



Mesoscale structure and oceanographic determinants of krill hotspots in the California Current: Implications for trophic transfer and conservation

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ABSTRACT

Krill (crustaceans of the family *Euphausiacea*) comprise an important prey field for vast array of fish, birds, and marine mammals in the California Current and other large marine ecosystems globally. In this study, we test the hypothesis that mesoscale spatial organization of krill is related to oceanographic conditions associated with coastal upwelling. To test this, we compiled a climatology of krill distributions based on hydroacoustic surveys off California in May–June each year between 2000 and 2009 (missing 2007). Approximately 53,000 km of ocean habitat was sampled, resulting in a comprehensive geo-spatial data set from the Southern California Bight to Cape Mendocino. We determined the location and characteristics of eight definite and two probable krill “hotspots” of abundance. Directional-dependence analysis revealed that krill hotspots were oriented in a northwest–southeast (135°) direction, corresponding to the anisotropy of the 200–2000 m isobath. Krill hotspots were disassociated (inversely correlated) with three upwelling centers, Point Arena, Point Sur, and Point Conception, suggesting that krill may avoid locations of strong offshore transport or aggregate downstream from these locations. While current fisheries management considers the entire coast out to the 2000 m isobath critical habitat for krill in this ecosystem, we establish here smaller scale structuring of this critical mid-trophic level prey resource. Identifying mesoscale krill hotspots and their oceanographic determinants is significant as these smaller ecosystem divisions may warrant protection to ensure key ecosystem functions (i.e., trophic transfer) and resilience. Furthermore, delineating and quantifying krill hotspots may be important for conservation of krill-predators in this system.

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1. Introduction

Due to their high biomass, lipid content, and tendency to form dense aggregations in epipelagic habitats, krill (crustaceans of the family *Euphausiacea*) comprise an important prey field and component of marine ecosystems worldwide (Siegel, 2000), including the California Current System (CCS) off the west coast of the US (Brinton, 1962, 1976; Brinton and Townsend, 2003). Most species of upper trophic level fishes, birds and marine mammals of societal interest depend directly or indirectly, through an intermediate prey species, on krill. Field et al. (2006) estimate that much of the energy flow in the northern CCS between primary producers and tertiary consumers is filtered through krill. Krill are important prey for all life stages of most rockfish (*Sebastes* spp.), salmonids (*Onchorhynchus* spp.), hake (*Merluccius productus*), and other economically important fish (Chess et al., 1988; Brodeur et al., 2007; Tanasichuk, 1999, respectively). Additionally, the endangered blue whale (*Balaenoptera musculus*), is an obligate krill-predator whose

foraging distribution is closely linked to krill distribution (Fiedler et al., 1998; Mate et al., 1999; Croll et al., 2005). Krill is important prey for locally breeding seabirds (Ainley et al., 1996; Abraham and Sydeman, 2006). For example, a major decline in krill availability was apparently responsible for reproductive failures of one species, Cassin's Auklet (*Ptychoramphus aleuticus*), in 2005 and 2006 (Sydeman et al., 2006; Santora et al., 2011). Understanding the foraging ecology and population biology of krill-predators (fish, birds, and mammals) in the CCS is therefore dependent on developing a better appreciation of both the relative abundance and spatial organization of krill in this ecosystem (Croll et al., 2005; Jahncke et al., 2008; Ainley et al., 2009; Santora et al., 2011). However, we largely lack reliable estimates of krill biomass throughout the California Current.

Two krill species, *Euphausia pacifica* and *Thysanoessa spinifera*, are numerically dominant in the CCS (Brinton, 1962; Siegel, 2000; Marinovic et al., 2002; Brinton and Townsend, 2003; Lu et al., 2003). *E. pacifica* is usually found in waters at or beyond the shelf-break (200–1000 m) and over submarine canyons, whereas *T. spinifera* apparently prefers coastal habitats extending to the outer-shelf (Brinton, 1962; Tanasichuk, 1998a,b; Feinberg and

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Peterson, 2003; Lu et al., 2003; Marinovic et al., 2002; Gómez-Gutiérrez et al., 2005; Dorman et al., 2005; Pinchuk et al., 2008). In comparison to high-latitude krill (e.g., *E. superba* in the Antarctic, and *T. rashii* in the Bering Sea) that usually undergo one major spawning season per year (Siegel, 2000), the reproductive ecology of *E. pacifica* and *T. spinifera* involves multiple spawning attempts throughout the year, the timing of which appears to be closely synchronized to upwelling in the CCS (Brinton, 1962, 1976; Tanasichuk, 1998a,b; Feinberg and Peterson, 2003; Shaw et al., 2010). Evidence exists suggesting that both species favor cooler oceanographic conditions over warm years in the CCS (Ainley et al., 1996; Tanasichuk, 1998a,b; Peterson et al., 2002; Marinovic et al., 2002; Brinton and Townsend, 2003; Sydeman et al., 2006).

Upwelling varies geographically in seasonality, strength and duration along the California coast (reviewed by Checkley and Barth, 2009; Bograd et al., 2009). The combination of seasonal north-westerly winds and geographic coastline features such as capes, points, and peninsulas produce spatial variability in the intensity of upwelling centers that can be assessed by calculating changes in wind stress and Ekman transport (Bakun and Parrish, 1982; Chelton, 1982; Pickett and Paduan, 2003; Chelton et al., 2007) and related to plankton distribution (Peterson and Keister, 2002; Keister et al., 2009). It is well-known that strong centers of upwelling along the California coast are located near Cape Mendocino (40°N), Point Arena (39°N), Point Sur (36°N), and Point Conception (34°N) (Strub et al., 1987; Pickett and Schwing, 2006; Chelton et al., 2007). All of these upwelling centers are linked to elevated ecosystem productivity (Checkley and Barth, 2009).

Since krill are active swimmers (e.g. speed range 1.8–3.0 cm s⁻¹; De Robertis et al., 2003) that are dependent on phytoplankton for food, we hypothesized that high krill concentrations (i.e. hotspots) would not be found near centers of upwelling, but instead are associated with adjacent regions, where offshore advection is weaker and food is concentrated (Bakun and Parrish, 1982). Conceptually, this idea is a hybrid of “upwelling shadows” (Graham et al., 1992; Wing et al., 1998) that result in downstream concentration of plankton, and “optimal environmental window” that leads to variable reproductive success and survivorship of fish in relation to upwelling intensity and its effect on food supply and larval displacement (Parrish et al., 1981; Bakun and Parrish, 1982; Cury and Roy, 1989). A hypothetical relationship between krill abundance and upwelling intensity is shown in Fig. 1. This model, expanded, modified, and applied in a spatial context from the original “optimal environmental window” of Cury and Roy (1989) suggests that the spatial distribution of krill is a function of the balance between Ekman transport and food availability from upwelling centers. That is, “hotspots” of krill are not located too far away from an upwelling center because food availability will be limited. Conversely, they are not located too close to upwelling centers because extensive advection transports krill from favorable habitat. The critical point is that both food availability and offshore Ekman transport act to limit, mechanistically, the optimal environmental conditions for krill and thus the locations of hotspots. To test this prediction we correlate latitudinal variation in krill density against latitudinal variation in offshore advection, using Ekman transport as a proxy for upwelling.

As high resolution information on preferred prey availability, specifically the abundance of diatoms (Ohman, 1984; Pinchuk et al., 2008) is not available, in this study we focus on the prediction that krill hotspots are disassociated (i.e. inversely correlated) with upwelling centers in the CCS. Although, satellite-based estimates of ocean color (e.g. SeaWiFS) may provide useful proxies for measuring and mapping phytoplankton concentrations, this information relates to ocean surface conditions and does not provide species level “prey” information (e.g. diatoms) that krill

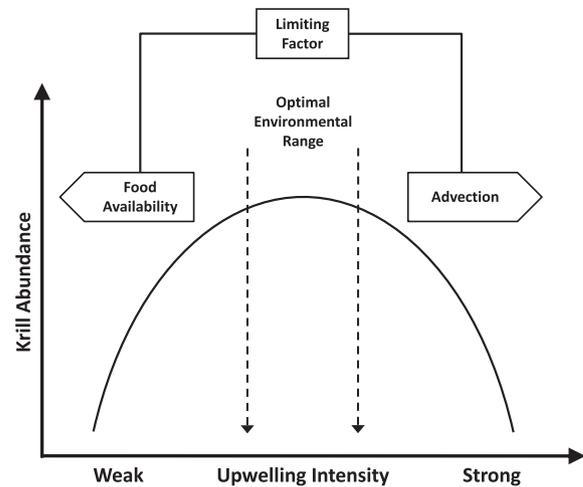


Fig. 1. This model, expanded, modified, and applied in a novel spatial context from the original “optimal environmental window” of Cury and Roy (1989) suggests that the spatial distribution of krill hotspots is based on upwelling intensity and advection (although in the original hypothesis, negative consequences of wind are due to excessive turbulence). Krill hotspots should not be located too far away from an upwelling center or food availability will be limited. In contrast, hotspots should not be located too close to upwelling centers because extensive transport (advection) may remove krill from favorable habitat.

prefer. Additionally, eddies and geostrophic flow may also influence where krill concentrate and this information along with remotely sensed phytoplankton and krill behavior (e.g. vertical migration, breeding, spawning) should be useful for designing a future study for modeling krill distributions and ocean conditions in the CCS (Hofmann et al., 2004; Goebel et al., 2010; Dorman et al., 2011).

We compiled a decade (2000–2009, minus 2007) of hydroacoustic survey data representing >50,000 km of survey effort to (i) map and measure the distributional patterns of krill, (ii) formulate a spatially-explicit climatology of krill hotspots, and (iii) assess the relationship of these hotspots to oceanographic conditions, particularly the spatial dynamics of upwelling. To analyze these data, we applied geo-statistical techniques to construct krill utilization distributions (i.e. mapped histograms) across the entire survey area. We employed the Nautical Scattering Coefficient (NASC) acoustic index that Santora et al. (2011) related primarily to abundance of *E. pacifica*. Although it is well-known that *E. pacifica* exhibits preference for shelf-break/slope habitats in the CCS (Brinton, 1962), the mesoscale (10–100 km) and directionality of krill aggregations has yet to be described. Consequently, we also predicted that krill distribution in the study region is more closely correlated at increasing spatial lags alongshore than in cross-shelf directions due to the general SW trend of the continental shelf-break.

