

## Triple check: Observations verify structural realism of an ocean ecosystem model

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[1] Improvements in fisheries and ecosystem management could be made if the prediction of key zooplankton, such as krill, were possible using ocean ecosystem models. To examine structural realism, hence the validity of a coupled physical-biogeochemical model, we compared measured spatiotemporal dynamics of krill and seabird abundance off California to hindcasted mesozooplankton derived from an independently designed model. Observed krill and modeled mesozooplankton (*Z2*) displayed latitudinal coherence but distinct longitudinal offsets, possibly related to unrealistic bathymetry in the model. Temporally, *Z2*, *Thysanoessa spinifera* (a neritic krill species) and seabird density and reproductive performance were well correlated, indicating that quantitative prediction regarding marine predators in upwelling ecosystems is within reach. Despite its basin-scale framework, the ROMS-CoSiNE model captures zooplankton and top predator dynamics regionally in the central California region, suggesting its utility for management of marine ecosystems and highlighting rapid advances that can be made through collaboration between empirical scientists and ecosystem modelers. **Citation:** Santora, J. A., W. J. Sydeman, M. Messié, F. Chai, Y. Chao, S. A. Thompson, B. K. Wells, and F. P. Chavez (2013), Triple check: Observations verify structural realism of an ocean ecosystem model, *Geophys. Res. Lett.*, 40, doi:10.1002/grl.50312.

### 1. Introduction

[2] Ecosystem oceanography forms the scientific backbone for ecosystem-based fisheries and ocean management [Cury *et al.*, 2008]. Ocean ecosystem models can play a substantial role in this developing field but require verification of structural realism before they will be accepted and widely

implemented in marine policy and management scenarios. To date, mass-balance models of food web dynamics have led the way in numerical simulations for fisheries impacts on marine ecosystems [Smith *et al.*, 2011]. Spatially explicit numerical models provide a framework for investigating mechanisms of biophysical interactions and sensitivities to climate variability and anthropogenic forces [Cury *et al.*, 2008]. However, these models often lack the structural complexity needed to adequately reproduce ecosystem dynamics, especially for mid and upper trophic levels [Arhonditsis and Brett, 2004]. Thus, there is a need to validate models by verifying contrasting modeled indicators with field-based observations. According to Cury *et al.* [2008], structural realism (*i.e.*, validation) of ocean ecosystem models is accomplished by comparing multiple patterns of association between model outputs and real-life observations. A model is likely to be structurally realistic when it reproduces more than one pattern of variability in space or time or both. Furthermore, a strong indicator of structural realism is whether a model is validated by patterns that are hindcasted by the model but not used (or even known) while developing the model.

[3] In pelagic food webs, zooplanktons are critical to biogeochemical cycling and energy transfer between primary producers (e.g., phytoplankton) and higher trophic levels. Zooplankton can exert top-down control on phytoplankton or bottom-up control on forage fish and, as such, may be used in a predictive context for management [Beaugrand *et al.*, 2003]. Numerical simulations of ocean ecosystems often include functional groups for zooplankton, but few studies have compared model output with observations of zooplankton in the wild [Arhonditsis and Brett, 2004]. Substantial effort has been devoted to validate ocean ecosystem models against physical oceanographic and phytoplankton observations, but there have been few studies that consider if modeled zooplankton capture observed temporal and spatial dynamics. We compare output from a coupled physical-biogeochemical model [Chai *et al.*, 2002; Polovina *et al.*, 2008] to measured zooplankton off central California. The goal of this study is to determine if empirical zooplankton data corresponds to output independently derived from a model. Specifically, we assess the model's ability to capture (1) mesoscale spatial organization, (2) temporal patterns of abundance, and (3) linkages to marine top predators, exemplified by seabirds. We focus on model output as an indicator of krill (Euphausiidae) because krill are globally important in epipelagic food webs, and the data for this taxa exist for this comparison. We used data on the spatiotemporal variation in krill abundance derived from acoustic and trawl surveys to assess the structural realism of the ocean ecosystem model. This study is significant because, while models are being

