and currents (Figs. 4–9).
The coastal upwelling area can be identified from the colder water at the surface along the Oregon and northern California coasts compared to the warmer water in the offshore areas (Fig. 4). Between Newport and Cape Blanco, Oregon, the upwelling area was parallel to the coast within a narrow 10–20 km band while south of Cape Blanco, the upwelling area extended offshore–ward approximately 100 km. Associated with these upwelling fronts, the currents from streamfunctions best–fitted with the detided currents from the mesoscale survey have revealed jets and eddies (Fig. 5). On Heceta Bank, the cold water of 10°C started inshore and spread over the bank area. South of Cape Blanco, associate with the broad upwelling area, the California Current departed from the coast to the southwestward. From Barnes interpolation, the California Current was steered offshore at Heceta Bank and Cape Blanco forming meanders (Fig. 5b) while from BDF interpolation, eddies were clearly formed over Heceta Bank and off Cape Blanco (Fig. 5c). The results from these two interpolations are significantly different due to different inherent assumptions in methods. Though both results are valid because both interpolation methods are well developed and tested, the significant differences in results have demonstrated the challenges in resolving physical processes and transport–retention of zooplankton populations.

Because the OPC was failed in the second half mesoscale survey, we used the CTD, fluorometer and OPC data from the mesoscale survey transects 1–7 and the southern fine–scale survey transects (Fig. 1). The chlorophyll distribution at 5 m was highly correlated with the upwelled cold water while the zooplankton biomass distribution at 5 m was not correlated with the upwelled cold water (Fig. 4). Elevated chlorophyll and zooplankton concentrations were found in the mesoscale eddy and the offshore transported cold water near Heceta Bank, and in the broad upwelling area south of Cape Blanco. The offshore transports of phytoplankton and zooplankton by the California Current were found west of Heceta Bank while the offshore water...
with low chlorophyll and zooplankton concentrations intruded into the coastal area between Heceta Bank and Cape Blanco.

The spatial patterns in the mean zooplankton abundance and biomass distributions between the surface and 153 m can visually be linked to the temperature patterns and mesoscale features of jets and eddies (Fig. 6). High zooplankton abundances and biomass were found along all coastal upwelling areas implying the effects of upwelling on primary and secondary productions. Zooplankton abundance maxima were found in most coastal areas while zooplankton biomass maxima were found only over Heceta Bank and Coos Bay areas.

**Vertical distributions of temperature, currents, chlorophyll and zooplankton**

The coastal upwelling and offshore stratification can be seen from the outcropped thermocline along mesoscale Transect 5 (Fig. 7). The upwelling area was limited near the coast with the temperature as low as 7–8°C. Crossing the upwelling front, the water was stratified with the surface temperature of 12–14°C and the thermocline depth of 20–30 m. The ADCP current measurements are superimposed on the temperature transect indicating the jets and eddies associated with slopes of thermocline.

Between 125° 00’W and 125°15’W on this transect, a jet was found southwestward at approximately 30 cm s⁻¹ consistent with the offshore–ward California Current steered by Heceta Bank (Fig. 5) (Barth et al., 2005). The along transect current component shows a convergent pattern in the depth range over 180 m occurring within this jet. This zonal convergence may lead to the deep penetration of phytoplankton and zooplankton biomasses (Fig. 7).

The surface chlorophyll maximum was found in the nearshore upwelling area (Fig. 7), and the subsurface maxima were found near thermocline areas in the offshore stratified water column.
Corresponding to such phytoplankton distributions, zooplankton were distributed over the entire water column with surface enhancements in the nearshore area, and strongly correlated with phytoplankton maxima in offshore areas.

**Zooplankton biomass transport**

The horizontal transport vectors of zooplankton biomass within the upper 153 m are calculated based on OPC biomass measurements and 2 current fields from Barnes and BDF interpolations (Fig. 8). All of them show similar large-scale patterns, for example, the dominant offshore and southward transports of zooplankton. The onshore and northward transports of zooplankton were revealed only at the mesoscale.