2. Materials and methods

2.1. Study area

The CCS is an eastern boundary current ecosystem characterized by high productivity and high variability in production across all trophic levels (Mann and Lazier, 1996; MacCall, 1996; Kudela et al., 2008). Productivity here is driven by coastal upwelling, with localized enhancement associated with coastline geography (e.g., Cape Mendocino and Pt. Conception, Fig. 2), wind stress curl over outer-shelf regions, and advection of source waters and nutrients from both the north and the south (Rykczewski and Checkley, 2008; Checkley and Barth, 2009). Flow dynamics in the coastal

region of the CCS have strong seasonal variability, although interannual variability can be as great or greater as seasonal changes. Specifically, increased advection of southern source water associated with El Niño events (warm phases of the El Niño–Southern Oscillation, or ENSO) events can result in dramatic declines in productivity and shifts in community structure, while during the cold phases of ENSO, the coastal ecosystem is characterized by intensified transport of nutrient-rich northern waters and increased productivity (Checkley and Barth, 2009). The 2000–2009 study period included both cold and warm ENSO events; cool ocean conditions associated with La Niña prevailed during 2000–2002; a weak El Niño event occurred in 2003; “normal” conditions characterized 2004 while, warm conditions and delayed upwelling extended across 2005–2006 and cool La Niña conditions again prevailed from 2008 through 2009 (Bograd et al., 2000; Goerick et al., 2004; Schwing et al., 2006; McClatchie et al., 2009; Bjorkstedt et al., 2010).

2.2. NMFS Juvenile Rockfish Survey

We used data collected by the National Marine Fisheries Service (NMFS) ‘Juvenile Rockfish/Ecosystem Survey’ (JRS), which focuses primarily on estimating the pre-recruit (young-of-year) abundance of rockfish (*Sebastes* spp.) during the period of high spring upwelling and productivity in May and June (Ralston and Howard, 1995). The shipboard sampling was conducted over a “Core” area within the central California Current that is bounded to north off Point Reyes (38°) and to the south off Monterey Bay, CA (36.5°), spanning approximately 350 km of coastline (Fig. 2). Embedded in this region are the National Marine Sanctuaries of Cordell Bank, Gulf of Farallones and Monterey Bay. In 2004, the survey was expanded coast-wide to the north off Cape Mendocino, CA (40°) and southward to San Diego, CA (32.5°), spanning approximately 1400 km of coastline (Fig. 2). This expansion of the survey enhanced information on regional oceanographic conditions, species distribution,

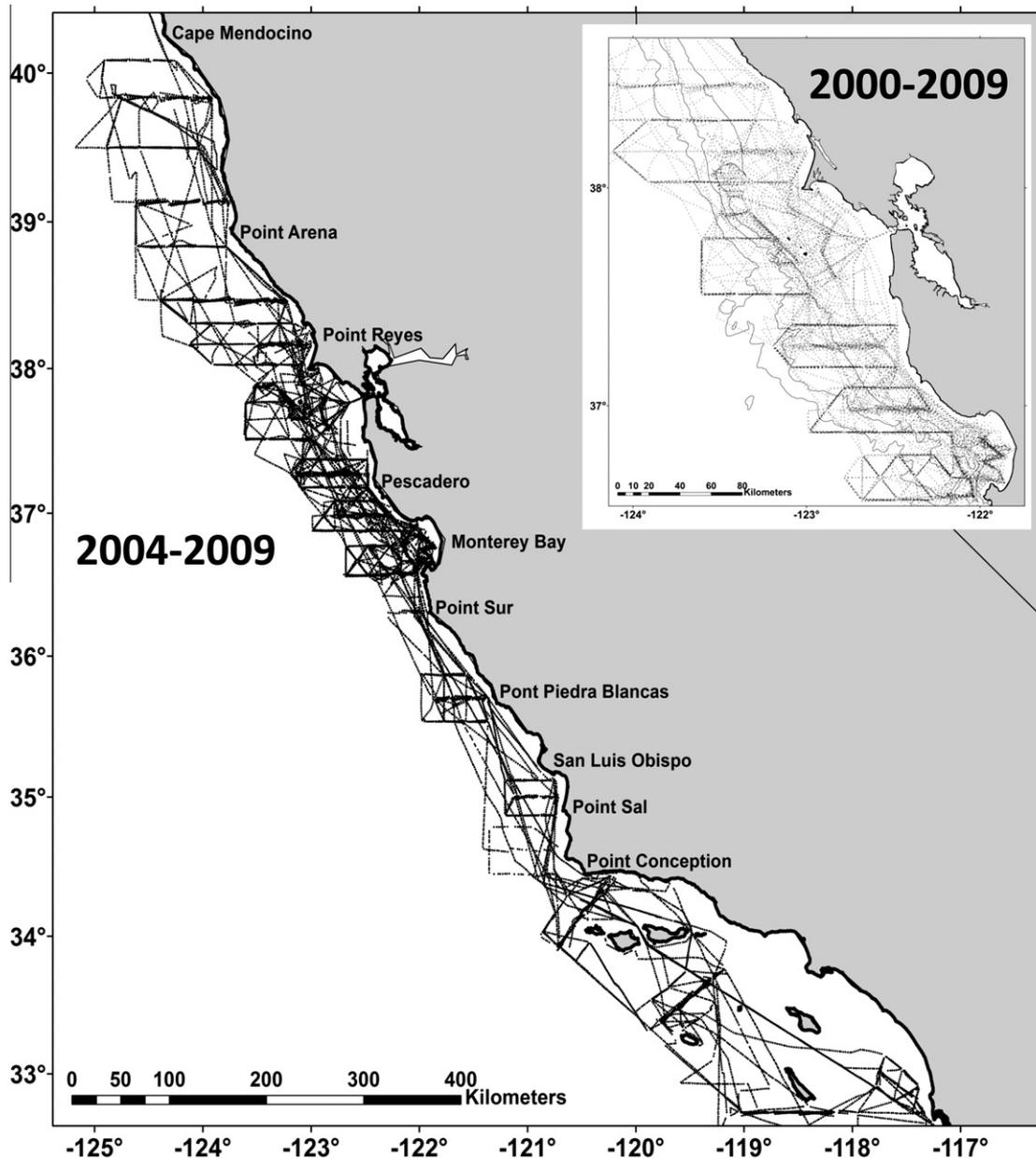


Fig. 2. Spatial coverage and ships trackline sampled during May–June aboard the NMFS Juvenile Rockfish survey; inset ‘core’ area 2000–2009 and coast-wide survey 04–09. A total of 53,180 km were sampled for krill using acoustics.

and bio-geographic boundaries (Sakuma et al., 2006). We used underway acoustics data to investigate spatial patterns of krill abundance (Santora et al., 2011) within the core area from 2000 through 2009 and coast-wide from 2004 through 2009. Unfortunately, acoustic data were not obtained in 2007.

2.3. Krill spatial distribution

Acoustic surveys are routinely used to map krill distributions in a variety of marine ecosystems worldwide (MacLennan and Simmonds, 2005). For the purpose of this study, we utilize acoustics to map krill distributions and identify concentrations of high abundance (i.e., krill hotspots). Acoustic volume backscattering data (S_v , dB) were collected using a multi-frequency echosounder (SIMRAD EK500 and EK60) configured with down looking 38, 120, and 200 kHz split beam transducers mounted on the hull of the ship at a depth of ~7 m (Santora et al., 2011). Acoustic data were processed using a multiple frequency target identification technique (Watkins and Brierley, 2002). Volume backscattering strength measured at different frequencies were used to identify the backscattering from krill by use of a three frequency ΔS_v method (Hewitt and Demer, 2000; Watkins and Brierley, 2002). We averaged volume backscattering and integrated signals over 1 nautical mile (nmi) horizontal segments, and from a depth of 300 m or the sea floor in shallow regions, to the transducer (10 m buffer added to transducer depth). We calculated the Nautical Acoustic Scattering Coefficient (NASC nmi^{-1}) as our basic measurement index of horizontal krill-plankton distribution and abundance (MacLennan and Simmonds, 2005). Due to their similar size range, 10–28 mm (Feinberg and Peterson, 2003; Croll et al., 2005; Ressler et al., 2005; Shaw et al., 2010; Santora et al., 2011), we are unable to separate backscatters of *E. pacifica* and *T. spinifera*.

2.4. Spatial analysis of krill distribution

Approximately 51,856 km of survey effort were integrated and stored in a geographic information system (GIS) designed for mapping krill and conducting spatial analysis within the core area (2000–2009; 29,443 km) and coast-wide survey (2004–2009; 35,158 km; Fig. 2). An important consideration is that nearly half (25,587 km) of this very large data set represents zero value estimates for the acoustic krill index. Part of this is attributed to acoustics techniques that provide high frequency sampling (MacLennan and Simmonds, 2005). Another factor is that krill are generally patchily distributed and densely concentrated particularly in specific geographic locations such as shelf-breaks and canyons (Mackas et al., 1997; Tanasichuk, 1998a,b; Lu et al., 2003; Ciannelli et al., 2008; Santora et al., 2011).

To evaluate the data, we compiled the acoustic survey effort into discrete 25 km^{-2} grid cells to summarize the acoustic krill index by sampling frequency (number of years a cell was sampled) and mean number of nautical miles sampled per cell. We then estimated the anomaly of krill abundance (mean per cell with total mean of all grid cells subtracted) and the coefficient of variation (CV) per grid cell (Fig. 3). The grid size was chosen to minimize effects of spatial autocorrelation (Fortin, 1999; Dungan et al., 2002; Ciannelli et al., 2008) and to match the spatial footprint of satellite products (e.g., sea surface temperature, chl-a) and top-predator atlases (see Ford et al., 2004) that may be used in future analysis with respect to krill. The grid size also reflects a reasonable trade-off between sampling density and spatial resolution. For example, in the core area (represented by nine survey years) the survey effort is highly repetitive, with nearshore and offshore waters being well sampled (Fig. 3A) and the mean number of nautical miles sampled per cell is relatively even along the coast (Fig. 3B). The krill abundance anomaly plot shows high concentrations along the

shelf-break and over the Monterey Canyon mouth (Fig. 3C). In addition, the Coefficient of Variation (CV) shows the variability of the krill index and highlights cells that appear to be more variable than others (Fig. 3D).

We quantified krill spatial distribution using the kernel smoothing method (Silverman, 1986) implemented in ArcView 9.2 (ESRI, Inc. Redlands, CA, USA) to estimate spatial utilization distributions (Worton, 1989; Keating and Cherry, 2009). Each acoustic sample had a longitude (x), latitude (y) and acoustic krill index (expressed as a z -value). Kernel density estimation, like any spatial interpolation method, involves estimating an attribute value (e.g., krill) at an un-sampled site given measurements at neighboring sampled sites, via an algorithm that incorporates a weighting function that prescribes relative contributions of individual sampled values as a function of the distance between the un-sampled and sampled sites. Kernel density estimation is a non-parametric method and assumes that spatial autocorrelation between samples decreases (e.g., their semivariance increases) asymptotically as distance increases (Silverman, 1986; Seaman and Powell, 1996; Legendre and Legendre, 1998; Ciannelli et al., 2008). The Gaussian kernel estimator for point location data (Silverman, 1986; Seaman and Powell, 1996) was modified for continuous data by multiplying values of krill abundance by kernel weights and computing a weighted average. The kernel width is adjusted by a search radius (bandwidth), which governs the degree of dispersion (rate of drop-off) of mass around the sampled value (see Fig. 2 for sampling distribution). Based on a previous analysis of the krill spatial organization from this data set, Santora et al., 2011 showed that the acoustic index of krill abundance was generally spatially autocorrelated at 5 nmi intervals. In order to achieve the mesoscale level of smoothing that we desired to detect krill hotspots, kernels were calculated using a search radius (bandwidth) equal to 5 nmi.