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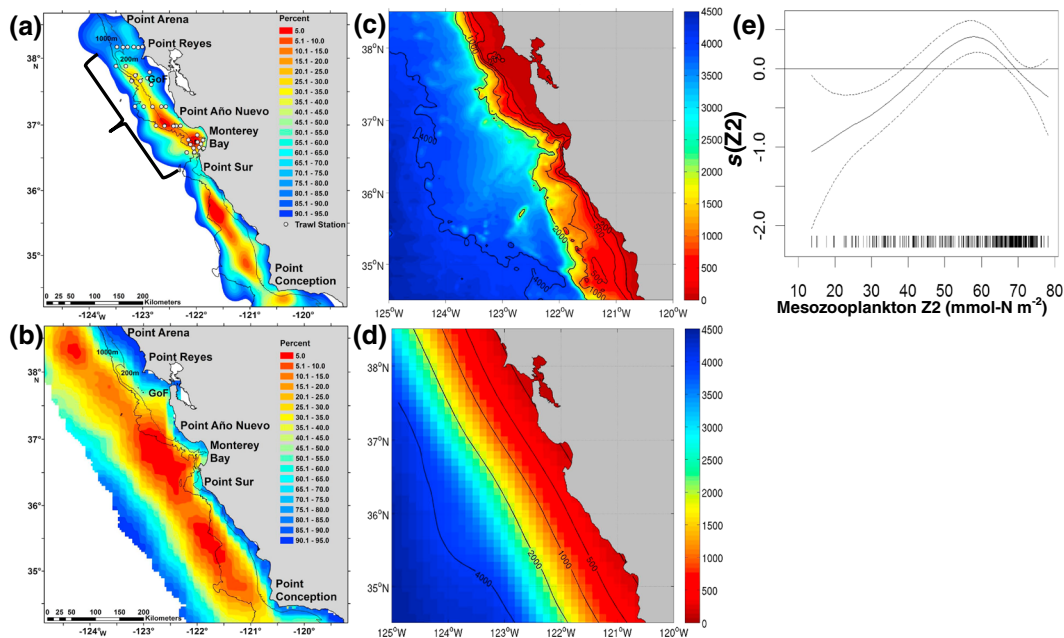
advanced for spatially explicit ecosystem-based management of pelagic systems [Plagányi, 2007], the ability of these models to realistically represent biological structures and processes within complex ecosystems has yet to be established.

## 2. Methods

[4] Modeled zooplankton originates from a coupled physical-biogeochemical simulation (years 1991–2010). The Regional Ocean Modeling System (ROMS) for the domain 45°S–65°N, 99°E–70°W [Wang and Chao, 2004] with a 1/8 degree horizontal resolution and 30 vertical layers is coupled with the biogeochemical model of Chai *et al.*, [2002]. Additional details of the ROMS are provided in Supplemental Material 1. Bathymetry is strongly smoothed in the model, resulting in the 500 and 1000 m isobaths being displaced 35–50 km further offshore than in reality (Figure 1). The biogeochemical ecosystem model is “CoSiNE” (Carbon, Si(OH)<sub>4</sub> and Nitrogen Ecosystem) and includes nutrient components of silicate, nitrate and ammonium, two phytoplankton groups, two zooplankton grazers, and two detrital pools [Chai *et al.*, 2002] (Supplemental Material 1). The coupled ROMS-CoSiNE configuration has been validated using remotely sensed observations of ocean conditions [Polovina *et al.*, 2008] but has not previously been compared to field-sampled zooplankton data. Here we focus on the model’s mesozooplankton component, denoted as “Z2” (mmol-N m<sup>-2</sup>). Z2 represents all mesozooplankton that graze on diatoms, small zooplankton, and detritus (Supplemental Material 1). The Z2 component includes krill, which comprise a major part (25%) of the California Current zooplankton assemblage by biomass expressed as mg C m<sup>-2</sup>

