

Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 Northern California coastal populations: Implications from a model study

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[1] A decrease in krill abundance during 2005 in regions of the California Current has been hypothesized to have had immediate (seabird) and long-term (salmon) negative impacts on upper trophic level predators. We use a suite of coupled models to examine the population biology and spatial and temporal distribution of the krill species *Euphausia pacifica* during the winter/spring of 2001, a “normal” year, and 2005, an “anomalous” year, to determine if this hypothesis is supported mechanistically. Ocean conditions were simulated using the Regional Ocean Modeling System (ROMS), which forced an individual-based model parameterized to simulate the population biology of *E. pacifica*. Poleward transport during winter 2005 advected particles north of Cape Mendocino, away from seabirds and salmon feeding in the Gulf of the Farallons region. Few of the particles that were advected north in 2005 returned to their region of release throughout the model run time (200 days). Moreover, the “condition” of those particles remaining within the domain was poor in 2005, with greater mortality from starvation and a decreased mean particle weight. Our results indicate that both physical processes (anomalous northern advection) and biological processes (greater starvation and less weight per individual) contributed to reduced krill availability to predators in the northern California region during 2005, and that the productivity and survival of seabirds and salmonids is dependent on krill during critical life history stages. **Citation:** Dorman, J. G., T. M. Powell, W. J. Sydeman, and S. J. Bograd (2011), Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 Northern California coastal populations: Implications from a model study, *Geophys. Res. Lett.*, 38, L04605, doi:10.1029/2010GL046245.

1. Introduction

[2] A key prey field and component of the California Current food web is krill, including the most common nearshore species *Euphausia pacifica* [Brinton, 1962]. This group of zooplankton is an important consumer of large phytoplankton (diatom) biomass, and are fed upon by a diverse suite of higher trophic level organisms including seabirds [Ainley *et al.*, 1996], marine mammals [Croll *et al.*, 2005], and commercially important fishes including salmon,

rockfish, and hake [Genin *et al.*, 1988; Yamamura *et al.*, 1998; Tanasichuk, 1999]. Even organisms that do not feed directly on krill in the California Current are rarely more than two trophic links removed from krill species at some point in their life history [Field *et al.*, 2006]. Due to their high connectivity and importance as a prey species to many organisms, the annual availability of krill can have an impact on the productivity and survival of many higher predators.

[3] Krill availability (abundance and spatial distribution) is linked to variability in the timing and amplitude of upwelling [Brinton, 1976; Tanasichuk, 1998], and resultant primary productivity. Upper trophic level predators demonstrate phenotypic plasticity in breeding or emigration, with limits imposed by photoperiod and other factors [Reed *et al.*, 2009]. The degree of match or mismatch in any one year of prey availability and predator demands has been hypothesized to impact predator productivity for that year [Cushing, 1990]. The year 2005 in the California Current was anomalous (see special section of Geophysical Research Letters 33, L22S01 – L22S11), with significantly delayed upwelling off the California & Oregon coast [Schwing *et al.*, 2006; Kosro *et al.*, 2006] and low chlorophyll *a* levels from January through May north of 37° N along the West Coast of the United States [Thomas and Brickley, 2006]. Delayed and reduced upwelling may have led to decreased abundance of krill during 2005, and has been hypothesized to have led to mismatches (both spatial and temporal) between krill (prey) and coastal seabird populations (low reproductive success in 2005 & 2006) [Sydeman *et al.*, 2006] and juvenile salmon entering the ocean (reducing returning adult populations in 2008 & 2009) [Lindley *et al.*, 2009]. The purpose of this study is to mechanistically determine how wintertime ocean conditions (currents and primary productivity) may have impacted the spatial and temporal distribution and biological condition of *Euphausia pacifica* off northern California in the spring of 2005. The year 2001 is considered as a “normal” year for comparison.

