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Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California

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Abstract

Changes in variance are infrequently examined in climate change ecology. We tested the hypothesis that recent high variability in demographic attributes of salmon and seabirds off California is related to increasing variability in remote, large-scale forcing in the North Pacific operating through changes in local food webs. Linear, indirect numerical responses between krill (primarily *Thysanoessa spinifera*) and juvenile rockfish abundance (catch per unit effort (CPUE)) explained >80% of the recent variability in the demography of these pelagic predators. We found no relationships between krill and regional upwelling, though a strong connection to the North Pacific Gyre Oscillation (NPGO) index was established. Variance in NPGO and related central Pacific warming index increased after 1985, whereas variance in the canonical ENSO and Pacific Decadal Oscillation did not change. Anthropogenic global warming or natural climate variability may explain recent intensification of the NPGO and its increasing ecological significance. Assessing non-stationarity in atmospheric-environmental interactions and placing greater emphasis on documenting changes in variance of bio-physical systems will enable insight into complex climate-marine ecosystem dynamics.

Keywords: central Pacific warming, climate change, ecological importance, euphausiids, forage fish, non-stationarity, North Pacific Gyre Oscillation, remote forcing, salmon, seabirds

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Introduction

According to the Intergovernmental Panel on Climate Change (IPCC, 2007), '*climate change refers to a change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer*'. Indeed, variability in indicators of aquatic and terrestrial ecosystem structure and functions are predicted to increase with anthropogenic global warming (Solomon *et al*., 2007). While the importance of variance in studies of climate change impacts is recognized (Jentsch *et al*., 2007), assessing changes in variance, especially in coupled bio-physical systems, has lagged behind treatments of change which focus on central tendency (Rosenzweig *et al*., 2008). Changes in means have also been the emphasis of studies of 'regime shifts' in marine ecosystems (Overland *et al*., 2010).

Recently, there have been signals of increasing variability in the demography of marine predators, including seabirds, salmon, and rockfish in the central-northern portion of the California Current ecosystem (CCE) (Sydeman *et al*., 2006; Lindley *et al*., 2009; Sydeman *et al*., 2009; Field *et al*., 2010). Early signals came in the late 1990s when one of the strongest El Niño events on record (1997–98) transitioned into a remarkably strong La Niña (Peterson & Schwing, 2003). Record coastal upwelling was observed in 1999 (Schwing *et al*., 2000) after significantly reduced upwelling throughout most of the 1990s. In 2002, the Cassin's auklet (species scientific names given in Table 1), a planktivorous seabird nesting on Southeast Farallon Island, initiated egg laying in February, an unprecedented timing, resulting in the highest productivity on record at that time (Abraham & Sydeman, 2004). Salmon returns in 2002 were also exceptionally high. However, in 2005, a non-El Niño year, the auklets abandoned their colony *en masse* and failed to produce any offspring (Sydeman *et al*., 2006), never before observed in over 35 years of investigation (Sydeman *et al*., 2001). In 2006 and 2007, similar auklet colony abandonment and reduced reproductive success were observed. Correspondingly, productivity of juvenile (age-0) rockfish, a key prey item for both salmon and seabirds (Mills *et al*., 2007), was the lowest on record from 2005 to 2007 (Field *et al*.,

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Table 1 Time series characteristics of physical and biological variables used in this study

