

Modeling spatiotemporal dynamics of krill aggregations: size, intensity, persistence, and coherence with seabirds

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Understanding aggregation dynamics of forage species is important for evaluating biophysical scaling in marine ecosystems and heterogeneity of trophic interactions. In particular, zooplankton aggregations are fundamental units of many pelagic systems, but are difficult to observe continuously through space and time. Using an established modeling framework that encompasses a coupled regional oceanographic and individual-based modeling system, we test the hypothesis that persistence (duration) of krill aggregations is dependent on their size, intensity, and location of formation within the coastal upwelling region of the California Current. In support of this hypothesis, we found that aggregation size is positively related to intensity, whereas persistence has a parabolic response to aggregation size and intensity, indicating the likelihood that large and highly persistent aggregations are rare. Persistence of krill aggregations also depends on formation location within coastal upwelling areas. We found that krill aggregations were more likely to form near a major seabird colony and that some coastal upwelling areas act as sources of aggregations for other areas. Observations of seabird aggregations were used to evaluate the potential structural realism of predicted krill aggregations. Seabird aggregations displayed marked coherence with predicted krill aggregations in space, providing important criteria on the scaling and availability of krill aggregations to breeding and migratory species. Predicting scales of krill aggregation dynamics will benefit ecosystem assessments, and numerical modeling of predator foraging and marine spatial management aimed at ensuring protection of ecologically important areas.

The tendency of organisms (e.g. coastal pelagic fishes, krill, and locusts) to form high-density aggregations is a universal aspect of aquatic and terrestrial ecosystems (Okubo 1986, Bonabeau et al. 1999, Flierl et al. 1999, Parrish and Edelstein-Keshet 1999, Atkinson et al. 2014). In some instances, aggregations influence the spatial structure of species interactions and ultimately, ecosystem function (Levin 1994). Animal aggregation is related to environmental conditions. Indeed, the interaction among heterogeneity in environmental conditions and species life histories is likely one of the causes of aggregation behavior (Okubo 1986, Grünbaum and Okubo 1994). For example, aggregation behavior may be attributed to a combination of concentrations in food supplies or reproduction occurring during short time frames due to an environmental signal (e.g. cicadas), or may be an anti-predation strategy (Sutherland 1983, Parrish and Edelstein-Keshet 1999, Brierley and Cox 2010, Atkinson et al. 2014). Aggregation of prey often begets swarming of predators, such that predators exhibit 'prey-taxis' due to the patchiness of their prey (Kareiva and Odell 1987). As such, patchiness of prey aggregations influences the rate of trophic transfer in ecosystems, especially when intensity of predator–prey interactions is highly concentrated in space and time (Levin 1994, Mangel 1994). Human activity and commercial harvest of natural resources may be intimately tied with

the ecology of aggregating species; systematic plantings of large crops are often targeted by swarms of insects and birds, and fisheries often target and extract the highest density of aggregations of schooling fish, squid and krill (Mangel 1994, Smith et al. 2011, Pitkitch et al. 2012, Atkinson et al. 2014). Therefore, in ecosystems where aggregations are integral to the spatiotemporal structure and function of the ecosystem, investigating the ecology of aggregations, in particular their scales of variability, is of great importance (Grünbaum and Okubo 1994, Bonabeau et al. 1999, Benoit-Bird et al. 2013a, b, Hazen et al. 2013).

In marine ecosystems, aggregation mechanisms vary for planktonic (drifters) versus nektonic (swimmers) organisms. For both groups, aggregation occurrence may be density-dependent, driven by food supply spatial heterogeneity and encounter rates of these aggregations (Grünbaum and Okubo 1994, Ritz 1994, Bonabeau et al. 1999). For plankton, aggregations are also related to concentration and retention mechanisms within suitable habitats (Hauray et al. 1978, Dower and Brodeur 2004). In upwelling ecosystems, concentration and retention mechanisms are integral drivers of lower and upper trophic level aggregations (Bakun 1996). For example, upwelling enriches nutrients to support phytoplankton production at high concentrations, which in turn would support zooplankton aggregations. At the same

time physical forcing (e.g. convergences, frontal features, or offshore transport) may act to retain or disperse planktonic organisms (Haury et al. 1978, Franks 1992, Bakun 1996). Production and concentration mechanisms of plankton support aggregation by predatory fishes and air-breathing predators (e.g. seabirds, whales) in response to the availability of prey (Croll et al. 2005, Gende and Sigler 2006, Santora et al. 2011a, Benoit-Bird et al. 2013b). Key characteristics for understanding spatiotemporal variability of forage fish aggregations, as well as their importance to predators, are continuous measurements of their spatial intensity (degree of clustering), size (area) and persistence (temporal duration). Furthermore, vertical distribution, volume and behavioral cues are also important characteristics of forage aggregations (Parrish and Edelman-Keshet 1999, Parrish et al. 2002, Viscido et al. 2004), but are not addressed in this study. However, observing aggregation dynamics of forage species continuously through space and time (over all spatial scales) is impossible due to expense as well as observer influence. Therefore, studies involving models of aggregation dynamics using realistic ocean-ecosystem models are one effective way of learning about zooplankton aggregation formation, dissipation, and their impact on ecosystem structure and function (Dorman et al. 2015a, b, Rose 2015).

Euphausiids (hereafter krill) are well-known swarming organisms (Mauchiline 1980, Siegel 2000). Post-larval krill always occur in swarms (Nicol 1986, Miller and Hampton 1989, Watkins 2000), exhibit hierarchical patchiness (swarms may be organized within larger swarms; Grünbaum and Okubo 1994), and are integral in marine food webs (Atkinson et al. 2014). A significant amount of energy flows from primary producers through krill to secondary consumers in many marine ecosystems worldwide (Siegel 2000). Thus, krill aggregations are fundamental units of many marine ecosystems (Mangel 1994). Krill aggregations are easily quantified using shipboard acoustic echosounders (Miller and Hampton 1989, Santora et al. 2011a, b), and much is known about their fine-scale horizontal and vertical distribution patterns, as well as their shape and size ranges (Cox et al. 2010). To date, however, no acoustic study has tracked the fate of an individual krill swarm for more than a day, or how swarms interact with other swarms and their environmental associations through time. Krill predators are numerous and the successful feeding and reproduction of their fish and air-breathing predators often depends on the occurrence, availability, and persistence of krill aggregations within particular habitats at critical time periods (Croll et al. 2005, Goldbogen et al. 2011, Santora et al. 2014). Furthermore, because krill have many predators, their aggregations often attract predators that are themselves prey for predators; schooling fish attracted to krill aggregations are also prey for seabirds and marine mammals. Therefore, if we want to understand trophic transfer in marine ecosystems, interactions with predators, and fishing vessel activity, then we need to focus on the aggregation scale of forage species.

Little is known on how krill aggregations are formed in marine ecosystems, and especially their characteristics and persistence on scales relevant to predator foraging, conservation and ecosystem-based fisheries management. To this end, we use an established modeling framework that integrates a coupled regional oceanographic modeling

system (ROMS) and an individual-based particle-tracking model (IBM) parameterized to represent krill *Euphausia pacifica* population dynamics in the California Current Ecosystem (CCE; Dorman et al. 2011, 2015a, b). Because krill are gregarious and rarely exist without other individuals, we consider each simulated krill particle a patch or ‘micro-swarm’ (Haury et al. 1978) and the concentration of particles an aggregation. Observations indicate individuals within krill swarms tend to be similar in size and sexually mature stage, and thus exhibit similar behavior and swimming capacity that is coherent at the patch scale (Watkins 2000, Tarling et al. 2009, Cox et al. 2010). In reference to spatiotemporal scales of plankton patchiness (Haury et al. 1978), our study focuses on temporal scales of days-weeks-months and spatial scales ranging from 10–100 km (Supplementary material Appendix 1, Fig. A1). This study does not investigate physical forces that influence the formation of krill aggregations, as that is addressed elsewhere (Dorman et al. 2015b).

