



Krill space: a comparative assessment of mesoscale structuring in polar and temperate marine ecosystems

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The spatial organization, mesoscale variability, and habitat associations of krill within portions of the Antarctic Peninsula and California Current marine ecosystems are compared. Using a decade of acoustic observations and remotely sensed oceanography (2000–2009), the hypothesis that mesoscale spatial organization of krill in both systems closely relates to geospatial variability of the shelf break and is non-linearly related to geostrophic flow and positively related to chlorophyll *a* (Chl *a*) is tested. Directional-dependence analysis to measure spatial variability of krill is used along with spatially explicit generalized additive models to quantify and compare the spatial relationships among krill and habitat characteristics in both systems. The results suggest the following aspects of krill spatial organization: (i) areas of dense aggregation, i.e. hot spots, are present in both systems and are orientated in the direction of the shelf break, (ii) moderate levels of eddy kinetic energy seem to concentrate krill in favourable habitats and lessen the likelihood of advection away from the system, and (iii) variable responses to surface Chl *a* concentration suggest that real-time Chl *a* values may not be useful as a global predictor of important krill habitat. The results provide valuable reference points for marine spatial management of krill and for refining ecosystem and foodweb models.

Keywords: Antarctic Peninsula, California Current, eddy kinetic energy, krill, mesoscale, spatial organization.

Introduction

It is well established that humankind has impacted most marine ecosystems worldwide (Halpern *et al.*, 2008). As we venture into the novel realm of marine ecosystem restoration, a better understanding of comparative ecosystem dynamics is required to understand fisheries- and climate-change-related impacts between systems (Bakun and Parrish, 1982; Megrey *et al.*, 2009; Murawski *et al.*, 2010). Regional- to local- to small-scale variations in oceanographic conditions serve to concentrate primary and secondary productivity, leading to substantial aggregations of mid- to upper trophic level marine populations, enhancing predator–prey interactions and energy and carbon cycling between trophic levels (Sydeman *et al.*, 2006). The causes and consequences of spatial aggregations vary by scale,

but their significance is not well known (Hewitt *et al.*, 2007). One clear impact, however, is that localized disruption of spatial aggregations of low-trophic-level organisms may be particularly important for central-place foraging marine top predators, such as seabirds or seals, which have restricted foraging ranges during breeding, and sometimes during other life-history stages (Santora *et al.*, 2009; Pichegru *et al.*, 2010; Santora and Reiss, 2011). Therefore, comparative studies of spatial organization of forage nekton have important implications for understanding predator requirements, trophic ecology, and functional and numerical responses between prey and predators. Ultimately, these factors need to be integrated into the myriad of ecosystem models gaining popularity for assessing the impacts of fisheries and climate in the marine environment (Batchelder

et al., 2002; Field *et al.*, 2006; Cury *et al.*, 2008; Levin *et al.*, 2009).

Because of their energy, nutritional content, and tendency to form large, dense, relatively long-term aggregations, euphausiids (hereafter, krill) provide an important prey field for a vast array of marine organisms globally, particularly in temperate and polar environments (Brinton, 1962; Siegel, 2000; Nicol, 2006). Consequently, improving knowledge of the distribution, abundance, and spatial organization of krill is important to understanding foodweb dynamics, fisheries- and climate-change impacts, and wildlife population dynamics across marine ecosystems (Smith *et al.*, 2011). Comparisons of krill spatial dynamics may provide valuable insight into emergent ecosystem properties, especially for systems with similarities in oceanography and top predator communities.

The Antarctic Peninsula ecosystem (APE) and the California Current ecosystem (CCE) are two marine ecosystems about which the ecology of the dominant krill species, *Euphausia superba* and *E. pacifica*, respectively, are reasonably well known (see Supplementary Table S1; Brinton, 1976; Batchelder *et al.*, 2002; Atkinson *et al.*, 2008). Although ubiquitous in both ecosystems, these krill species are known to concentrate near shelf breaks and shallow-water topographies (Brinton, 1962; Atkinson *et al.*, 2008; Santora *et al.*, 2011a). Advective processes are thought to determine krill distribution and abundance in both ecosystems (Brinton and Townsend, 2003; Atkinson *et al.*, 2008; Loeb *et al.*, 2009; Santora *et al.*, 2011b). However, the mechanistic details and scales of distributional characteristics remain unclear and could be understood better if generalities between ecosystems can be developed. Here, we examine if mesoscale advective processes similarly structure krill distribution and abundance in both the CCE and the APE. Mesoscale variability in time and space has been recognized as singularly important in ecosystem oceanography, yet few comparative tests of this concept have been undertaken (Hunt and Megrey, 2005; Hewitt *et al.*, 2007; Cury *et al.*, 2008; Megrey *et al.*, 2009). We follow Cury *et al.* (2008) in considering mesoscale events as operating at intermediate spatial scales of between 10 and 100 km and at temporal scales of weeks to months.

The primary objective of this study is to compare the spatial organization, mesoscale variability, and habitat associations of krill within portions of the APE and the CCE. Using extensive datasets representing a decade of hydroacoustic observations (2000–2009), we compare the long-term spatial patterns of krill in relation to bathymetry and climatologies of remotely sensed oceanographic indices: geostrophic eddy kinetic energy (EKE) and surface chlorophyll *a* (Chl *a*) concentrations. It is beyond the scope of this paper to consider interannual variability, so this topic will be addressed elsewhere. We hypothesize that because of shared bathymetric associations and sensitivity to hydrographic drivers, krill in both systems exhibit similar patchiness and mesoscale structuring. Specifically, the hypothesis is that the spatial variability of krill along the shelf break in both systems is related non-linearly to geostrophic flow and positively, perhaps linearly, to Chl *a*. This study has the potential to provide baseline information for calibrating mesoscale structuring for large-scale ecosystem models. The comparative approach will reveal if there is a coherent scale for krill patchiness or if ecosystem-specific values must be used for model parametrization.

Methods

The APE at the northeastern tip of the Antarctic Peninsula is an important spawning and nursery ground of Antarctic krill (*E. superba*) as well as an important area for the commercial krill fishery (Hewitt *et al.*, 2004; Atkinson *et al.*, 2008). The hydrography and circulation of the region is complex and variable, and it reflects inputs and mixing of waters from the Antarctic Circumpolar Current (ACC) within Drake Passage, the western portion of the Weddell Gyre, and upstream regions along the western Antarctic Peninsula that enter through the Gerlache and western Bransfield Straits (Orsi *et al.*, 1995; Loeb *et al.*, 2009, 2010). The rugged bathymetry of the region, which includes the continental shelf around the islands, the deep basins of Bransfield Strait, and the South Shetland Trench and Shackleton Fracture Zone ridge in Drake Passage, provides additional hydrographic and circulation variability (Figure 1). The ACC transports warm Circumpolar Deep Water (CDW) to the region, and this is an essential component of krill reproductive success (Hofmann and Murphy, 2004; Atkinson *et al.*, 2008). *Euphausia superba* spawning in the region is limited to the ice-free austral summer (December–March), supported by elevated primary production.