Percent volume contours were calculated at 5% intervals from kernel densities to summarize spatial utilization distributions (i.e. histograms) of krill (Worton, 1989; Keating and Cherry, 2009). Essentially, this procedure is a cumulative histogram approach that partitions the interpolated krill abundance index into percentiles of abundance. We mapped utilization distributions and considered percentage levels of 5–20% as “high” and 20–40% as “medium” hotspots; we calculated metrics for describing their respective location (e.g., mean center, distance to isobaths and land, etc.). For interpreting utilization distributions, it is important to keep in mind that the outer 95% elliptical contours depict the extent (total area or volume observed/sampled during shipboard sampling) containing the majority of survey effort. Moving inward, the utilization distributions are concentric ellipses that reflect an increase in the spatial heterogeneity of krill, revealing localized concentration zones of repeatedly detected higher values of the acoustic index (i.e., the probability of finding similar values of krill decreases by increasing distance and area). That is, lower percent utilization contours (<40%) indicate areas of high krill abundance, especially those smaller than 20%.

2.5. Spatial variability of krill

Little is known about how krill aggregations vary spatially by latitude in the CCS (but see Ressler et al., 2005; Lu et al., 2003; Swartzmen et al., 2005). To describe these patterns, one needs to examine cross-shelf and alongshore directionality. This concept (anisotropy) focuses on the idea that a measurement property (krill distribution) varies spatially with direction (Legendre and Legendre, 1998; Ciannelli et al., 2008). We measured the spatial variability of krill distribution using directional-based correlogram methods (Moran's I) to quantify scale-dependent patterns of krill (Legendre and Legendre, 1998). Correlograms allow determination of the characteristic scale of krill patchiness by counting the

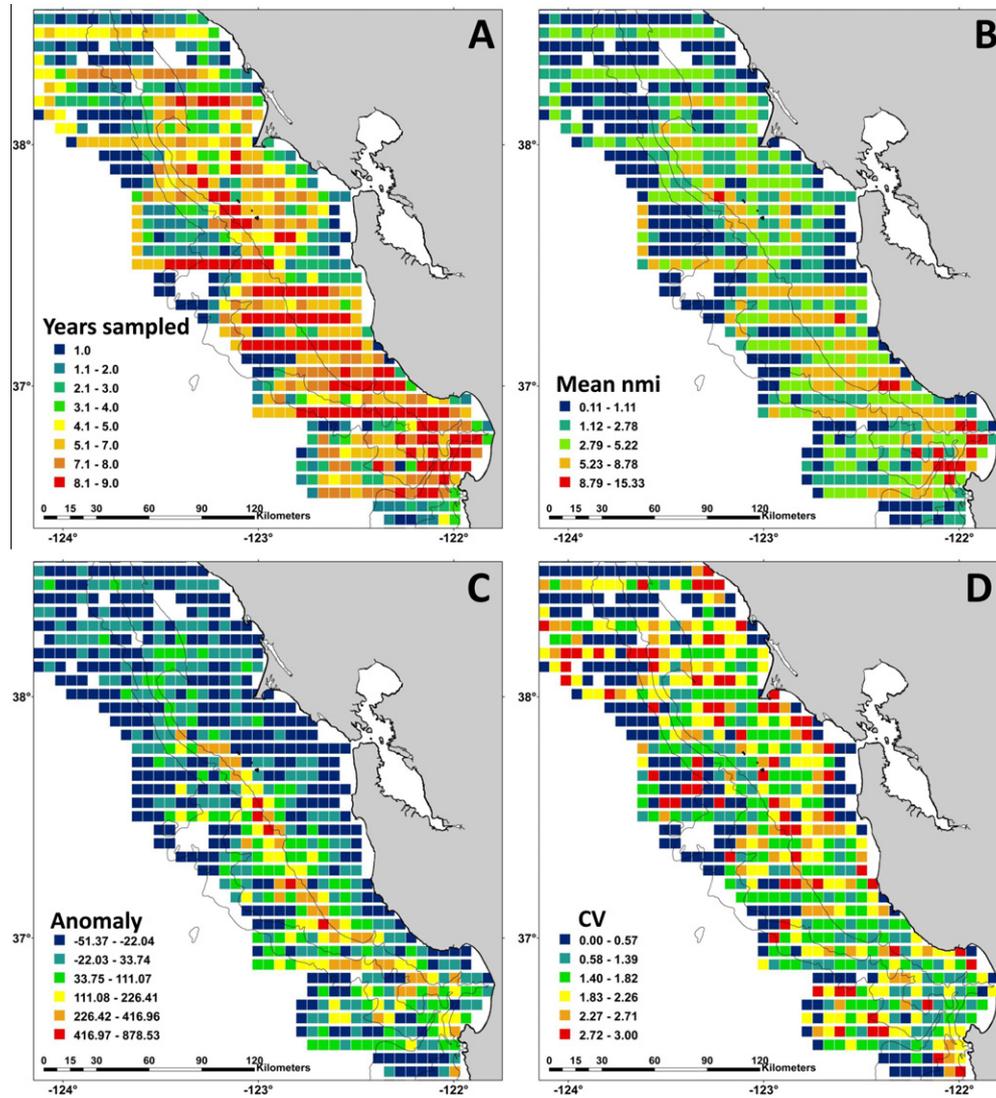


Fig. 3. Grid-based analysis (cell $\sim 25 \text{ km}^{-2}$) of acoustic krill index off central California: (A) summary of sampling effort by grid (years sampled, max 9), (B) mean nautical miles sampled per cell per year, (C) standardized block-averaged anomaly of krill abundance (subtracted mean from mean cell value) and (D) coefficient of variance (CV) of krill abundance per cell.

successive number of lags with positive correlations before becoming negative (i.e. zero-crossing). We calculated modes of krill directional spatial variability for isotropic (all-directional, invariant with respect to direction), 0° for north/south variation, 90° for cross-shelf-break variation, and 135° for alongshore variation.

2.6. Ekman transport and upwelling

Meridional wind stress (North–South) data measured from the QuikSCAT satellite scatterometer were obtained from NOAA Coastwatch (<http://coastwatch.pfeg.noaa.gov/erddap/search/index.html?searchFor=QuikSCAT>). QuikSCAT uses active microwave radar to measure electromagnetic backscatter from wind roughened ocean surface (Pickett and Paduan, 2003; Pickett and Schwing, 2006; Chelton et al., 2007). Wind vector measurements from the QuikSCAT satellite have been validated and have good agreement with wind vectors measured from National Data Buoy Center (NDBC) buoys (Pickett and Paduan, 2003). We calculated wind stress from wind velocities as described in Smith (1988). QuikSCAT data were plotted onto a 0.125° by 0.125° grid (14 km). Zonal (East–West) mass transport is simply calculated

from: $Mex = Ty(0)/f$; where Mex is the zonal (East–West) Ekman mass transport, $Ty(0)$ is the wind stress at the sea surface, and f is the coriolis parameter. The unit of Ekman transport is $\text{kg}/(\text{ms})$. Negative values of wind stress (winds directed from North to the South) result in negative Mex values. Therefore, increasingly negative Mex values indicate more transport of water in the Ekman layer offshore. To calculate the zonal Ekman mass transport climatologies, monthly means in May and June for the years 2000–2009 were averaged to reveal locations along the coast where advection was intense.

2.7. Ekman transport, upwelling centers and krill hotspots

We compared the latitudinal distribution of Ekman transport (from QuikSCAT) and mean krill abundance along the California coastline. Comparisons were made between 34.4°N and 40.0°N , representing approximately 716 km. To test our hypothesis that the optimal environmental window for krill is related to distance to/from upwelling centers we calculated mean Ekman transport at locations 50 km from the coast and mean abundance of krill by 0.2° bins of latitude. The distance of 50 km is approximately

where the 1000 m isobath is along the California coast and includes the shelf and shelf-break habitat. We used cross-correlations to examine how the association between Ekman transport and krill vary by increasing latitudinal distance (Legendre and Legendre, 1998). To accomplish this we lagged (lag size is 0.2° bins of latitude ~ 25 km) krill against Ekman transport and plotted the resulting correlogram from -15 lags to $+15$ lags (a total 350 km in either direction). Data were de-trended prior to cross-correlation analysis and significance per lag was determined at the 95% confidence interval.

3. Results

3.1. Identification and location of krill hotspots

3.1.1. 'Core' area: Cordell Bank (38°N) to Monterey Bay (36.5°N)

Utilization distributions for the core area averaged over 9 years indicated four hotspots within the central California area (labeled A–D in Fig. 4, Table 1). One hotspot is located approximately 50 km due west of Pt. Reyes peninsula, centered on Cordell Bank (38°N , 123.4°W , labeled A in Fig. 4). The center of this location (38°N , 123.4°W) is 7 km, 12.5 km and 18 km east of the 200 m, 1000 m and 2000 m isobaths, respectively. Inspection of the 200 m isobath, indicates that the unique twist in bathymetry

may facilitate krill concentration here (Fig. 4). The southwestern edge of Cordell Bank forms the beginning of the Farallon Escarpment, an area of steep bathymetric change and krill hotspot B, located on the shelf-break at the western edge of the Gulf of the Farallones. The center (37.5°N , 122.9°W) of B is 53 km from the coast, directly over the 200 m isobath and 11 km and 35 km, respectively, from the 1000 m and 2000 m isobaths. On the southern edge of B, lies Pioneer submarine canyon, which bisects hotspots B and C (Fig. 4). Both the Pioneer and the Ascension canyon systems have previously been described as hotspots for shortbelly rockfish (*Sebastes jordani*), an important krill-predator and key prey of salmon, seabirds and marine mammals (Chess et al., 1988; Ralston et al., 2003). Hotspot C has a NW orientation parallel to the coast, and is centered on the 200 m isobath. Its center (37°N , 122.6°W) is 38 km from Año Nuevo on the coast and 12.5 km and 32 km, respectively, from the 1000 m and 2000 m isobaths (Fig. 4). The southeastern edge of this hotspot is associated with Ascension submarine canyon and forms a boundary with Monterey submarine canyon, the location of hotspot D (Fig. 4). Hotspot D is positioned over the 1000 m isobath with its center (36.7°N , 122.0°W) 23 km from Moss Landing and 5 km and 9 km, respectively, from the 1000 m and 2000 m isobaths (Fig. 4). Monterey submarine canyon is a well-known location of large numbers of krill and their predators (Marinovic et al., 2002; Croll et al., 2005).