The simulations of krill aggregations described herein complement an array of observational studies of krill population dynamics and aggregations in the region relative to oceanographic drivers (Dorman et al. 2005, Santora et al. 2011a, b, 2012a, b). Observational studies however are limited in their ability to illuminate the variability in krill aggregations as most are made on relatively short time scales. The development of models that reproduce krill aggregations (Dorman et al. 2011) has opened up the ability to explore ocean conditions and occurrence of krill aggregations (Dorman et al. 2015a, b) and finer-scale temporal variation (days to months) of aggregation dynamics, which is the focus of this study. Other previous assessment of models (i.e. comparison of model output to observations) of krill in this region include Santora et al. (2013) who found that a coupled ocean-ecosystem model reproduces observed spatiotemporal variability of krill hotspots, and Schroeder et al. (2014) that described how ocean conditions may modulate seasonal krill production in coastal waters. This study is different in that we use an IBM embedded within a ROMS to quantify the emergent behavior and spatiotemporal aspects of krill aggregations (Dorman et al. 2015b). Our overarching objective is to investigate how the spatiotemporal dynamics of krill (particles) give rise to the emergent properties and characteristics of aggregations. In particular, we address the spatial aspects (intensity, size, formation and dissipation locations) and temporal aspects (duration) of aggregation formation through the coalescence of particles in geographic space. For broader context and model evaluation, we examine if emergent properties of modeled krill aggregations are coherent with seabird aggregations by relating observed foraging distribution patterns of a resident central-place breeder (murre) and a trans-hemisphere migrant (shearwater).

Methods

Model background and simulations

To investigate the dynamics of krill aggregations, we use a particle-tracking IBM (Batchelder et al. 2002, Dorman et al. 2015a) coupled with a regional oceanographic modeling

system – nutrient/phytoplankton/zooplankton/detritus (ROMS-NPZD) model designed specifically for the CCE (Powell et al. 2006). The goal of the physical modeling is to provide realistic physical conditions to force biological models. The modeled domain ranged from Newport, Oregon to Point Conception, California and extended 1000 km offshore (Fig. 1). Model grid resolution is approximately 6 km in the alongshore and 3 km in the cross-shore direction; grid cells are 18 km². ROMS was forced with data from the National Centers for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) data set. Boundary and initial conditions are from the Simple Ocean Data Assimilation (SODA) model (Carton and Giese 2008). Model simulations spanned the 9 yr, 2000–2008. Additional detail on the ROMS configuration, including coherence with observed ocean physics is provided by Dorman et al. (2011, 2015a, b).

The IBM (POPCYCLE) is derived from Batchelder and Miller (1989) and parameterized for particles of the krill *E. pacifica* based on their life history characteristics in the California Current (see Dorman et al. 2015a for a thorough description of the IBM). Particle movements are implemented by interpolating currents spatially (from model grid points) and temporally (from saved ROMS model output) to the particle location, then integrated using a Runge–Kutta 4th-order advection scheme to update particle location. Vertical diffusivity is included in particle tracking using a non-naïve random walk (Visser 1997); diurnal vertical migration (DVM) is implemented using a methodology similar to Batchelder et al. (2002), with a maximum swimming speed of approximately 0.1 m s⁻¹ (Torres and Childress 1983). Based on regional field-based studies and previous sensitivity analyses of the model (Dorman et al. 2015a, b), we set the upper limit of DVM to 20 m below the ocean surface; generally, this limit corresponds to the chlorophyll *a* maximum depth layer and where krill aggregations were regularly observed from acoustics off central California (Santora et al. 2011b). Downward vertical migration of particles was based on light levels (e.g. daily change in sunrise). No additional biological parameterization (e.g. growth, life-stage development, reproduction, mortality) was implemented in this study, so aggregation dynamics were driven exclusively by advective and retention processes. A total of 18 realizations of the IBM were simulated and model runs ran for 90 d from start date. We simulated model runs for spring (9 yr) and summer (9 yr) with start dates of 15 February and 15 May each year, respectively; each run was seeded with 40 000 particles in a uniform distribution throughout the domain (Fig. 1). Due to the influence of initial physical conditions on distribution of seeded particles, as a standardization procedure, we omitted model days 1–30 from geospatial analyses. An example of our model simulation and tracking of daily krill aggregations can be viewed in a supplemental movie file (Supplementary material Appendix 2).

From individuals to aggregations

In simulations, krill particles (essentially concentrated individuals) and the aggregations they produced were identified daily. Statistically significant aggregations were identified

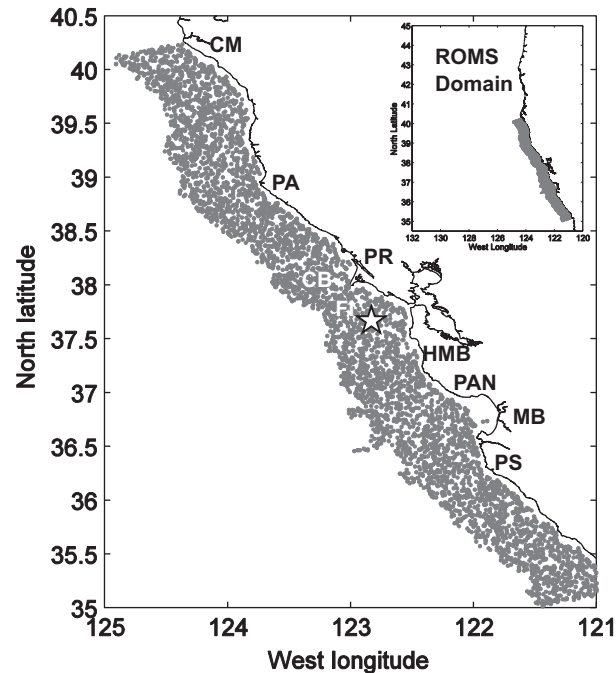


Figure 1. Study area of the central California Current large marine ecosystem. Dots indicate an example of a simulated krill particle configuration map and the inset shows the extent of regional oceanographic modeling system (ROMS) domain. Particle seeding was predetermined by the extent of previously identified krill hotspots (Santora et al. 2011a, b). Star indicates the location of the Farallon Islands (FI), a major seabird colony. CM is Cape Mendocino, PA is Point Arena, PR is Point Reyes, CB is Cordell Bank, HMB is Half Moon Bay, PAN is Point Año Nuevo, MB is Monterey Bay and PS is Point Sur.

based on the distribution of particle concentrations within all grid cells (Dorman et al. 2015b). We used the Getis–Ord statistic (G_i^* ; Getis and Ord 1992) to quantify both swarm occurrence and to index the spatial intensity of each aggregation. The G_i^* is a statistical measurement (a z -score) of local clustering relative to the background spatial mean and standard deviation of all particle densities and distribution within the model domain. To estimate G_i^* , a spatial neighborhood must be selected. We set the neighborhood for the clustering routine as 42 km in the alongshore and 15 km in the across-shore dimension based on 2-D Moran's I tests of anisotropic spatial autocorrelation in acoustic observations of krill hotspots (Santora et al. 2011a, 2012a). Significant aggregations were assigned a unique ID (e.g. 'HS01') and their geospatial aspects were tracked until they dissipated, where dissipation is defined as point in which an aggregation on the ROMS grid is no longer a statistically significant cluster of particles. For each day, we measured the aggregations' geographic position (longitude and latitude), spatial intensity (G_i^*), size (km²), distance traveled (km) and bearing, as well as its persistence (number of days since formation). The size (in km²) of an aggregation was calculated using the number of contiguous grid cells in the ROMS that contained a significant cluster of individual particles. The ROMS grid cell resolution set a lower limit on aggregation size at 18 km², but this size is within the lower range provided by the Stommel diagram of plankton swarms

(Supplementary material Appendix 1, Fig. A1). To quantify persistence (in days), we counted the number of days of significant G_i values per aggregation for each model run until the aggregation diffused. Distance traveled (km) and bearing (direction) was quantified by measuring the linear distance and direction (radians) between daily centroid locations of an aggregation. We also calculated bottom depth from the ROMS-based bathymetry and distance to the coastline as additional geographic covariates for every day each aggregation persisted.

We focused on 4 inter-related questions regarding the dynamics of krill aggregations: Q1) what are the characteristic scales of variability of aggregation spatial intensity, size and persistence? Q2) How do these characteristics of aggregations evolve over time? Q3) What are the functional relationships among aggregation spatial intensity, size and persistence? Q4) Where are aggregations most likely to form and dissipate? To determine the scales of variability (Q1), we constructed histograms; these figures also demonstrated the likelihood of finding intense, large, and persistent aggregations which may be most important to krill predators. To assess Q2, we examined a subset of aggregations with the highest persistence (longest lasting; e.g. > 2 weeks) and estimated their variance regarding temporal changes in spatial intensity, size and distance traveled. To assess Q3, we used generalized additive models (GAM) to quantify the functional responses among spatial intensity, size, and persistence, with the ultimate goal of determining the shape of relationships (e.g. linear, asymptote, parabolic). Due to their flexibility, GAMs are appropriate for this synthesis, because spatiotemporal dynamics of plankton patchiness tends to exhibit complex non-linear relationships. GAMs were implemented using the 'mgcv' package in the R statistical program (R Development Core Team) and smoothness parameters (s) were estimated with generalized cross-validations (Wood 2006). We calculated GAMs to assess functional relationships with and without persistence. For example, a GAM to examine the effect of size and persistence on spatial intensity is: $\text{Intensity} \sim s(\text{Size}) + s(\text{Persistence})$. The effect of each covariate in the GAM was plotted to visually determine its functional form.