The CCE is a productive eastern boundary current upwelling ecosystem. Off California, the combination of seasonal northwesterly winds and coastline features such as capes, promontories, and points produce spatial variability in the intensity of upwelling centres and jets that vary by latitude and season, influencing primary and secondary plankton abundance and distribution (Checkley and Barth, 2009). For example, strong centres of upwelling along the California coast are next to localized krill hot spots (Santora *et al.*, 2011b). *Euphausia pacifica* is the numerically dominant krill species in the northern CCE (Brinton, 1962) and is found in waters at or beyond the shelf break (200–1000 m) and over submarine canyons (Lu *et al.*, 2003; Santora *et al.*, 2011a).

Surveys

The National Marine Fisheries Service (NMFS) Antarctic Marine Living Resources (AMLR) programme conducts an ecosystem assessment of the coastal and pelagic waters around the South Shetland Islands annually during the austral summer (January–March; Figure 1). The survey focuses on monitoring krill demography and mapping the spatial distribution and abundance of krill and krill predators on a fixed grid of stations and transects. The survey consists of a series of north–south transects within four strata: the Elephant Island region, “West”, i.e. the shelf north of the South Shetland Islands, “South”, i.e. the Bransfield Strait, and near Joinville Island (for a review of the sampling methodology, see Reiss *et al.*, 2008; Santora *et al.*, 2010). The NMFS Groundfish Analysis Team conducts an ecosystem assessment of coastal and pelagic waters along the coast of southern and central California. The survey focuses on monitoring juvenile rockfish (*Sebastes* spp.) and other forage nekton, including krill, and predators. The survey is conducted during the boreal spring/summer upwelling period in May and June (Sakuma *et al.*, 2006). Data were analysed from Point Arena (39°N) to Point Conception, CA (34°N), spanning ~350 km of coast (Figure 1).

Acoustic surveys facilitate mapping krill distribution and abundance over a variety of spatial scales. In both ecosystems, acoustic volume backscattering data (S_v , dB) were collected during daylight using multifrequency echosounders (Simrad EK 60 and EK 500)

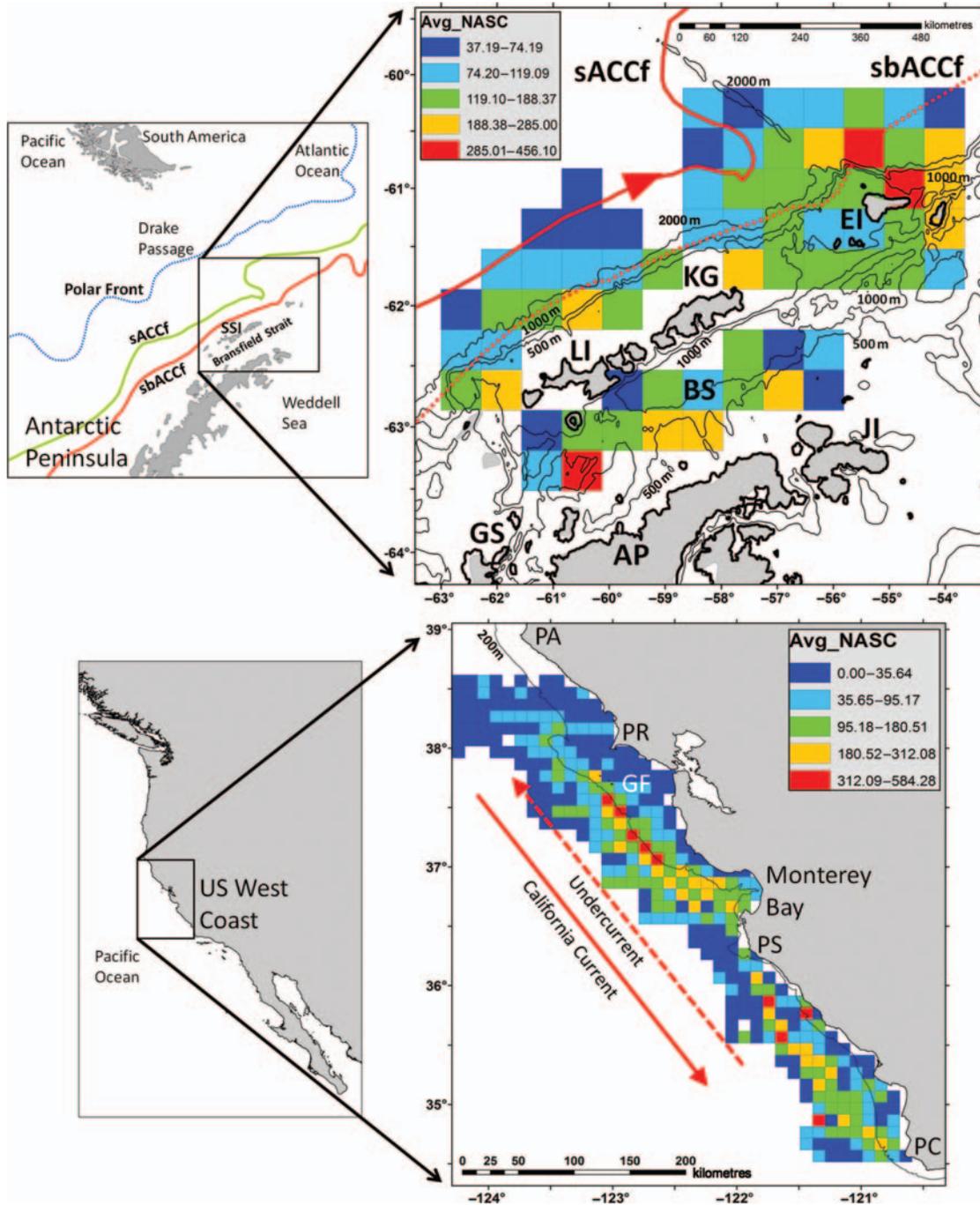


Figure 1. Mean spatial abundance of krill (NASC) within the (top) Antarctic Peninsula (January–March 2003–2009; cell size 1000 km²) and (bottom) California Current (May and June 2000–2009; cell size 100 km²) large marine ecosystems (note the difference in scale). The survey area (125 000 km²) in the Antarctic is located in the southwest Atlantic Ocean around the South Shetland Islands and has complex bathymetry and water circulation as a result of the influence of the ACC and Weddell Sea and coastal currents. Bathymetric contours in the Antarctic study area are the 500-, 1000-, and 2000-m isobaths. The average position of the southern ACC front (sACCF) and its southern boundary (sbACCF) are shown in red and generally follow the contour of the shelf break north of the South Shetland Islands (Orsi *et al.*, 1995); BS, the Bransfield Strait; LI, Livingston Island; KG, King George Island; EI, Elephant Island; JI, Joinville Island; GS, Gerlache Strait; AP, Antarctic Peninsula. The shelf break in the California study area is shown as the 200-m isobath. The California Current runs south, whereas its Undercurrent runs north; PA, Point Arena; PR, Point Reyes; GF, Gulf of the Farallones; PS, Point Sur; PC, Point Conception.

configured with downlooking 38, 120, and 200 kHz transducers mounted on the hull of the ship at a depth of ~10 m (Antarctic) and ~7 m (California). Details of sampling and

analysis in both regions are provided by Hewitt *et al.* (2003), Reiss *et al.* (2008), and Santora *et al.* (2011a, b). The Nautical Area Scattering Coefficient (NASC nautical mile⁻¹) was calculated

as the basic measurement of horizontal krill distribution and abundance. Only daytime survey effort was processed to avoid potential bias attributable to diel vertical migration by krill. During the years 2003–2009, 12 110 nautical miles of shipboard trackline was collected in the AMLR survey area, and during the years 2000–2009, 28 000 nautical miles of shipboard trackline was collected off California.