The depth integrated zooplankton biomass gradient advection is calculated based on Eq. (4) using the OPC biomass measurements and the mesoscale current field based on BDF interpolation (Fig. 9a). Positive advection implies that higher biomass water mass is displacing the lower biomass water mass, and vice versa. Negative advection was found in the onshore current south of Heceta Bank where the shoreward current transported low biomass water northeastward. Positive values were found in coastal regions where the currents had transported higher zooplankton biomass into the area. Within the advection terms as expressed in Eq. (4), the advection of biomass gradients dominated the processes, especially in the areas of offshore transport. To compare the biomass advection with zooplankton growth rates, the specific convergence rate of biomass advection is computed by the ratio of depth integrated biomass gradient advection to depth integrated zooplankton biomass in the survey area (Fig. 9b). The convergence rate varies between –0.5 and 0.5 day\(^{-1}\) in June, the early summer season, indicating the importance of physical advective processes on zooplankton distributions.
To estimate the magnitude of zooplankton biomass offshore transport and coastal retention, we define a coastal area by the 153 m isobath and survey Transects 1 and 12 (Fig. 1). Assuming there was no flux crossing the coast, the transport fluxes crossing northern, western and southern boundaries in Eq. (5) were estimated based on the current fields from both Barnes and BDF interpolations (Table 1). The results show the flux estimates are extremely sensitive to the current fields, especially the estimates at 153 m isobath.

Zooplankton size structure

To investigate zooplankton size structures and species, 6 representative areas are selected in the survey area (Fig. 6a): Area 1 represents the offshelf low biomass area west of Heceta Bank, Area 2 is the high productive Heceta Bank region, Area 3 is in the offshore–ward jet off Heceta Bank with both chlorophyll and zooplankton maxima, Area 4 is in the offshelf water with both low chlorophyll and zooplankton, Area 5 represents the nearshore chlorophyll and zooplankton biomass maxima off Cape Blanco, and Area 6 is within the offshore jet with both chlorophyll and zooplankton maxima southwest of Cape Blanco. The biomass spectra in Fig. 10a–c are paired between offshelf Areas 1 and 4, between nearshore Areas 2 and 5, and offshore jet Areas 3 and 6.

To evaluate the effects of zooplankton vertical migration on zooplankton distributions, the OPC data were separated into day and night time based on PAR (photosynthetically available radiation) which was predicted as a function of latitude and Julian day. The night period was defined as PAR equal to zero corresponding to the local time approximately between 19:00 and 05:00 h during the survey period. Daytime and nighttime biomass spectra were constructed between the surface and the maximum depth the SeaSoar reached (Fig. 10d). We exclude the coastal area shallower than 153 m isobath for this study because high biomass measurements in shallow coastal regions could lead to high biomass estimates in upper water columns and bias the
estimates. The regression relationship between daytime and nighttime biomass spectra indicates the significant similarity ($y = 1.06x -0.29$, $r^2 = 0.99$).

**DISCUSSIONS**

**Mesoscale current fields from two interpolation methods**

Both Barnes and BDF interpolation methods and stream functions have revealed coastal jets, meanders and eddies (Figs. 5b and 5c). The coastal jets and eddies are significantly steered by shallow banks and capes in the Oregon and northern California section (Brink & Cowles 1991; Barth et al., 2000; Barth et al., 2002). Though both interpolations have provided large scale currents, meanders and eddies, significant differences exist. For example, the California Current was turned to the offshore direction forming large crossing–isobath currents and a meander over Heceta Bank from Barnes interpolation and forming small crossing–isobath currents and an eddy over Heceta Bank from BDF interpolation. Comparing both to the original detided ADCP currents, Barnes interpolation provides a smoother large scale circulation pattern with less mesoscale features while BDF interpolation remains more detailed mesoscale features under the nondivergent condition. The differences in the circulation patterns between different interpolation methods are resulted from the inherent assumptions within the methods.

The differences between current fields are critically important in understanding transport and retention mechanisms of biota in coastal areas, for example Heceta Bank. Barnes interpolation has shown a crossing–isobath offshelf transport in the southwestern part of the bank, while BDF interpolation has shown a much reduced crossing–isobath current controlled by isobaths. The magnitude of crossing–isobath currents obviously plays an important role for the population dynamics of zooplankton on Heceta Bank. It is feasible to adjust parameters and methods to converge results from these two different interpolation methods though any
subjective adjustment will not make any new understanding. Though both these current fields are valid but focus on different features of the current fields, how can we choose interpolation methods and current fields for computing transport and retention of biological fields? The ultimate test has to compare to observations of both physical and biological fields. These methods are originally developed for analyzing and filtering imperfect field data. New progresses in both observations and analytical methods need to be made for better physical and biological fields.