A variety of mapping procedures and frequency distribution statistics were used to address Q4. We mapped the coordinates of formation and dissipation for aggregations lasting over 2 d and compared them to known geographic features (e.g. sub-marine canyons and submerged banks) to determine if there are regions where aggregations either were repeatedly formed or dissipated. Important geographic features associated with observed krill hotspots include Cordell Bank, Año Nuevo, Pioneer and Monterey submarine canyon systems (Fig. 1; Santora et al. 2011a). Moreover, as a geospatial summary for all simulations, we averaged spatial intensity, size and persistence of all identified aggregations by half-degree latitude bins (corresponding to ~ 55 km or ~ 3000 km²) to assess potential geographic shifts in swarms. This latitudinal resolution is justified because Santora et al. (2011a) and Dorman et al. (2015b) revealed that the distribution of krill hotspots off California at that scale is related to strong upwelling zones (e.g. Points Arena, Sur, and Conception), which are roughly 25–50 km apart on the central-northern CA coastline.

Model coherence with seabirds

We compared and contrasted intensity, size and persistence of krill aggregations with observations of summertime seabird abundance that were mapped within the modeling domain during same time period (2000–2010). Standardized ship-board surveys of seabirds were made in conjunction with the annual NOAA-NMFS Rockfish Recruitment Ecosystem Assessment Survey (RREAS) during May–June each year (Yen et al. 2004). The relative abundance (total per 3 km²) of seabirds was estimated using strip-transect methods during daylight hours while the vessel transited between sampling stations. We examined the coherence in spatial scaling between aggregations of modeled krill and abundance of two of the most abundant seabird species in the CCE, the locally-breeding common murre *Uria aalge* and the trans-hemisphere migrant sooty shearwater *Puffinus griseus*. Within this region seabird aggregations at sea tend to be highly skewed and patchy, with observations of very large flocks being rare (Santora et al. 2011a). For the comparative purposes of this analysis, we only mapped aggregations greater than 10 and 20 individuals per 3 km for murre and shearwaters, respectively. Both species are known to feed on krill directly or on prey that feed on krill within krill patches (e.g. juvenile rockfish *Sebastes* and squid; Santora et al. 2012a). Common murre are diving seabirds and the most abundant breeding seabird on the Farallon Islands (centrally located in the Gulf of the Farallones, GoF; Fig. 1). Murre are gregarious colonial nesters and depend on availability of high density prey patches (Davoren et al. 2003). During late May–June, murre are rearing chicks (one chick per pair) and behave as central-placed foragers (Orians and Pearson 1979) making daily trips most within 50 km from the colony in search of prey patches (Ainley and Boekelheide 1990). It is very likely that murre maintain a daily memory of where the most profitable prey patches are located and they often forage in dense flocks (Davoren et al. 2003). The sooty shearwater is a near-surface feeder and is the most abundant seabird off California during spring and summer (Veit et al. 1997); they may occur in extremely dense aggregations (numbering in the thousands), mostly along the shelf-slope environment (Santora et al. 2011a). We qualitatively evaluate coherence of krill aggregations and observed seabird aggregations to assess scales of variability (size and persistence) and availability of krill aggregations potentially utilized by seabirds. As our previous studies have indicated, there is distinctive observed latitudinal variability of krill and seabird hotspots due to changes in locations of strong upwelling cells along the California coast (Dorman et al. 2015b). Therefore, we assess if seabird abundance reflects changes in the intensity, size and persistence of krill aggregations as a function of latitude.

Results

Scales and functional aspects of krill aggregations

A total of 475 and 380 aggregations were identified during spring and summer, respectively. Persistence of aggregations ranged from 1 to 60 d (the entire duration of the model

simulation; Fig. 2). Across all simulation years, regardless of season, temporal scales of total aggregations revealed that 30% formed and dissipated in one day, 35% lasted for 2–4 d, 20% lasted 5–10 d, while those lasting greater than 15 d occurred ~ 5% (Fig. 2). Aggregations with the highest persistence (> 20 d) accounted for less than 5% of total aggregations, occurred less than 5% of the time, indicating these aggregations are rare. These high persistence aggregations were also some of the largest (800–1000 km²), most intense (high G_i), and closest to land (10–30 km) that tended to shift no more than a few km (4–10 km) during their existence (Fig. 2–3, Supplementary material Appendix 1, Fig. A2). Conversely, low persistence aggregations were more likely to be small (< 400 km²), formed further from land, and traveled greater distances during their short existence (Fig. 2, Supplementary material Appendix 1, Fig. A2). Spatial intensity covaried with aggregation size, indicating that larger aggregations tended to exhibit higher values of spatial intensity (Supplementary material Appendix 1, Fig. A2). Spatial scales of aggregations ranged from a minimum 18 km² (grid cell minimum) to 1900 km² (Fig. 2). As with persistence, the majority of aggregations (75%) ranged from 18 to 800 km², while only a few (25%) tended to exhibit sizes greater than 900 km² (Fig. 2).

Figure 3 shows the variability of the 4 most persistent aggregations (2 per season). These aggregations were tracked for upwards of 60 d and provide insight on temporal changes of large aggregations (i.e. evolution). It should be noted that the variability in size and intensity of aggregations is likely due in part to the continued coalescence of particles joining, and particles diffusing away from aggregations. In all 4 instances, after formation, aggregations tend to remain in their local neighborhood for 2–3 weeks before starting to drift very slowly at about 5–10 km over the next month of their existence. A month post formation, they tended to move further distances up to 30 km from their origin before dissipating (Fig. 3). The intensity of these aggregations tended to either increase steadily over time or remained stable. Increasing aggregation intensity and size may indicate the continued growth of aggregations through the coalescence of smaller swarms joining the aggregation. Two aggregations that started out fairly large (1400–1600 km²), declined in size after 2 weeks, but then exhibited a second peak in size similar to their initial formation size; after this second peak, they tended to stabilize at moderate sizes (400–800 km²). The other aggregations formed at relatively smaller sizes (400 km²) but grew substantially, with one aggregation peaking at 1600 km² before declining to moderate levels (Fig. 3).

GAMs applied to all identified aggregations (i.e. persistence of 1–60 d) revealed that the functional relationship between intensity and size is generally linear, but exhibit a small step function at moderate values (intensity levels of 5–7 G_i and sizes of 900–1200 km²; Fig. 4a–b), with a pronounced linear increase at greater values. GAMs that included only those aggregations that lasted more than 2 d, thus having a measure of persistence, yielded interesting non-linear functional relationships among intensity, size and persistence (Fig. 5). The effect of intensity on aggregation persistence indicates a steady increase in intensity to an asymptote (Fig. 5a), where