For mapping, we compiled the acoustic survey effort into grid cells, then calculated block averages by dividing the acoustic krill by sampling frequency (the number of years a cell was sampled) and the mean number of nautical miles sampled per cell. We estimated the anomaly of krill abundance (mean per cell minus the mean of all grid cells for all years; Santora et al., 2011b). Off California the cell size is 100 km² and in the Antarctic it is 1000 km². The larger Antarctic cell size is because of the larger survey area relative to that off California (~125 000 vs. 40 000 km²). Additionally, this cell size has been used extensively during previous Antarctic krill and predator studies (Atkinson et al., 2008; Santora et al., 2010). The resulting maps are used to identify and describe areas of abundance (Figure 1). However, data used to model habitat associations of krill in both systems are the same dimension (100 km²; see below).

Spatial variability of krill

To quantify scale-dependent patterns of krill, we used direction-based correlogram methods (Moran's *I*; Legendre and Legendre, 1998). This concept focuses on the idea that a measurement property (krill distribution) varies spatially with direction (Lu et al., 2003; Ciannelli et al., 2008). Correlograms allow determination of the characteristic scale of krill patchiness by counting the successive number of lags yielding positive correlations before becoming negative (i.e. zero-crossing; Santora et al., 2009, 2011a, b). NASC nautical mile⁻¹ data are used for this analysis. Modes of krill directional spatial variability were calculated for isotropic (all-directional, invariant with respect to direction), 0° for north/south variation, 90° (longitudinal variation in APE and cross-shelf break variation in CCE), and 135° (cross-shelf break variation in APE and alongshore variation in CCE). In making between-ecosystem comparisons of krill spatial variability, it is important to keep in mind the size of the respective regions, the sampling resolution and the transect layout (north/south transects vs. cross-shelf transects), and the underlying structure of the bathymetry and coastal geomorphology.

Spatial covariates and modelling

Satellite data were used to construct climatologies of EKE and surface Chl *a* concentration. Bathymetric data (m; 0.016° resolution) were obtained from the ETOPO1 Global Relief Model (www.ngdc.noaa.gov/mgg/global/global.html). A digital elevation model in GIS was used to estimate slope (degrees) and general bathymetric curvature (radians per decimal degree; high values are convex and low values are concave) to index bathymetric features such as seamounts and submarine canyons (i.e. rugosity). Sea surface height and geostrophic velocity data (level 3) were generated by the Archiving, Validation, and Interpretation of Satellite Oceanographic (AVISO) source, and EKE (cm² s⁻²; 0.25° resolution) was calculated from $EKE = 1/2(U^2 + V^2)$, where *U* and *V* are the zonal and meridional geostrophic current components, respectively (<http://www.aviso.oceanobs.com>). For a review of EKE in the Antarctic and the California Current, see Lenn et al. (2007) and Strub and James (2002), respectively. We

used Chl *a* concentration data (level 3; mg m⁻³; 0.08° resolution) from SeaWiFS (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>) to index surface phytoplankton concentrations and computed the spatial mean of EKE and Chl *a* over the years 2000–2009 in May (California) and January (Antarctic). All remotely sensed data were acquired from NOAA's Coastwatch website (<http://coastwatch.pfeg.noaa.gov/erddap/index.html>).

We used generalized additive models (GAMs) to investigate similarities in the relationship of krill with geospatial features (e.g. depth, slope, distance to features; Santora and Reiss, 2011; Santora et al., 2011a). To make ecosystem comparisons at the appropriate scale, both datasets were standardized by averaging krill abundance over all years into grid cells of the same dimension (100 km), then linking spatial covariates to the cells. Note that for the APE, these cells do not correspond directly to the cells in Figure 1. The covariates used in GAMs were depth (m), slope (change in sea depth, °), bathymetric curvature, distance to shelf break (km; 200 m isobath off California and 1000 m isobath off Antarctic Peninsula), and the spatial coordinate (longitude, latitude). The fitted GAM for log-transformed krill abundance was specified with a Gaussian distribution and an identity-link function: $Krill = s(\text{Depth}) + s(\text{Slope}) + s(\text{Curvature}) + s(\text{DistShelf break}) + s(\text{EKE}) + s(\text{Chl } a) + lo(\text{long, lat})$, where DistShelf break is the distance (km) to the 200 m (California Current) and 1000 m isobaths (Antarctic), and *lo*(long, lat) is the smoothed interaction term between longitude and latitude. Smoothing functions *s*() and *lo*() are regression splines. Backward stepwise model selection through AIC (Akaike's information criterion) is used to perform model selection (Zuur et al., 2009). The GAM analysis was done using the "gam" package in R (R Development Core Team, 2009). The effect of each geospatial covariate included in the GAM was plotted to inspect visually the functional form to determine whether krill exhibit similar peaks or changes in relation to geospatial covariates between the two ecosystems.

Results

Spatial distribution patterns

The maps of mean spatial abundance (NASC) show where krill are highly concentrated in both ecosystems (Figure 1). Areas of abundance were patchy throughout both, and in general reflected favourable krill habitats that equate to the position of the shelf break and the distance from land, possibly reflective of convergence zones (fronts) maintained by aspects of physical forcing particular to each region. In the APE, krill are concentrated north of the South Shetland Islands along the shelf break, where the southern boundary of the ACC follows the steep bathymetry from west to east. Krill are also concentrated within the Bransfield Strait, where they are associated with deep basins, narrow channels, and the convergence of waters with Drake Passage and Weddell Sea origins. In contrast, krill in the California upwelling system are distributed along the coast with concentrations in proximity to highly productive upwelling cells (Figure 1). For example, north of Monterey Bay, areas of high abundance are along the 200-m isobath and also associated with submarine canyons. There, concentrations are greatest in the upwelling shadow south of Point Reyes (Figure 1), but south of Monterey Bay, there are concentrations between the upwelling cells off Point Sur and Point Conception.

