

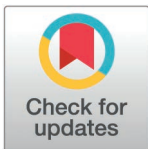
RESEARCH ARTICLE

Ecological vs. climate uncertainty in future marine ecosystems: Lessons learned from krill in a major upwelling region

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Abstract

Krill is a central organism in the food web of many marine ecosystems and eastern boundary current upwelling regions specifically. Here, a superensemble of climate and ecological models is used to determine drivers of future change, variability, and uncertainty in krill abundance for the California Current. While krill is projected to slowly decrease throughout the 21st century, the long-term trend consistently exceeds natural variability only under extreme warming. Similarly, unprecedented low krill years are expected to progressively increase, but their frequency of occurrence will depend on background abundances tied to low-frequency climate variability. The relative contributions of warming rate and ecological model formulation to projected uncertainty are comparable and reflect latitudinal changes in the magnitude of climate forcing and availability of empirical data to parameterize krill models. This finding highlights the fact that uncertainty in climate change impacts on coastal upwelling ecosystems may depend as strongly on model formulation as they do on anthropogenic forcing. Furthermore, the increasingly divergent krill model responses outside of the core domain for which they were originally implemented advocate for regionally tailored projections and models to reduce overall uncertainty. By identifying and quantifying uncertainty sources in future krill abundance across relevant time scales, the present study lays the foundation for understanding how the superposition of long-term trends, low-frequency variability, and extreme events may lead to unprecedented ecosystem states, and for assessing their broader impacts on altered presence, distribution, and recovery of species that directly or indirectly depend on krill.

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1. Introduction

Due to their integral position in the food web of many large marine ecosystems, euphausiids (hereafter, krill) play an important role in transferring energy to higher trophic level species and, as such, support important ecosystem services world-wide [1,2]. In the California Current Ecosystem (CCE), one of the four major eastern boundary current upwelling regions, krill abundance and distribution undergo substantial seasonal to decadal fluctuations and reflect spatial heterogeneity associated with coastal upwelling intensity and bathymetric features [3–7]. Oftentimes, this spatiotemporal variability impacts the distribution, behavior, and overall population dynamics of higher trophic level predators relying directly or indirectly on krill [8–11]. For instance, studies have revealed that alongshore locations where krill hotspots (i.e., persistent areas of high abundance) occur in the CCE coincide with observed increased presence of whales and seabirds [4–7,12], demonstrating the close linkage between krill and higher trophic levels that contributes to ecosystem scale patterns. As many of these higher trophic level species have important ecological, cultural, and commercial values, projecting changes in krill abundance and distribution is critical for assessing future ecosystem states and informing fishery management actions [13,14].

In the North Pacific, increases in krill abundance have historically occurred during years of cooler waters and declines during periods of warmer ocean conditions [15–17]. In the CCE, unfavorable conditions can result from isolated events, such as El Niño years [18] and marine heatwaves [10,19], or prolonged periods of basin-scale variability associated with positive phases of the Pacific Decadal Oscillation (PDO; [20]) and negative phases of the North Pacific Gyre Oscillation (NPGO; [21]). While multi-decadal ecosystem monitoring of krill and concurrent environmental variability have informed the development of novel predictive models aimed at understanding the location, persistence, and intensity of krill hotspots [2], the limited spatial and seasonal coverage of these surveys remains a challenge in the CCE and elsewhere. Therefore, numerical models that couple ocean climate variability and lower trophic level ecosystem processes are important tools for exploring historical and future patterns and drivers of krill variability.

Three fundamentally different krill model formulations are used here to produce high-resolution (~10 km) regional projections of 21st century krill abundance in the CCE under lower, average, and higher warming rates associated with the Representative Concentration Pathway 8.5 (RCP8.5) high emissions scenario [22,23]. While associated with RCP8.5, the lower warming rate considered here is also representative of the expected mean warming under the more moderate RCP4.5 emissions scenario. All three krill models have demonstrated skill in reproducing observed alongshore, seasonal, and interannual variability of krill aggregations in the CCE and consist of a Eulerian deterministic Nutrient-Phytoplankton-Zooplankton model [6], a Lagrangian deterministic growth-advection model [7], and a Eulerian statistical species distribution model [5]. By incorporating uncertainty associated with warming rate and krill dynamics, this superensemble approach not only yields insights into responses

robustly identified across projections but also quantifies the relative importance of uncertainty sources associated with anthropogenic change and ecological processes. One of the main results highlighted here is that, despite extensive calibration and evaluation under historical conditions, functionally different krill models can exhibit divergent responses to future climate conditions, with uncertainty comparable to that of the projected warming range under RCP8.5. This finding reinforces the notion that accurately predicting the long-term evolution of fundamental ecological properties of Large Marine Ecosystems depends at least as strongly on model formulation as it does on anthropogenic forcing (e.g., [24]).

2. Methods

2.1. Downscaled climate projections

Future climate change and variability in the CCE are described by three regional ocean projections forced by the GFDL-ESM2M [25], IPSL-CM5A-MR [26], and Hadley-GEM2-ES [27] earth system models (ESMs) under the RCP8.5 high emissions scenario. These models were selected for their inclusion of marine biogeochemical fields and to represent the spread of physical and biogeochemical futures in the CMIP5 ensemble. GFDL-ESM2M (hereafter referred to as “Lo8.5”) has a lower warming rate and higher primary production; IPSL-CM5A-MR (hereafter referred to as “Av8.5”) has a rate of warming and primary production representative of the CMIP5 ensemble mean; and Hadley-GEM2-ES (hereafter referred to as “Hi8.5”) has a higher warming rate and lower primary production [22,28]. While the projections are all run under the RCP8.5 high emissions scenario, the magnitude of the ensemble spread is such that the GFDL solution provides a realistic approximation for the mean warming rate expected under the more moderate RCP4.5 emissions scenario (Fig A in [S1 Text](#)). Hence, the three projections can be regarded as representative of mean RCP4.5 warming (GFDL, “Lo8.5”), mean RCP8.5 warming (IPSL, “Av8.5”), and extreme RCP8.5 warming (Hadley, “Hi8.5”).

The ocean circulation component of the downscaled projections is an implementation of the Regional Ocean Modeling System (ROMS) [29,30] for the broader California Current region (30°N to 48°N and 116°W to 134°W), with a horizontal grid resolution of 1/10° (ca. 10 km) and 42 non-uniform terrain-following vertical levels. The biogeochemical component, called NEMUCSC, is a customized version of the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) model [31] specifically parameterized for the CCE [6,32]. NEMUCSC includes three limiting micronutrients (nitrate, silicate, ammonium), two phytoplankton functional groups (nanophytoplankton and diatoms), three zooplankton functional groups (micro, meso, and predatory zooplankton), and dissolved and particulate detritus. The downscaled projections use a time-varying delta method to produce a continuous, bias-corrected solution of 21st century climate change effects in the CCE [22,33] and they have served as the basis for many studies addressing future ecosystem states from physical and biogeochemical properties [22,23] to forage fish [34,35] and top predators [36].