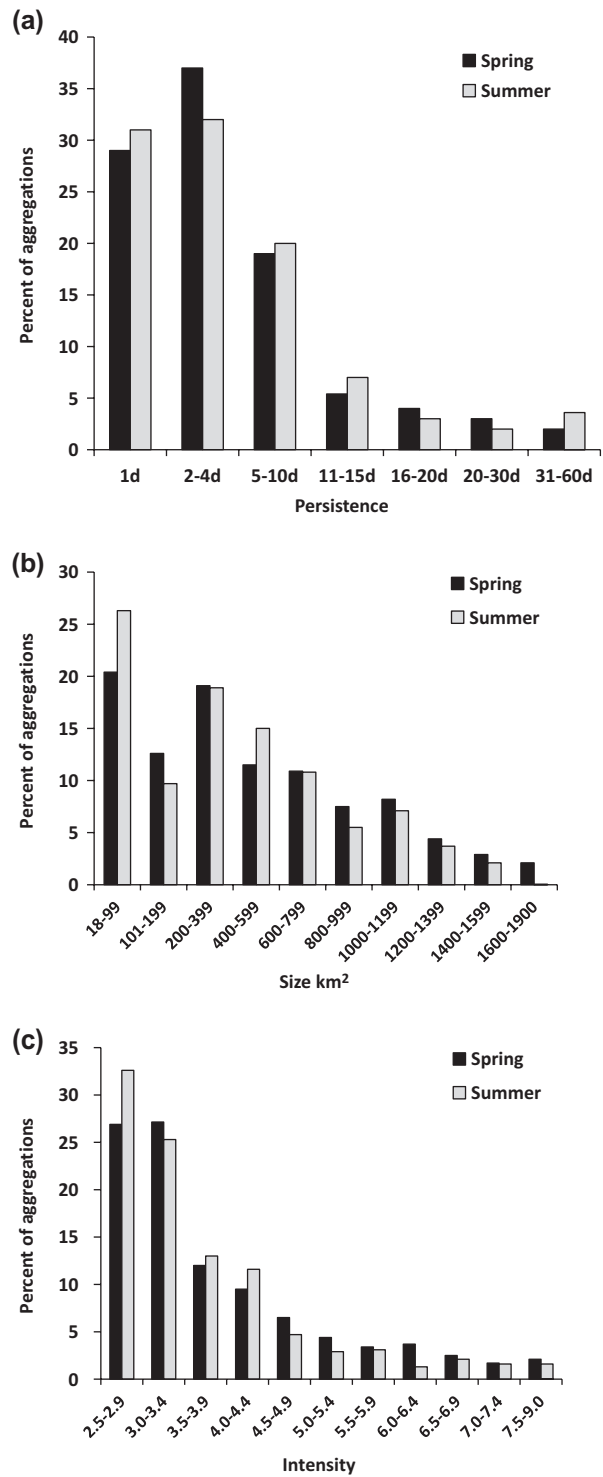


Figure 2. Scales of variability of simulated krill aggregations (a) persistence, (b) size and (c) intensity.

most persistent aggregations exhibit highest intensities (Fig. 5c). The effect of size on persistence yielded a dome-shaped relationship, with a peak around 900–1200 km² (Fig. 5b–d). This relationship confirms that aggregations with moderate levels of persistence (20–30 d) likely have an optimal size window, and furthermore, high persistence aggregations are indeed rare and likely unstable at very large sizes (> 1400 km²; Fig. 5b–d).

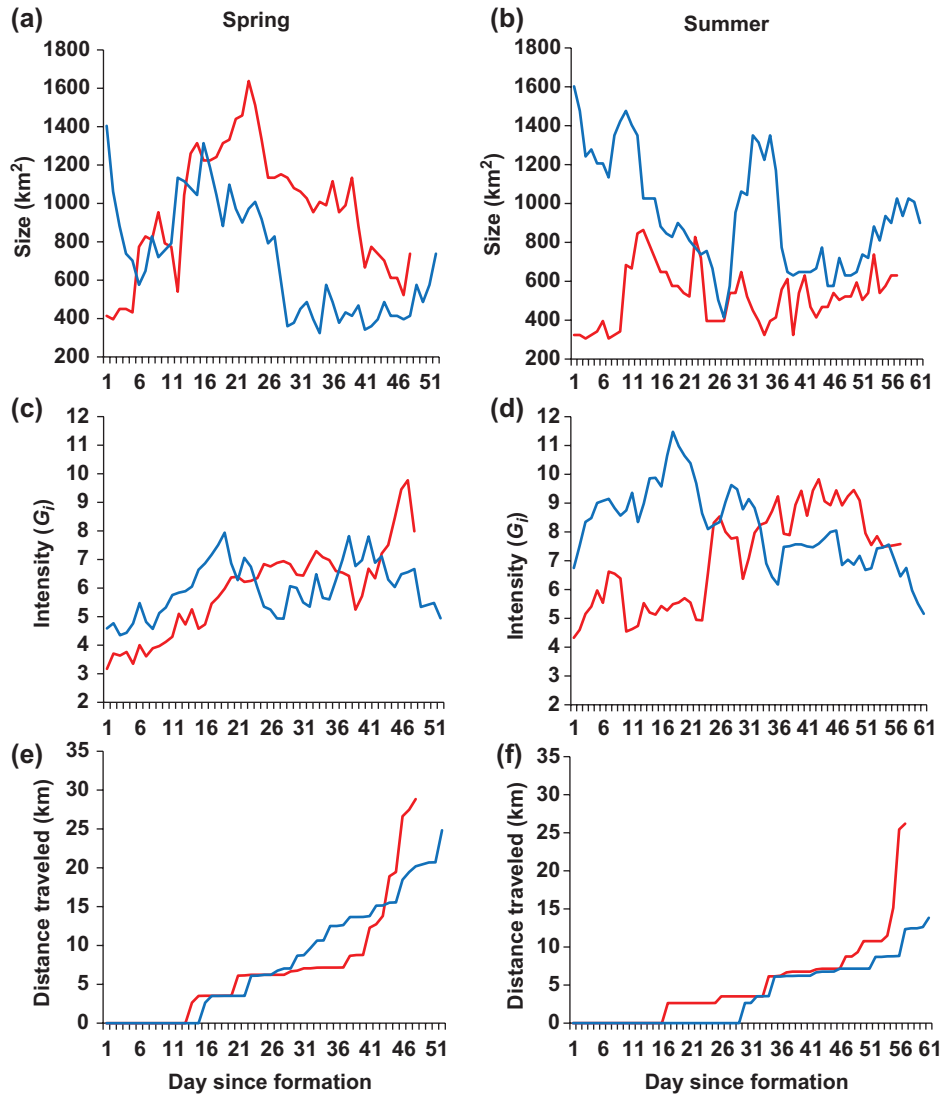


Figure 3. Temporal variability and evolution of krill aggregation aspects. Examples of the 4 most persistent aggregations during spring (a, c and e) and summer (b, d and f) simulations illustrating temporal variability of aggregation size, intensity, and distance travelled since formation.

Formation and dissipation of krill aggregations

In spring and summer simulations, most krill aggregations formed between 36° and 38.5°, with a clear peak around 37° (in the GoF), coinciding with the extensive continental shelf there (Fig. 6–7). Furthermore, most aggregations tended to shift slightly to the north (~ 0.2°–0.4°) within the inner shelf (Supplementary material Appendix 1, Fig. A3). By comparison to summer, spring aggregations were larger at all latitudes and formed in deeper water further from the coast, and their intensity was generally consistent across latitudes (Fig. 6; Supplementary material Appendix 1, Fig. A3). Average persistence of aggregations during spring was about 7 d between 37.5° to 39° (Fig. 6). Summer aggregations exhibited clear latitudinal peaks in size at 37.5°, 38° and from 39°–39.5° (Fig. 6; Supplementary material Appendix 1, Fig. A4–A5) and on average, persisted for a week.

At finer scales, many aggregations are associated with several regionally important bottom topographies, such as Cordell Bank, Pioneer Canyon, Pt Año Nuevo and Monterey submarine canyons (Fig. 7). During spring, high persistence aggregations are formed north of Pt Reyes, within the GoF and off Half Moon Bay (Fig. 7a). The last spring location of high persistence aggregations indicate they become even more clustered within the GoF (Fig. 7c). Spring aggregations with ~ 22–34 d persistence tended to form on the shelf off Half Moon Bay and shifted into the GoF (Fig. 7a, c). During summer, high persistence aggregations (21–60 d) formed within the GoF, Half Moon Bay and off Pt Año Nuevo in the northern sector of the Monterey submarine canyon system (Fig. 7b, d). Prior to dissipating, these high persistence aggregations shifted north along the shelf and were clustered off Half Moon Bay and within the GoF, especially near the Farallon Islands (Fig. 7b, d). Moreover, several aggregations

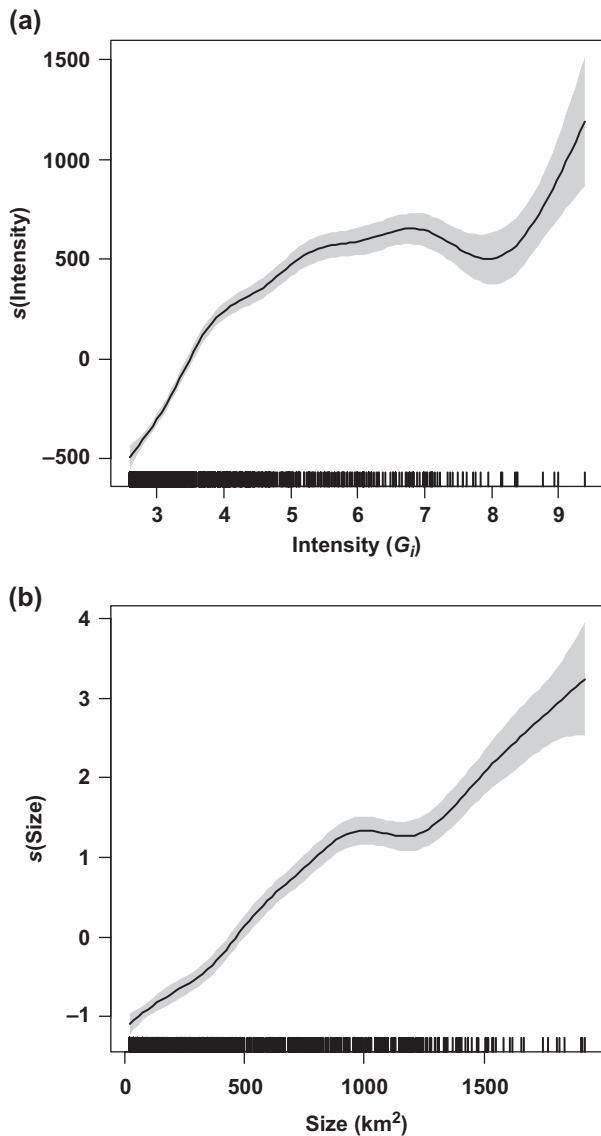


Figure 4. GAM results showing the functional relationship between size and intensity derived from the average of all simulated krill aggregations; (a) effect of intensity on size and (b) effect of size on intensity.

ended up further offshore of Pt Reyes on top of Cordell Bank, potentially indicative of a source/sink dynamic.