[Lavaniegos and Ohman, 2007]. Because this model is not individual based or state dependent, there are no aspects of zooplankton behavior or memory to consider. Z2 growth (*i.e.*, accumulation of biomass) is determined by a balance of grazing (G), detritus production ( $\gamma$  = assimilation efficiency), excretion of ammonium ( $e$  = excretion rate), and loss term to higher trophic levels ( $\mu$  = specific mortality rate):  $d(Z2) / dt = G - (1 - \gamma) * G - e * Z2 - \mu * Z2^2$ . This equation is kept in check (density-dependent mortality) by the closure term  $\mu * Z2^2$ , which is a function of Z2 itself since there are no Z2 predators in the model.

[5] Observations of krill using acoustic-trawl methods are made by NOAA-NMFS-SWFSC and partners during May–June each year (Supplemental Material 2). Over 28,000 nmi of acoustic surveys are used to map krill distribution [Santora *et al.*, 2011a, 2011b]. The acoustic krill index is based on the Nautical Area Scattering Coefficient (NASC nautical mile<sup>-1</sup>), integrated to 300m water depth. NASC is averaged over the region 38.5°N–36°N for time series analysis. We also summarized data on the relative abundance [(CPUE) = (log) number individual haul<sup>-1</sup> [Wells *et al.*, 2012] of *Euphausia pacifica* and *Thysanoessa spinifera* obtained from mid-water trawls at 35 sampling stations over 8 years, 2002–2009. Krill catches are log-transformed due to high numbers of krill caught. *E. pacifica* is the numerically dominant krill species occurring along the continental shelf-break and slope habitats; *T. spinifera*, a neritic krill species, is distributed within the Gulf of the Farallones [Brinton, 1962]. Additionally, seabird abundance at sea was determined during each NMFS survey (density; birds km<sup>-2</sup>) [Santora *et al.*, 2011a]. Daily seabird densities were averaged to produce survey-wide estimates for each year. Total bird density (all



**Figure 1.** The California Current area showing utilization distributions of (a) acoustically determined krill (NASC nmi<sup>-1</sup>) and (b) modeled mesozooplankton (Z2; mmol-N m<sup>-2</sup>), (c) realistic bathymetry derived from ETOPO-1 and (d) the model’s coarse bathymetry. For interpreting utilization distributions, the outer 95% contour depicts the extent; lower percentages represent higher values. (e) GAM result showing relationship ( $\pm 95\%$  confidence intervals) between krill and Z2. The y-axis indicates a smoothed function for the relationship between krill and Z2; the y-axis is specific to the acoustic krill index. The black vertical bars below curve depict the distribution of grid points compared. The bracket in Figure 1a indicates the region used for temporal comparison between net-sampled krill and Z2.

species) is used, 80% of which is composed of four species: common murre (*Uria aalge*), Cassin’s auklet (*Ptychoramphus aleuticus*), sooty shearwater (*Puffinus griseus*), and pink-footed shearwater (*P. creatopus*). Data on seabird reproductive performance (number chicks/pair) and phenology (average egg-laying date for auklets and murres) were recorded at Southeast Farallon Island (March–July), details in *Schroeder et al.* [2009]. Seabird data from 2000–2007 (density, breeding success, and timing of breeding) were combined using principal component analysis (PCA) to construct an integrated, multivariate index of predator responses.

[6] We “triple check” the structural realism of the ROMS-CoSiNE model by assessing the spatial and temporal coherence between field-sampled krill (NASC and CPUE), seabirds, and Z2 distributions. Spatial comparisons between modeled and observed zooplankton distributions (Figures 1a and 1b) utilize all available empirical data and modeled output (2000–2009). Both data sets were standardized; this was done by averaging acoustically derived krill abundance and Z2 density over all years (2000–2009) according to grid cells (100 km<sup>2</sup> in size; n = 1037 cells) and subtracting the grand mean (of all cells) to produce spatial anomalies. We interpolated both Z2 and observed krill (NASC) using kernel density smoothing and express these as percent utilization