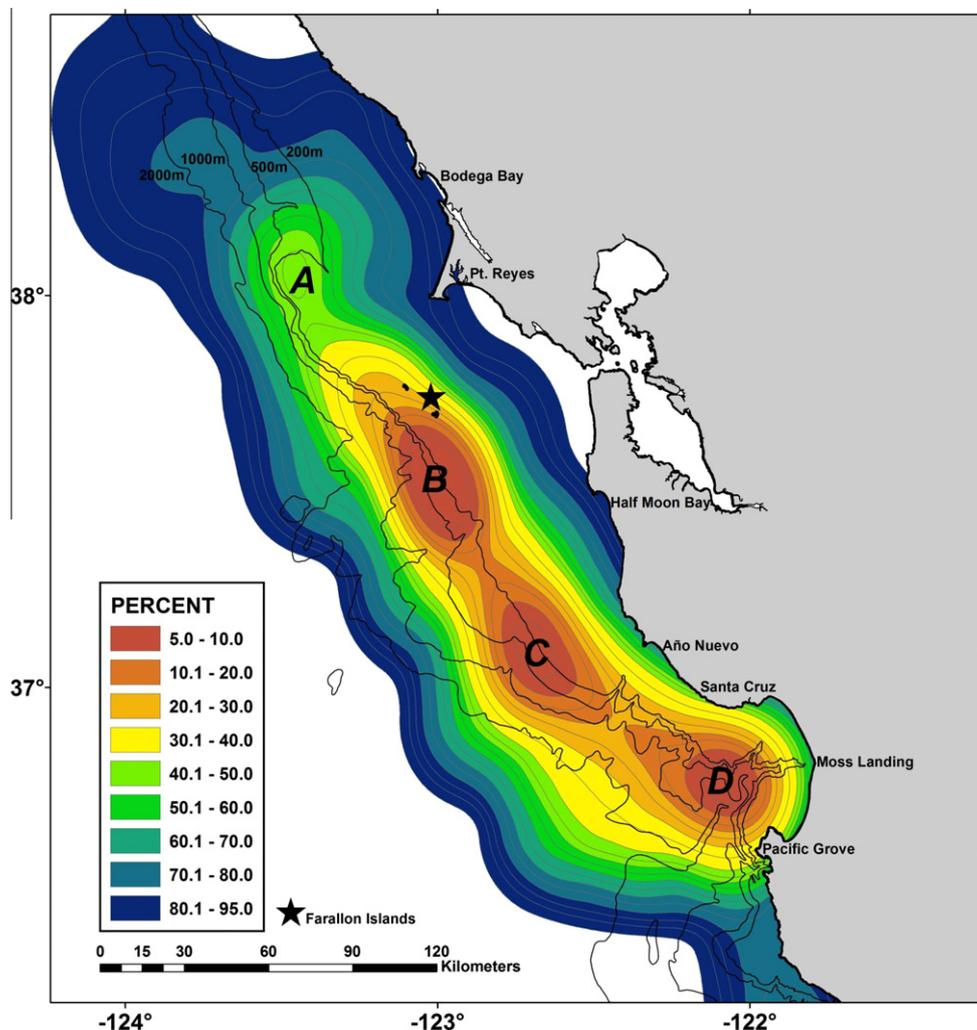


Fig. 4. Krill hotspots off central California, during May–June, 2000–2009. Percent utilization distributions were estimated and mapped using kernel density interpolation; regions containing dense krill concentrations are labeled A–D. See Table 1 for additional information on labeled krill hotspots.

Table 1

Summary of krill hotspots (ID, Geographic name, Location) identified in the central California region, May–June, 2000–2009 (see Fig. 4). Dist. is distance to feature (isobath, coast) in km; values in parentheses indicate (–) inshore and (+) offshore. Ref. land point is reference to nearest land on California coast or island.

ID	Name	Mean center	Area, km ²	Dist. 200 m	Dist. 1000 m	Dist. 2000 m	Dist. Coastline	Ref. land point
A	Cordell Bank	38.0 N, –123.4 W	200	7(+)	12.5(+)	18(+)	50(–)	Pt. Reyes Peninsula
B	Gulf of Farallones	37.5 N, –122.9 W	890	0	12.5(+)	35(+)	53(–)	Half Moon Bay
C	San Mateo	37.0 N, –122.6 W	671	0	12.5(+)	32(+)	38(–)	Año Nuevo Island
D	Monterey Bay	36.7 N, –122.0 W	578	5(–)	0	9	23(–)	Moss landing
	Mean ± SD		584.7 ± 287	3 ± 3	9 ± 6	23 ± 12	41 ± 13	

3.1.2. California coast-wide: Pt. Arena to the Channel Islands

The expanded survey effort in 2004 allowed us to map krill hotspots between Cape Mendocino and Point Conception using 5 years of data (Fig. 5). Between Cape Mendocino and Point Arena to the south are two closely spaced locations of elevated krill concentrations (1; Table 2, Fig. 5), but these are too small to be considered hotspots. South of this was a medium inshore hotspot (2) off Bodega Bay, north of Point Reyes (Table 2, Fig. 5). This is centered (38.3 N, –123.2 W) 20 km east of Bodega Head, and 11 km, 26 km, and 48 km, respectively, from the 200 m, 1000 m and 2000 m isobaths. Within the Gulf of Farallones and Monterey Bay the previously detected hotspots B, C and D are found in identical locations (labeled 3–5; Figs. 4 and 5), but varied slightly in their

mean centers (Tables 1 and 2). These results indicate that the central California krill hotspots based on nine survey years were also identified using 5 years of data.

It is important to note that the bathymetry south of Monterey Bay is quite different than that to the north, particularly with respect to the 200 m isobath. South of Monterey Bay the 200 m isobath runs southeast within a few kilometers of the coastline (Fig. 5) whereas in the Gulf of the Farallones it is located 20–60 km offshore. South of Monterey Bay along the Big Sur coast, two portions of the largest hotspot detected are located on the relatively wide shelf extending between the 200 and 1000 m isobaths over the Santa Lucia Bank (Table 2, Fig. 5, labeled 6). The northern edge of this location is bounded by Sur and Lucia Canyons. The first portion

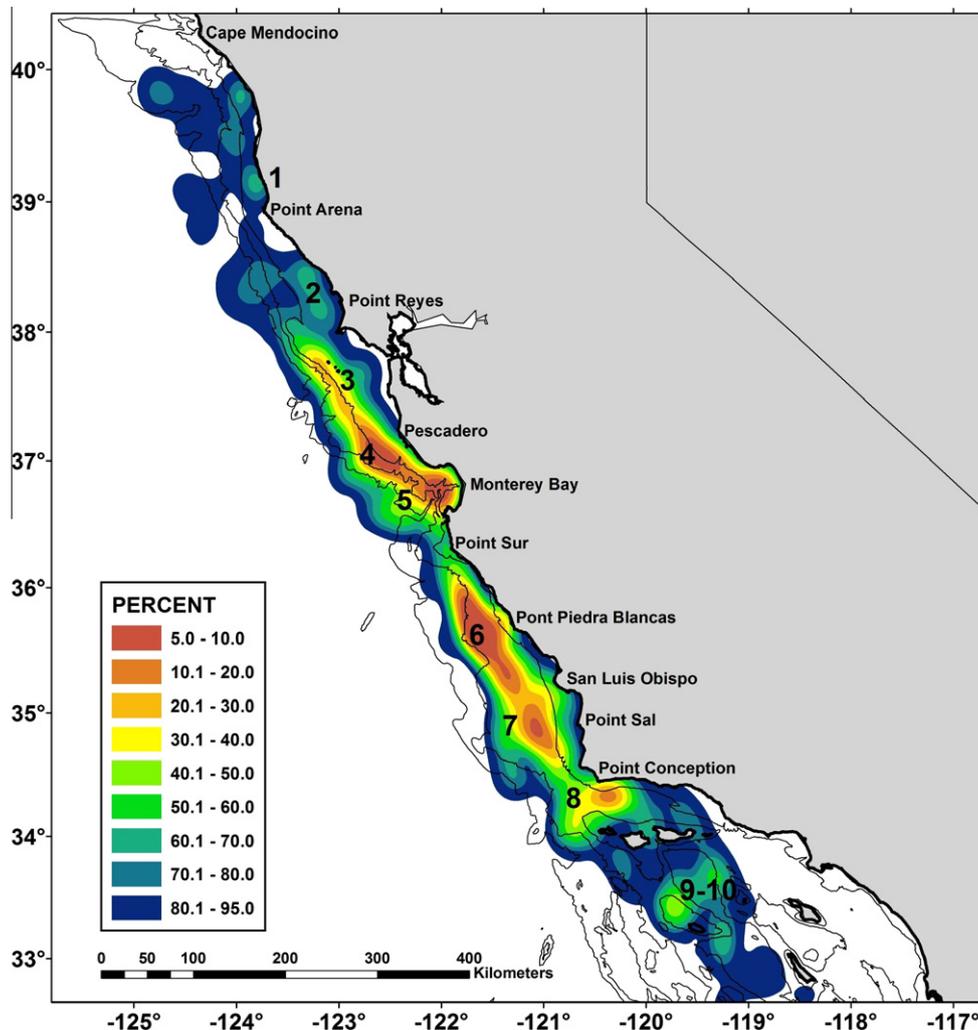


Fig. 5. Krill hotspots California coast-wide during May–June, 2004–2009. Percent utilization distributions were estimated and mapped using kernel density interpolation; regions containing dense krill concentrations are labeled 1–10. Depth contours are the 200 m, 1000 m and 2000 m isobaths respectively. See Table 2 for additional information on labeled krill hotspots.

Table 2
Summary of krill hotspots from coast-wide surveys, May–June, 2004–2009 (see Fig. 5). Dist. is distance to feature (isobath, coast) in km; values in parentheses indicate (–) inshore and (+) offshore. Ref. land point is reference to nearest land on California coast or island.

ID	Name	Sub areas	Mean center	Area, km ²	Dist. 200 m	Dist. 1000 m	Dist. 2000 m	Dist. coastline	Ref. land point
1	Point Arena	1	39.8°N, 123.9 W	216	11(+)	26(+)	48(+)	12(–)	Pt. Arena
		2	39.1°N, 123.8 W	320	15(+)	28(+)	48(+)	7.5(–)	
2	Bodega Head	1	38.3°N, 123.2 W	950	17(+)	40(+)	56(+)	20(–)	Bodega Head
3	Gulf of Farallones		37.6°N, 123.0 W	740	0	6(+)	10(+)	10(–)	SE Farallon Island
4	Pescadero		37.0°N, 122.5 W	823	0	17.5(+)	36.5	28.8(–)	Pescadero
5	Monterey Bay		36.7°N, 122.0 W	578	5(–)	0	9(+)	23(–)	Moss Landing
6	Big Sur	1	35.6°N, 121.6 W	2100	22(–)	17(+)	57(+)	33(–)	Big Sur
		2	35.3°N, 121.3 W	700	36(–)	32(+)	60(+)	50(–)	
7	Point Sal		34.8°N, 121.0 W	1060	21(–)	50(+)	73(+)	43(–)	Pt. Sal
8	Point Conception		34.3°N, 120.4 W	780	3(–)	19(+)	49	14(–)	Pt. Conception
9–10	Channel Islands	1	33.4°N, 119.7 W	430	3(–)	14(+)	28(+)	25(–)	San Nicholas Island
		2	33.6°N, 119.3 W	210	29	0	82	36(–)	
Mean ± SD				742.2 ± 509	13.5 ± 12	20.8 ± 15	46.4 ± 22	25.2 ± 13	

of hotspot 6 extends southward of Point Sur with a mean center (35.6°N, 121.6 W) situated 33 km west of Point Piedras Blancas (Fig. 5). The second portion is to the south with a mean center (35.3°N, 121.3 W) located 50 km west of San Luis Obsipo (Fig. 5).