2.2. Krill model formulations

The three krill models considered here predict the spatiotemporal distribution patterns of *Euphausia pacifica*, the most abundant euphausiid (krill) in the CCE [3,4,15], and are informed by decades of ecosystem surveys involving acoustics, mid-water trawls for krill abundance, and applied visual surveys of predators [2,37]. Specifically, the models reproduce observed spring and summer occurrence and persistence of krill hotspots associated with known upwelling centers in the southern, central, and northern regions of the CCE. Predicted krill abundance is typically higher in the central bioregion (due to the presence of extensive shelf, slope, and submarine canyon habitat) and lower in the northern bioregion with fewer persistent hotspots. In the southern bioregion, the models consistently indicate the presence of a large and persistent krill hotspot around Point Conception (~34.5°N). The ability of the three krill models to account for observed variability during the recent historical period justifies their implementation in the downscaled projections to evaluate how the abundance and distribution of krill in the CCE may shift under changing climate conditions. A summary of the three krill model formulations, including input variables, strengths, and limitations, is provided in Table A in [S1 Text](#).

The Eulerian krill model (hereafter referred to as “NPZ”) is simply represented by the predatory zooplankton functional group of NEMUCSC. This zooplankton group has been parameterized to represent *Euphausia pacifica*, the numerically dominant euphausiid in the CCE, via growth rates and diet preferences reported in the literature [38,39]. Based on a 1990–2010 hindcast, the coupled ROMS-NEMUCSC model exhibits substantial skill in reproducing observed krill hotspots and identifies strong patterns of alongshore and seasonal variability in the intensity of these hotspots [6].

The Lagrangian growth advection model (hereafter referred to as “GA”) is a method that couples horizontal Lagrangian surface trajectories originating at the coast with a plankton model initialized by nutrient input from coastal upwelling [40]. The plankton model predicts the evolution of phytoplankton and zooplankton functional groups within surface water masses as they get advected offshore, with the large zooplankton group parameterized to represent krill. The plankton model output is mapped onto the Lagrangian trajectories and combined into daily, then monthly maps at 1/8° resolution. Despite solely incorporating information about coastal nitrate supply (via nearshore upwelling intensity and nitrate concentration at 60 m depth), near-surface advection (via 0–30 m depth-averaged currents), and temporal lags created by plankton dynamics, GA is able to reproduce climatological and interannual variability of hindcast krill concentrations from the full ROMS-NEMUCSC model when forced by the same fields, and compares favorably with in situ surveys [7].

The species distribution model (hereafter referred to as “SDM”) is a statistical tool that merges observed krill abundance (catch-per-unit-effort; CPUE) with coincident environmental data to evaluate habitat associations of a species, and then use those relationships to predict geographic distribution for places and times where direct observations are not available. The krill SDM is based on a previously published version [5] but updated to extend predictions back to 1990, across spring and summer months (i.e., May–August), and include all krill observations from 35 to 42°N. For model fitting, bathymetric and environmental variables (e.g., wind stress, ocean surface currents, temperature, and stratification) were taken from the hindcast period corresponding to the downscaled projections [22]. Boosted regression trees trained on monthly data for May–June were used to model krill distributions and performed similar to published models [5], capturing ~48% of the variance and exhibiting similar species-habitat relationships.

2.3. Analysis framework

The analysis focuses on the region between 35 and 42°N and months from May to August (hereafter referred to as the “upwelling season”) because all three krill models have been primarily calibrated and evaluated for this latitudinal range and season. Since GA and SDM do not explicitly resolve depth, only the uppermost layer values for NPZ are considered here for consistency. To enable comparison across projections, standardized relative abundances are calculated independently for each krill model (NPZ, GA, or SDM) as:

$$\text{Standardized Krill} = (\text{Krill} - \text{Mean}) / \text{SD}$$

$$\text{where Mean} = (\text{Mean}_{\text{Lo8.5}} + \text{Mean}_{\text{Av8.5}} + \text{Mean}_{\text{Hi8.5}}) / 3$$

$$\text{SD} = (\text{SD}_{\text{Lo8.5}} + \text{SD}_{\text{Av8.5}} + \text{SD}_{\text{Hi8.5}}) / 3$$

with “Mean_{xxx}” and “SD_{xxx}” denoting the 2000–2020 mean and standard deviation of krill abundance spatially averaged over the central CCE region (i.e., 35–42°N and 0–100 km offshore; see black outline in Fig 1). This approach yields unitless krill values comparable across models (i.e., NPZ, GA, and SDM) and ESM solutions (i.e., Lo8.5, Av8.5, and Hi8.5) that can be combined into a 9-member superensemble integrating the effects of differing rates of anthropogenic warming and krill dynamics. Standardized krill abundances are further averaged from the coast to