2. Materials and Methods

[4] The coastal ocean was simulated using the Regional Ocean Modeling System (ROMS) [Shchepetkin and McWilliams, 2005; Haidvogel *et al.*, 2008], a commonly used tool that has been successfully implemented to model coastal upwelling in the California Current [Marchesiello *et al.*, 2003; Powell *et al.*, 2006, Di Lorenzo *et al.*, 2008]. Our ROMS model has 3 km cross-shore resolution, 6 km along-shore resolution, and 40 vertical levels. ROMS was forced with North American Regional Reanalysis (NARR) atmospheric data from the National Center for Environmental

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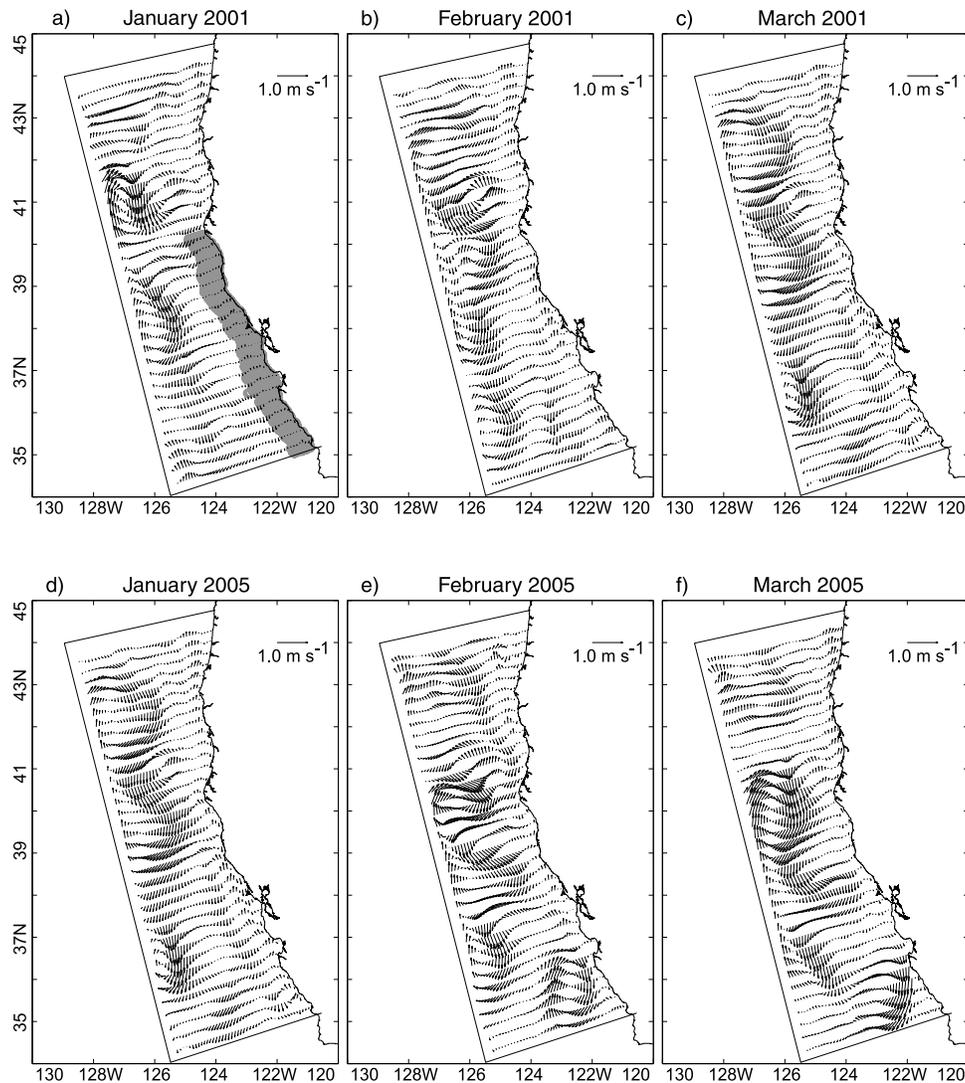


Figure 1. January, February, and March mean surface currents during (a–c) 2001 and (d–f) 2005. Initial particle seeding location on year-day 5 is shown in gray in Figure 1a.