Measurement	Survey area	Time span	Species/area surveyed	Data source
Aleutian Low (AL)		1950–2011		National Center for Environmental Prediction Reanalysis II, Sea Level Pressure
North Pacific Oscillation (NPO)		1950–2011		National Center for Environmental Prediction Reanalysis II, Sea Level Pressure
Canonical ENSO index		1950–2011		http://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Data/nino34.long.data
Non-Canonical ENSO index		1950–2011		http://www.jamstec.go.jp/frcgc/research/d1/iod/modoki_home.html.en
Pacific Decadal Oscillation (PDO)		1950–2011		http://jisao.washington.edu/pdo/PDO.latest
North Pacific Gyre Oscillation (NPGO)		1950–2011		http://pgo.o3d.org
Bakun upwelling index	39°N 125°W	1946–2011		ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon
Prey				
Krill net-derived abundance	Point Reyes-Point Sur	2002–2008	*Thysanoessa spinifera* *Euphausia pacifica*	National Marine Fisheries Service surveys
Krill Acoustic Index (NASC)	Point Reyes-Point Sur	2000–2008	Euphausiids	National Marine Fisheries Service surveys
Juvenile (age-0) rockfish abundance	Point Reyes-Point Sur	1983–2010	*Sebastes* spp.	National Marine Fisheries Service surveys
Predators				
Seabird phenology (mean lay date)	Southeast Farallon Island	1972–2006	Common Murre (*Uria aalge*)	PRBO Conservation Science/USFWS
			Cassin's Auklet (*Ptychoramphus aleuticus*)	PRBO Conservation Science
Seabird productivity (chicks fledged/pair/year)	Southeast Farallon Island	1971–2007	Brandt's Cormorant (*Phalacrocorax penicillatus*)	PRBO Conservation Science
		1971–2007	Pelagic Cormorant (*P. pelagicus*)	PRBO Conservation Science
		1971–2007	Pigeon Guillemot (*Cepphus columba*)	PRBO Conservation Science
		1986–2007	Rhinoceros Auklet (*Cerorhinca monocerata*)	PRBO Conservation Science
		1972–2007	Common Murre	PRBO Conservation Science
		1971–2007	Cassin's Auklet	PRBO Conservation Science
Seabird density (#/km^2)	Point Reyes-Point Sur	1996–2009	Common Murre	Farallon Institute surveys
			Cassin's Auklet	National Marine Fisheries Service surveys
			Pink-footed Shearwater (*Puffinus creatopus*)	National Marine Fisheries Service surveys
			Sooty Shearwater (*Puffinus griseus*)	National Marine Fisheries Service surveys
Chinook salmon abundance (#)	Russian River	2000–2009	*Oncorhynchus tshawytscha*	Sonoma County Water Agency
	Sacramento River	1983–2011		Pacific Fishery Management Council

2010). The immediate ecosystem impacts in 2005–2007 gave rise to delayed impacts on salmon fisheries (Lindley *et al.*, 2009). From 2007 to 2009, the Sacramento River fall run Chinook (SRFC) population fell below conservation goals resulting in the first ever west coast fisheries closures (Pacific Fisheries Management Council, 2009). Chinook salmon escapement to the nearby Russian River system covaries with that of the SRFC (Thompson *et al.*, 2012), and showed similar declines in 2008–2009. Moreover, sockeye salmon (*Oncorhynchus nerka*) at the northern extent of the California Current showed similar population fluctuations, with record low returns in these years (McKinnell *et al.*, 2012). Then, remarkably, the largest return of Fraser River sockeye salmon since the early 1900s was observed in 2010. Considering the broad-scale nature of these observations across trophic levels, species, and approximately 12° of latitude along the west coast of North America, the causes of change were undoubtedly operating at the basin scale.

Changes in 'ocean climate' and prey availability are leading explanations for these notable rockfish, seabird, and salmon fluctuations in the 2000s, but connections between the physical environment and biological observations have yet to be fully investigated. Fundamentally, productivity in the CCE is determined by remote, basin-scale oceanographic factors including transport as well as localized regional upwelling (Checkley & Barth, 2009). Upwelling, the vertical flux of cold, nutrient-laden waters, stimulates phytoplankton growth and reproduction and food web development. Currents transport waters, nutrients, and plankton from the subarctic and subtropical regions into the CCE. Thus, the epipelagic food web that has affected predators over the past decade could be related to changes in either upwelling or patterns of large-scale circulation. Garcia-Reyes & Largier (2010) reported generally increasing upwelling in the region of 36°N to 39°N over 27 years (1982–2008). Keister *et al.* (2011) developed a process model on copepod community structure and showed how transport associated with the variability in the Pacific Decadal Oscillation (PDO) could result in different copepod communities off Oregon. In a related study using satellite observations of sea surface height, Bi *et al.* (2011) showed that the biomass of subarctic, lipid-rich copepods off Oregon was positively related to the enhanced southward transport generally found during negative (cold) phases of the PDO. Lastly, key epipelagic forage nekton, including euphausiid crustaceans (also known as 'krill') and juvenile (age-0) rockfish, were related to positioning of the North Pacific Current; when the current was distributed to the north, krill and juvenile rockfish were more abundant (Sydeman *et al.*, 2011). These recent studies and other classics from the past (Chelton *et al.*, 1982) suggest key linkages between large-scale gyre circulation in the Northeast Pacific and predator-prey numerical responses in the north-central CCE.