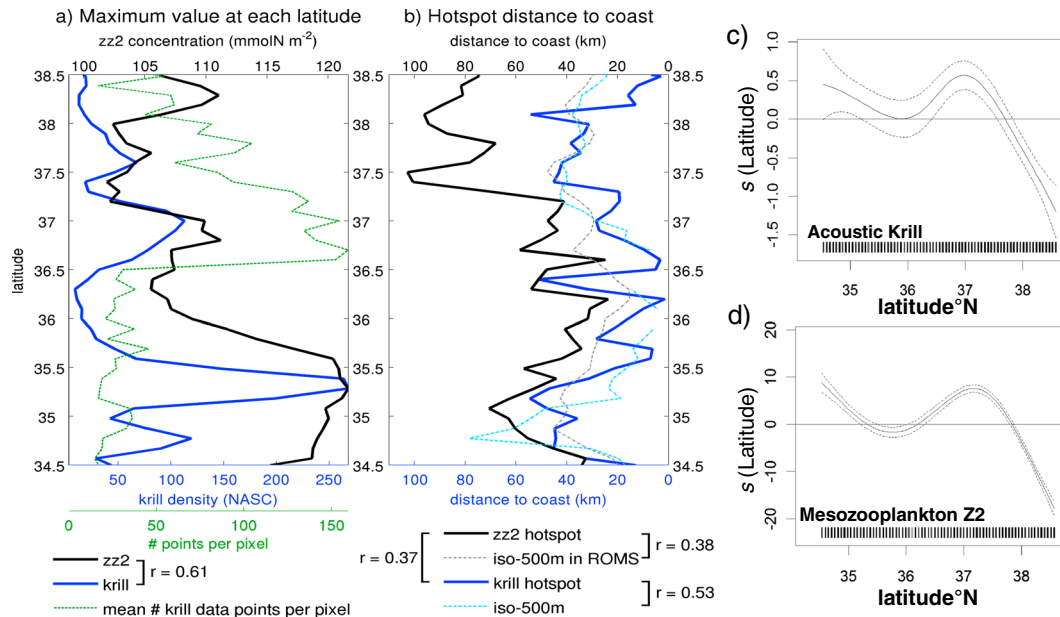
distributions [*Santora et al.*, 2011b]. Geospatial covariates were related to cell-specific anomalies and include latitude, water depth and bathymetric slope, distance to shelf break (200 m isobath), and near-surface Chl-*a* concentration. Bathymetric data (m; 0.016° resolution) were obtained from the ETOPO1 Global Relief Model. Near-surface Chl-*a* concentration data (Level 3; mg m<sup>-3</sup>; 0.08° resolution) was derived from SeaWiFS (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>).

[7] Generalized additive models (GAM) are used to investigate similarities and differences in geospatial associations between spatially averaged modeled and observed mesozooplankton [*Santora et al.*, 2012a]. We tested the spatial association between observed krill (NASC) and modeled zooplankton (Z2) adjusted by spatial coordinates using GAM<sub>1</sub>: Krill = *s*(Z2) + *te* (longitude, latitude), where *s*() and *te*() are smoothing functions (regression splines). We then compared “habitat associations” of observed krill and modeled zooplankton based on depth (m), slope (change in sea depth, degrees), distance to shelf-break (km; 200 m isobath “Dist.200m”), chlorophyll-*a* (mg m<sup>-3</sup>), and latitude as covariates. The relative effect of each geospatial covariate included in GAM<sub>2</sub> was plotted to visually inspect the functional form to determine whether krill and Z2 exhibit similar peaks or changes in relation to geospatial covariates (Supplemental Material 3).