**Zooplankton maxima vs. mesoscale current fields**

The meander or eddy over Heceta Bank can remain for several weeks according to Lagrangian drifter studies (Barth et al. 2000; Geen et al. 2000). At Cape Blanco, the California Current separates from the coast, and typically forms jets and eddies (Barth et al., 2000, 2005). These eddies and meanders increase the residence time and in turn can potentially affect phytoplankton and zooplankton productivities. The strong correlations between coastal upwelling, eddies, chlorophyll concentrations and zooplankton biomass are clearly shown in Figs. 4, 5 and 6, suggesting that upwelling drives the productive coastal ecosystem off Oregon and northern California. Downwelling wind events did occur during the survey (Fig. 2). Would a downwelling event erases chlorophyll and zooplankton maxima in nearshore areas? In a short downwelling wind event, the downwelling wind could prevent biota from offshore transport and retain biomass along coastal regions by its onshore Ekman transport. Though currents varied between upwelling and downwelling favorable winds, the effect of enhanced productivity in coastal areas was persistent.

In offshelf areas, the zooplankton biomass maxima were found associated with offshore–ward jets and meanders (Figs. 5 and 6). Some of these maxima could be related to the offshore
transport by jets. For example, the deep zooplankton maximum between 125°15´W and
124°55´W along Transect 5 (43°45´N) was associated with an offshore–ward jet off Heceta Bank.
Offshore transports of phytoplankton and zooplankton biomasses have been observed (Washburn et al. 1991; Huntley et al. 1995, 2000; Barth et al. 2002). Our study further shows the
relationship between coastal productive areas and offshore zooplankton maxima associated with
offshore–ward jets.

Zooplankton deep maximum

A zooplankton deep maximum was found along Transect 5 (43°45´N) between 125°15´W
and 125°50´W in the offshore jet region (Fig. 7). Similar chlorophyll and zooplankton deep
maxima were also found in other studies within the California Current system (Huntley et al.
2000; Barth et al. 2002). The primary cause of deep biomass maxima has been interpreted as the
subduction of coastal biota with subducting waters during offshore transport. In these deep
maxima, both coastal and offshore zooplankton species can be found representing the transport
and mixing of coastal and offshore waters.

The zooplankton deep maximum had a zonal scale of 40 km which is equivalent to the
internal Rossby Radius in this area (Chereskin et al. 1994). No zooplankton deep maximum was
found in either survey Transect 4 or 6, implying that the meridional scale of this deep maximum
is less than 40 km. We can speculate that when jets and eddies are formed at the scale similar to
the internal Rossby Radius, their advection of zooplankton gradients can lead to the increase in
zooplankton patchiness at the similar scales.

The high zooplankton biomass in deep waters should be associated with subduction of
surface waters (Barth et al. 2002). Studies of quasigeostrophic dynamics of jets and fronts
indicate that denser water tends to slide underneath less dense water (Rudnick 1996; Shearman et al. 2000; Barth et al. 2002). In the offshore–ward currents off Heceta Bank and Cape Blanco, the upwelled deep water near coasts could subduct near upwelling fronts with coastal biota and then be transported offshore with the currents that led to a convergent zone or subduction zone of zooplankton around the currents.

There is no significant difference between daytime and nighttime biomass spectra from this study (Fig. 10d). In studies of zooplankton vertical diel migration processes, it was found that krill migrated to the surface layer at the beginning of sunset, and then they spread into a broad water column depending on prey fields (Zhou et al. 2005). It is also found that the migration patterns of mesopelagic boundary communities could be complicated by different migration speeds of different species (Benoit-Bird & Aub 2003). To examine detailed diel migration pattern, the depth center of biomass distribution in the water column was calculated as a function of time. The zooplankton biomass data were binned into 8 m depth bins from the surface to 153 m, and then averaged along the ship track within a longitudinal interval of 0.05°. The depth center ($Z$) of biomass distribution was determined by

$$Z = \frac{\sum_i B_i \cdot z_i}{\sum_i B_i},$$

where $B_i$ is the biomass at the depth of $z_i$. In order to avoid the shallow bottom which could bias the estimates of biomass depth centers, the calculations were also made from individual OPC profiles deeper than 153 m west of 124°48´N (Fig. 12). Taking the hourly averaging, the biomass depth centers varied in the ranges of $54\pm21$ m and $60\pm21$ m during the daytime and nighttime periods, respectively. The two sample $t$–test (df = 174) led to the $p$–value less than 0.29. Though there is a difference in the depth centers between daytime and nighttime, it is clear that
zooplankton did not aggregate in the upper water column more during the night than they did
during the day. Previous studies also found that total copepod biomass and individual species
showed no day–night difference in both net and OPC samples among the California Current
region (Mackas et al. 1991; Huntley et al. 1995; Peterson et al. 2002).