South of San Luis Obispo, the 200 m isobath moves further offshore then bends nearly 90° to the east around the coastline off Point Conception. This region comprises a major bio-geographic boundary along the US west coast that separates oceanic and climatic conditions to the north from those within the California Bight of southern California (Fig. 5; Checkley and Barth, 2009). Kill hotspot 7 is located north of Point Conception; centered (34.8°N, 121.0 W) 43 km west of Point Sal, this is the southernmost krill hotspot within the central California region (Table 2, Fig. 5). Hotspot 8, centered at 34.3°N, 120.4 W, is 14 km due south of Point Conception within the western edge of Santa Barbara channel. Longitudinal survey coverage south of this, within the southern California Bight, was reduced and the near shore coastal area was not sampled (see boundary of 95% kernel in Fig. 5). However, offshore surveys conducted near San Nicholas and Santa Barbara Islands included two medium hotspots, 9 and 10 (Table 2, Fig. 5). Hotspot 9 was centered 25 km north of San Nicholas Island (33.4°N, 119.7 W) over the 200 m isobath while hotspot 10 (33.6°N, 119.3°W) was centered 36 km northwest of Santa Barbara Island over the 1000 m isobath (Fig. 5).

3.2. Modes of directional spatial variability of krill hotspots

Krill hotspots (Figs. 4 and 5) are spatially orientated along the prominent southeast bathymetric trend of the California coastline. Based on Moran's *I* we found concordance in the spatial variability of krill among isotropic (all-directional), 0° (north–south) and 90° (east–west) directional correlograms, indicating a common characteristic spatial scale of 1–7 nmi or 13 km (Fig. 6). That is, krill exhibit similar scales of patchiness in north/south and cross-shelf directions. The alongshore (135° direction) spatial variability showed a characteristic spatial scale of 1–23 nmi, 43 km, that is substantially larger than other directions (Fig. 6). However, krill demonstrated increased spatial variability at even larger scales (>23 nmi.) for cross-shelf directions (Fig. 6) that we attribute to large-scale spatial similarity associated with the shelf-break extending throughout the California Current marine ecosystem.

3.3. Spatial relationships between krill hotspots and strong upwelling regions

Krill hotspots are located in proximity to known upwelling centers (Figs. 5 and 7A). The climatology of zonal Ekman transport (Fig. 7A) shows strong east–west transport (increasing negative

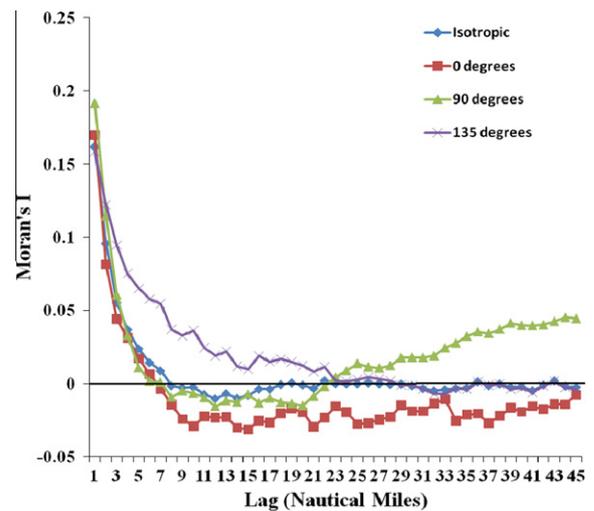


Fig. 6. Modes of directional spatial variability of krill off central California: 2-dimensional correlograms (Moran's *I*) depicting direction spatial variability for isotropic (all-directional), 0° (north/south variation), 90° (cross-shelf, east/west variation) and 135° (alongshore, parallel to bathymetry). The characteristic scale is largest in the alongshore direction (~1–42 km). (For interpretation to colours in this figure, the reader is referred to the web version of this paper.)

values of Ekman transport) near Cape Mendocino, Point Arena, Point Sur and Point Conception. In contrast, relatively weak transport occurs between the Point Reyes Peninsula and Monterey Bay and along the coast south of Point Sur to just north of Point Conception (features labeled in Fig. 7A). Placing krill hotspots (Fig. 5) in context with Ekman transport (Fig. 7A), shows that krill are not concentrated near the Cape Mendocino region where Ekman transport is strongest. To illustrate and quantify the role of variable Ekman transport by latitude on krill abundance we selected data between 34.4°N and 40°N (~715 km of coastline; Fig. 7). The plotted mean Ekman transport at 50 km from the coast and mean krill abundance by 0.2°N latitude bins (~25 km) shows concordant inverse fluctuation between high krill abundance and Ekman transport (Fig. 7C). That is, geographically along the coast higher (less negative) values of Ekman transport indicate the likelihood of reduced advection (i.e., increased retention) which coincides with elevated krill abundance. In fact, the relationship between mean Ekman transport and krill abundance is negative and strong ($r^2 = 0.54$, $r = -0.77$, $p < 0.01$, Fig. 7C). In addition, cross-correlation was used to measure the association of Ekman transport and lagged krill abundance (at lags of 0.2°N, ~25 km) to determine the sensitivity of their association (Fig. 7D). We found that Ekman transport and krill abundance are generally in phase with changes

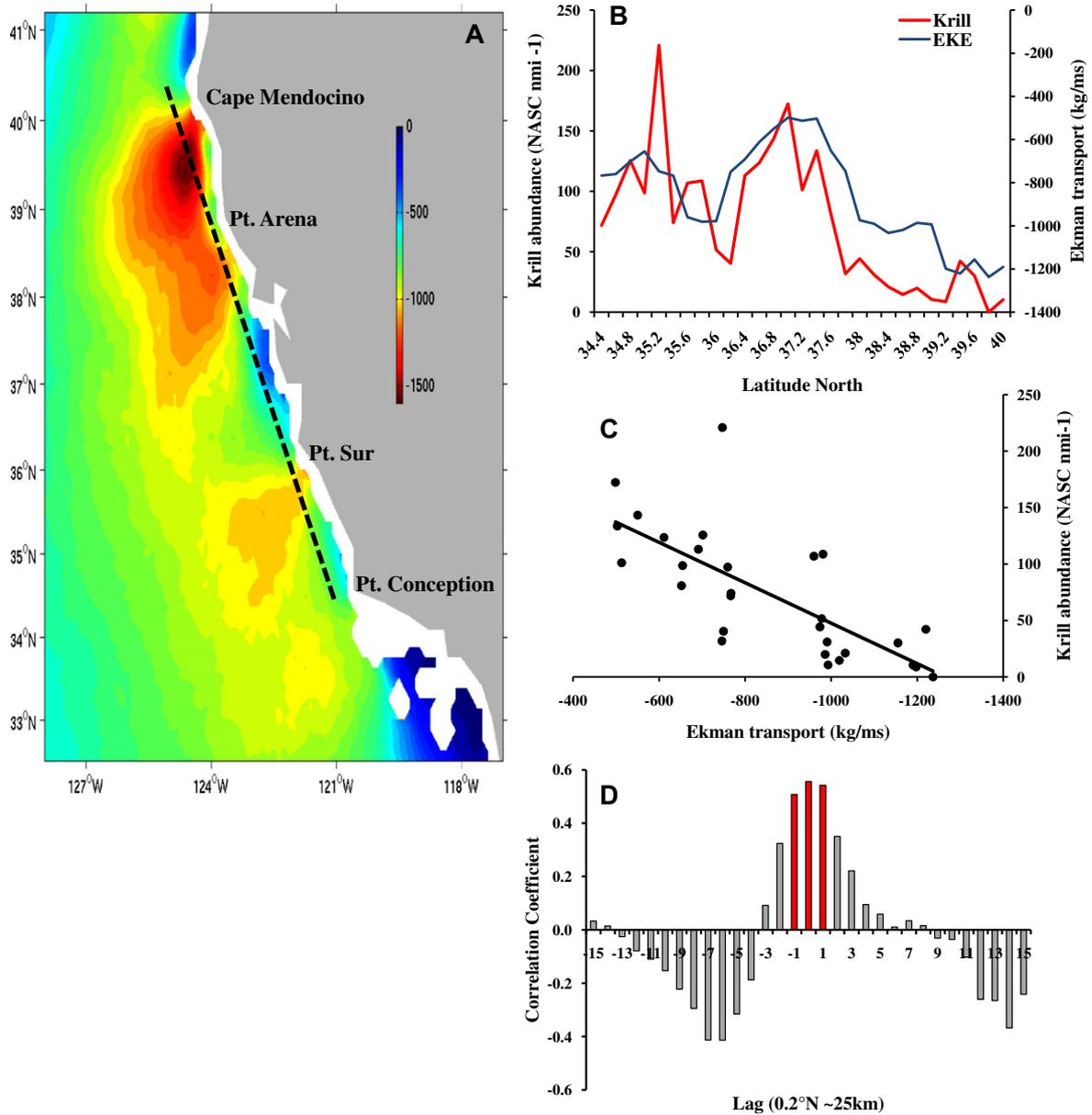


Fig. 7. Ekman transport and krill distribution. (A) Climatology of May and June zonal Ekman Mass transport for the time span 2000–2009. The mass transport (kg/ms) is driven by the upwelling winds that are present during this time of year, and the resultant transport is directed offshore (from east to west). Larger values are located at south of Cape Mendocino, Point Arena and Point Sur. The dashed line marks the distance of ~50 km from the shore; this distance is approximately the same location as the –1000 m isobath. (B) Covariation of mean Ekman transport (50 km from coast) and mean krill abundance (NASC nmi⁻¹) by 0.2°N latitudinal bins (~25 km); higher Ekman values indicate lower transport, (C) relationship between krill abundance and Ekman transport (based on data in b), and (D) cross-correlation between Ekman transport and lagged krill abundance showing positive and significant associations at –1 to +1 lags (red bars) and disassociations or out of phase at larger lags (<–3 and +5).

at small lags to the north and south (–2 to +2, ~100 km; Fig. 7D), but were strongly out of phase at larger lags (Fig. 7D).

4. Discussion

In the CCS, krill are of great interest because a large amount of energy flows through them to upper trophic levels, particularly to commercially important species (Batchelder et al., 2002; Field et al., 2006). Therefore, describing description of the spatial organization of krill on relatively large spatio-temporal scales is warranted for understanding and managing living marine resources of the California Current ecosystem. This study builds on the classic work of Brinton (1962, 1976), who developed a geographic atlas of krill to establish broad scale patterns of krill abundance,

distribution and reproductive behavior in relation to oceanographic and climatic conditions in the CCS and elsewhere in the North Pacific. Specifically, this study focused on indentifying zones of elevated krill abundance at a previously unattainable resolution, quantifying the orientation of these spatial patterns along the coast and quantifying the spatial relationships between the long-term mean of krill distribution and upwelling intensity.