**Table 1.** Results of Generalized Additive Models for Spatial Distribution Patterns of Acoustically Derived Krill and Modeled Mesozooplankton (Z2) in Relation to Geospatial Covariates

| Variable | Depth           | Slope           | Distance to 200m Isobath | Latitude        | Chl- <i>a</i> * |
|----------|-----------------|-----------------|--------------------------|-----------------|-----------------|
| Krill    | 7.53, (<0.001)  | 1.52, (0.06)    | 7.79, (<0.001)           | 3.55, (<0.01)   | 3.12, (<0.02)   |
| Z2       | 94.41, (<0.001) | 12.17, (<0.001) | 35.67, (<0.001)          | 83.34, (<0.001) | 51.68, (<0.001) |

Values are nonparametric F statistic and significance (p-value; bold is significant). \* Chl-*a* for krill is derived from SeaWiFS and Chl-*a* for Z2 is derived from ROMS-CoSiNE (see Supplemental Material 3 for details).



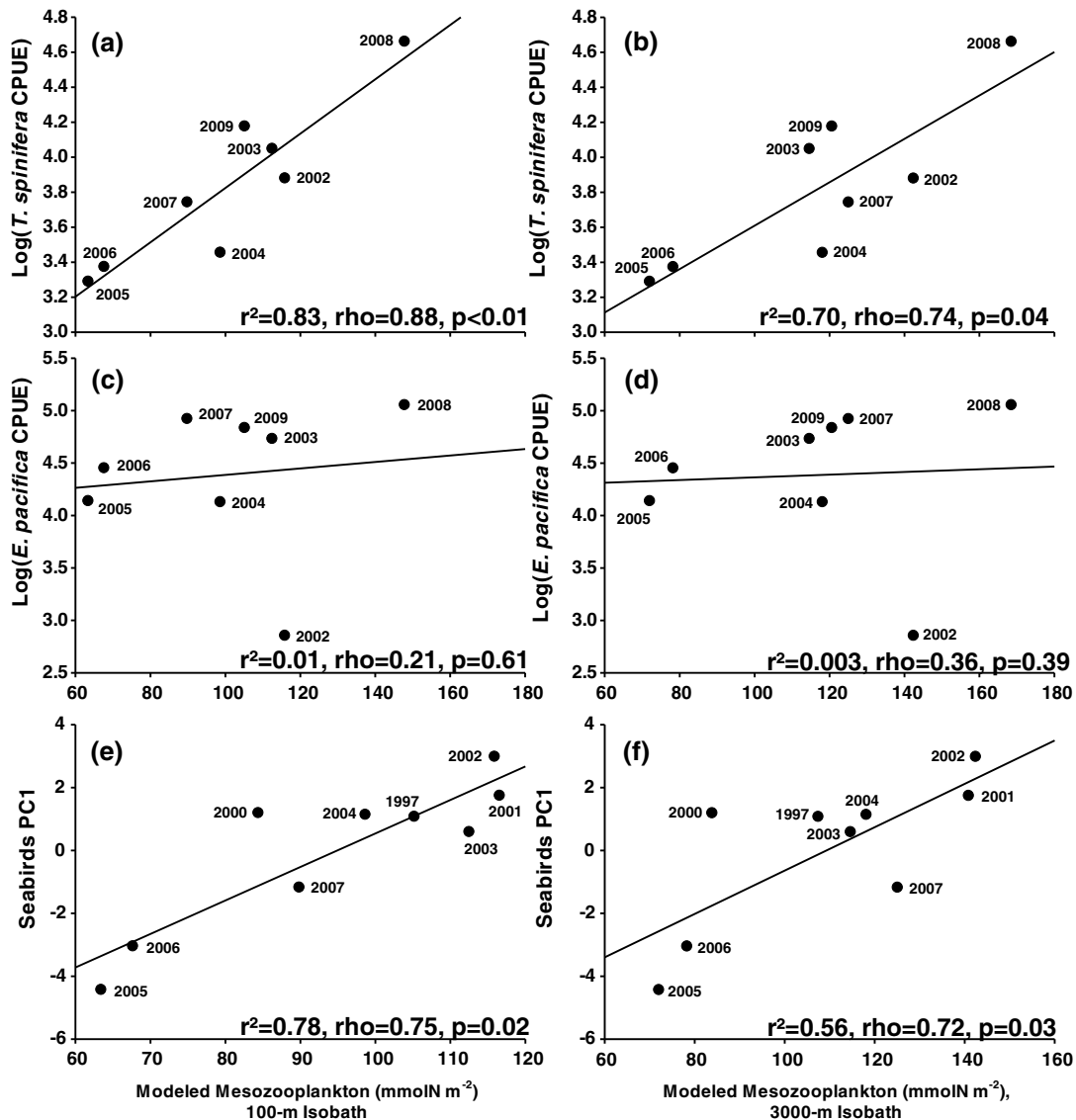
**Figure 2.** Comparison of intensity (a) and location (b) of krill hotspots as a function of latitude as obtained from NASC and mesozooplankton (Z2) maps averaged in May–June. (c, d) Results of GAM showing the relationship ( $\pm 95\%$  confidence intervals) for effect of latitude °N on distributions of (c) acoustic krill and (d) Z2. The black vertical bars below curves depict grid samples.