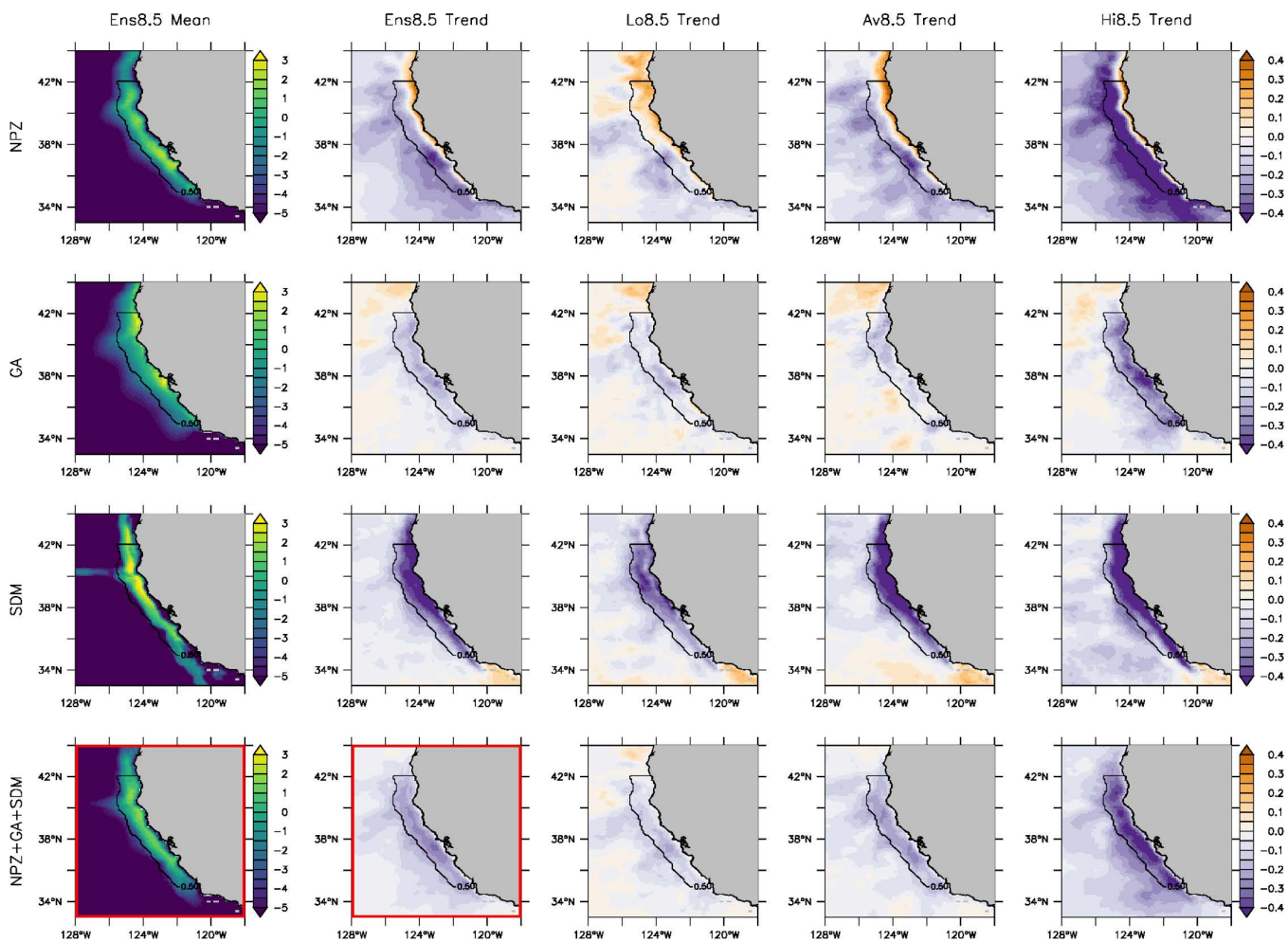


Fig 1. Projected relative krill abundance (standardized) in the central CCE for 2000-2100 from the 9-member superensemble. Column 1: Lo8.5+Av8.5+Hi8.5 ensemble mean. Column 2: Lo8.5+Av8.5+Hi8.5 ensemble trend. Column 3-5: Lo8.5, Av8.5 and Hi8.5 trends. From top to bottom: NPZ, GA, SDM, and NPZ+GA+SDM ensemble. The 9-member superensemble mean and trend are displayed in the first and second panels of the bottom row and highlighted with a red outline. All trends represent a change in standardized abundance per decade. The black outline in all panels identifies the central CCE coastal region (35–42°N, 0–100 km offshore). The coastline information is from [geo_borders_intermed.nc](https://github.com/NOAA-PMEL/FerretDatasets/archive/refs/tags/v7.6.zip) openly distributed in <https://github.com/NOAA-PMEL/FerretDatasets/archive/refs/tags/v7.6.zip>.

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100 km offshore (black outline in Fig 1) to characterize alongshore patterns of climate change, variability, and extremes. Since the three krill models have different native units, “abundance” is used here as a collective term referring to the standardized (unitless) values.

The long-term trend (i.e., climate change signal) is quantified using a linear regression analysis applied either by grid cell or to spatially averaged values over the full 2000–2100 projection period. Since krill values are standardized, the trend is relative to the historical standard deviation and expressed here as a change per decade (i.e., equivalent change in krill abundance over a 10-year period based on the 2000–2100 trend). Attributing long-term change to a specific mechanism for each krill model is determined by linearly regressing trends in relative krill abundance with those from explanatory environmental variables (i.e., upwelling-favorable wind stress, sea surface temperature, surface nitrate concentration, and total surface phytoplankton concentration) as a function of warming rate.

Low-frequency climate variability is identified using a multivariate Empirical Orthogonal Function (mEOF) decomposition combining projected krill abundances and environmental variables (i.e., sea surface height, temperature, nitrate concentrations, phytoplankton concentrations, and meridional wind stress). To eliminate the climate change signal and facilitate the identification of low-frequency variability, all variables are detrended and smoothed with a 5-year running mean prior to analysis. The environmental variables are also scaled by their respective historical (2000–2020) standard deviation averaged over 35–42°N and 0–100 km offshore (black outline in Fig 1) to remove units and normalize variability in the mEOFs. Since temporal variability is not expected to be synchronous across ESM solutions (i.e., each ESM is a free running evolution of the Earth’s coupled land-ocean-atmosphere system), low-frequency patterns must be identified separately for the Lo8.5, Av8.5, and Hi8.5 ensembles. The mEOF modes for each warming rate are subsequently recast into the superensemble framework by combining their spatial (alongshore) patterns and fast Fourier transform (FFT) of their temporal amplitudes (i.e., while temporal variability across ESM solutions is not expected to be synchronous, identifiable modes of low-frequency variability should nonetheless exhibit similar dominant frequency contents). Only the leading mEOF mode is presented here, as it accounts for ~40% of the explained variance in the projections and is readily attributable to a known mode of basin-scale climate variability (i.e., Pacific Decadal Oscillation).

Krill “extremes” are defined as years when relative abundances during the upwelling season (i.e., May–August) exceed 2 standard deviations above or below the mean for a given latitude, where the mean and standard deviation are calculated based on the 2000–2020 reference (“historical”) period. Similarly, unprecedented conditions (climate “novelty”) are defined as years when relative krill abundances during the upwelling season exceed the minimum or maximum historical values. While the meaning of “unprecedented” is relatively straightforward (i.e., conditions for which no historical analog exists), the definition of “extreme” is more variable and context dependent in the literature. Using 2 standard deviations above or below the mean is a relatively strict criterion as it represents extreme highs or lows occurring only ~2.5% of the time (i.e., ~1 in 40 year event). Here, these definitions are explicitly meant to identify how the superposition of interannual fluctuations, low-frequency climate variability, and long-term change will lead to anomalously high or low krill abundances relative their present-day range of expected variability. Spatiotemporal changes in extreme and unprecedented conditions produced by each superensemble member are identified as the fraction of years above or below the thresholds by decade and 0.5° latitude bins. Note that unprecedented years generally represent a subset of extreme years, except for latitudes where the minimum or maximum value for 2000–2020 does not exceed 2 standard deviations from the mean.