Comparing spatial structure

The isotropic (all-directional) analysis showed that the characteristic scale of krill patchiness in the Antarctic was much larger (1–17 nautical miles) than in the California Current (1–7 nautical miles; Figure 2). In the Antarctic, krill spatial variability in the north/south (0°) and longitudinal (90°) direction exhibited a characteristic scale of 1–10 nautical miles (Figure 2). However,

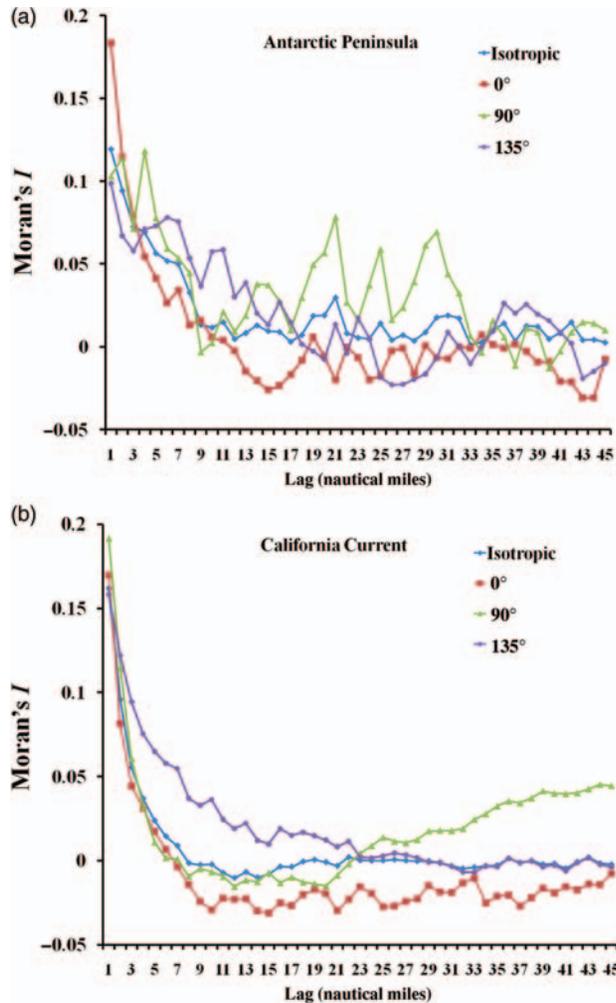


Figure 2. Modes of directional spatial variability of krill within the (a) Antarctic Peninsula and (b) central California Current marine ecosystems: two-dimensional correlograms (Moran's *I*) depicting direction spatial variability for isotropic (all-directional), 0° (north/south variation), 90° (cross-shelf off California and east/west variation in the Antarctic study area), and 135° (cross-shelf in the Antarctic study area and alongshore off California).

spatial variability in the longitudinal (90°) direction displayed increased correlation at scales ranging from 20 to 30 nautical miles, reflecting the east/west transect spacing, and also suggests similar scale peaks in krill abundance along the northeast-trending shelf break of the Antarctic Peninsula. Off California, krill exhibited 1–7-nautical mile scales of patchiness in both the north/south (0°) and cross-shelf directions (90°; Figure 2). The along-shore (135° direction; parallel to the coastline) spatial variability had a characteristic scale of 1–23 nautical miles that is substantially larger than the other directions (Figure 2). Moreover, krill distribution in the cross-shelf direction showed increased spatial variability at larger scales (>23 nautical miles) that we attribute to general homogeneity of the shelf break extending south through that portion of the California coast.

Comparing habitat associations

Regarding bathymetry, GAMs indicate that in both regions water depth is a significant factor underlying krill distribution; this supports the patterns depicted in the maps of krill abundance (Table 1, Figures 1 and 3a and b). In the Antarctic, the effect of water depth on krill is positive from 500 to 2000 m and declines at greater depths. Off California the effect of water depth on krill is positive at shallow depths (100–1000 m), but declines at depths >1000 m. Although seafloor slope is not a very influential factor, the effect of slope on krill abundance increased with increasing change in slope in both systems (Figure 3c and d). The index of bathymetric curvature was not a significant factor in predicting changes in krill distribution and abundance in either ecosystem (Figure 3e and f). However, this finding may be due in part to the coarse scale of the investigation; at finer scales, abrupt and convoluted topographies could possibly contain elevated concentrations of plankton as a result of enhanced turbulence or retention. Therefore, the complicated non-linear relationship between krill and unique topographies may be better understood at finer scales (e.g. <10 km).

In general, there is an association between krill and the shelf break, as shown in the abundance maps for both ecosystems (Figure 1). GAMs confirmed this, but showed different relationships between ecosystems. In the Antarctic, krill are associated with the 1000-m isobath, but were increasingly abundant with increasing distance from this isobath (Figure 4a and b), highlighting their tendency to form dense aggregations in offshore waters of the ACC (Figure 1; reviewed by Atkinson *et al.*, 2008). In the California study area, krill are associated with the 200-m isobath within and north of Monterey Bay, but are farther from the 200-m isobath south of Monterey Bay along the Big Sur coastline (Figure 1; reviewed by Santora *et al.*, 2011b).

We used EKE to index the geostrophic flow of water with the underlying assumption that the spatial distribution of krill aggregations may relate similarly to mesoscale energy in both

Table 1. Results of GAMs for comparing the relationships between krill spatial distribution and abundance within the Antarctic Peninsula and California Current large marine ecosystems: (first two rows) full model, (last two rows) selected model by backward stepwise AIC, the values being non-parametric *F*-statistics, and their significance (i.e. the *p*-value; emboldened values indicating statistical significance).

System	Depth	Slope	Curvature	Distance to shelf break	EKE	Chl <i>a</i>	Lon, Lat	AIC
Antarctic Peninsula	6.38 (<0.001)	2.07 (0.1)	0.98 (0.39)	3.72 (0.01)	20.15 (<0.001)	8.47 (<0.001)	31.44 (<0.001)	5 489.07
California Current	5.72 (<0.001)	0.96 (0.41)	1.15 (0.32)	2.10 (0.09)	4.59 (0.003)	8.91 (<0.001)	7.29 (<0.001)	4 063.42
Antarctic Peninsula	6.40 (<0.001)	2.16 (0.09)	–	3.74 (0.01)	20.47 (<0.001)	8.76 (<0.001)	31.50 (<0.001)	5 484.45
California Current	7.39 (<0.001)	–	–	1.75 (0.15)	5.24 (0.001)	10.28 (<0.001)	9.50 (<0.001)	4 056.67