*Effects of advection on zooplankton community structure*

The biomass spectra from 6 selected areas had the similar feature that is high abundances at
small size classes and low abundances at large size classes (Fig. 10). Such a feature has been
observed in most of ocean and freshwater environments (Sheldon et al. 1967, 1972; Rodríguez &
Mullin 1986; Sprules & Manuwar 1986). Results from net samples collected in the same survey
period over Heceta Bank indicate the zooplankton assemblage in the body size range between
10^0 and 10^3 μgC in the California Current is dominated by a small number of species similar to
previous findings (Huntley et al. 2000). Body sizes between 0.5 and 1100 μgC contained early
to adult stages of copepod species, *Pseudocalanus spp.*, *Acartia spp.*, *Centropages spp.*, *Calanus
marshallea* and *Calanus pacificus*, and early stages of *Euphausia pacifica* and *Sergestes similis*.

Body sizes larger than 1100 μgC were dominated by middle to adult stages of *Euphausia
pacifica*, *Sergestes similis* and *Thysanoessa spinifera* (Mackas et al., 1991; Huntley et al., 2000;
Peterson et al., 2002).

Among the biomass spectra, the values in the size range between 16 and 250 μg C (1.2–2.4
in the log_{10} scale) over Heceta Bank (Area 2) were higher than those of other areas (Fig. 10).
Within this size range, the net tow samples in the same area (124.51°W, 44.25°N) and at the
same time indicate a biomass composition of 35% by *Pseudocalanus spp.* and 33% by *Calanus
marshallea* which are two of the most common copepod species in Oregon upwelling areas (Fig.
11) (in courtesy of W. Peterson). Such elevated biomass spectra from the linear relationship have
also been found in other coastal regions during spring such as the Norwegian shelf where the elevated biomass spectra were contributed by *Calanus finmarchicus* CV and adults and euphausiid larvae (Zhou 2009).

Two types of biomass spectra were observed during the survey: the linear spectra found in the offshore area (Area 1) and along the onshore intruding current (Area 4); and the nonlinear spectra found in coastal upwelling areas (Area 2) and the offshore jets (Area 3). Because the offshore and onshore–ward jets carried the biota from their origins, the spectrum of zooplankton in an offshore jet inherited the dome–shaped biomass spectrum of a coastal cohort and the spectrum in an onshore jet inherited the linear spectrum of an offshore cohort. Thus, the dome–shape of the biomass spectra in the offshore eddies marked by Areas 2 and 3 were contributed by *Pseudocalanus spp.* and *C. mashiellae* from coastal upwelling zones. These coastal zooplankton communities can be entrapped in eddies and advected further into offshelf region on an order of 100 days. The coastal zooplankton communities entrapped in a mesoscale eddy and advected 100 km off the shelf were also found (Huntley et al. 1995, 2000).

The offshore transport of coastal communities can be seen from the association between extending tongues of high zooplankton biomass from Heceta Bank and Cape Blanco, and the offshore currents (Figs. 5 and 6). In contrast, the onshore currents transported low zooplankton biomass waters to nearshore regions with zooplankton minima, such as the low zooplankton biomass band south of Heceta Bank extending from the offshore region to the coast region corresponding to a negative gradient advection (Fig. 9). In the Heceta Bank region, these onshore and offshore transports led to a biomass convergence.
Coastal convergence and offshore export of zooplankton biomass