Prediction (NCEP) at three-hour intervals. The forcing was parameterized using an approximation detailed by *Fairall et al.* [1996]. Data for initial conditions and boundary conditions is from a monthly climatology from the Estimating the Circulation and the Climate of the Ocean, Phase II (ECCO2) model [Menemenlis et al., 2008]. A Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) ecosystem model was incorporated into ROMS and run simultaneously. NPZD model equations and parameterization are described by *Powell et al.* [2006] and *Fiechter et al.* [2009] with the only change in parameterization being the detritus remineralization rate reduced to 0.1 d^{-1} . The ROMS/NPZD model was spun up from initial conditions for one year before the collection of data began and averaged daily values of model variables were saved for analysis. ROMS results were validated using MODIS-A (Moderate Resolution Imaging Spectroradiometer – Aqua satellite) data products.

[5] *Euphausia pacifica* population biology was simulated using the individual-based model (IBM) POPCYCLE [Batchelder and Miller, 1989; Batchelder et al., 2002].

POPCYCLE uses output from the ROMS/NPZD model to provide physical ocean conditions and phytoplankton (food source) to the particles. For each time step, particles undergo growth using results from *Ross* [1982a, 1982b]. Growth is scaled according to phytoplankton concentration based on an empirical equation of feeding rates of *E. pacifica* under varying food conditions [Ohman, 1984]. Life stage progression is determined by weight gain based on laboratory studies of development [Ross, 1981; Feinberg et al., 2006]. Weight loss beyond the midpoint weight of the previous life stage results in starvation mortality. Diel vertical migration was implemented in a similar fashion to *Batchelder et al.* [2002] using a maximum swim speed reported by *Torres and Childress* [1983]. Particles younger than furcilia IV did not vertically migrate, furcilia IV–VII larvae weakly migrated, and juveniles and adults consistently migrated. Particles were seeded over the continental shelf from the southern model boundary to Cape Mendocino (4,911 total particles). Particles representing furcilia III larvae (weight of $40 \mu\text{g}$ carbon) were seeded on January 5, based on the