Producing a superensemble offers the possibility to quantify different sources of uncertainty in the projections. Here, uncertainty is separated into two components: “climate uncertainty” referring to the spread associated with different climate models (and consequently different warming rates), and “krill uncertainty” referring to the spread associated with different krill model formulations. The two quantities are defined and calculated as:

$$\text{Climate Uncertainty} = \left[\left((Krill_{Lo8.5} - Krill_{Mean})^2 + (Krill_{Av8.5} - Krill_{Mean})^2 + (Krill_{Hi8.5} - Krill_{Mean})^2 \right) / 3 \right]^{0.5}$$

$$\text{where } Krill_{Lo8.5} = (Krill_{NPZ,Lo8.5} + Krill_{GA,Lo8.5} + Krill_{SDM,Lo8.5}) / 3$$

$$Krill_{Av8.5} = (Krill_{NPZ,Av8.5} + Krill_{GA,Av8.5} + Krill_{SDM,Av8.5}) / 3$$

$$Krill_{Hi8.5} = (Krill_{NPZ,Hi8.5} + Krill_{GA,Hi8.5} + Krill_{SDM,Hi8.5}) / 3$$

$$\text{Krill Uncertainty} = \left[\left((Krill_{NPZ} - Krill_{Mean})^2 + (Krill_{GA} - Krill_{Mean})^2 + (Krill_{SDM} - Krill_{Mean})^2 \right) / 3 \right]^{0.5}$$

$$\text{where } Krill_{NPZ} = (Krill_{NPZ,Lo8.5} + Krill_{NPZ,Av8.5} + Krill_{NPZ,Hi8.5}) / 3$$

$$Krill_{GA} = (Krill_{GA,Lo8.5} + Krill_{GA,Av8.5} + Krill_{GA,Hi8.5})/3$$

$$Krill_{SDM} = (Krill_{SDM,Lo8.5} + Krill_{SDM,Av8.5} + Krill_{SDM,Hi8.5})/3$$

For both quantities, $Krill_{Mean}$ represents the full ensemble mean defined as the mean of the 9 ensemble members. Note that because of cross-contributions, the sum of climate and krill uncertainty is not identical to total uncertainty defined as the full ensemble spread where the contribution of each ensemble member relative to the ensemble mean is independently considered (i.e., $Krill_{Mean}$ remains the same, but the spread calculation includes 9 distinct terms).

3. Results

Projected 21st century ensemble means for NPZ, GA, and SDM exhibit comparable krill patterns, with maximum abundance occurring within ~100 km from the coast and decreasing offshore (Fig 1, left column). These patterns are consistent with the observed geographical range of krill along the U.S. west coast [4] and those produced by the three models for recent historical conditions [5–7]. Projected long-term change is more variable across model formulations and warming rates, ranging from a mix of increasing and decreasing krill abundances for NPZ under lower warming to a substantial region-wide decline for SDM under higher warming (Fig 1, columns 2–5). However, NPZ, GA, and SDM have qualitatively similar responses across warming rates, with the smallest long-term change occurring for Lo8.5 and the largest being associated with Hi8.5.

The following sections examine the dominant climate change, variability, and extreme patterns emerging from the superensemble, and the extent to which these signals are robustly identified considering uncertainty associated with krill model formulation and warming rate. To reflect the area of largest change predicted by all 9 ensemble members, trends, variability, and extremes are characterized for the region 35–42°N using longitudinally averaged quantities between 0–100 km offshore (Fig 1, black outline in all panels).

3.1. Climate change

The 2000–2100 superensemble trend indicates that long-term change in the central CCE will be characterized by a reduction in relative krill abundance at all latitudes (Fig 2, top panels). The magnitude of the change is relatively uniform with latitude and suggests a decrease per decade equal to ~20% of present-day variability (i.e., 2000–2020 standard deviation). In contrast, the relative importance of uncertainty sources for the trend exhibits a clear latitudinal pattern, with krill model uncertainty becoming progressively more important as latitude increases (from ~30% at 35°N to ~70% at 42°N) (Fig 2, top panel). For NPZ and GA, the long-term decrease in relative krill abundance is strongly related to changes in coastal upwelling intensity and nitrate concentrations, whereby the central CCE is becoming progressively less productive as warming rate increases (Fig B in S1 Text). For SDM, which does not explicitly include biogeochemical forcing, the projected decrease in relative krill abundance is directly associated with increasing sea surface temperature but also reflects reduced upwelling intensity and nitrate concentrations.

Based on relative krill abundances averaged latitudinally over the central CCE, the “emergence” of the anthropogenic signal (i.e., year when the standardized trend falls 1 historical standard deviation below the historical mean) varies substantially across warming rates and krill models (Fig 2, bottom panels). For the lower and moderate warming rates (Lo8.5 and Av8.5), SDM emerges relatively rapidly (~2030), while NPZ and GA do not emerge by the end of the century. In contrast, under higher warming (Hi8.5), all three model formulations emerge by mid-century. Furthermore, the responses of the three krill models are remarkably in-phase for a given warming rate (cross-correlations between NPZ, GA, and SDM in the range of 0.41–0.63 for Lo8.5, 0.52–0.63 for Av8.5, and 0.65–0.76 for Hi8.5), which suggests that environmental forcing on projected relative krill abundances in the central CCE manifests similarly in the models despite their functionally different formulations.