Indeed, due to their abundance, high lipid content, and tendency to form aggregations, krill may be singularly important to climate-mediated impacts on epipelagic food webs and predator-prey relationships in the CCE (Field *et al.*, 2006) and other pelagic ecosystems globally. Here, we investigate how recent variance in demography (reproductive success, recruitment, and returns) of seabirds, salmon, and rockfish of the central CCE may be related to krill and changing variance in regional upwelling and remote forcing of ocean climate in the region. Specifically, we test the hypothesis that relative abundance of two species of krill, *Thysanoessa spinifera* and *Euphausia pacifica,* is related to the reproductive success of seabirds and rockfish and the relative abundance of seabirds and salmon (the latter lagged two years to correspond with ocean conditions during the year of ocean entry). To test this hypothesis, we developed indices of krill abundance within a 10-year period (2000–2009) and investigated the numerical responses of seabirds and salmon to variation in the relative abundance (catch per unit effort (CPUE)) of krill and juvenile rockfish. In turn, we evaluated relationships between krill abundance and indices of upwelling (Schwing *et al.*, 1996) and circulation (using the North Pacific Gyre Oscillation (NPGO) index; Di Lorenzo *et al.*, 2008). We place these observations in context by evaluating changes in variance of the NPGO in relation to the canonical El Niño and other flavors of tropical Pacific cycles over the past 50 years (Newman *et al.*, 2011). In particular, it has been recently suggested that climate change may be altering the noncanonical central Pacific, or 'Modoki', El Niño (Yeh *et al.*, 2009), with corresponding teleconnections to the North Pacific, including effects on the NPGO (Di Lorenzo *et al.*, 2010). We therefore focus on change in variability of the central Pacific warming and NPGO as hypothesized remote drivers of krill and predator-prey variability in the north-central CCE.

Materials and methods

Ecosystem surveys

The distribution and abundance of krill, age-0 juvenile rockfish, and seabirds was studied during surveys conducted by National Marine Fisheries Service and others in may–june from 1983 to present (Table 1). The study design is described by Sakuma *et al.* (2006). Details of mid-water trawl sampling are provided by Field *et al.* (2010). During transit between stations, acoustic surveys of krill (Santora *et al.*, 2011a,b) and counts of marine birds were conducted; details of the seabird surveys are provided by Yen *et al.* (2004).

Indices of krill abundance

Data on the relative abundance of *E. pacifica* and *T. spinifera* (as well as juvenile rockfish, see below) were obtained from 35 stations between Pt. Sur and Pt. Arena, California (Table 1, Appendix). Krill were separated from the catch of fish, volumetrically subsampled, and identified and enumerated by one of us (BM). We used (ln) number individuals haul^{-1} in analyses. Volume backscattering strength measured at different frequencies was used to identify krill (methods in Santora *et al*., 2011a,b). We used the Nautical Acoustic Scattering Coefficient (NASC nmi^{-1}) as our index of krill-plankton backscatter which is proportional to biomass. From 2000 to 2009 (missing 2007), approximately 16 000 nmi (29 500 km) of habitat was surveyed. Previous comparisons of this krill index with net samples indicated the acoustic krill index primarily reflected *E. pacifica* (Santora *et al*., 2011a).

Indices of juvenile rockfish abundance

Juvenile rockfish indices were calculated using a delta-GLM approach after the raw catch was adjusted to a common age of 100 days to account for interannual differences in age structure (Field *et al*., 2010). The total sum of the indices for the ten most frequently occurring species (which cumulatively account for over 97% of all juvenile rockfish catches in this region) was used to index relative abundance.

Indices of seabird abundance

At-sea relative abundance (density; birds km^{-2}) for seabirds was calculated by summing daily counts for each species and dividing each daily species sum by the daily area surveyed. Species examined were Cassin's auklet, common murre, sooty shearwater, and pink-footed shearwater. Total bird density (including all species observed on these surveys, not just those listed above) was also used in analysis. Daily densities were averaged to produce survey-wide estimates for each year. The four species examined contributed about 80% of the total bird density in the study region.

Indices of seabird productivity

To examine the timing of breeding and reproductive success of seabird species, a sample of focal breeding pairs was studied throughout each nesting season on Southeast Farallon Island, Farallon National Wildlife Refuge (37°42′N 123°W; Sydeman *et al*., 2001). Species monitored included Brandt's cormorant, common murre, pigeon guillemot, pelagic cormorant, Cassin's auklet, and rhinoceros auklet. For each species, individual nest sites were monitored (n = 15-500 nests per species per year) at 1–7 day intervals for breeding activity. Reproductive performance was defined as the number of offspring departing the colony per breeding pair per year; details provided by Sydeman *et al.* (2001). Timing of breeding (or 'phenology') was defined as the average egg-laying date for auklets and murres; details and data provided by Schroeder *et al.* (2009). Timing of breeding and breeding success are interrelated, with earlier reproductive timing generally resulting in better reproductive success (Abraham & Sydeman, 2004; Reed *et al*., 2008). As such, both of these parameters can be interpreted as indicators of 'seabird productivity'.