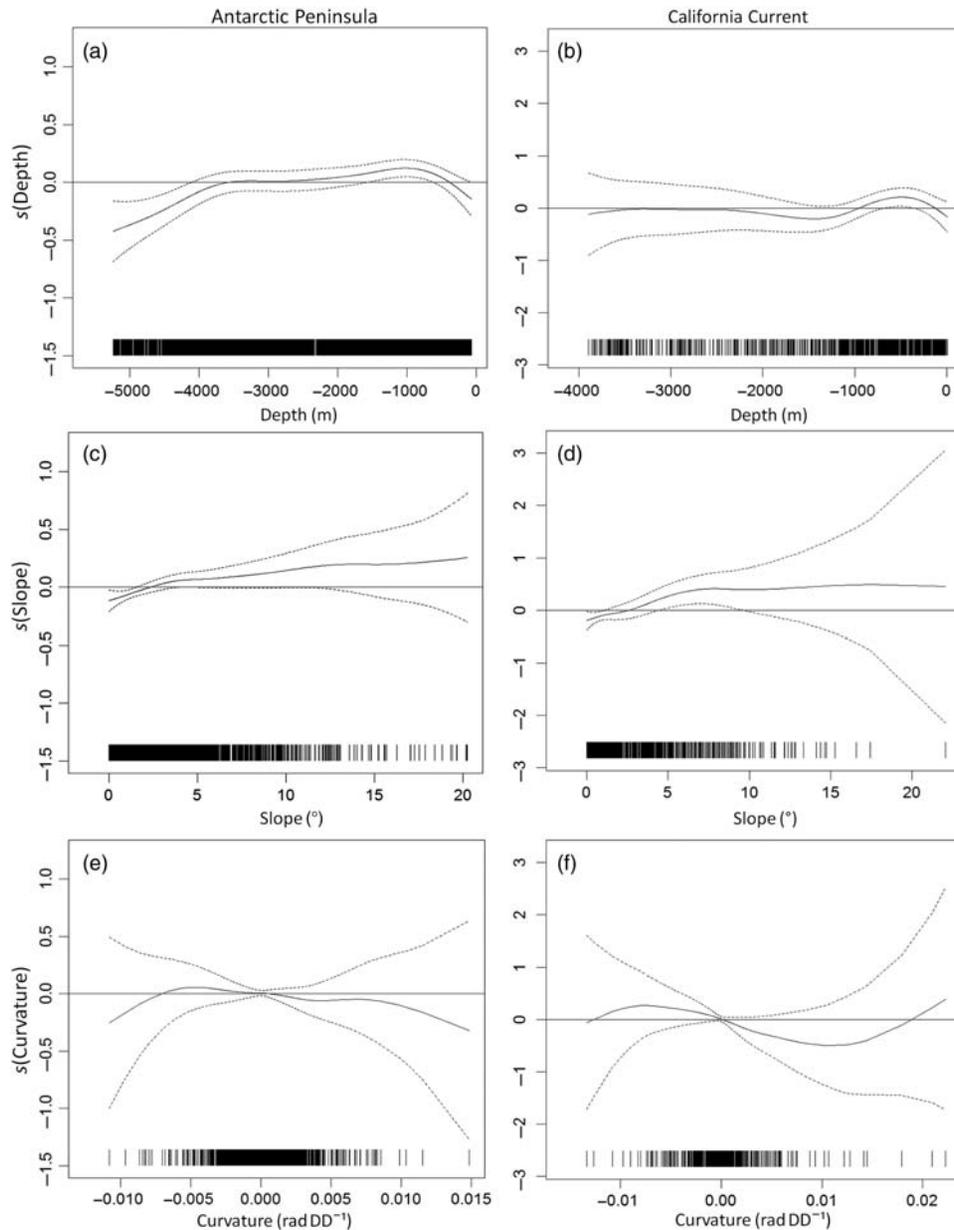


Figure 3. Fitted GAM results showing the relationship between predictor variables (x -axis; a and b) water depth, (c and d) slope, and (e and f) curvature on changes in krill abundance (response variable; y -axis) and spatial distribution near the Antarctic Peninsula (left) and in the California Current (right). Data availability is indicated on the x -axis, and dashed lines are the 95% confidence intervals.

ecosystems. The GAMs indicate that the effect of EKE on krill is indeed a significant factor in both regions (Table 1, Figure 4c and d). The EKE effect is positive at intermediate levels of EKE, indicating that krill spatial distribution is probably related to enhanced geostrophic flow along the shelf break and in the wake of islands (Figures 1 and 4c and d). Krill may avoid regions of higher EKE to remain in favourable habitat for growth and development. In the APE, there were relatively fewer dense concentrations of krill north of the ACC, because krill caught in that current are most likely advected out of the APE and into the Scotia Sea. Likewise off the California coast, the largest concentrations of krill are in areas between upwelling cells in waters generally classified as retentive (e.g. the Gulf of the Farallones, Monterey Bay; Santora et al., 2011b).

Surface phytoplankton concentration in the California coastal upwelling system is much greater than in the Antarctic Peninsula study area (Figure 4e and f). The GAMs indicate that the effect of Chl a on krill is a significant factor in both ecosystems (Table 1). Interestingly, off California the effect of Chl a on krill abundance rises steeply at low Chl a levels, but plateaus with increasing Chl a concentration (Figure 4e and f). This indicates the high spatial overlap between krill and surface phytoplankton along the shelf break in this highly productive upwelling ecosystem. In the much lower productivity waters off the Antarctic Peninsula, the GAM shows that the effect of Chl a on krill is non-linear (Figure 4e and f); the effect is positive at low levels of Chl a , but also shows a gradual positive increase with increasing levels of Chl a , possibly indicating that overlap between krill and Chl a is