Using nearly a decade of acoustic surveys we tested the hypothesis of mesoscale (10s–100s of km) structuring of krill populations in the southern to central-northern California Current. We quantified a climatology of krill abundance and distribution to resolve spatial structuring and to identify and describe characteristics of krill hotspots. Our study shows where krill are concentrated along the California coast during typically the strongest periods of upwelling in this environment (May–June; Rykaczewski and

Checkley, 2008; Bograd et al., 2009; Checkley and Barth, 2009). We confirmed mesoscale structuring of the krill population in this region of the California Current (Brinton, 1962) and demonstrate that krill hotspots are aligned with the predominant orientation of the shelf-break in the study region (135°). This conclusion is, in part, related to the acoustic signatures we obtained. Using about half of this dataset (2002–2006), Santora et al. (2011) demonstrated that the acoustic signals relate more strongly to the relative abundance of *Euphausia pacifica* than *Thysanoessa spinifera*. According to previous studies of these species off California, *E. pacifica* is more abundant than *T. spinifera* and occupies more of the outer-shelf, shelf-break, and slope habitats (Brinton, 1962; Brinton and Townsend, 2003). Therefore, we surmise that the overall pattern of mesoscale structuring evident in this study reflect *E. pacifica* more so than other species of krill in this ecosystem. Ongoing and future research will include a refinement of acoustic estimates by species across different habitats with coupled analysis of trawl and bongo net data. We can improve our understanding of essential krill habitats and their connectivity in the food web, by quantifying the location, spatial arrangement and directional orientation of krill hotspots. Zooplankton patchiness has been studied for decades and it is generally assumed that correlation scales vary more rapidly in the cross-shelf rather than along-shelf direction (Haury et al., 1978; Mackas, 1984). Krill hotspots were generally 20 nmi in length in the alongshore direction and only 5–7 nmi in the cross-shelf direction. We also found that the area of krill hot spots ranged in size from 200 to 2100 km² and suspect this variation relates to regional oceanographic conditions (e.g., Ekman transport, turbulence) and bathymetric characteristics such as submarine canyon size and shelf habitat.

Our study confirmed that there is substantial regional variability in the spatial distribution of krill in the California Current. We did not identify any krill hotspots in the northern California region from Cape Mendocino (40°N) south to Pt. Arena (39°N), a region of strong upwelling (Bakun and Parrish, 1982; Pickett and Schwing, 2006). Along the central California coast, we quantified the spatial organization of krill hotspots within a region of low upwelling between 38°N and 36.5°N (Fig. 4). Here we identified four krill concentration zones centered along the shelf-break-slope within the boundaries of Cordell Bank (A), Gulf of the Farallones (B), and Monterey Bay (C and D) National Marine Sanctuaries (see Fig. 4). The bathymetry within this region is a complex network of submarine canyons (e.g., Pioneer Canyon, Monterey Canyon) that is interspersed with steep shelf-break (e.g., Farallon Escarpment) and wide shelf-slope habitat. Moreover, there is evidence that the flow of water over Monterey Canyon within Monterey Bay forms an offshore eddy (Graham and Largier, 1997), a location that we identified as a krill hotspot and previously described as an important location for foraging cetaceans (Benson et al., 2002; Croll et al., 2005).

South of Monterey Bay, at Point Sur, the coastal flow of the California Current is influenced by steep changes in nearshore bathymetry (200 m isobath lies directly at the coastline) and widening of the shelf-break (Hickey, 1979; Breaker and Mooers, 1986). This region is also considered an important upwelling region where geostrophic flow is intensified by wind resulting in high primary productivity to the south along the Big Sur coast (Breaker and Mooers, 1986; Pickett and Paduan, 2003; Pickett and Schwing, 2006). We found three relatively large krill hotspots within this region that ranged in area of 1000–2000 km² and were centered on the 1000 m isobath approximately 30–50 km from the coastline (Fig. 5). South of this region, is the geographic boundary formed by Point Conception (34°N), a location containing high concentrations of top-predators and recognized as a “biological hotspot” in the California Current (Checkley and Barth, 2009). We identified krill hotspots adjacent to the north and south of this important region.

Our comparison of the mesoscale structure of krill hotspots with Ekman transport (calculated from QuikSCAT winds) by latitude from 34°N to 40°N showed disassociations (inverse correlation) with upwelling centers; krill were found in regions of generally weaker Ekman transport (e.g. Greater Gulf of the Farallones). Previous work on wind stress, upwelling and Ekman transport off the California coast (Bakun and Parrish, 1982; Pickett and Paduan, 2003; Pickett and Schwing, 2006; Chelton et al., 2007; Rykaczewski and Checkley, 2008) showed that regions of substantial upwelling coincide with coastal geomorphology (e.g. bathymetry and coastal mountains) such as the coastal promontories at Cape Mendocino, Point Arena, Point Sur and Point Conception. We found that although krill hotspots are separated from these sites they are found adjacent to these upwelling centers in regions where Ekman transport is decidedly weaker (Fig. 7). The fact that krill are disassociated with strong upwelling centers during May and June, when upwelling is substantial, supports our conceptual model of an “optimal upwelling window” for krill. This model depends on both nutrient input and advection as mechanisms for understanding their spatial distribution. We did not address the nutrient input/food availability part of this mechanism in this study due to lack of data on diatoms, the primary prey resource for krill (Ohman, 1984; Pinchuk et al., 2008). Krill hotspots should persist throughout the summer as long as upwelling at these locations is relatively active, driving the opposing mechanisms of nutrient input (food availability) and advection (transport). Furthermore, synthesis is needed on the behavior of krill, specifically diel vertical migration, which may help to counter displacement of krill from favorable habitat. Future analysis is needed to investigate seasonal variation in mesoscale structuring of krill distributions especially during winter and fall months when upwelling is less active and geostrophic flow is stronger in the northward direction due to intensification of the Davidson Current and California Undercurrent (Hickey, 1979; Huyer, 1983). This information would be useful for predicting changes in krill spatial organization and perhaps population dynamics of krill between seasons and years (Swartzmen et al., 2005; Dorman et al., 2011).

In recognition of the key role of krill in the food web, the PFMC implemented a ban on the development of krill fisheries in the US waters of the California Current, a move preceded by actions taken by West Coast states in coastal waters and widely supported by academic, conservation, and fishing communities (PFMC, 2008). The action recognized krill as an “essential component” of the marine ecosystem, in particular as forage to species of considerable economic significance in each of the four Fishery Management Plans (FMP) administered by the PFMC. This includes all stocks in the coastal pelagic species FMP, particularly market squid (*Doryteuthis opalescens*) for which krill typically represent over 90% of prey (Karpov and Cailliet, 1979). However, krill are also important prey of Pacific sardine (*Sardinops sagax*, Hand and Berner, 1959; Emmett et al., 2005), anchovies and jack mackerel (*Engraulis mordax* and *Trachurus symmetricus*; Brodeur et al., 1987) as well as juvenile and adult stages of both species of Pacific salmon (Merkel, 1957; Brodeur et al., 1987; Daly et al., 2009). Krill are preyed upon by most of the largest groundfish populations on the US west coast, notable among which are Pacific hake (*Merluccius productus*) the largest West Coast fishery by volume (Rexstad and Pikitch, 1986; Buckley and Livingston, 1997; Tanasichuk, 1999) and most species of rockfish (*Sebastes* spp., Brodeur and Percy, 1984; Chess et al., 1988; Lee and Sampson, 2009). Although most highly migratory fish species feed higher on the food web, both albacore tuna (*Thunnus alalunga*) and blue sharks (*Prionace glauca*) will feed on euphausiids in coastal waters (Harvey, 1989; Glaser, 2010). Finally, as noted earlier, krill are critical components of the diets of many seabirds and marine mammals, including several threatened or vulnerable species.

In enacting their protective management measures for krill, the PFMC defined krill habitat very broadly as “the area between the 2000 m isobath and coastline with topographic and oceanographic features that consistently serve to concentrate krill and support stock productivity (while incidentally supporting predator feeding)” (PFMC, 2008). However, the Council action also recognized that within this broad region there are specific areas of krill aggregation and high abundance, many of which support high densities of mobile predators such as salmon, seabirds and marine mammals. These areas are generally well-known but have not been formally quantified with respect to long-term patterns of distribution and abundance. Although the PFMC decision did not identify such regions with a higher level of habitat protection (e.g., definition of these areas as Habitats of Particular Concern, or HAPCs), due largely to the fact that the ban on directed fishing precluded this need, future management actions by the PFMC or other management entities may benefit from the improved identification and quantification of such habitats in the Central California region. In particular, the location, size and spacing of krill hotspots within this region may be particularly valuable for future consideration of marine protected areas aimed at offering additional protection for krill-dependent predators (Hyrenbach et al., 2000; Roberts et al., 2003; Parnell et al., 2006). Notably, we identified krill hotspots within the boundaries of three National Marine Sanctuaries off Central California. The size, spacing and center of these distributions may be informative for sanctuary managers in developing conservation and management plans for maintaining the functional role of krill within sanctuary boundaries, particularly if integrated with distribution data on a variety of their fish, seabird and mammal predators (Halpern et al., 2008).

Our summary of krill hotspots should be useful for understanding and predicting changes in the spatial distribution, abundance and demography of krill-dependent predators. This, in turn, should help inform management and conservation measures by any number of management agencies or bodies. For example, endangered blue whales have been involved in lethal ship-strikes incidents off California, which poses additional threats to their conservation (Berman-Kowalewski et al., 2010). Additional insight may be gained by relating blue whale foraging behavior and distributions to krill hotspots, as a means to possibly prevent future ship-strike incidents. We identified krill hotspots near Point Conception and the Channel Islands (see Fig. 5), a region recognized as an important feeding ground for blue whales (Fiedler et al., 1998; Mate et al., 1999; Bailey et al., 2010) and also a heavily traveled route for commercial shipping (Halpern et al., 2009); whale-ship-strike incidents are highly clustered here (Berman-Kowalewski et al., 2010). Future effort is needed to determine how the location of krill hotspots relate to commercial shipping traffic and other human disturbances to the marine environment of the California Current ecosystem (Halpern et al., 2009). As the distribution of whales, and thus their vulnerability to strikes, varies considerably from year to year, an integrated approach that considers both long-term spatial hotspots with shorter-term forecasts of temporal variability in krill abundance (Santora et al., 2010) could lead to information that would reduce the risk of whale mortalities.