Indices of salmon abundance

The Sonoma County Water Agency (SCWA) assessed the escapement of Russian River fall Chinook salmon (RRFC) using photographic documentation of individual adult salmon as they returned to the river each year (Table 1). During the run, salmon were counted on a daily basis by means of two underwater video cameras located in fish ladders adjacent to an inflatable dam on the Russian River. The video used high resolution monochrome wide-angle lenses to capture the images of migrating salmon and were operated 24 h/day between August and January. Daily counts were summed to produce an annual estimate of escapement, which is used as the population estimate for this stock. Beginning in 2008, the Pacific Fishery Management Council (PFMC) Salmon Technical Team began using a new index of abundance specific to the Sacramento River fall Chinook (SFRC; Sacramento Index, SI). This index used the formula $SI = H_{o,S} + E$, where $H_{o,S}$ is the September 1 through August 31 ocean harvest of SRFC south of Cape Falcon (45°N) and E is the escapement of fish that return to spawn, which includes a river harvest component (O'Farrell *et al*., 2009). One important difference between the RRFC and the SI is that the SI is an overall measure of abundance, whereas the RRFC is a measure of escapement.

Indices of North Pacific climate and remote forcing

We selected climate indices that are known drivers of marine ecosystems of the North Pacific to examine whether increasing variance may explain recent changes in biology in the CCE (Table 1). The Pacific Decadal Oscillation (PDO) index was acquired from http://jisao.washington.edu/pdo/PDO.latest, and the North Pacific Gyre Oscillation (NPGO) index (Di Lorenzo *et al*., 2008) from http://npgo.o3d.org. Over the North Pacific domain north of 20°N, the Aleutian Low (AL) and North Pacific Oscillation (NPO) are atmospheric indices computed as the first and second principal components of sea level pressure anomalies from the National Center for Environmental Prediction (NCEP) Reanalysis II. The canonical and noncanonical ENSO indices were derived from the first and second principal components of the National Oceanic and Atmospheric Administration (NOAA) extended sea surface temperature anomalies over the tropical Pacific region [20°S to 20°N], consistent with previous studies (Ashok *et al*., 2007). The canonical ENSO is the standard first empirical orthogonal function, describing SST anomalies in the equatorial Pacific, whereas the noncanonical ENSO is the Central Pacific El Niño index (also known as 'Modoki') and is related to SST anomalies concentrated in the central equatorial Pacific.

Indices of regional upwelling

The timing and amplitude of upwelling was proxied by the Bakun Upwelling Index (UI), calculated by NOAA's Environ-

mental Research Division, from estimates of the magnitude of the offshore component of the Ekman transport driven by wind stress (Bograd *et al.*, 2009). Positive values indicate upwelling while negative values indicate downwelling. Methods and details of computation are available from http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/how_computed.html. For this study we used UI for the location 39°N, 125°W. Monthly upwelling values were seasonally averaged (winter: December–February; spring: March–May; summer: June–August; fall: September–November) for analyses.

Statistical analyses

We used Principal Components Analysis (PCA) to create multivariate indicators of predator productivity and abundance by combining information on salmon and seabirds ($PC1_{predators}$ and $PC2_{predators}$; Table 2). The seabird data (at-sea abundance (birds/km^2), timing of breeding (egg-laying date) and breeding success (number chicks/pair)) were summarized for the years 2000–2008. Salmon data (abundance in numbers of fish) were obtained for 2002–2010 and lagged by 2 years to align with krill, rockfish, and seabird data for each salmon cohort's year of ocean entry (Wells *et al.*, 2012). We used the sum of juvenile rockfish abundance for analyses. We used Spearman rank correlation, multiple linear regression, and path analysis (Mitchell, 2001) to investigate the numerical responses of the predator index to krill and age-0 rockfish abundance. Spearman rank correlations also were used to examine the relationships between krill abundance and seasonal upwelling and the NPGO. Specifically, krill abundance (CPUE) was compared to upwelling and the NPGO for winter and spring of the current year, as well as each season (winter, spring, summer, fall) of the previous year. Winter upwelling in the current year has previously been shown to influence many species and biological processes in the region (Black *et al.*, 2011; Thompson *et al.*, 2012) and was hypothesized to be most relevant in this study.