The transport flux estimates crossing the boundaries surrounding the coastal region are extremely sensitive to the current fields, especially the estimates at 153 m isobath (Table 1). The current field from Barnes interpolation leads to significant crossing–isobath transport while the current field from BDF interpolation is mostly in parallel to 153 m isobath minimizing the crossing–isobath transport. Based on these estimates, the major transport flux into the Oregon coastal region occurred in the northern boundary (Transect 1) where the California Current transports zooplankton biomass southward approximately $2.5 \times 10^3$ and $1.0 \times 10^3$ ton C d$^{-1}$ based on Barnes and BDF interpolations, respectively. Across the southern boundary (Transect 12), the transport flux was relatively small and negligible comparing to the northern boundary. The offshore transport across the 153 m isobath was on the same order of magnitude as that across the northern boundary. The offshelf transport across the 153 m isobath computed from the currents based on Barnes interpolation is approximately $3.7 \times 10^3$ ton C d$^{-1}$ 4–5 times higher than that of BDF interpolation approximately $0.8 \times 10^3$ ton C d$^{-1}$. The difference in transport estimates primarily occurred at the shelf break south of Heceta Bank. The smaller crossing–isobaths transport from the current field based on BDF interpolation was caused by both the mesoscale currents being more in parallel to the 153 m isobath and the mesoscale returning currents associated with offshore jets. The crossing–isobath transport of biota due to crossing–isobath currents from Barnes interpolation occurs south of Heceta Bank and Cape Blanco.

The total zooplankton biomass integrated within the coastal area shallower than 153 m isobath is approximately $4 \times 10^4$ ton C. The net transport crossing the boundaries of this coastal area was $-1.4 \times 10^3$ and $0.3 \times 10^3$ ton C d$^{-1}$ using the current fields derived from Barnes and BDF interpolations leading to the biomass accumulation at the rates of $-0.04$ and $0.01$ d$^{-1}$, respectively.
The differences between transport fluxes estimated using different interpolation methods do not imply any unreliability of these mathematical methods. The differences indicate the differences between these methods in dealing with uncertainties from field data. Thus to verify results from mathematical methods in field observations is challenging but necessary for us to study coupled physical and biological processes.

The growth rate of zooplankton is approximately 0.1 d\(^{-1}\) in 8\(^\circ\)C water within upwelling areas using a general formula (Huntley & Lopez 1992; Hirst & Bunker 2003; Bi et al. 2010; Zhou et al. 2010), or 0.08 d\(^{-1}\) for overall copepod species from a time series in upwelling waters off Newport, Oregon (Gómez–Gutiérrez and Peterson 1999). The local specific convergence rates of biomass advection were between −0.5 and 0.5 day\(^{-1}\) which were significantly higher than local zooplankton growth rates (Fig. 9b). The dominancy of physical advective processes in zooplankton biomass variations elucidates the difficulty in studying in–situ zooplankton population dynamics processes which requires following a specific zooplankton cohort. Though the local convergence rate is dominant 5 times higher than the local growth rate, the area mean of convergence rates becomes less while integrating the convergence rate over a larger region. The accumulation rates due to the convergence of biomass gradient advection in the entire coastal area shallower than 153 m isobaths off Oregon are approximately −0.04 and 0.01 d\(^{-1}\) based on 2 different interpolations, respectively. These accumulation rates are approximately one order of magnitude smaller than the growth rate, indicating the high zooplankton production in the Oregon coastal region was enhanced by the local primary production.

The local convergence of zooplankton transport is dominated by advection of zooplankton gradients because the convergence of currents is secondary. In the survey area, the advection of zooplankton biomass gradients shows alternating negative and positive patches.
associated with currents and biomass gradients (Fig. 9). The signs simply indicate the advection of a high biomass center or a low biomass center into a local area. In the offshore–ward jets, the positive sign indicates an offshore transport of nearshore–produced zooplankton biota while in an onshore current the negative sign indicates an intrusion of offshelf low zooplankton water. Thus, the mosaic of zooplankton gradient advection in Fig. 9 also represents the horizontal exchange–mixing processes of zooplankton nearshore and offshelf biota due to advective transports. These results, especially the different estimates using Barnes and BDF interpolations, elucidate the nonlinearity of zooplankton gradient advection processes, and potential biases by linear averaging removing mesoscale features. Can we improve measurements of currents and biomass so that estimates of advection and population process rates can be improved? What a research vessel can do is limited by its cruise speed and limited sensors can be deployed at the same time. The recent development of autonomous underwater vehicles and miniaturized optical and acoustic sensors may provide the mean to resolve higher spatial and temporal resolution physical and biological fields, and also to release the ship from mapping for conducting process rate experiments. Most importantly, a detailed analysis of errors from sampling methods and designs must be taken prior to a cruise so that potential errors can be estimated and possibly avoid.