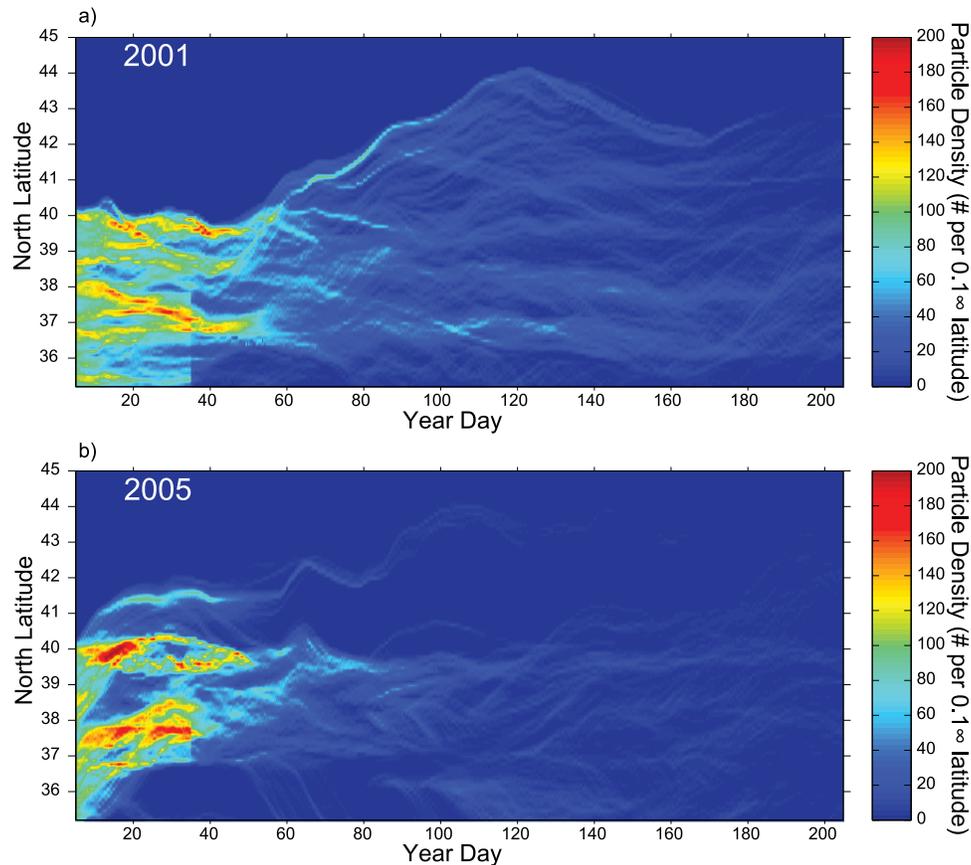


Figure 2. Particle density (number per 0.1° latitude) within 100 km of the coastline during (a) 2001 and (b) 2005. Note the northward advection of particles in January 2005 and greater number of particles in 2001.

dominance of early larval stages in January 2002 samples [Dorman *et al.*, 2005]. For the results reported in this manuscript, predation mortality and reproduction were not implemented during the model runs.

3. Results

[6] We contrasted along-shore currents in 2005 with those in 2001. In 2001, equatorward (poleward) currents were stronger (weaker) than in 2005 (Figure 1). Averaged monthly currents inshore of the continental shelf break (~ 60 km) from Point Reyes to Cape Mendocino exhibited weak equatorward (negative sign) currents during January (-0.016 m s $^{-1}$) and March (-0.007 m s $^{-1}$) of 2001, and weak poleward currents during February 2001 (0.035 m s $^{-1}$). Strong poleward currents were observed in January 2005 (0.131 m s $^{-1}$), and weak equatorward currents during February (-0.010 m s $^{-1}$) and March (-0.029 m s $^{-1}$) of 2005. Mean chlorophyll *a* concentration within 100 km of the coastline was low during winter of both years (Figure S1 of the auxiliary material).¹ Increased chlorophyll *a* concentration occurred later in the year during 2005, with only one upwelling event prior to year-day 150 (Figure S1).

[7] Particles released in 2005 moved much further to the north earlier in the year than in 2001 (Figure 2 and S2). On February 1, March 1, and April 1 of 2001, the cumulative

number of particles advected north of 40.5° N latitude (the approximate latitude of Cape Mendocino) was 34 (0.6%), 228 (4.6%), and 528 (10.8%), respectively. On February 1, March 1, and April 1 of 2005, the cumulative number of particles advected north of 40.5° N latitude was 521 (10.6%), 527 (10.7%), and 731 (14.9%), respectively.

[8] Mortality due to starvation occurred in both years, but was greater in 2005 than in 2001. Starvation of particles that

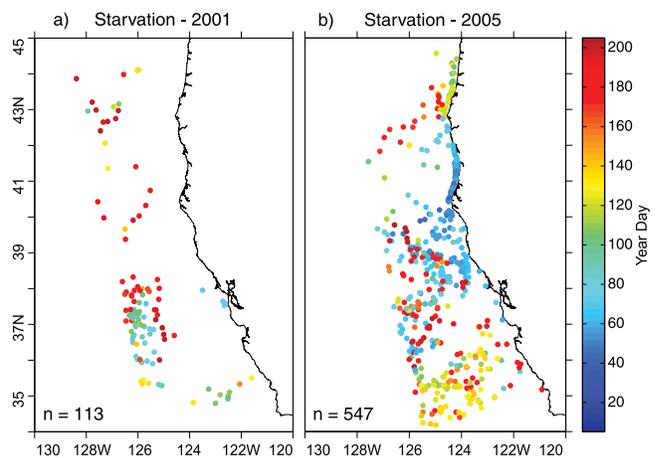


Figure 3. Starvation location of furcilia IV–VII, juvenile and adult *Euphausia pacifica* during (a) 2001 and (b) 2005. Color axis shows year-day of starvation.