[8] Temporal comparisons between krill (CPUE of *E. pacifica* and *T. spinifera*) and Z2 were limited to the Gulf of the Farallones region during 2002–2009 (Figure 1). Two Z2 time series were constructed: one based on spatial integrations of data from the coast to the 100m isobath, and one from the coast to 3000 m isobaths, thereby encompassing the habitat of both krill species. Because Z2 is not parameterized to track the timing and life history dynamics of krill (e.g., physiology, feeding preferences), we assess temporal coherence in observed krill and Z2 distributions using the maximum monthly value of Z2 within each spatial integration per year (i.e., value corresponding to the annual peak concentration). We chose this value of Z2 because sampled krill distributions were obtained during a few weeks in May–June, and it is unrealistic to assume model performance with such temporal accuracy. During 2002–2009, the maximum monthly value of Z2 occurred on average during June with a median of July. Nonparametric rank correlation, linear regression, and Monte Carlo randomization tests were used to assess

interannual coherence between observed krill CPUE and modeled zooplankton concentration.

### 3. Results

[9] We found substantial spatial coherence between observed krill and modeled zooplankton distribution (Table 1; Figures 1 and 2). The spatial climatology of observed krill shows a patchy distribution along the shelf-break and apparent density concentrations (“hotspots” of abundance) downstream of key upwelling cells near Points Arena, Reyes, Año Nuevo, and Sur. Z2 exhibits a smooth distribution (Figure 1b), undoubtedly related to the bathymetry used. Krill and Z2 concentrations are similar with respect to latitude; both krill and modeled zooplankton display high concentrations within the Gulf of the Farallones and Monterey Bay and along the coast between Points Sur and Conception. In contrast, to the north,  $>37^{\circ}\text{N}$ , high concentrations of Z2 correspond to an area of low observed krill density (Figures 1 and 2). Despite these latitudinal similarities, Z2



**Figure 3.** Temporal comparison of (a, b) mean CPUE of *T. spinifera* and modeled mesozooplankton (Z2), (c, d) mean CPUE of *E. pacifica* and Z2, and (e, f) seabird principal component 1 and Z2.

clearly exhibits spatial offset with measured krill in longitude. This difference, as illustrated by GAM<sub>1</sub>, indicates that areas characterized by low abundance of observed krill and Z2 are in agreement, but this association dissipates from intermediate to high levels of krill and Z2 (Figure 1e). GAM<sub>2</sub> indicates that spatial covariates were significant predictors of acoustic krill and Z2 spatial distribution patterns (Table 1; Supplemental Material 3). GAM<sub>2</sub> indicates that observed krill and Z2 exhibit similar “habitat” associations, with two principal concentration regions, 34°N–35.5°N and 36.5°N–37.5°N (Table 1; Figures 2c and 2d). Furthermore, relationships between observed krill, Z2, and surface Chl-*a* are structurally similar (Supplemental Material 3). Relative to the model’s coarse bathymetry, the distribution of Z2 exhibits a peak in concentration centered on the 1000 m isobath (GAM<sub>3</sub>) indicating the importance of these isobaths in the model (Supplemental Material 3). Therefore, it appears that distribution of zooplankton resulting from this model (Z2) can realistically reflect those observed for krill within the shelf/coastal zone to the shelf-break but not further offshore.