Coherence with seabirds

Murre aggregations are distributed throughout the shelf and inshore of the 200 m isobath (Fig. 8a), and as expected, murre aggregations are clustered in the vicinity of their breeding colony within the GoF. Murre aggregations also occurred to the north and to the east of Pt Reyes (near another colony), and to the south of Half Moon Bay and Pt Año Nuevo, where they are especially clustered inshore of the 200 m isobath (Fig. 8a). Sooty shearwater aggregations were also highly concentrated over the shelf to the north and south of Pt Año Nuevo, and within inner Monterey Bay (Fig. 8b). However, unlike murre aggregations, shearwaters aggregations are distributed further offshore in pelagic

waters, with aggregations located between the 200 and 1000 m isobaths. Clusters of shearwater aggregations are located near Pioneer Canyon and on the eastern edge of Cordell Bank (Fig. 8b). No shearwater aggregations were observed within the inner GoF where murre aggregations tend to be concentrated (Fig. 8a–b).

Qualitatively, seabird aggregations are coherent with the spatial distribution and clustering of highly persistent krill aggregations (Fig. 7–8), indicating the model is capable of reproducing realistic scaling patterns of prey patches off central California. First, clustering of murre aggregations within GoF, due in part to the location of their breeding colony, overlap within an area that fosters krill aggregations with some of the highest levels of persistence recorded (Fig. 7–8). Second, murre and shearwater aggregations also overlap with highly persistent krill aggregations formed and retained off Half Moon Bay and Pt Año Nuevo. Third, shearwater aggregations are repeatedly observed on Cordell Bank, a location where multiple highly persistent krill aggregations occurred before dissipation, and near Pioneer Canyon, where numerous krill aggregations were located between the 200 and 1000 m isobaths (Fig. 7–8).

Latitudinal coherence between spatial mean seabird density and aspects of krill aggregation indicates important sub-regions along the CA coast. Due to the location of their large breeding colony on the Farallon Islands (Fig. 8a), murre are clearly associated with peaks in persistence, size and intensity of krill aggregations between 37° – 37.5° (Fig. 9). Within the GoF, murre are likely to encounter krill aggregation persisting for greater than a week and ranging in size from 400–800 km² (Fig. 9); this area of high aggregation formation and retention is likely critical to the foraging and breeding success of murre. Shearwater density appears to be somewhat offset with local peaks in krill aggregation size and intensity, but their density peak is associated with a peak in persistence at 37° , where krill aggregations are likely to persist on average for greater than a week (Fig. 9). This latitudinal peak is where numerous shearwater aggregations were encountered off Pt Año Nuevo (Fig. 9), a location with a narrow shelf region where several submarine canyons terminate at the coast, and where numerous krill aggregations were formed (Fig. 7, 9).

Discussion

Quantifying dynamics of forage species aggregations is fundamental to understanding marine ecosystem structure and function, but is difficult to study given the complexity of interacting biological and physical forces on aggregations across multiple scales. Our modeling study addressed the frequency of occurrence and persistence of krill aggregations, as well as their transient dynamics over time, including their size, intensity and distance traveled. We address the following dynamics of krill aggregations resulting from our simulations: a) scales of variability and relationships among aggregation size, intensity and persistence, b) formation and dissipation locations, c) evolution over time, and d) evaluate their coherence with observed seabird aggregations to assess structural realism of our model and to identify scales

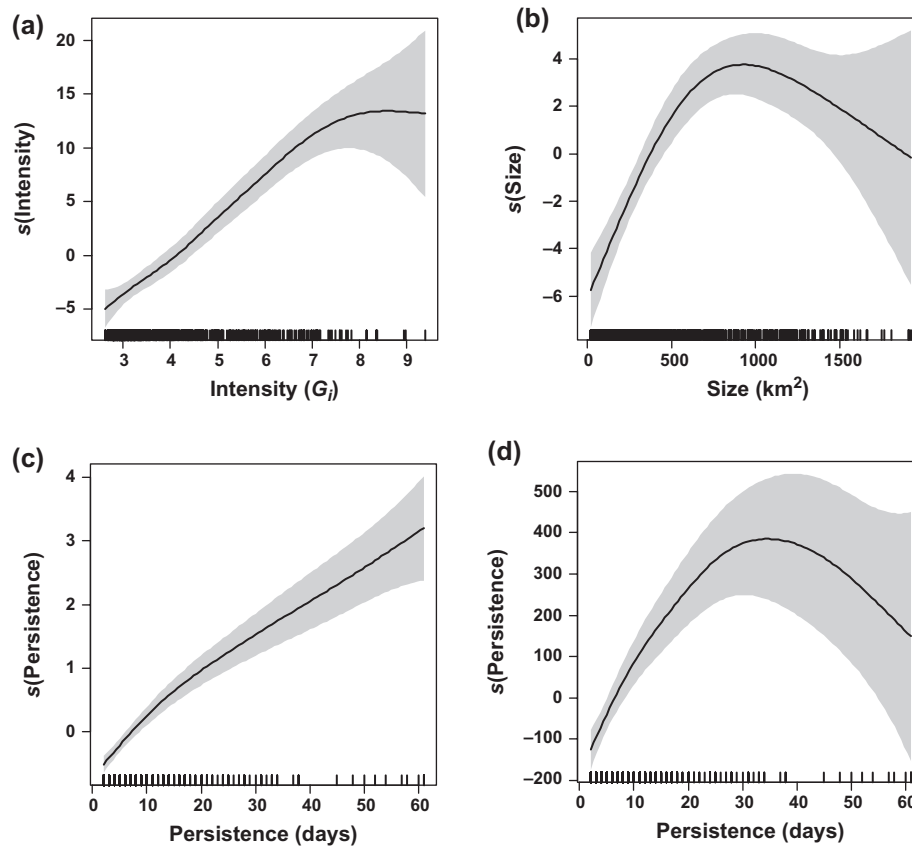


Figure 5. GAM results showing the functional relationships among intensity, size and persistence derived from all simulated krill aggregations that exhibited persistence (> 2 d); effect of persistence on (a) intensity, (b) and size, and effect of intensity (c) and (d) size on persistence.

of krill aggregations that may be important to air-breathing predators.

Krill aggregation scales and marine ecosystem function

The Stommel diagram of plankton patchiness (Supplementary material Appendix 1, Fig. A1; Haury et al. 1978) illustrates a theoretical ‘swarm scale’ where plankton patches are concentrated between 10–100 km over days, weeks and months. This scaling is coherent with the distribution of krill aggregations simulated by our model in the upwelling zone off central California. Approximately, 55% of krill aggregations persisted between 2–10 d, while 5% persisted for 15 d or more, and only a few occurred for a month or more. The event scale of wind-driven upwelling, an important physical driver of nutrients and formation of frontal structures that may accumulate plankton in retention zones (Bakun 1996, Wing et al. 1998), also has a characteristic spatiotemporal scale of 1–2 weeks (Botsford et al. 2006, García-Reyes and Largier 2012). Spatially, the location of strong upwelling and retention zones off California is linked to occurrence of krill abundance hotspots (Santora et al. 2011a, Dorman et al. 2015b). Our simulations clearly indicate that the size, intensity, and persistence of krill aggregations display a peak off central California. This region is bounded to the north and south by strong upwelling zones (Pt Reyes and Pt Sur), has

a wide continental shelf and a network of deep submarine canyon systems that favors the concentration and retention of dense krill aggregations.