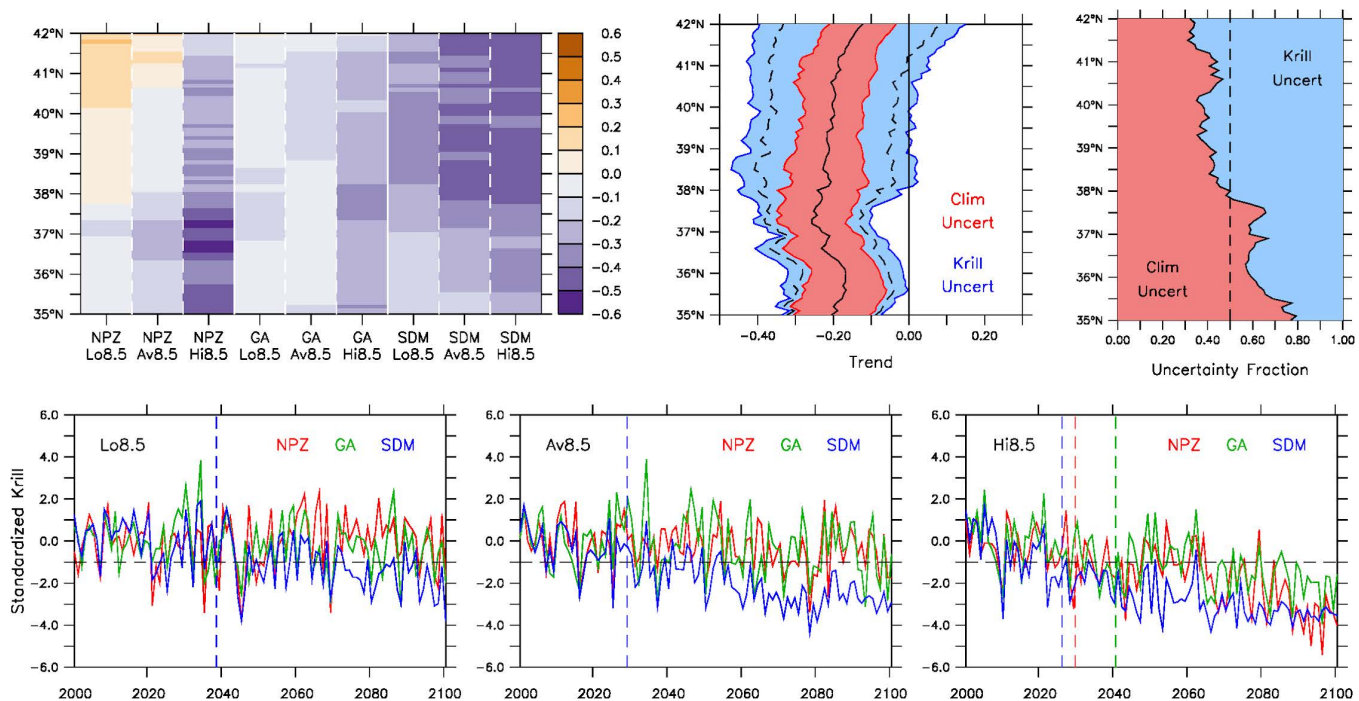


Fig 2. Projected trend, uncertainty, and year of emergence of zonally-average (0-100 km offshore) relative krill abundance for 2000-2100 in the central CCE (see black outline in Fig 1). Top left: trend for the 9 superensemble members. Top center: super ensemble trend (black line) with climate uncertainty (red shading), krill uncertainty (blue shading), and ensemble spread (black dashed lines). Top right: fraction of superensemble trend uncertainty associated with climate uncertainty (red shading) and krill uncertainty (blue shading). Bottom: latitudinally-averaged (35-42°N) relative krill abundances for Lo8.5 (left), Av8.5 (center), and Hi8.5 (right) ensembles; the vertical dashed lines indicate the year when the 2000-2100 trend for NPZ (red), GA (green), and SDM (blue) exceeds 1 standard deviation (horizontal dashed line) below the 2000-2020 mean (note that not all models reach the threshold).

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3.2. Climate variability

The leading detrended mode of climate variability identified by the multivariate Empirical Orthogonal Function (mEOF) analysis is consistent across warming rates and accounts for 45%, 39%, and 46% of the total explained variance in Lo8.5, Av8.5, and Hi8.5, respectively. The mode is characterized by a synchronous response across latitudes, with projected relative krill abundance in NPZ, GA, and SDM varying in phase with nitrate, phytoplankton concentrations, and equatorward wind stress, and out of phase with sea surface height and sea surface temperature (Fig 3, top panels). The amplitude of krill abundance associated with mode 1 is relatively uniform with latitude in the northern part of the domain (38-42°N) and becomes progressively weaker at lower latitude (35-38°N) (Fig 3, bottom panels). The relative importance of uncertainty sources is opposite to that of the long-term trend, whereby uncertainty associated with warming rate increases progressively with latitude (from ~30% at 35°N to ~70% at 42°N).

As expected, the temporal amplitudes of mode 1 for Lo8.5, Av8.5, and Hi8.5 exhibit similar, but not necessarily in-phase, variability, which precludes direct averaging (Fig 3, middle panels). In the frequency domain, spectral (FFT) peaks are reliably identified across all warming rates (i.e., low climate uncertainty) at periods of approximately 14 and 24 years (Fig 3, bottom right panel). Furthermore, correlations between the temporal amplitude of mode 1 for Lo8.5, Av8.5, and Hi8.5 from the downscaled projections and sea surface heights and temperatures in the North Pacific from their respective earth system model solutions exhibit a strong correspondence with the known spatial expression of the PDO (Fig C in S1 Text).