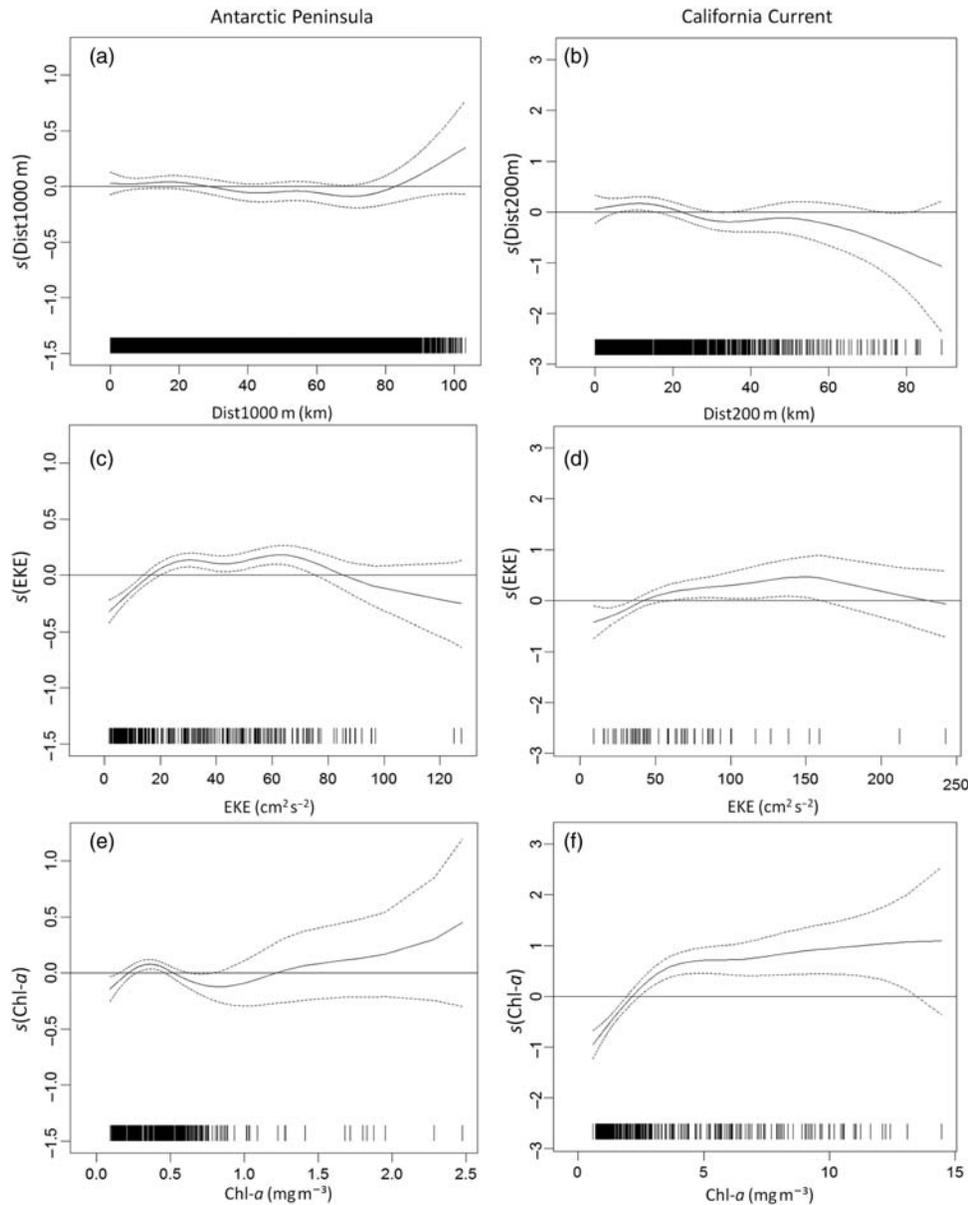


Figure 4. Fitted GAM results showing the relationship between predictor variables (x-axis; a and b) distance to the shelf break, 1000 and 200 m isobaths, (c and d) EKE, and (e and f) Chl *a* on changes in krill abundance (response variable; y-axis) and spatial distribution near the Antarctic Peninsula (left) and in the California Current (right). Data availability is indicated on the x-axis, and dashed lines are the 95% confidence intervals.

more patchy there than off California. However, these results should be taken with caution because the surface conditions may not reflect Chl *a* concentrations at the daytime depth where krill tend to concentrate. Additionally, estimates of surface Chl *a* concentration may be affected by cloud cover in both regions.

Model selection criteria (AIC) revealed which suite of spatial covariates was important for understanding krill spatial distribution and abundance patterns in both ecosystems (Table 1). In the Antarctic, the best model (i.e. lowest AIC) contained water depth, slope, distance to the shelf break, EKE, Chl *a*, and spatial position. In the California Current, the best model selected contained water depth, distance to the shelf break, EKE, Chl *a*, and spatial position. The models selected in both marine ecosystems

were similar, except slope, which was not included in the California Current.

Discussion

Krill is important to the structure of marine foodwebs in both the Antarctic Peninsula and California Current marine ecosystems. Following Megrey *et al.* (2009) and Murawski *et al.* (2010), we undertook a comparative analysis of krill by focusing on mesoscale structuring to determine if rules governing krill spatial distributions and habitat associations could be established. The motivation for this work is the need to quantify the spatial structure of lower trophic level species to provide a spatial context for modelling (Batchelder *et al.*, 2002; Cury *et al.*, 2008; Smith *et al.*, 2011;

Santora *et al.*, 2011b). Furthermore, the work was motivated by concerns about the possible decline in krill populations in various sectors of the Southern Ocean (Atkinson *et al.*, 2004) and the consequent impacts on predators. Although there were some differences in spatial organization and patchiness, including larger patch size in the APE, krill in both systems were related to bathymetric and oceanographic features.

Similarities and differences between the APE and the CCE

A novel approach was used in comparing krill distribution across the two ecosystems. Multiple years of acoustic surveys were combined to map krill hot spots, defined as grid cells of relative abundance, and to measure patchiness. These maps provide a long-term perspective and, although undoubtedly somewhat variable between years, should provide a robust representation of krill spatial organization in these ecosystems. We also integrated acoustically derived indices of distribution and abundance with remotely sensed hydrographic variables to permit the implementation of cross-system habitat models. Habitat modelling suggested that apparent krill hot spots in both ecosystems were the result of oceanographic and bathymetric features, possibly coupled with favourable feeding conditions. The results of this study may be summarized as follows: (i) areas of dense krill aggregations, i.e. hot spots, are present in both ecosystems, (ii) geospatial variability of the shelf break and other complex bathymetric characteristics provide habitat presumably essential for feeding and reproduction, (iii) moderate levels of EKE may facilitate krill concentrations and lessen the likelihood of offshore advection away from favourable shelf break/slope habitats, and (iv) variable responses to surface Chl *a* concentration suggest that real-time Chl *a* conditions may not be useful as a global predictor of important krill habitat.

Although the spatial organization of krill in the APE and the CCE revealed many similarities, there were also some notable contrasts. Overall, the shelf break area in both systems contained the largest krill concentrations. However, krill aggregations (patches) in the APE were larger, i.e. they displayed positive correlations on larger spatial scales than those in the CCE. This could be attributed to the larger study scale and/or transect orientation in the APE (Figure 1), but it may also be due to basic differences in bathymetric and oceanographic properties in this system. Compared with the CCE, the APE study area shows additional oceanographic complexity, including greater current flows. In the study region, there is the northeast-flowing ACC offshore of the South Shetland Islands, a clockwise flow within Bransfield Strait resulting from mixing of waters from the Weddell Sea to the east and Bellingshausen Sea from the southeast and north, and anticlockwise flow around the South Shetland Island shelf break (Figure 1). Frontal features here result from topographically related interactions of these disparate waters. In contrast, the oceanography within the CCE study area, comprising the California Current and Davidson countercurrent, is somewhat more homogeneous; there, convergence of fronts throughout the shelf break environment is attributable to localized coastal upwelling plumes (Checkley and Barth, 2009).

Mesoscale structuring

A mesoscale eddy is a circular movement of water formed alongside a main current with a spatial scale of 10–100 km and a temporal scale of 10–30 d (Cury *et al.*, 2008). We found krill in both systems to be concentrated within waters characterized by

moderate EKE levels. Therefore, the strong pelagic and coastal currents in both systems may concentrate krill in particular locations with optimal EKEs. In the APE, convergence zones around the South Shetland Islands support recirculation zones. Notable among these are eddies along the northern shelf break of the South Shetland and Elephant Islands, northeast of Joinville Island and Tower Island, respectively, in southeast and southwest Bransfield Strait, and northeast of Elephant and Clarence Islands; these are regions with relatively sluggish currents and elevated primary production (Ichii *et al.*, 1998; Thompson *et al.*, 2009). In particular, the mesoscale eddy along the northern island shelf break next to the slope region where krill spawn forms an essential part of the coupled advective–retentive circulation system critical for maintaining local populations (Hofmann *et al.*, 2004; Nicol, 2006). In the CCE, wind-driven upwelling along the coast promotes the formation of eddies along the shelf break and of retention zones in the lee of coastal promontories (Checkley and Barth, 2009). The distribution of krill hot spots off California are associated with low levels of Ekman transport, indicating that krill tend to concentrate in areas characterized as retentive (Santora *et al.*, 2011b). In both systems, it is clear that mesoscale eddies influence biological properties, and the results of this study show such eddies to be important for understanding the mesoscale variability of krill. If mesoscale eddies are locations of elevated primary productivity, then it would be advantageous for krill to exploit them for feeding, unless they risk advection from source areas as a consequence of increased transport.