Our simulations of krill aggregations correspond to differences imposed by spring and summer upwelling conditions. During spring, northwesterly winds intensify and nutrient rich water is upwelled along the coast during regular weekly intervals, and coastal waters are transported in the cross-shelf direction promoting development of upwelling plumes and alongshore fronts at the shelf-slope (Checkley and Barth 2009). Comparatively, this process is more consistent during spring than in summer, whereby prolonged week long relaxation periods are more typical during summer, promoting retention of nutrients, primary production and subsequent growth of zooplankton populations (Botsford et al. 2006). By comparison, we found that krill aggregations were generally larger but displayed less persistence and were located further offshore during spring compared to summer. Furthermore, aggregation size, intensity and persistence were also less variable across latitude during spring compared to summer, which showed a clear peak in all aggregation aspects within the retention zone of the GoF. These novel modeling results highlight there are potential different scaling mechanisms of krill aggregations during the more intense spring upwelling season compared to the more relaxed summer upwelling period.

Large and persistent aggregations of forage species often account for high percentages of total biomass of forage species

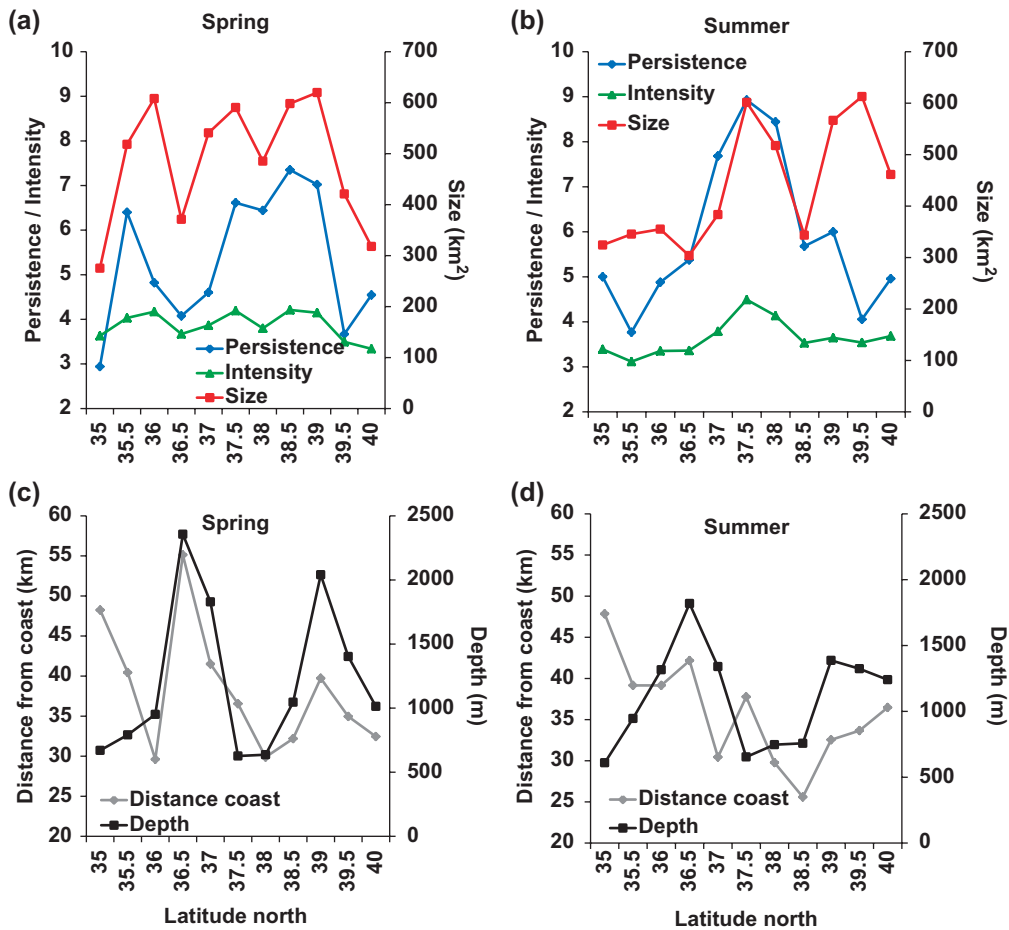


Figure 6. Latitudinal variability (0.5° bin) of averaged krill aggregations aspects off of central California derived from all simulated aggregation during spring and summer: (a–b) intensity, size and persistence and (c–d) distance from the coast and sea depth.

(Atkinson et al. 2014), making their identification important as potential ecosystem indicators and for informing how ecosystem survey design may be modified to study their occurrence. Although the relationship between size and intensity of krill aggregations is positively linear, we found that persistence of krill aggregations appears to have an optimal environmental window of 20–40 d at sizes of 800–1200 km². This suggests a threshold functional response between size and persistence in geographic space, indicating that the location of formation is important to the outcome of krill aggregations (Cury and Roy 1989, Santora et al. 2011b). Krill aggregation formation, growth (change in size) and persistence should depend on the encounter rate of individual krill swarms (particles), and the intensity at which smaller swarms are concentrated and retained within a given area (Sutherland 1983, Levin 1994, Mangel 1994). We found that krill aggregations formed with initial higher intensity (i.e. more packing of individual particles) tend to be larger in size and have higher persistence. Dissipation of krill aggregations may be due to degradation of retention forces and/or the transport of individual krill swarms out of key retention zones and forces impacting krill aggregation size and intensity. We found that more krill aggregations tended to form and dissipate off central California between 36.5° and 37.5°N, and that these aggregations were, compared to other regions, of higher persistence, size and intensity. Aggregations

formed with this region tend to maintain their position for several days and then shift into adjacent retention zones, or move to offshore locations such as Cordell Bank, an ecologically important area where high concentrations of fish, seabirds, and marine mammals frequently occur (Santora et al. 2012a). During spring and summer, the Gulf of the Farallones and Half Moon Bay are both important areas as a source and a sink of krill aggregations having high persistence, while Monterey submarine canyon system to the south is important for producing high persistence swarms that may potentially shift to the north during summer.

Evolution of krill aggregations over time

Quantifying variability of forage aggregations through space and time is one of the most challenging aspects in the study of swarming organisms (Parrish and Edelman-Keshet 1999, Parrish et al. 2002). This is due to the difficulty of observing an aggregation and following it through the course of its existence without influencing the behavior of the aggregation. Moreover, disentangling the biophysical forces, behavioral responses and social interactions acting on keeping the aggregation together is extremely complicated (Okubo 1986, Ritz 1994, Parrish and Edelman-Keshet 1999). Although observed forage species aggregations have been linked to