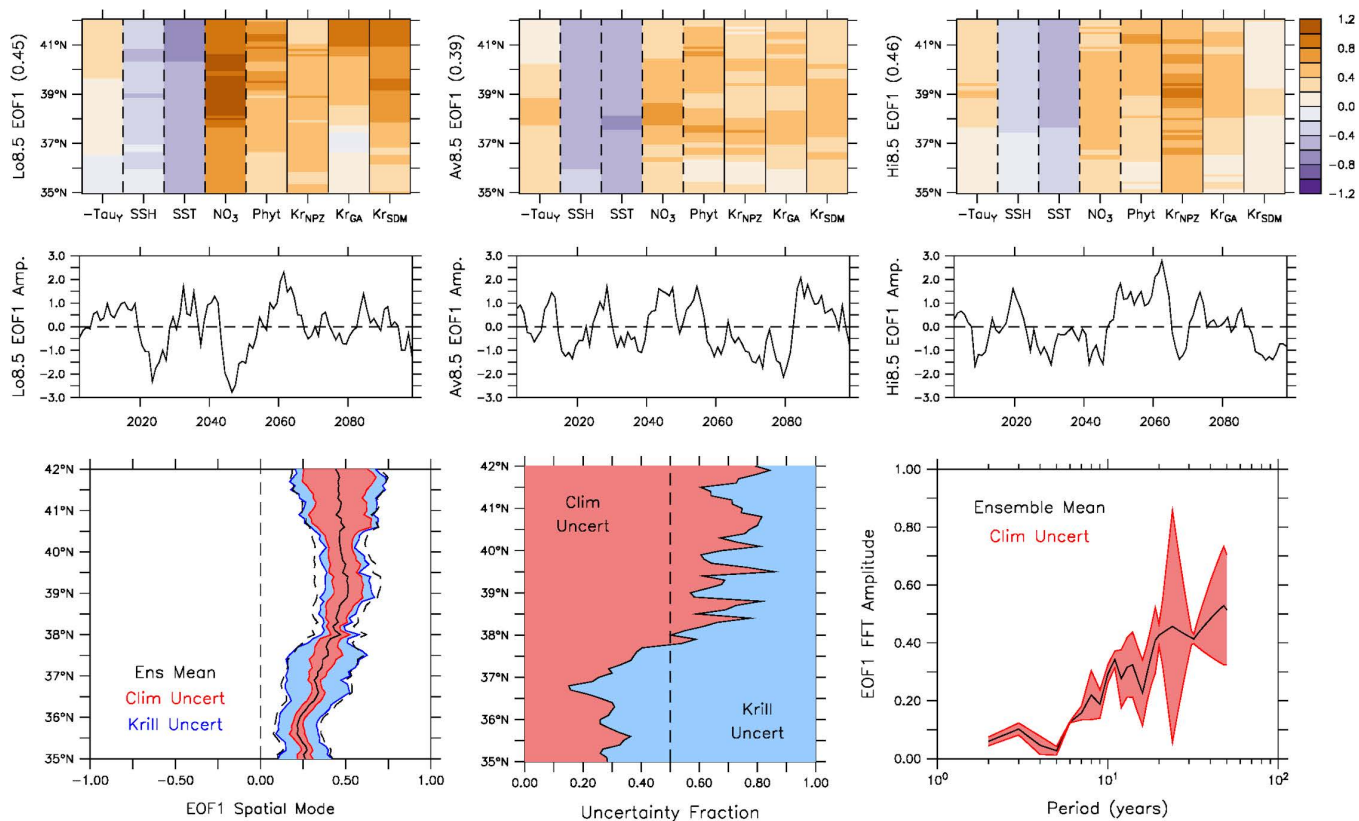


Fig 3. Projected climate variability and uncertainty of relative krill abundance in the central CCE for 2000–2100. Top: EOF 1 spatial amplitudes for standardized upwelling-favorable wind stress ($-\tau_y$), SSH, SST, surface nitrate concentration, surface phytoplankton concentration, and surface krill abundance from NPZ, GA, and SDM for Lo8.5 (left), Av8.5 (center), and Hi8.5 (right). Middle: EOF 1 temporal amplitude for Lo8.5 (left), Av8.5 (center), and Hi8.5 (right). Bottom left: superensemble mean EOF 1 spatial amplitude (black line) with climate uncertainty (red shading), krill uncertainty (blue shading), and ensemble spread (black dashed lines). Bottom center: fraction of superensemble EOF 1 spatial amplitude uncertainty associated with climate uncertainty (red shading) and krill uncertainty (blue shading). Bottom right: fast Fourier transform (FFT) amplitude of superensemble EOF 1 temporal amplitude (black line) with climate uncertainty (red shading). The percent of the total variance explained by EOF 1 is 45% for Lo8.5, 39% for Av8.5, and 46% for Hi8.5. All variables are detrended, low-pass filtered (5-year running mean), and standardized prior to computing the EOFs.

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3.3. Climate extremes and novelty

The projected occurrence of extreme and unprecedented high and low relative krill abundances in the central CCE exhibits substantial differences across model formulations and warming rates, ranging from limited change for NPZ and GA under Lo8.5 to a pronounced increase in extreme and unprecedented lows under Hi8.5, especially for NPZ and SDM (Fig D and Fig E in [S1 Text](#)). Given the overall tendency of the 9 ensemble members toward a long-term reduction in krill abundance, the results focus here on the future occurrence of anomalously low conditions.

Relative to the historical baseline (i.e., 2000–2020 mean and standard deviation), the frequency of extreme and unprecedented conditions in the central CCE is projected to increase from about 1 in 10 years during 2020–2040 to 3–4 extreme years and 2–3 unprecedented years per decade by the end of the century (2070–2100) (Fig 4, top left panel). Considering that the frequency of occurrence of extreme and unprecedented conditions track each other, severely anomalous low krill years in the future will likely coincide with abundances below the present-day envelope. However, there is relatively large uncertainty in projected occurrences, as evidenced by comparable superensemble mean and spread for most decades. While warming rate and model formulation contribute similarly to uncertainty in the frequency

of occurrence of extreme years before 2050, the latter becomes more dominant (~70% of uncertainty) by the end of the century (Fig 4, top right panel). A similar pattern exists for unprecedented conditions, but with an overall larger impact of warming rate on uncertainty (i.e., approximately equivalent to that of model formulation during the second half of the century). The dominant source of uncertainty also exhibits noticeable multi-decadal variability (i.e., 2030–2050 vs. 2050–2070 vs. 2080–2100), suggesting that the superposition of low-frequency climate variability and climate change determines the occurrence of extreme krill abundances as the two processes are differentially affected by uncertainty due to warming and model formulation.

When averaged over the last 30 years of the century, the projected response is relatively uniform alongshore, although southern latitudes (35–37°N) generally exhibit a lower frequency of occurrence of extreme and unprecedented conditions, a smaller ensemble spread, and a relatively larger contribution of warming rate to uncertainty (Fig 4, bottom panels). This pattern presumably reflects the large negative trend in krill abundance projected by SDM in the northern half of the domain, which increases both the spread across model formulations and the occurrence of severely low conditions by the end of the century (see Fig 2). Most extreme low krill years at a given latitude will also coincide with unprecedented abundances, and the impact of warming on uncertainty is larger for unprecedented conditions than for extreme conditions. Furthermore, the relative contributions of emissions scenario and model formulation to uncertainty parallel those of the