[10] The mean CPUE of neritic *T. spinifera* and the annual monthly maximum of Z2 were significantly correlated with the strongest relationship occurring with Z2 integrated from the coast to 100 m isobath ( $\rho = 0.88$ ,  $p < 0.001$ ; Figures 3a and 3b). For the full time series (2002–2009), there was no correlation between mean CPUE of *E. pacifica* and Z2 (Figures 3c and 3d), but when year 2002 is omitted, *E. pacifica* is significantly correlated with Z2 integrated to the 3000 m isobath ( $r^2 = 0.53$ ,  $\rho = 0.79$ ,  $p < 0.05$ ). The acoustic krill index is not correlated with Z2 in either bathymetric division ( $\rho = 0.17$ ,  $p = 0.68$  and  $\rho = -0.05$ ,  $p = 0.90$ , respectively). However, seabird population responses (integrated reproductive success, phenology of egg laying, and at-sea density) were equally correlated with coastally integrated ( $\rho = 0.75$ ,  $p = 0.02$ ) as well as offshore Z2 ( $\rho = 0.72$ ,  $p < 0.03$ ; Figures 3e and 3f), suggesting that modeled zooplankton abundance may be useful to resolve interannual population variability of higher trophic levels.

#### 4. Discussion

[11] Predictive, process-oriented planktonic ecosystem models are important for developing principles of ecosystem oceanography which in turn could be useful in fisheries and climate change impact assessments [Cury *et al.*, 2008]. The utility of these models, however, is dependent upon their realism. Plankton dynamics are usually studied through ship-based observations and numerical simulations. Alone, both approaches are imperfect, but combined results may be robust. A key challenge, however, in the combined approach is communication and collaboration between observational scientists and modelers. This study, one of the first of its type, shows that krill distribution measured from ships matches mesozooplankton output derived from an independently designed coupled physical-biogeochemical model. In this study, we made “three checks” to assess the structural realism of the ROMS-CoSiNE performance in hindcasting mesozooplankton distribution off central California relative to empirically measured patterns of krill distribution and predator (seabirds) dynamics. The Z2 model component includes all mesozooplankton; therefore, caution is required in interpreting covariation between Z2 and krill distribution as Z2 is not calibrated to track life history or behavioral

aspects (e.g., feeding, growth, and reproduction) of krill. Furthermore, a straightforward comparison of modeled and observed zooplankton abundance remains difficult due to limited net sampling and modeling units that do not reflect abundance. Improving measures of abundance in sampling and models should be explored in the future to better our understanding of trophic transfer in marine ecosystems.

[12] *First check*: the mesoscale spatial structuring between observed krill and Z2 are similar, particularly with latitude along the central California coastline. Latitudinal coherence of krill/Z2 is probably explained by an interaction between winds, coastal geomorphology, and bathymetry (e.g., favorable shelf-slope habitat) [Santora *et al.*, 2011b; 2012a]. Winds are a primary environmental driver of ROMS-CoSiNE. The interaction between winds and coastal geomorphology produces latitudinal variability in advection-retention patterns off California that previously has been related to “hotspots” of krill abundance in the region [Santora *et al.*, 2011b]. Z2, however, exhibits considerable difference in longitude from observed krill distributions, and this is likely due to the smoothed bathymetry that does not resolve key krill habitats such as canyons, the shelf break, and shallow water topographies [Santora *et al.*, 2012a; 2012b]. The model hindcasted zooplankton distribution in several areas directly offshore of coastal promontories, presumably resulting from strong cross-shelf Ekman transport there [Keister *et al.*, 2009], but no acoustically detected krill was found in these areas. In summary, from a spatial perspective, current limitations of the model seem to be the use of inappropriate bathymetric gradients and lack of behavioral considerations (e.g., the diel vertical migration used by krill to remain in place) [Dorman *et al.*, 2011]. Vertical migration has been shown to retain zooplankton in a ROMS circulation model [Carr *et al.*, 2008]. Thus, to improve spatial coherence of the model, use of more realistic bathymetry and vertical migration behavior of zooplankton should help.