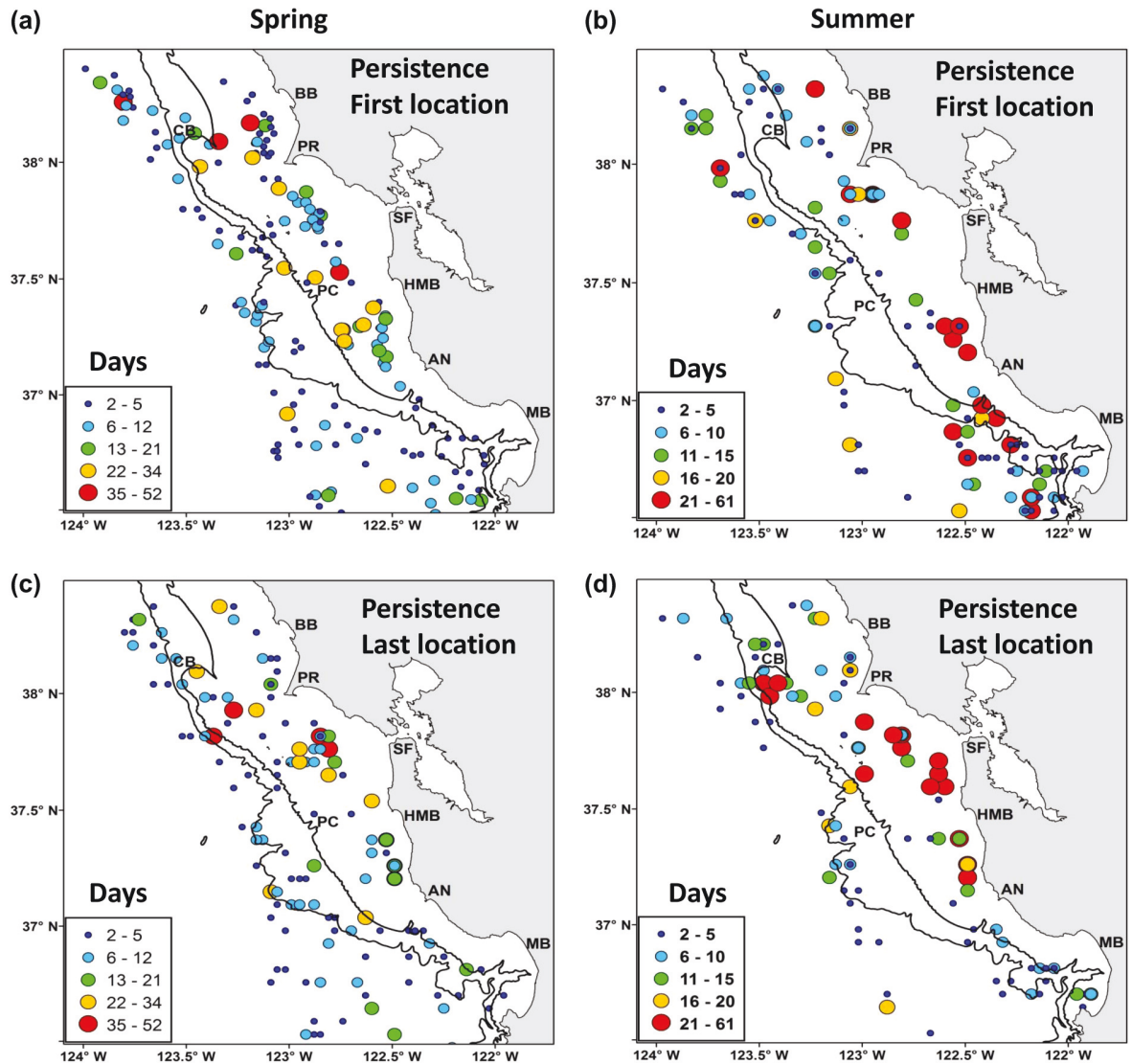


Figure 7. Geospatial variability and classification of aggregation persistence illustrating the location of formation and dissipation of aggregations (a, c) spring and (b, d) summer. Contour lines are the 200-m and 1000-m isobaths. North to south, BB is Bodega Bay, CB is Cordell Bank, PR is Point Reyes, SF is San Francisco, PC is Pioneer Canyon head, HMB is Half Moon Bay, AN is Año Nuevo, and MB is Monterey Bay. See Supplementary material Appendix 1, Fig. A6 for variation in size between location of formation and dissipation.

bathymetry (Allen et al. 2001, Santora et al. 2012b) and persistence of frontal features (Woodson and Litvin 2015), few empirical studies have followed individual aggregations continuously over time (Tarling et al. 2009, Cox et al. 2010). Although most krill aggregations formed and dissipated within 1 d, many aggregations persisted for multiple days. For simplicity and comparative purposes, we examined the 4 most persistent aggregations, which lasted for over a month. After initial formation, we found that these aggregations tended to increase in size and intensity until they reached a maximum, and then either decreased or remained constant until their dissipation. After formation, these aggregations did not move for weeks. However, a few days prior to their dissipation, they moved rapidly from nearshore retention areas to deep offshore waters. This may indicate that physical forces acting to retain a krill aggregation, such as an upwelling relaxation event (Botsford et al. 2006), were optimal for aggregation growth, but likely advection and

increased current strength started to act on the aggregation by sheering apart particles (Dorman et al. 2015b) or coastal eddy propagation resulted in transport of the aggregation offshore. Several studies documented increased abundance of zooplankton within upwelling plumes and eddies moving offshore (Keister et al. 2011), so it is likely that these features are also important for understanding movement of krill aggregations offshore. We incorporated DVM behavior into our model, and this is presumed to assist krill in their retention within productive coastal waters (Haury et al. 1978). Furthermore, due to complexity of tracking the fate of individual particles, in our simulations we did not examine whether persistent large aggregations split and form new aggregations, and whether this process influenced rates of formation and dissipation. Although we examined the interactive effects of sea temperature and current strength in our previous study (Dorman et al. 2015b), future research on how ocean physics varies within highly persistent

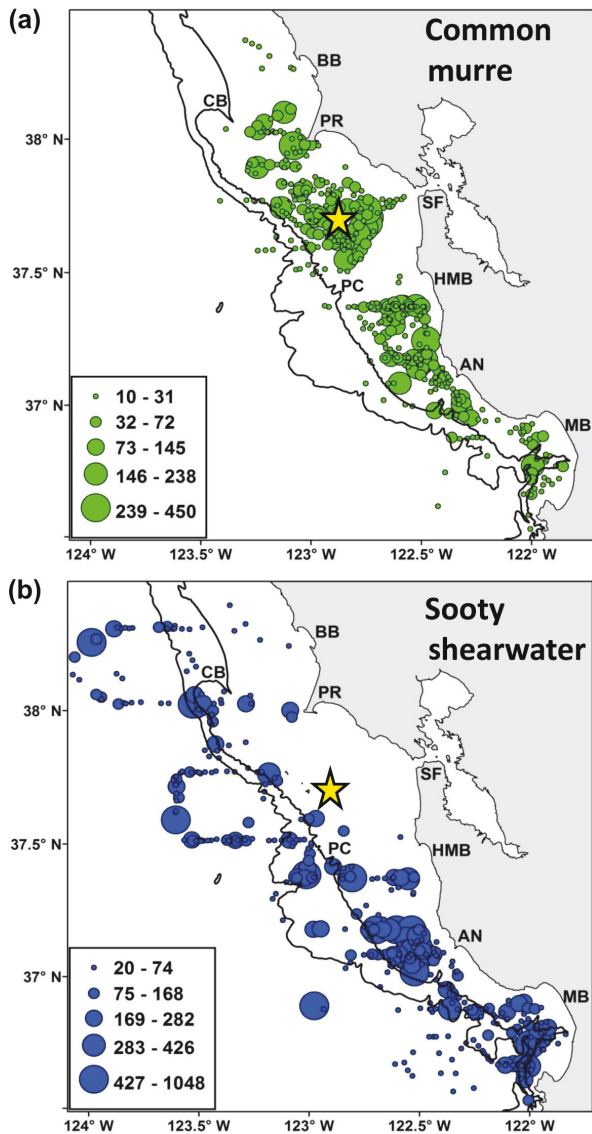


Figure 8. Abundance patterns of observed seabird aggregations (where aggregation size is greater than 10 or 25 individuals for murre and shearwaters, respectively) derived from a decade (2000–2010) of visual surveys collected on the Rockfish Recruitment and Ecosystem Assessment survey during May–June: (a) common murre and (b) sooty shearwater. North to south, BB is Bodega Bay, CB is Cordell Bank, PR is Point Reyes, SF is San Francisco, PC is Pioneer Canyon head, HMB is Half Moon Bay, AN is Año Nuevo, and MB is Monterey Bay.

aggregations should be paramount for understanding the evolution of krill aggregations.

Caveats and krill simulations

There are several caveats regarding our simulation approach that could be improved upon. Since we wanted to examine emergent properties of krill aggregation formation within the California Current Ecosystem using a ROMS-IBM, initial particle seeding was uniform and made to match our previous empirical research using acoustics to infer krill hotspot distribution (Santora et al. 2011b, Dorman et al. 2015b).

New simulations may want to generate a seeding scheme based on where persistent krill aggregations are observed to study their emergence based on the background density and heterogeneity of particles. For example, initial starting points could use random aggregations with variable patch size and intensity. Our krill model included simple DVM behavior, but we turned off other biological aspects of the model such as growth and reproduction to avoid changing population size due to mortality and egg production (Dorman et al. 2015a, b). Future simulations could account for vertical migration depth based on the concentration of food and or physical features, such as pycnocline variation, to assess the sensitivity of aggregations to changes in food availability. Predation on krill aggregations is also an important aspect that should be considered. Our aggregation model could be combined with a behavioral model containing krill predators to investigate not only the effect of predators on aggregation size, intensity and persistence, but also how krill aggregations influence the searching behavior, foraging success and aggregations of fish, seabirds and marine mammals.

Of krill aggregations and predators

Our model of krill aggregations within the GoF encompasses a critical area for large populations of seabirds breeding on the Farallon Islands, and an area utilized by migratory seabirds and baleen whales. We found the spatial distribution of krill aggregations corresponds to the distribution of observed seabird aggregations, suggesting our model displays structural realism at relevant biophysical scales in the California Current Ecosystem (Cury et al. 2008, Santora et al. 2013). Common murre, a central-place breeding species which forages in neritic shelf waters, are highly aggregated throughout the shelf and the vicinity of their breeding colony within the inner GoF where the model indicated some of the most persistent and large krill aggregations were likely to form and reoccur over several weeks. Sooty shearwater, a migratory species that feeds in the shallow sub-surface, was aggregated along the outer shelf-slope and near the sub-marine canyons where krill aggregation are likely to form and persist for several days. Although simple in approach, this evaluation with observed seabird aggregations provides context for future implementation of upper-level predators in behavioral models and understanding scaling of predator-forage interactions in marine ecosystems (Rose 2015).