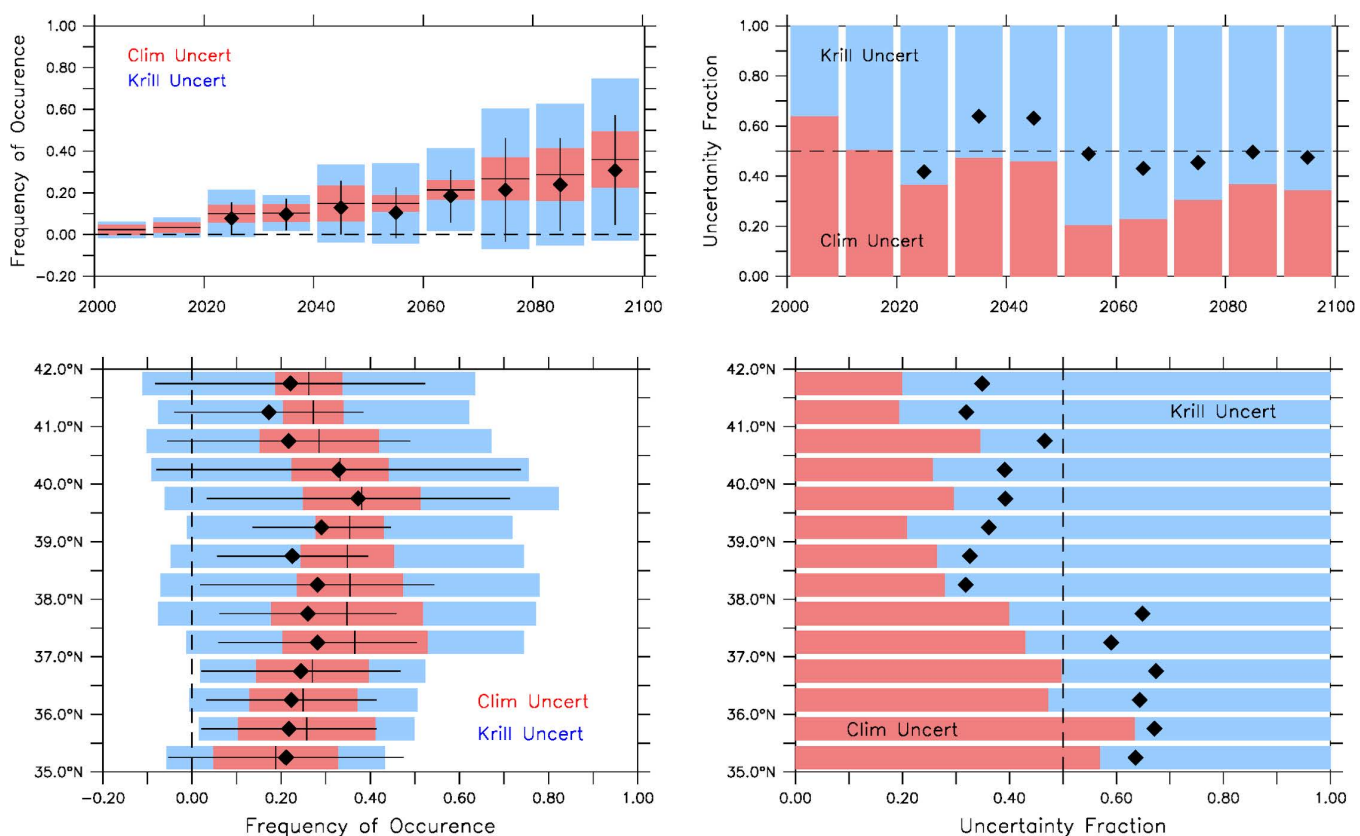


Fig 4. Projected climate extremes, novelty, and uncertainty of relative krill abundance in the central CCE. Top: Frequency of occurrence (left) and uncertainty fraction (right) of extreme (bars) and unprecedented (diamonds) low abundances averaged over 35–42°N by decade. Bottom: Frequency of occurrence (left) and uncertainty fraction (right) of extreme (bars) and unprecedented (diamonds) low abundances averaged over 2070–2100 by 0.5° latitude bins. For extreme lows (2 standard deviations below the mean for the 2000–2020 reference period), red shading represents climate uncertainty and blue shading represents krill uncertainty. For unprecedented lows (below the minimum for the 2000–2020 reference period), vertical lines denote superensemble spread.

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long-term trend (see Fig 2), which suggests that uncertainty patterns associated with climate change may similarly influence the detection of climate extremes.

4. Discussion

The consensus across superensemble members is that the central CCE (35–42°N) will experience a long-term decline in relative krill abundance over the course of the 21st century, resulting in progressively more frequent extreme and unprecedented low conditions. By 2100, relative krill abundance is projected to decrease by about twice the magnitude of present-day variability, with a spread ranging from limited change to 4 standard deviations. However, based on latitudinally-averaged abundances, the long-term trend from each krill model only exceeds natural variability before the end of the century under a higher warming rate (Hi8.5). For all krill models, the long-term decline in krill abundance is directly (NPD and GA) or indirectly (SDM) associated with decreases in both coastal upwelling intensity and nutrient supply, although recent work suggests that nutrient content in upwelled waters may be the stronger determinant to reduced productivity in the CCE [23].

Incorporating functionally different krill model formulations into the projections is particularly valuable for understanding how uncertainty about climate change and krill dynamics influence the predictability of future ecosystem properties, such as long-term trends, low-frequency variability, and extreme events. The present findings highlight the fact that climate and krill uncertainty sources are comparable, but that their relative importance exhibits regional differences and depends on the property considered. While all properties suggest a transition in the dominant source of uncertainty around 38°N, warming rate has a stronger influence on the long-term trend and extreme events at lower latitudes and on low-frequency variability at higher latitudes. This north-south separation likely reflects latitudinal variations in the strength of the climate signal and limitations in data availability to parameterize and evaluate the krill models. For long-term change and extremes, krill model formulations produce comparable patterns in relative abundance for a particular warming rate in the region for which they were originally implemented but exhibit progressively more divergent behaviors to climate forcing when moving away from that region. This behavior is likely magnified for extreme and unprecedented conditions since their identification requires the krill models to consistently predict a combination of two properties (i.e., trend and variability). For low-frequency variability, the relationship between cumulative upwelling and the PDO (i.e., dominant mode of variability identified here) in the CCE is known to strengthen with latitude [41], thereby suggesting that uncertainty depends more strongly on krill model formulation where climate forcing is weaker (i.e., at lower latitudes) and on differences in the PDO signal across earth system models and warming rates where climate forcing is stronger (i.e., at higher latitudes) [42].

By quantifying uncertainty (and its sources) in future krill abundance across relevant time scales associated with climate variability and change, this study lays the foundation for understanding how the superposition of long-term trends, low-frequency variability, and extreme events may lead to unprecedented conditions that could ultimately impact broader ecosystem function. For instance, knowing the upper and lower bounds of expected krill variability under future compound disturbances would yield useful insight into the likelihood of altered presence, distribution, and recovery of ecologically, economically, and culturally important species that directly or indirectly depend on krill [43–45]. While the analysis presented here focuses on uncertainty generated by structural model formulation, it is important to recognize that parameter selection will also lead to additional uncertainty in the results [46]. However, performing a comprehensive parameter sensitivity study with the three krill models for each of the downscaled projections would be computationally prohibitive, especially considering that appropriate parameter selection and range should be first determined in a historical context to avoid generating unrealistic responses. Expanding the scope of the analysis to parameters would also deemphasize the key finding highlighted here that “best-available” model formulations carefully evaluated under recent historical conditions may exhibit substantially divergent responses under climate change forcing.