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GL046245.

never progressed beyond the initial seeded stage (furcilia III) was prominent during winter of both years, with 31.9% and 45.2% of furcilia III larvae dying in 2001 and 2005, respectively. Starvation of furcilia IV–VII larvae, juvenile, and adult stages was more prominent during 2005, with 3.8% and 21.8% of those particles that molted beyond the furcilia III stage dying in 2001 and 2005, respectively (Figure 3). Starvation of particles advected north of 40.5° N latitude in January was high in 2001 and 2005 with 82.4% and 92.9% of particles starving, respectively. Starvation was much lower to the north of 40.5° N latitude in February and March of 2001, with 3.6% and 10.0% of particles starving, respectively. In this region during 2005, 100% and 31.8% of particles starved in February and March, respectively.

4. Discussion

[9] These modeling results do not attempt to explore interannual differences in the krill population biology leading up to January or differences in predation during the winter/spring that might impact our results. By limiting the variability of the initial population, we are able to highlight the impacts of the physical and environmental conditions on the population biology. There is very little wintertime information on the population biology of krill in our region of interest and no data to suggest there would be extreme differences in wintertime populations during 2001 and 2005. Additionally, primary producers and consumers in the northern California Current are generally considered to be controlled by bottom-up (physical) forces [Largier *et al.*, 2006], thus it seems reasonable to limit predation as a variable that impacts our model results.

[10] Differences in winter alongshore currents during the years 2001 and 2005 resulted in variation in the spatial distribution of *Euphausia pacifica* particles. The most striking advection event during these simulations was in January 2005, when particles were advected poleward by nearshore northward flowing currents (Figure 2b). This event effectively moved all particles that were seeded below Point Sur, California, to the north of Monterey Bay and advected over 10% of the population north of Cape Mendocino. There is often poleward flow in the California Current during wintertime [Hickey, 1998], but 2005 was unique in the strength and duration of the poleward advection. As the upwelling season occurs later in the year as one moves poleward in the California Current, particles in 2005 were transported into a region of reduced southerly transport that was still months away from upwelling-driven phytoplankton blooms. Thus, these particles experienced high starvation mortality and weak equatorward currents over the subsequent months, resulting in few of the surviving particles returning to the south. A poleward advection event in late February of 2001 resulted in much less starvation mortality as food resources were more prevalent at this later time of the year and particles were ultimately distributed back to the seeded model domain later in the year as persistent equatorward currents developed in the region.

[11] Lower food resources throughout the model domain during 2005 also impacted survivorship and the biological condition of particles. The initial cohort of particles (seeded as furcilia III larvae) experienced high mortality within the first 40 days of the model run during both 2001 and 2005 (albeit higher in 2005). The high mortality of larvae

observed near day 35 of both years (Figure 2) is a byproduct of seeding all particles the same weight, but high mortality of larvae, with lower energy reserves, is to be expected during winter in the California Current when food resources are generally low and were particularly poor in 2005. Particles that progressed to late larval (furcilia IV–VII), juvenile and adult stages experienced high starvation mortality during 2005, with particles starving both nearshore and offshore due to the delayed onset of upwelling-driven primary productivity. During 2001, late larval, juvenile and adult stages rarely experienced starvation except in unproductive offshore regions. Through advection and starvation, fewer particles remained in the model domain during 2005, and those particles that remained had a lower mean weight due to reduced food resources.

[12] Reduced krill availability and decrease in krill condition during 2005 likely impacted many higher trophic level predators that rely on them as a food source. Smaller prey size can impact predators in a variety of ways depending on predator foraging strategies, but in general, smaller prey size requires increased predator foraging effort to achieve comparable energy gain. Seabirds, such as Cassin's auklets (*Ptychoramphus aleuticus*) in the Gulf of the Farallons, require food resources within about 60 km of their colonies to successfully reproduce [Abraham and Sydeman, 2004, 2006]. Similarly, young salmon entering the ocean require abundant prey for successful first-feeding and initial survival at sea. Our model indicates that the diminished prey availability in the northern California region was due to anomalous poleward transport during winter 2005 and low survival of krill during spring 2005. The effect of these oceanographic anomalies has been long-term, with reductions in salmon populations through at least 2009, resulting in the closure of critical fisheries and causing socio-economic damage in excess of \$1B. The importance of this result and understanding krill population dynamics to societal concerns, therefore, is substantial.

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