Our simulations provide context about the occurrence and residence time of statistically large and persistent krill aggregations that predators are likely dependent on for survival and population growth. The occurrence of krill aggregations within the GoF are critically important for the successful feeding of juvenile salmon, juvenile rockfish, and breeding seabirds. For example, previous studies have shown that if juvenile salmon do not encounter sufficient concentrations of krill upon their ocean entry in the GoF, than they will experience higher mortality, resulting in weaker recruitment 2 yr later (Wells et al. 2012). Breeding seabirds are also sensitive to krill availability during a limited time window needed for successful chick survival (Sydeman et al. 2006). Importantly, our simulations indicate there is an increase likelihood of krill aggregations forming and

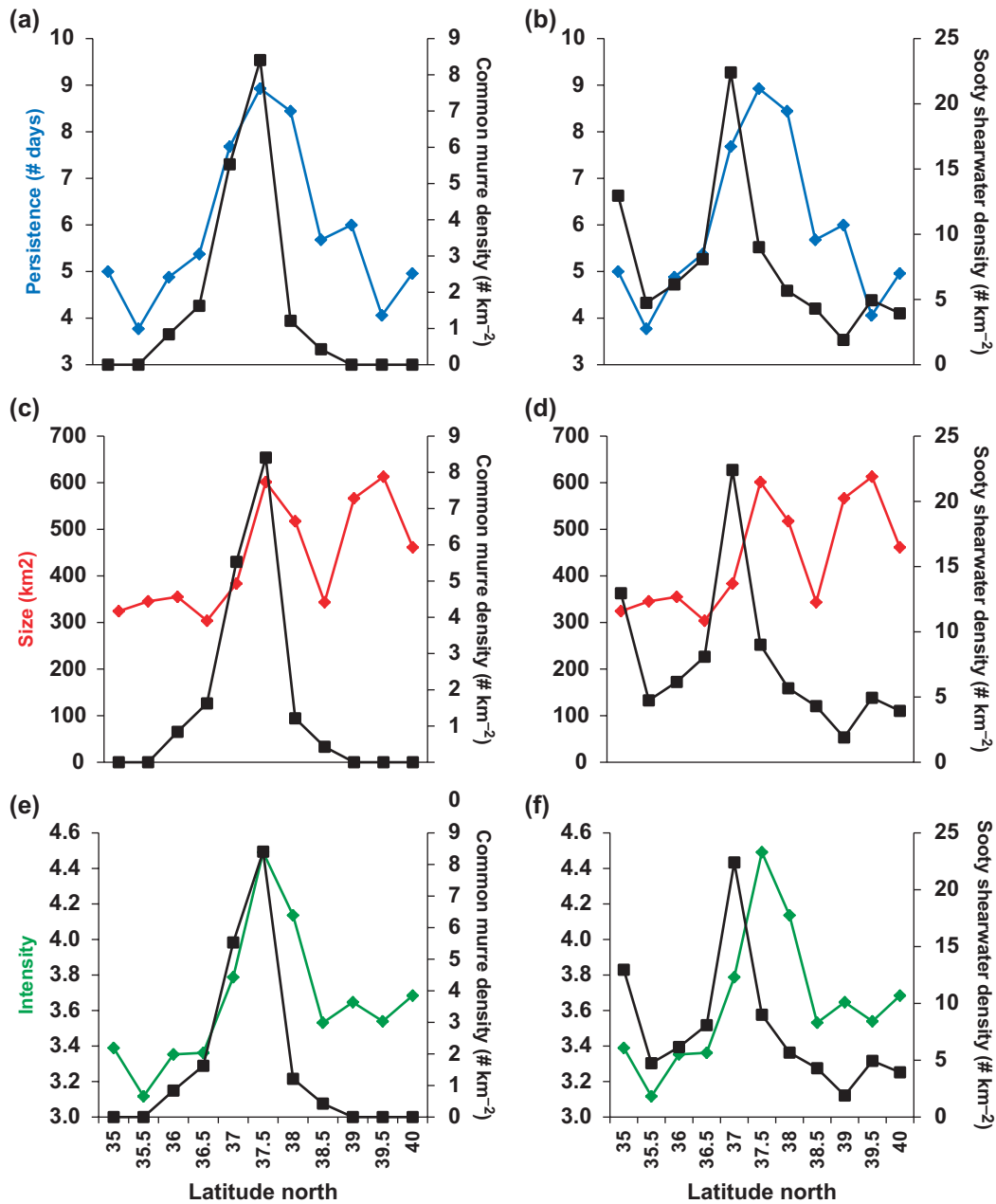


Figure 9. Latitudinal coherence among mean density (km⁻²; May–June) of seabirds (left, common murre; right, sooty shearwater) and (a–b) persistence, (c–d) size and (e–f) intensity of simulated summer time krill aggregations (June).

persisting for multiple weeks in the vicinity of the Farallon Islands. Common murres make daily decisions on where to forage during chick rearing. Their foraging behavior varies with breeding cycle (e.g. different energetics during egg and chick rearing stages), and is ultimately based on forage patch availability, which may be expressed as a function of time/distance spent traveling to and from the colony balanced by the density, number of and distance among prey patches. The increased likelihood of krill aggregations forming in proximity to the Farallon Islands, as well as concentrating aggregations from other regions, makes the GoF incredibly important for the population growth and survival of locally breeding seabirds and juvenile fish.

Migratory species, such as shearwaters and baleen whales, time their migrations to feed in the upwelling waters of the California Current Ecosystem, and it's likely that their decision to forage within this region is based on the availability and patchiness of krill and fish aggregations (Veit et al. 1997, Bailey et al. 2009, Irvine et al. 2014). For example, satellite tracking and theoretical studies of the foraging behavior of blue whales *Balaenoptera musculus*, have shown, through measures of increased residence time, where whales are likely to spend time foraging (Bailey et al. 2009, Irvine et al. 2014). Given the dependency of some species of baleen whales on krill, our simulations of krill aggregation are likely useful for parameterizing whale behavioral and movement

models. Parameters such as encounter rate of krill aggregations expressed as a function of their size, intensity and persistence, are important parameters for modeling investigations on the energetics of feeding whales (Goldbogen et al. 2011) and for making conservation decision regarding preserving critical forage habitat and mitigating potential lethal ship strikes (Redfern et al. 2013). For example, if krill aggregations are more likely to form in particular locations and persist for several weeks, this information could be used to infer probabilities for assessing whale residence time and feeding efficiency in future whale behavioral simulations (Bailey et al. 2009, Goldbogen et al. 2011).

Conclusion

Uncertainty about marine ecosystem spatial structure may be improved if realistic oceanographic-ecosystem models are used to assess the scales of variability of krill aggregations. Importantly, empirical and modeling studies are needed to understand where krill aggregations are likely to occur, and our work builds on several field-based and modeling investigations. Although not discussed here, we previously evaluated the coherence among observed and modeled krill aggregations patterns (Santora et al. 2013, Dorman et al. 2015b), but here we expanded our evaluation process by assessing the coherence between modeled krill and observed seabird aggregation patterns. In summary, our study revealed: a) there are clear functional relationships among size, intensity and persistence of krill aggregations, b) large and persistent krill aggregations are rare and dependent on location of formation, c) coastal upwelling areas may act as sources of aggregations for other areas, d) highly persistent krill aggregations were more likely to form near a major seabird colony, and e) observations of seabird species distribution verify structural realism of predicted krill aggregations.

Our previous modeling work evaluated the importance of DVM for assessing coherence between modeled and observed krill aggregations off California (Dorman et al. 2015b). Here we've shown that including simple DVM, an important krill behavior that plays a key role in the formation and retention of krill aggregations, along with ocean physics (e.g. upwelling and transport patterns) and a hotspot clustering index can lead to realistic distribution patterns of krill aggregations and inform scaling aspects of aggregation size, intensity and persistence. This critical finding may allow our approach to be generalized to other krill-centric ecosystems (e.g. Antarctic). Understanding the scaling of krill aggregations will benefit future ecosystem assessment research and survey design, and future modeling aimed at predicting the impact of the availability of krill aggregations on the foraging success of krill predators.

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Supplementary material (Appendix ECOG-02250 at <www.ecography.org/appendix/ecog-02250>). Appendix 1–2.