The progressively diverging trends across krill models in the northern CCE (i.e., outside the core region for which they were parameterized and evaluated) primarily reflect differences in the environmental variables driving long-term change

in each formulation (Fig B in [S1 Text](#)). For instance, sea surface temperature trends are relatively uniform over the entire CCE, meaning that SDM responses (primarily associated with temperature) should be consistent inside and outside the core region. In contrast, trends in surface and subsurface nitrate concentrations (driving variables for NPZ and GA, respectively) exhibit different signs and magnitude in the northern CCE relative to the core region. This spatial heterogeneity implies that krill model formulations responding mainly to nutrient supply will inherently have diverging trends in the central vs. northern CCE. However, while both NPZ and GA suggest similar latitudinal patterns (i.e., an overall krill decrease in the central CCE and increase in the northern CCE), the NPZ projections also hint at cross-shore differences characterized by predominantly positive trends nearshore and negative trends offshore. Since curl-driven upwelling is not included in GA, the NPZ model may reflect a contrasted impact of climate change on coastal upwelling vs. curl-driven upwelling, whereby nutrient supply from coastal upwelling may be enhanced in the future by strengthening upwelling favorable winds [\[47\]](#), but nutrient supply associated with curl-driven upwelling may be reduced by increased warming and stratification. In that sense, relative krill abundance in the CCE could exhibit progressively more pronounced nearshore habitat compression throughout the 21st century, such as that observed during the 2014–2016 large marine heatwave [\[10\]](#).

Considering that surface warming intensity may not always reliably predict changes in upwelling efficiency, the lack of information about nitrate concentrations in SDM may explain its more strongly divergent response relative to NPZ and GA under lower and moderate warming rates, especially in the northern CCE where upwelling-favorable winds are expected to intensify in a warmer climate [\[48\]](#). Furthermore, the krill models used here have not been evaluated for winter and early spring and may not account for potential phenological shifts, whereby an earlier onset of the upwelling season in the future [\[23,47\]](#) could lead to an apparent decrease in krill abundance for May–August that may be at least partially compensated by an increase during the preceding months. Since only one of the three krill models explicitly includes temperature dependent metabolic rates (NPD; $Q_{10}=2$), it is difficult to robustly assess its overall impact on long-term trends. However, considering that (i) NPZ krill and nitrate do not have significant trends under Lo8.5 despite a ~20% Q_{10} increase in metabolic rates by 2100, and (ii) GA krill and nitrate have significant matching trends under Hi8.5 without a Q_{10} effect, the direct impact of warming on metabolism as a cause for long-term change is presumably small. However, the higher R-squared value between NPZ krill and temperature compared to that between GA krill and temperature (0.88 vs 0.68; Fig B in [S1 Text](#)) could reflect the secondary contribution of a Q_{10} effect in the NPZ projections, especially under higher warming rates. While direct attribution to environmental or metabolic changes is not feasible for SDM, the model has a known tendency to predict reduced relative krill abundance during warmer years compared to neutral or cooler conditions [\[5\]](#). It is also worth noting that *Euphausia pacifica* (the krill species considered here) occurs throughout the north-east Pacific [\[49\]](#) and can likely adapt to a greater range of temperatures than the warming differences across the three projections.

Low-frequency variability is an important contributor to ecosystem response along the U.S. west coast and often coincides with the occurrence of so-called “regime shifts” [\[50–52\]](#). Furthermore, since the superposition of decadal fluctuations on the long-term trend is expected to dampen or exacerbate climate change impacts over prolonged periods, identifying the magnitude, frequency, and underlying drivers of dominant modes of low-frequency variability has important implications for predicting future ecosystem states and whether they represent natural oscillations of the system or potential shifts to unprecedented regimes. The projected dominant mode of low-frequency variability identified here for krill is associated with the PDO and exhibits a strong signature across model formulations and warming rates. This finding not only suggests that past ecosystem states and regime shifts linked to the PDO will persist in the future, but also that anthropogenic impacts in the CCE will be modulated by low-frequency basin-scale variability (e.g., long-term change could “emerge” sooner equatorward of 38°N where low-frequency variability has a reduced amplitude). However, it is important to note that the dominant period associated with low-frequency krill variability is not robustly identified across ensemble members, which suggests either inconsistencies in the decadal variability

produced by the three ESMs [42] or a non-stationary relationship between decadal variability and ecosystem properties [53,54]. This second caveat highlights the need to identify consistent processes controlling ecosystem response (as done here by establishing the link between dominant low-frequency krill variability and fundamental explanatory variables, such as alongshore winds and nutrient supply) instead of simply relying on correlative relationships with known climate indices.

Given the central role of krill in the pelagic food web of coastal upwelling systems, the compound effect of low-frequency variability and long-term change has direct implications for assessing the vulnerability of other species of ecological, economical, and cultural importance ranging from forage fish to higher trophic level predators. A question of particular importance is the extent to which future krill abundance will be able to sustain a rewinding of the CCE with growing seabird and whale populations [14,55]. However, considering that none of the krill models include explicit mortality from higher trophic level predators, the trends identified here do not reflect potential top-down control on relative krill abundance. While these effects are presumably largest at local and interannual scales (e.g., [56]), more robust information on long-term changes in the abundance, distribution, and diet of krill predators in the CCE is needed to fully answer the question. Furthermore, several decades of historical observations in the southern California Current suggest that the CCE food web is strongly bottom-up driven at decadal scales, with no evidence of significant top-down control on lower and mid trophic level species [57].

While the rate of warming associated with RCP8.5 may be unrealistically high (e.g., [58]), the point emphasized here is not the exact determination of the timing and magnitude of changes, but rather the range of responses that functionally different krill models extensively calibrated with present-day observations can exhibit under future climate conditions. For instance, while the direction of long-term change and environmental variability tend to manifest similarly across the three krill model formulations, the exact magnitude of the trends and the frequency of occurrence of extreme conditions are less consistent and display uncertainty comparable to that associated with representative warming rates for the RCP8.5 emissions scenario. Fundamentally, this finding highlights the need for a more pragmatic incorporation of anthropogenic and ecological uncertainty sources when projecting the fate of marine ecosystems in a changing climate, especially in regions where substantial interannual and decadal variability can obscure the anthropogenic signal, even under high emissions and warming (e.g., [59]). Further compounding the issue is the fact that not all environmental and ecological variables will emerge simultaneously, as their signal-to-noise (i.e., anthropogenic trend to natural variability) ratio differs [60]. For instance, variables directly related to warming (e.g., sea surface temperature, upper ocean stratification, and subsurface dissolved oxygen) may exhibit unprecedented values in the California Current during the 21st century [61], while other ecosystem properties may not exceed their present-day envelope as rapidly [23,34]. Since a large fraction of the uncertainty in projecting net primary productivity changes for large marine ecosystems stems from natural variability and model formulation as opposed to emissions scenario [24], the work presented here ultimately highlights the need for climate change studies that include a diverse representation of key marine organisms, such as krill, to better differentiate their responses to natural variability and anthropogenic forcing.

Supporting information

S1 Text. Supplementary material.
(DOCX)

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