In conclusion, our study resolved mesoscale spatial distribution patterns of krill, identified regions of high abundance (i.e., hotspots) that were disassociated with strong upwelling centers, and confirmed the likelihood of spatial “optimal environmental windows” for krill in the CCS. This long-term study provides information on where krill are most likely to occur along the California coast and has important implications for the spatial ecology and management of krill and their predators. A novel aspect of this study is the spatially-explicit linkage between ship-based acoustically determined krill abundance and Ekman transport derived from remotely sensed wind stress (NASA QuikSCAT). Integration

of other satellite-based data products with information on krill and krill-predators would likely be a promising way forward in the developing field of marine spatial management.

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References

- Abraham, C.L., Sydeman, W.J., 2006. Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacific* and *Thysanoessa spinifera*. *Marine Ecology Progress Series* 313, 271–283.
- Ainley, D.G., Spear, L., Allen, S.G., 1996. Variation in the diet of Cassin's auklet reveals spatial, seasonal and decadal occurrence patterns of euphausiids off California, USA. *Marine Ecology Progress Series* 137, 1–10.
- Ainley, D.G., Dugger, K.D., Ford, R.G., Pierce, S.D., Reese, D.C., Brodeur, R.D., Tynan, C.T., Barth, J.A., 2009. Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. *Marine Ecology Progress Series* 389, 271–294.
- Bailey, H., Mate, B.R., Palacios, D.M., Irvine, L., Bograd, S.J., Costa, D.P., 2010. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research* 10, 93–106.
- Bakun, A., Parrish, R.H., 1982. Turbulence, transport, and pelagic fish in the California and Peru Current Systems. *CalCOFI Reports* 23, 99–112.
- Batchelder, H.P., Barth, J.A., Kosro, P.M., Strub, T., Brodeur, R.D., Peterson, W.T., Tynan, C.T., Ohman, M.D., Botsford, L.W., Powell, T.M., Schwing, F.B., Ainley, D.G., MacKas, D.L., Hickey, B.M., Ramp, S.R., 2002. The GLOBEC Northeast Pacific California Current System Program. *Oceanography* 15, 36–47.
- Benson, S.R., Croll, D.A., Marinovic, B.B., Chavez, F.P., Harvey, J.T., 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. *Progress in Oceanography* 54, 279–291.
- Berman-Kowalewski, M., Gulland, F.M.D., Wilkin, S., Calambokidis, J., Mate, B., Cordaro, J., Rotstein, D., Leger, J.S., Collins, P., Fahy, K., Dover, S., 2010. Association between blue whale (*Balaenoptera musculus*) mortality and ship strikes along the California Coast. *Aquatic Mammals* 36, 59–66.
- Bjorkstedt, E.P., Goericke, R., McClatchie, S., Weber, E., Watson, W., Lo, N., Peterson, P., Emmett, B., Peterson, J., Durazo, R., Gaxiola-Castro, G., Chavez, F., Pennington, J.T., Collins, C.A., Field, J., Ralston, S., Sakuma, K., Bograd, S., Schwing, F., Xue, Y., Sydeman, W., Thompson, S.A., Santora, J.A., Largier, J., Halle, C., Morgan, S., Kim, S.Y., Merckens, J., Hildebrand, J., Munger, L., 2010. State of the California Current 2009–2010: regional variation persists through transition from La Niña to El Niño (and back?). *California Cooperative of Oceanographic Fisheries Investigations, Reports* 51, 39–69.
- Bograd, S.J., DiGiacomo, P.M., Durazo, R., Hayward, T.L., Hyrenbach, D., Lynn, R.L., Mantyla, A.W., Schwing, F.B., Sydeman, W.J., Baumgartner, T., Lavaniegos, B., Moore, C.S., 2000. The state of the California Current, 1999–2000: forward to a new regime? *California Cooperative of Oceanographic Fisheries Investigations, Reports* 41, 26–52.
- Bograd, S.J., Schroeder, I., Sakar, N., Qiu, X., Sydeman, W.J., Schwing, F.B., 2009. The phenology of coastal upwelling in the California current. *Geophysical Research Letters* 36. doi:10.1029/2008GL035933.
- Breaker, L.C., Mooers, C.N.K., 1986. Oceanic variability off the central California coast. *Progress in Oceanography* 17, 61–135.
- Brinton, E., 1962. The distribution of Pacific euphausiids. *Bulletin of Scripps Institute of Oceanography* 8, 51–270.
- Brinton, E., 1976. Population biology of *Euphausia pacifica* off southern California. *Fisheries Bulletin* 74, 733–762.
- Brinton, E., Townsend, A., 2003. Decadal variability in abundances of the dominant euphausiid species in the southern sectors of the California Current. *Deep-Sea Research Part II* 50 (14–16), 2449–2472.
- Brodeur, R.D., Pearcy, W.C., 1984. Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the Northeastern Pacific Ocean. *Fishery Bulletin* 82, 2.

- Brodeur, R.D., Lorz, H.V., Percy, W.G., 1987. Food Habits and Dietary Variability of Pelagic Nekton off Oregon and Washington, 1979–1984. NOAA Technical Report, NMFS: 57.
- Brodeur, R.D., Daly, E.A., Schabetsberger, R.A., Mier, K.L., 2007. Interannual and interdecadal variability in juvenile coho salmon diets in relation to environmental changes in the Northern California current. *Fisheries Oceanography* 16, 395–408.
- Buckley, T.W., Livingston, P.A., 1997. Geographic variation in the diet of Pacific hake, with a note on cannibalism. California Cooperative of Oceanographic Fisheries Investigations, Reports 23, 130–148.
- Checkley, D.M., Barth, J.A., 2009. Patterns and processes in the California Current. *Progress in Oceanography* 83, 49–64.
- Chelton, D.B., 1982. Large-scale response of the California Current to forcing by the wind stress Curl. California Cooperative of Oceanographic Fisheries Investigations, Reports 23, 130–148.
- Chelton, D.B., Schlax, M.G., Samelson, R.M., 2007. Summertime coupling between sea surface temperature and wind stress in the California Current System. *Journal of Physical Oceanography* 37, 495–517.
- Chess, J.R., Smith, S.E., Fischer, P.C., 1988. Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. California Cooperative of Oceanographic Fisheries Investigations, Reports 29, 129–136.
- Ciannelli, L., Fauchald, P., Chan, K.S., Agostini, V.N., Dingsør, G.E., 2008. Spatial fisheries ecology: recent progress and future prospects. *Journal of Marine Systems* 71, 223–236.
- Croll, D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., Ternullo, R., Tershy, B.R., 2005. From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series* 289, 117–130.
- Curry, P., Roy, C., 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences* 46, 670–680.
- Daly, E.A., Brodeur, R.D., Weitkamp, L.A., 2009. Ontogenetic shifts in diets of juvenile and Subadult Coho and Chinook Salmon in coastal marine waters: important for marine survival? *Transactions of the American Fisheries Society* 138, 1420–1438.
- De Robertis, A., Schell, C., Jaffe, J.S., 2003. Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen. *ICES Journal of Marine Science* 60, 885–898.
- Dorman, J.G., Bollens, G., Slaughter, A.M., 2005. Population biology of euphausiids off northern California and effects of short time-scale wind events on *Euphausia pacifica*. *Marine Ecology Progress Series* 288, 183–198.
- Dorman, J.G., Powell, T.M., Sydeman, W.J., Bograd, S.J., 2011. Advection and starvation cause krill (*Euphausia pacifica*) decrease in 2005 Northern California coastal populations: implications from a model study. *Geophysical Research Letters* 38, L04605.
- Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.-J., Jakomulska, A., Miriri, M., Rosenberg, M.S., 2002. A balanced view of scale in spatial statistical analysis. *Ecography* 25, 626–640.
- Emmett, R.T., Brodeur, R.D., Miller, T.W., Pool, S.S., Krutzikowsky, G.K., Bentley, P.J., McCrae, J., 2005. Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. *CalCOFI Reports* 46, 122–143.
- Feinberg, L.R., Peterson, W.T., 2003. Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. *Progress in Oceanography* 57, 262–379.
- Fiedler, P.C., Reilly, S.B., Hewitt, R.P., Demer, D., Philbrick, V.A., Smith, S., Armstrong, W., Croll, D.A., Tershy, B.R., Mate, B.R., 1998. Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Research Part II* 45 (8–9), 1781–1801.
- Field, J.C., Francis, R.C., Aydin, K., 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography* 68, 238–270.
- Ford, R.G., Ainley, D.G., Casey, J.T., Keiper, C.A., Spear, L.B., Ballance, L.T., 2004. The biogeographic patterns of seabirds in the central portion of the California Current. *Marine Ornithology* 32, 77–96.
- Fortin, M.-J., 1999. Effects of quadrat size and data measurement on the detection of boundaries. *Journal of Vegetation Science* 10, 43–50.
- Glaser, S.M., 2010. Interdecadal variability in predator–prey interactions of juvenile North Pacific albacore in the California Current System. *Marine Ecology Progress Series* 414, 209–221.
- Goebel, N.L., Edwards, C.A., Zehr, J.P., Follows, M.J., 2010. An emergent community ecosystem model applied to the California Current System. *Journal of Marine Systems* 83, 221–241.
- Goerick, R., Bograd, S.J., Gaxiola-Castro, G., Gomez-Valdes, J., Hoof, R., Huyer, A., Hyrenbach, K.D., Lavanigos, B.E., Mantyla, A., Peterson, W.T., Schwing, F.B., Smith, R.L., Sydeman, W.J., Vernick, E., Wheeler, P.A., 2004. The state of the California Current, 2003–2004: a rare “normal” year. California Cooperative of Oceanographic Fisheries Investigations, Reports 41, 27–59.
- Gómez-Gutiérrez, J., Peterson, W.T., Miller, C.B., 2005. Cross-shelf life-stage segregation and community structure of the euphausiids off central Oregon (1970–1972). *Deep-Sea Research Part II: Topical Studies in Oceanography* 52, 289–315.
- Graham, W.M., Field, J.G., Potts, D.C., 1992. Persistent “upwelling shadows” and their influence on zooplankton distributions. *Marine Biology* 114, 561–570.
- Graham, W.M., Largier, J.L., 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Continental Shelf Research* 17, 509–532.
- Halpern, B.S., McLeod, K.L., Rosenberg, A.A., Crowder, L.B., 2008. Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean & Coastal Management* 51, 203–211.
- Halpern, B.S., Kappel, C.V., Selkoe, K.A., Micheli, F., Ebert, C.M., Kontgis, C., Crain, C.M., Martone, R.G., Shearer, C., Teck, S.J., 2009. Mapping cumulative human impacts to California Current marine ecosystems. *Conservation Letters* 2, 138–148.
- Hand, C.H., Berner, L., 1959. Food of the Pacific Sardine. *Fishery Bulletin of the Fish and Wildlife Service* 60, 175–184.
- Harvey, J.T., 1989. Food habits, seasonal abundance, size and sex of the blue shark, *Pristiurus glauca* in Monterey Bay, California. *California Fish and Game* 75, 33–44.
- Haurry, L.R., McGowan, J.A., Wiebe, P.H., 1978. Patterns and processes in the time-space scales of plankton distributions. In: Steele, J.H. (Ed.), *Spatial Pattern in Plankton Communities*. Plenum Press, New York.
- Hewitt, R.P., Demer, D.A., 2000. The use of acoustic sampling to estimate the dispersion and abundance of euphausiids, with an emphasis on Antarctic krill, *Euphausia superba*. *Fisheries Research* 47, 215–229.
- Hickey, B.M., 1979. The California current system – hypotheses and facts. *Progress in Oceanography* 10, 191–279.
- Huyer, A., 1983. Coastal upwelling in the California current system. *Progress in Oceanography* 12, 259–284.
- Hofmann, E.E., Haskel, A.G.E., Klinck, J.M., Lascara, C.M., 2004. Lagrangian modelling studies of Antarctic krill (*Euphausia superba*) swarm formation. *ICES Journal of Marine Science* 61, 617–631.
- Hyrenbach, K.D., Forney, K.A., Dayton, P.K., 2000. Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10, 437–458.
- Jahncke, J., Saenz, B.L., Abraham, C.L., Rintoul, C., Bradley, R.W., Sydeman, W.J., 2008. Ecosystem responses to short-term climate variability in the Gulf of the Farallones, California. *Progress in Oceanography* 77, 182–193.
- Karpov, K.A., Cailliet, G.M., 1979. Prey composition of the market squid, *Loligo opalescens* Berry, in relation to depth and location of capture, size of squid, and sex of spawning squid. California Cooperative of Oceanographic Fisheries Investigations, Reports 20, 51–57.
- Keating, K.A., Cherry, S., 2009. Modeling utilization distributions in space and time. *Ecology* 90, 1971–1980.
- Keister, J.A., Cowles, T.J., Peterson, W.T., Morgan, C.A., 2009. Do upwelling filaments result in predictable biological distributions in coastal upwelling ecosystems? *Progress in Oceanography* 83, 303–313.
- Kudela, R.M., Banas, N.S., Barth, J.A., Frame, E.R., Jay, D.A., Largier, J.L., Lessard, E.J., Peterson, T.D., Vander Woude, A.J., 2008. New insights into the controls and mechanisms of plankton productivity of the Northern California Current System. *Oceanography* 21, 46–59.
- Lee, Y.W., Sampson, D.B., 2009. Dietary variations in three co-occurring rockfish species off the Pacific Northwest during anomalous oceanographic events in 1998 and 1999. *Fishery Bulletin* 107, 510–522.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Science, Amsterdam, The Netherlands.
- Lu, B., Mackas, D.L., Moore, D.F., 2003. Cross-shore separation of adult and juvenile euphausiids in a shelf-break alongshore current. *Progress in Oceanography* 57, 381–404.
- MacCall, A.D., 1996. Patterns of low-frequency variability in fish populations of the California Current. California Cooperative of Oceanographic Fisheries Investigations, Reports 37, 100–110.
- Mackas, D.L., 1984. Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. *Limnology and Oceanography* 29, 451–471.
- Mackas, D.L., Kieser, R., Saunders, M., Yelland, D.R., Brown, R.M., Moore, D.F., 1997. Aggregations of euphausiids and Pacific Hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 1–18.
- MacLennan, D.N., Simmonds, E.J., 2005. *Fisheries Acoustics*. Fish and Fisheries Series, vol. 5. Chapman & Hall, New York.
- Mann, K.H., Lazier, J.R.N., 1996. *Dynamics of Marine Ecosystems*. Blackwell, Cambridge.
- Marinovic, B.B., Croll, D.A., Gong, N., Benson, S.R., Chavez, F.P., 2002. Effects of the 1997–1999 El Niño and La Niña events on the zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. *Progress in Oceanography* 54, 265–277.
- Mate, B.R., Lagerquist, B.A., Calambodkiddis, J., 1999. Movements of North Pacific blue whale during the feeding season off southern California and their southern fall migration. *Marine Mammal Science* 15, 1246–1257.
- McClatchie, S., Goericke, R., Schwing, F.B., Bograd, S.J., Peterson, W.T., Emmett, R., Charter, R., Watson, W., Lo, N., Hill, K., Collins, C., Kahru, M., Mitchell, B.G., Koslow, J.A., Gomez-Valdes, J., Lavanigos, B.E., Gaxiola-Castro, G., Gottschalk, J., L’Heureux, M., Xue, Y., Manzano-Sarabia, M., Bjorkstedt, E., Ralston, S., Field, J., Rogers-Bennett, L., Munger, L., Campbell, G., Merckens, K., Camacho, D., Havron, A., Douglas, A., Hildebrand, J., 2009. The state of the California Current, 2008–2009: Cold conditions drive regional difference. California Cooperative of Oceanographic Fisheries Investigations, Reports 50, 43–68.
- Merkel, T.J., 1957. Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. *California Fish and Game* 43, 249–270.
- Ohman, M.D., 1984. Omnivory by *Euphausia pacifica*: the role of copepod prey. *Marine Ecology Progress Series* 19, 125–131.
- Pacific Fishery Management Council (PFMC), 2008. Management of krill as an essential component of the California Current Ecosystem. Amendment 12 to the