Interestingly, the relationship between krill and surface Chl *a* concentration varied between the two systems. Although the GAMs indicated that Chl *a* is positively related to krill abundance, the functional relationships showed different patterns in the two systems. In the CCE, the relationship increased sharply and levelled out with increasing Chl *a* concentration, perhaps following a classical type II functional response curve. In the APE, in contrast, krill displayed positive association with lower levels of Chl *a* and marked increases at relatively few high levels of Chl *a*. This may be because the scale and magnitude of Chl *a* is far greater in the CCE than in the APE survey area. In addition, the greater scale of Chl *a* in the CCE may have produced a saturation effect between krill and Chl *a*. Krill occupy a variety of depths (through vertical migration) and generally concentrate within the pycnocline to feed (Atkinson *et al.*, 2008). Additionally, in the Antarctic, krill feed on ice algae and the extent of sea ice in winter and the timing of break-up in spring is critical for krill development (Nicol, 2006). Therefore, surface measurements of Chl *a* may not be appropriate for modelling the horizontal spatial distribution of krill. More work is required to disentangle the link between krill and phytoplankton spatial distribution, which may be improved using *in situ* data collected at different depths during surveys. Lastly, this study focused solely on the horizontal distribution of krill, and more research is needed to examine how the mesoscale structure of krill varies according to vertical distribution.

Krill life history: the missing link

Although the focus was mainly on krill relationships with the physical environment, krill behaviour, age, and reproduction are important factors affecting their distributions (Brinton, 1976; Siegel, 2000). Both *E. superba* and *E. pacifica* have extremely broad ranges; the distribution of *E. superba* is circumpolar, whereas that of *E. pacifica* extends across the north Pacific, so

the study regions addressed here represent just a small portion of their respective ranges (Brinton, 1962; Atkinson *et al.*, 2008). Both species are subject to advective processes that potentially remove them from optimal coastal habitats, and they have developed physiological and behavioural modifications in relation to ambient ecosystem processes to maximize retention within these habitats. Common behavioural traits are diel and ontogenetic vertical migrations that permit local retention through differential transport of surface waters and deeper layers (e.g. countercurrents) and relaxation following upwelling events. Short-lived *E. pacifica* adjust to enhanced localized primary production through a rapid spawning response to relaxation events that allow them to reproduce throughout the year (Feinberg and Peterson, 2003; Shaw *et al.*, 2010). Reproduction by *E. superba* is seasonally constrained by sea-ice cycles and long dark winters; reproductive activity and output results from feeding conditions prevailing across spring months of sea-ice retreat and water column stratification; the consequences of years with poor recruitment success are buffered by the multiyear reproductive life of the species. Despite their radically different life histories, *E. superba* and *E. pacifica* have similar population responses to physical processes driven by *El Niño*–Southern Oscillation forcing, with strong reproductive output and recruitment success associated with *La Niña* conditions (Brinton and Townsend, 2003; Loeb *et al.*, 2009, 2010).

Conclusions: krill for thought

California Current krill are important prey of wild salmon (MacFarlane and Norton, 2002), whereas harvested Antarctic krill are fed to farm-raised salmon (Naylor *et al.*, 2009). The meso-scale spatial structuring of krill described in this paper is important to the management perspective for both ecosystems. In the Southern Ocean, the Commission for the Conservation of AMLR (CCAMLR) uses an ecosystem approach to manage quotas for the krill fishery within small-scale management units, and harvest control rules are set to prevent krill from becoming depleted near land-based predator breeding sites (e.g. seal rookeries and penguin colonies; Croll and Tershy, 1998; Croxall *et al.*, 1999; Constable *et al.*, 2000; Hewitt *et al.*, 2004; Hill *et al.*, 2009; Trivelpiece *et al.*, 2011). Importantly, there is no reason to believe that krill fishing is evenly distributed within a designated fishing ground. Krill predators do not forage in a uniform manner either. In both cases, the “harvest” is most often concentrated in time and space within the most predictable locations for exploiting krill, whether the predators are seabirds, whales, or humans.

In contrast, in the CCE, the Pacific Fishery Management Council (PFMC) implemented a ban on the development of krill fisheries (PFMC, 2008). This 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 administered by the PFMC (coastal pelagic species, groundfish, salmon, and highly migratory species). In addition to commercially important species, the plan also recognized that krill are critical components of the diets of many seabirds and marine mammals, including several threatened or vulnerable species. The PFMC 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. In particular, the management plan recognized that the location, size, and

spacing of krill hot spots would be valuable habitat information for future consideration of spatial management measures aimed at offering additional protection for krill-dependent predators.

The mesoscale patterns and habitat associations of krill quantified in this study are useful reference points for resolving spatially explicit fisheries impacts and parametrizing ecosystem models for both the CCE and the APE in future. The spatial “climatologies” of krill distribution are also relevant to marine spatial planning and the protection of ecosystem functions (Cury *et al.*, 2008; Smith *et al.*, 2011). Ecosystem models that combine regional ocean models with krill life-cycle models have been implemented to understand the population dynamics of krill in both the APE and the CCE (Hofmann *et al.*, 2004; Dorman *et al.*, 2011). Although ecosystem models in both systems have focused on understanding the role of advection and retention on krill survival and reproduction, the baseline spatial distributions of krill developed in this study, using multiple years of surveys along with remote sensing of oceanography, are needed to implement spatially explicit ecosystem models to predict krill and krill predator–prey dynamics.

Supplementary material

Supplementary material is available at the ICES/JMS online version of this manuscript in the form of a table reflecting on comparative aspects of krill within a polar and a temperate marine ecosystem.

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References

- Atkinson, A., Siegel, V., Pakhomov, E. A., and Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, 432: 100–103.
- Atkinson, A., Siegel, V., Pakhomov, E. A., Rothery, P., Loeb, V., Ross, R. M., Quetin, L. B., *et al.* 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series*, 362: 1–23.
- Bakun, A., and 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., *et al.* 2002. The GLOBEC Northeast Pacific California Current System Program. *Oceanography*, 15: 36–47.
- Brinton, E. 1962. The distribution of Pacific euphausiids. *Bulletin of the Scripps Institute of Oceanography*, 8: 51–270.
- Brinton, E. 1976. Population biology of *Euphausia pacifica* off southern California. *Fishery Bulletin US*, 74: 733–762.
- Brinton, E., and Townsend, A. 2003. Decadal variability in abundances of the dominant euphausiid species in the southern sectors of the California Current. *Deep Sea Research II*, 50: 2449–2472.
- Checkley, D. M., and Barth, J. A. 2009. Patterns and processes in the California Current. *Progress in Oceanography*, 83: 49–64.
- Ciannelli, L., Fauchald, P., Chan, K. S., Agostini, V. N., and Dingsøer, G. E. 2008. Spatial fisheries ecology: recent progress and future prospects. *Journal of Marine Systems*, 71: 223–236.

- Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I., and Miller, D. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES Journal of Marine Science*, 57: 778–791.
- Croll, D. A., and Tershy, B. R. 1998. Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. *Polar Biology*, 19: 365–374.
- Croxall, J. P., Reid, K., and Prince, P. A. 1999. Diet, provisioning and productivity of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, 177: 115–131.
- Cury, P. M., Shin, Y. J., Planque, B., Durant, J. M. N., Fromentin, J.-M., Kramer-Schadt, S., Stenseth, N. Ch., et al. 2008. Ecosystem oceanography for global change in fisheries. *Trends in Ecology and Evolution*, 23: 338–346.
- Dorman, J. G., Powell, T. M., Sydeman, W. J., and 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.
- Feinberg, L. R., and Peterson, W. T. 2003. Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. *Progress in Oceanography*, 57: 262–379.
- Field, J. C., Francis, R. C., and 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.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., et al. 2008. A global map of human impact on marine ecosystems. *Science*, 319: 948–952.
- Hewitt, J. E., Thrush, S. F., Dayton, P. K., and Bonsdorff, E. 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *The American Naturalist*, 169: 398–408.
- Hewitt, R. P., Demer, D. A., and Emery, J. H. 2003. An 8-year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Islands during the austral summers of 1991/1992 through 2001/2002. *Aquatic Living Resources*, 16: 205–213.
- Hewitt, R. P., Watters, G., Trathan, P. N., Croxall, J. P., Goebel, M. E., Ramm, D., Reid, K., et al. 2004. Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. *CCAMLR Science*, 11: 81–97.
- Hill, S. L., Trathan, P. N., and Agnew, D. J. 2009. The risk to fishery performance associated with spatially resolved management of Antarctic krill (*Euphausia superba*) harvesting. *ICES Journal of Marine Science*, 66: 2148–2154.
- Hofmann, E. E., Haskel, A. G. E., Klinck, J. M., and Lascara, C. M. 2004. Lagrangian modeling studies of Antarctic krill (*Euphausia superba*) swarm formation. *ICES Journal of Marine Science*, 61: 617–631.
- Hofmann, E. E., and Murphy, E. J. 2004. Advection, krill, and Antarctic marine ecosystems. *Antarctic Science*, 16: 487–499.
- Hunt, G. L., and Megrey, B. A. 2005. Comparison of the biophysical and trophic characteristics of the Bering and Barents Seas. *ICES Journal of Marine Science*, 62: 1245–1255.
- Ichii, T., Katayama, K., Obitsu, N., Ishii, H., and Naganobu, M. 1998. Occurrence of Antarctic krill (*Euphausia superba*) concentrations in the vicinity of the South Shetland Islands: relationship to environmental parameters. *Deep Sea Research I*, 45: 1235–1262.
- Legendre, P., and Legendre, L. 1998. *Numerical Ecology*. Elsevier, Amsterdam. 853 pp.
- Lenn, Y.-D., Chereskin, T. K., Sprintall, J., and Firing, E. 2007. Mean jets, mesoscale variability and eddy momentum fluxes in the surface layer of the Antarctic circumpolar current in Drake Passage. *Journal of Marine Research*, 65: 27–58.
- Levin, P. S., Fogarty, M. J., Murawski, S. A., and Fluharty, D. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology*, 7: e1000014. doi:10.100010.1001371/journal.pbio.1000014.
- Loeb, V. J., Hofmann, E. E., Klinck, J. M., and Holm-Hansen, O. 2010. Hydrographic control of the marine ecosystem in the South Shetland–Elephant Island and Bransfield Strait region. *Deep Sea Research II*, 57: 519–542.
- Loeb, V. J., Hofmann, E. E., Klinck, J. M., Holm-Hansen, O., and White, W. B. 2009. ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. *Antarctic Science*, 21: 135–148.
- Lu, B., Mackas, D. L., and Moore, D. F. 2003. Cross-shore separation of adult and juvenile euphausiids in a shelf-break alongshore current. *Progress in Oceanography*, 57: 381–404.
- MacFarlane, R. B., and Norton, E. C. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. *Fishery Bulletin US*, 100: 244–257.
- Megrey, B. A., Link, J. S., Hunt, G. L., and Moksness, E. 2009. Comparative marine ecosystem analysis: applications, opportunities, and lessons learned. *Progress in Oceanography*, 81: 2–9.
- Murawski, S. A., Steele, J. H., Taylor, P., Fogarty, M. J., Sissenwine, M. P., Ford, M., and Suchman, C. 2010. Why compare marine ecosystems? *ICES Journal of Marine Science*, 67: 1–9.
- Naylor, R. L., Hardy, R. W., Bureau, D. P., Chiu, A., Elliot, M., Farrell, A. P., Forster, I., et al. 2009. Feeding aquaculture in an era of finite resources. *Proceedings of the National Academy of Sciences of the USA*, 106: 15103–15110.
- Nicol, S. 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *BioScience*, 56: 111–120.
- Orsi, A. H., Whitworth, T., and Nowlin, W. D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Research I*, 42: 641–673.
- PFMC (Pacific Fishery Management Council). 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/wpcontent/uploads/CPS_Am12_Krill_DraftEA.pdf.
- Pichegru, L., Gremillet, D., Crawford, R. J. M., and Ryan, P. G. 2010. Marine no-take zone rapidly benefits threatened penguin. *Biology Letters*, 6: 498–501.
- R Development Core Team. 2009. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <http://www.r-project.org/>.
- Reiss, C. S., Cossio, A. M., Loeb, V., and Demer, D. A. 2008. Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. *ICES Journal of Marine Science*, 65: 497–508.
- Sakuma, K. M., Ralston, S., and 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. *CalCOFI Reports*, 47: 127–139.
- Santora, J. A., Ralston, S., and Sydeman, W. J. 2011a. Spatial organization of krill and seabirds in the central California Current. *ICES Journal of Marine Science*, 68: 1391–1402.
- Santora, J. A., and Reiss, C. S. 2011. Geospatial variability of krill and top predators within an Antarctic submarine canyon system. *Marine Biology*, 158: 2527–2540.
- Santora, J. A., Reiss, C. S., Cossio, A. C., and Veit, R. R. 2009. Interannual spatial variability of Antarctic krill (*Euphausia superba*) influences seabird foraging behavior near Elephant Island, Antarctica. *Fisheries Oceanography*, 18: 20–35.
- Santora, J. A., Reiss, C. S., Loeb, V. J., and Veit, R. R. 2010. Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Marine Ecology Progress Series*, 405: 255–269.

- Santora, J. A., Sydeman, W. J., Schroeder, I. D., Wells, B. K., and Field, J. C. 2011b. Mesoscale structure and oceanographic determinants of krill hotspots in the California Current: implications for trophic transfer and conservation. *Progress in Oceanography*, 91: 397–409.
- Shaw, C. T., Peterson, W. T., and 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.
- Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., *et al.* 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science*, 26: 1147–1150.
- Strub, P. T., and James, C. 2002. Altimeter-derived surface circulation in the large-scale NE Pacific Gyres. 1. Seasonal variability. *Progress in Oceanography*, 53: 153–183.
- Sydeman, W. J., Brodeur, R. D., Grimes, C. B., Bychkov, A. S., and McKinnell, S. 2006. Marine habitat “hotspots” and their use by migratory species and top predators in the North Pacific Ocean. Introduction. *Deep Sea Research II*, 53: 247–249.
- Thompson, A. F., Heywood, K. J., Thorpe, S. E., Renner, A. H. H., and Trasvina, A. 2009. Surface circulation at the tip of the Antarctic Peninsula from drifters. *Journal of Physical Oceanography*, 39: 3–26.
- Trivelpiece, W. Z. T., Hinke, J., Miller, A. K., Reiss, C. S., Trivelpiece, S. G., and Watters, G. M. 2011. Variability in krill biomass links harvesting and climate warming to penguin populations in Antarctica. *Proceedings of the National Academy of Sciences of the USA*, doi:10.1073/pnas.1016560108.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York. 574 pp.

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