**SUMMARY**

The high resolution observations of physical–biological fields obtained in the California Current system off Oregon during June 2002 revealed the strong correlations between coastal upwelling areas and zooplankton biomass maxima. Primary productivity in the coastal region off Oregon is enhanced by upwelling, which supports the ecosystem in the region. However the zooplankton productivity within the region not only depends on local growth and regeneration,
but also the convergence of zooplankton biomass gradient advection. In the coastal area shallower than the 153 m isobaths between 41°44’N and 44°37’N, the mesozooplankton biomass was approximately $4 \times 10^4$ ton C. There are significant differences in transport flux estimates from different current fields based on Barnes and BDF interpolation methods indicating inherent uncertainties from the field data and the importance to resolve these differences in field. In spite of these discrepancies, the results indicate the influx of zooplankton biomass into the coastal area occurred primarily at the northern boundary at Newport, Oregon by the southward California Current approximately $1 - 2.5 \times 10^3$ ton C d$^{-1}$ at a rate of $0.03 - 0.06$ day$^{-1}$ based on two different analytical methods which are close to the mean growth rate of zooplankton (Huntley & Lopez 1992; Hirst & Bunker, 2003; Bi et al. 2010; Zhou et al. 2010). The flux at the southern boundary is one order of magnitude less than that of the northern boundary. The offshore transport of high zooplankton biomass water was found off Heceta Bank and Cape Blanco while the onshore intrusions of low zooplankton biomass waters were found between Heceta Bank and Coos Bay. The net offshore transport of zooplankton crossing the 153 m isobaths was approximately $0.8 - 3.7 \times 10^3$ ton C d$^{-1}$ at a rate of $0.02 - 0.09$ day$^{-1}$ significantly contributing to the loss of coastal communities during June 2002. Thus in the Oregon coast, the physical advection processed are on the same order of magnitude of zooplankton growth rate, and of important processes in determining zooplankton retention and productivity.
ACKNOWLEDGEMENTS

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LITERATURE CITED


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Table 1. Zooplankton biomass transport fluxes ($\times 10^3$ ton C d$^{-1}$) into the coastal area shallower than 153 m isobaths between 41°44′N (Transect 12) and 44°37′N (Transect 1) (Fig. 1) and corresponding rates (d$^{-1}$). A positive or negative value represents a net flux of biomass into or out of the coastal area. The rate estimate is based on the estimated total standing biomass of $4 \times 10^4$ ton C within the control area.

<table>
<thead>
<tr>
<th>Current field</th>
<th>Transect 1</th>
<th>Transect 12</th>
<th>153 m</th>
<th>Net</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flux Rate</td>
<td>Flux Rate</td>
<td>Flux Rate</td>
<td>Flux Rate</td>
</tr>
<tr>
<td>Detided ADCP currents</td>
<td>2.1 0.05</td>
<td>0.1 0.003</td>
<td>1.4 0.04</td>
<td>3.6 0.09</td>
</tr>
<tr>
<td>Streamfunction$^1$</td>
<td>2.5 0.06</td>
<td>-0.2 -0.005</td>
<td>-3.7 -0.09</td>
<td>-1.4 -0.04</td>
</tr>
<tr>
<td>Streamfunction$^2$</td>
<td>1.0 0.03</td>
<td>0.1 0.003</td>
<td>-0.8 -0.02</td>
<td>0.3 0.01</td>
</tr>
</tbody>
</table>

$^1$ The streamfunction is derived from an isotropic covariance function with a scale of 50 km.

$^2$ The streamfunction is derived from an anisotropic covariance function with a zonal scale of 33 km and a meridional scale of 88 km.
Figure Captions

Fig. 1. Bathymetry of the study area off Oregon. The thin black lines are isobaths of 50, 100, 153 and 2000 m, the thick black lines are mesoscale survey transects from 1 to 7 and southern fine-scale survey transects from 8 to 12 indicated by the labels next to these lines, and the black cross at Transect 1 indicates the location of NDBC buoy 46050.

Fig. 2. Autocorrelations calculated from temperature data: (a) zonal and (b) meridional components. The black dots are calculated data, the dash lines are the best–fit covariance function \((1-r)e^{-r}\), and the solid lines are the best–fit covariance function \((1-r^2)e^{-r^2}\). The zero crossings are 33 km and 88 km in the zonal and meridional directions, respectively.