[13] *Second check*: the interannual variability of *T. spinifera* (and to a lesser extent, *E. pacifica*) abundance is strongly correlated with modeled mesozooplankton abundance. Primary productivity in the system, especially in the inner shelf where *T. spinifera* reside [Santora *et al.* 2012b], is derived from a balance between upwelling, turbulence, and advection [Largier *et al.*, 2006]. That the model output correlates best with the neritic krill species suggest it captures these processes reasonably well. We attribute this result to the ability of ROMS to capture wind-driven ocean circulation patterns along the California coast and reproduce cool/warm productive/unproductive years well. The model output did not correlate as well with variation in *E. pacifica* abundance, the dominant shelf-break/slope krill species. The lack of temporal coherence between *E. pacifica* and Z2 may be primarily related to poor bathymetric representations. *E. pacifica* and *T. spinifera* exhibit varying abundance peaks at multiple time scales from seasonal to interannual [Lavaniegos and Ohman, 2007; Santora *et al.*, 2011a], so perhaps the weaker correlation with *E. pacifica* is related to the relatively short time series used in this study. Another explanation may be that the growth parameter of Z2 relative to food availability is not accurate for krill. Individual-based models capable of tracking the life history stages and behavior of krill species may improve understanding of ecosystem dynamics further [Dorman *et al.*, 2011]. Nonetheless, the fact that ROMS-CoSiNE generates modeled zooplankton

estimates that correlate exceedingly well with interannual variability of *T. spinifera* is promising and verifies its utility for capturing realistic aspects of the neritic community. This is relevant to upper trophic level organisms as krill is predictive of fish, seabird, and marine mammal productivity and distribution [Thompson et al., 2012; Wells et al., 2012].

[14] *Third check:* the modeled zooplankton is significantly correlated to interannual variability of marine top predators, represented in this case by seabirds. This promising result is key to our interpretation of structural realism as relating model output to upper trophic level organisms is a key element for ecosystem oceanography and management. Similar links would likely be found with other species (*i.e.*, salmon) that depend on mesozooplankton for growth and reproduction [Wells et al., 2012]. Sydeman et al. [2006] showed that anomalous atmospheric-oceanographic conditions may negatively influence krill populations resulting in large-scale redistributions of plankton-dependent seabirds in the California Current. Therefore, the temporal coherence between modeled zooplankton and seabirds has potential for understanding ecosystem-wide aspects of trophic transfer. These results also have implications for developing studies of habitat use and foraging behavior of krill predators [Santora et al., 2011a; 2012b]. Currently, ecosystem-scale predictive habitat models of seabirds mostly rely on bathymetry and/or remotely sensed Chl-*a* [Suryan et al., 2012]. While Chl-*a* may serve as a proxy for prey, it does not exhibit the spatiotemporal structuring of zooplankton, which is key for understanding predator foraging and habitat use. Thus, the inclusion of modeled mesozooplankton in top predator habitat models may be a robust approach toward predicting changes in populations of valuable species.

[15] Estimates of mesozooplankton distribution and abundance derived solely from empirical sampling or output from models is often equivocal. However, by assessing similarities and differences from both approaches, zooplankton dynamics may be illuminated with greater precision. This study provides an important first step in the process of determining the feasibility of realistically tracking zooplankton populations with a coupled physical-biogeochemical model. Moreover, its potential for connections to higher trophic levels has been revealed. Quantifying the validity of model-based zooplankton estimates bodes well for developing a deeper understanding of trophic transfer in epipelagic food webs, thereby improving fisheries, wildlife, and other marine ecosystem assessments.

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