- Coastal Pelagic Species Fishery Management Plan. Pacific Fishery Management Council, Portland, OR. <http://www.pcouncil.org/wp-content/uploads/CPS_Am12_Krill_DraftEA.pdf>.
- Parnell, P.E., Daton, P.K., Lennert-Cody, C.E., Rasmussen, L.L., Leichter, J.J., 2006. Marine reserve design: optimal size, habitats, species affinities, diversity, and ocean microclimate. *Ecological Applications* 16, 945–962.
- Parrish, R.H., Nelson, C.S., Bakun, A., 1981. Transport mechanisms and reproductive success of fishes in the California current. *Biological Oceanography* 1, 175–203.
- Peterson, W.T., Keister, J.E., Feinberg, L.R., 2002. The effects of the 1997–98 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast. *Progress in Oceanography* 54, 381–398.
- Peterson, W.T., 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 (2–4), 389–411.
- Pickett, M.G., Paduan, J.D., 2003. Ekman transport and pumping in the California Current based on the US Navy's high-resolution atmospheric model (COAMPS). *Journal of Geophysical Research* 108, 3327. doi:10.1029/2003JC001902.
- Pickett, M.H., Schwing, F.B., 2006. Evaluating upwelling estimates off the west coasts of North and South America. *Fisheries Oceanography* 15, 256–269.
- Pinchuk, A.I., Coyle, K.O., Hopcroft, R.R., 2008. Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003. *Progress in Oceanography* 77, 203–216.
- Ralston, S., Howard, D.F., 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. *Fishery Bulletin* 93, 710–720.
- Ralston, S., Bence, J.R., Eldridge, M.B., Lenarz, W.H., 2003. An approach to estimating rockfish biomass based on larval production, with application to *Sebastes jordani*. *Fishery Bulletin* 101, 129–146.
- Ressler, P.H., Brodeur, R.D., Peterson, W.T., Pierce, S.D., Vance, P.M., Røstad, A., Bart, J.A., 2005. The spatial distribution of euphausiid aggregations in the Northern California Current during August 2000. *Deep-Sea Research II* 52, 89–108.
- Rexstad, E.A., Pikitch, E.K., 1986. Stomach contents and food consumption estimates of Pacific Hake, *Merluccius productus*. *Fishery Bulletin* 84 (4), 947–956.
- Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B., Lafferty, K.D., Leslie, H., Lubchenko, J., McArdle, D., Possingham, H.P., Ruckelshaus, M., Warner, R.R., 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13, S199–S214.
- Rykaczewski, R.R., Checkley, D.M., 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences* 105, 1965–1970.
- Sakuma, K.M., Ralston, S., Wespestad, V.G., 2006. Interannual and spatial variation in the distribution of young-of-the-year rockfish (*Sebastes* spp.): expanding and coordinating a survey sampling frame. *California Cooperative of Oceanographic Fisheries Investigations, Reports* 47, 127–139.
- Santora, J.A., Ralston, S., Sydeman, W.J., 2011. Spatial organization of krill and seabirds in the central California Current. *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsr046.
- Santora, J.A., Reiss, C.S., Loeb, V.J., Veit, R.R., 2010. Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill (*Euphausia superba*) suggest size-dependent predation. *Marine Ecology Progress Series* 405, 255–269.
- Schwing, F.B., Bond, N.A., Bograd, S.J., Mitchell, T., Alexander, M.A., Mantua, N., 2006. Delayed coastal upwelling along the US West Coast in 2005: a historical perspective. *Geophysical Research Letters* 33 (22), L22S01.
- Seaman, D.E., Powell, R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77, 2075–2085.
- Shaw, C.T., Peterson, W.T., Feinberg, L.R., 2010. Growth of *Euphausia pacifica* in the upwelling zone off the Oregon coast. *Deep-Sea Research II* 57, 584–593.
- Siegel, V., 2000. Krill (Euphausiacea) life history and aspects of population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 130–150.
- Silverman, B., 1986. *Density Estimation for Statistics and Data Analysis*. Monographs in Statistics and Applied Probability. Chapman & Hall, London, UK.
- Smith, S.D., 1988. Coefficients for sea surface wind stress, heat flux, and wind profiles as a function of wind speed and temperature. *Journal of Geophysical Research* 93, 15467–15472.
- Strub, P.T., Allen, J.S., Huyer, A., Smith, R.L., Beardsley, R.C., 1987. Seasonal cycles of currents, temperatures, winds, and sea level over the northeast Pacific continental shelf: 35 N to 48 N. *Journal of Geophysical Research* 92, 1507–1526.
- Swartzmen, G., Hickey, B., Kosro, P.M., Wilson, C., 2005. Poleward and equatorward currents in the Pacific Eastern Boundary Current in summer 1995 and 1998 and their relationship to the distribution of euphausiids. *Deep-Sea Research II* 52, 73–78.
- Sydeman, W.J., Bradley, R.W., Warzybok, P., Abraham, C.L., Jahncke, J., Hyrenbach, K.D., Kousky, V., Hipfner, J.M., Ohman, M.D., 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmosphere blocking? *Geophysical Research Letters* 33 (22), L22S09.
- Tanasichuk, R.W., 1998a. Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada with special reference to the 1992 and 1993 warm ocean years. *Marine Ecology Progress Series* 173, 163–180.
- Tanasichuk, R.W., 1998b. Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada with special reference to the 1992 and 1993 warm ocean years. *Marine Ecology Progress Series* 173, 181–195.
- Tanasichuk, R.W., 1999. Interannual variation in the availability of euphausiids as prey for Pacific hake (*Merluccius productus*) along the southwest coast of Vancouver Island. *Fisheries Oceanography* 8, 150–156.
- Watkins, J.L., Brierley, A.S., 2002. Verification of acoustic techniques used to identify and size Antarctic krill. *ICES Journal of Marine Science* 59, 1326–1336.
- Wing, S.R., Botsford, L.W., Ralston, S.V., Largier, J.L., 1998. Meroplankton distribution and circulation in a coastal retention zones of the Northern California upwelling system. *Limnology and Oceanography* 43, 1710–1721.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168.