Fig. 3. The time series of wind measurements at NOAA NDBC buoy 46050 during the survey period: (a) wind speed, (b) zonal component and (c) meridional component. The shaded areas indicate the periods of the mesoscale, northern and southern fine–scale surveys.

Fig. 4. Horizontal distributions at 5 m: (a) temperature in °C represented by false colors with black dash contours at 1°C intervals, (b) chlorophyll in mg m⁻³ represented by false colors with black dash contours at 1 mg m⁻³ intervals, and (c) zooplankton biomass in mg C m⁻³ represented by false colors and zooplankton abundance in individuals m⁻³ represented by solid black contours. The solid white contour lines indicate the 153 m isobath.

Fig. 5. Horizontal current distributions at 25 m in m s⁻¹ represented by vectors: (a) 30 minute averaged detided ADCP currents, (b) currents derived from Barnes interpolation, (c) currents derived from the BDF interpolation. The solid contour lines indicate the 153 m isobath.

Fig. 6. Depth averaged distributions between 0 and 153 m: (a) zooplankton abundance in individual m⁻³ and (b) zooplankton biomass in mg C m⁻³ represented by false colors. The
numbers 1–6 in (a) are used to mark the six $20 \times 20$ km$^2$ areas representing: 1) the southward jet area in the northern boundary, 2) the high biomass area on Heceta Bank, 3) the high biomass area within the southwestward jet off Heceta Bank, 4) the low biomass area within the onshore return flow, 5) the high biomass area in the coastal region north of Cape Blanco, and 6) the high biomass area within the offshore jet south of Cape Blanco.

Fig. 7. Cross–shelf vertical transects along mesoscale Transect 5: (a) temperature in $^\circ$C represented in false colors with ADCP currents represented by the horizontal vectors for the zonal components and the $45^\circ$ vectors for the meridional components, (b) chlorophyll in mg m$^{-3}$ represented in false colors, and (c) zooplankton biomass in mg C m$^{-3}$ represented in false colors and zooplankton abundance in individuals m$^{-3}$ represented by solid black contours.

Fig. 8. Depth (0–153 m) integrated zooplankton biomass horizontal transport in mg C m$^{-1}$ s$^{-1}$: (a) the transport derived from 30 minute averaged detided ADCP currents, (b) the transport derived from the Barnes interpolation, and (c) the transport derived from the BDF interpolation. The solid contour lines indicate the 153 m isobath.

Fig. 9. Depth (0–153 m) integrated biomass gradient advection: (a) the biomass gradient advection in mg C m$^{-2}$ s$^{-1}$ derived from the BDF interpolation, and (b) the specific rate of biomass gradient advection in day$^{-1}$ based on the ratio of the depth integrated biomass gradient advection to the depth integrated biomass. The dash lines indicate the zero contours.

Fig. 10. Biomass spectra from OPC measurements: (a) Areas 1 and 4, (b) Areas 2 and 5, (c) Areas 3 and 6, and (d) daytime (05:00–19:00 h) and nighttime (19:00–05:00 h) in the survey area deeper than 153 m. The areas are indicated in Fig. 6a. The dots represent the
means and solid vertical lines indicate 95% confidence intervals.

Fig. 11. Percentage composition of dominant zooplankton species from zooplankton samples collected in Area 2 indicated in Fig. 6a.

Fig. 12. Depth centers of zooplankton biomass derived from individual vertical profiles in the survey area deeper than 153 m as a function of nighttime (19:00–05:00) represented by open circles and daytime (05:00–19:00) represented by solid gray dots. The solid black dots represent the hourly means and the vertical black lines are their standard deviations.
Fig. 1
Fig. 2
Fig. 3

Mesoscale
Northern fine-scale
Southern fine-scale

(a)

(b)

(c)

June 2002

Zonal (m s⁻¹)

Meridional (m s⁻¹)

Speed (m s⁻¹)
Fig. 4
Fig. 5
Fig. 7
Fig. 9
Fig. 10

(a) (b) (c) (d)

log_{10} (body weight in μgC) vs. log_{10} (biomass spectrum in m^{-3})

Area 1
Area 2
Area 3
Area 4
Area 5
Area 6

Day
Night
Pseudocalanus spp.
Thysanoessa spp.
Euphausia spp.
Calanus marshallea
Centropages spp.
Calanus pacifica
others

Fig. 11
Fig. 12