We used a Monte Carlo randomization approach (Manly, 2007) to test whether the variability (variance) of climate indices (e.g., PDO, NPGO) differed significantly between the periods 1950 through 1984 and 1985 through 2011. Initially, we considered splitting these time series at the median year of the entire series, which would have resulted in a break point between 1980 and 1981. However, this would have resulted in the large climatic deviation of 1982–1983 El Niño falling into the second time period when El Niño had apparently become longer lasting and more frequent (Trenberth & Hoar, 1996). Thus, to minimize any potential biases due to the 1983 El Niño, we chose to place the years 1982–1984 in the first time period. We believe this is an appropriately conservative approach for the simulations we developed. Next, for each climate index, we calculated a time-dependent autocorrelation parameter for use within an auto-regressive model (order 1) to generate 10 000 realizations of red noise time series (Di Lorenzo *et al.*, 2010). Importantly, these random time series have the same spectral slope as the original time series and the same degrees of freedom (i.e., the rate at which an index

Table 2 Results of Principal Component Analysis (PCA) on the relative abundance, timing of breeding, and breeding success of eight species of seabird, and two populations of Chinook salmon in central-northern California. Results from the first three PC and parameter loadings (unrotated) are shown

Component	Eigenvalue	Difference	Proportion	Cumulative
1	7.97	4.75	0.53	0.53
2	3.22	1.63	0.21	0.75
3	1.58	0.41	0.11	0.85
	Eigenvectors			
Variable	1	2	3	
Density				
Total birds	0.066	−0.384	0.551	
Common murre	0.012	0.352	0.569	
Cassin's auklet	0.302	−0.061	0.266	
Pink-footed shearwater	−0.129	−0.120	−0.395	
Sooty shearwater	−0.012	−0.539	−0.028	
Phenology				
Common murre	−0.337	0.039	0.104	
Cassin's auklet	−0.289	0.046	0.072	
Reproductive success				
Brandt's cormorant	−0.006	0.535	−0.144	
Pigeon guillemot	0.328	0.010	−0.181	
Pelagic cormorant	0.309	−0.197	−0.207	
Rhinoceros auklet	0.316	0.221	−0.006	
Common murre	0.287	0.113	0.080	
Cassin's auklet	0.343	−0.103	−0.075	
Salmon abundance				
Russian river	0.305	0.140	−0.110	
Sacramento river	0.306	−0.016	0.108	

changes at high or low frequencies is similar). We calculated differences in variance between the periods 1985–2011 and 1950–1984 and estimated a probability distribution of all variance differences. From this distribution, we estimated the significance of the changes in variance for the selected climate index. If the changes in variance fell beyond the 95% of occurrences, we considered the change significant.

Results

Overlapping time series for all variables were restricted to the 6-year period 2002–2007. Examples of some of the time series used in this study are provided in Fig. 1, including winter NPGO and upwelling indices, abundance of juvenile rockfish in the region, reproductive success of murres and auklets, and population abundance of Chinook salmon from the Sacramento River. For these examples, interannual variability in the reproductive success (offspring raised $pair^{-1}$) of auklets and abundance of salmon increased over time, while that for murres and rockfish did not change. For the auklet, the coefficient of variation increased from 9% in the 1970s to 75% in the 2000s, while mean reproductive success decreased from 0.76 in the 1970s to 0.61 in the 2000s. Mean juvenile rockfish abundance (log(standardized CPUE)) varied from 34.5 in the 1980s to 9.6 in the 1990s, to 13.9 in the 2000s, with the corresponding coefficients of variation varying from 69% to 99% to 87%, respectively, in each decade. For salmon, the coefficient of variation for the Sacramento Index (SI) increased from 42% in the 1980s (39% in the 1990s) to 72% in the 2000s, while mean annual abundance decreased from approximately 924K fish in the 1980s to approximately 731K in the 2000s.

Multivariate indicators of predator responses

$PC1_{predators}$ accounted for 53.1% of the variation in the 15 parameters (Table 2). $PC2_{predators}$, however, also accounted for a significant amount (21.5%) of the variation in predator response parameters. $PC1_{predators}$ was representative of Cassin's auklet density at sea, the timing of breeding of auklets and murres, the reproductive success of all seabirds except Brandt's cormorant, and the lagged return values of both salmon populations. The loadings were similar across these parameters (0.28 –0.33), and we interpret PC1 to be a generalized predator productivity index. $PC2_{predators}$ was representative of the density of murres and shearwaters at sea, total (all species) bird density at sea, and Brandt's cormorant breeding success. Notably, the loadings for murre density and cormorant success were positive while those of shearwaters and 'all species' density were negative. The cormorant reproductive success was trending upwards during the 1990s while for the other species, the trend was negative or flat (Sydeman *et al*., 2001); the cormorant population on the island was also increasing rapidly at that time (PRBO Conservation Science, unpubl. data). During the same decade, the murre breeding population on the island was increasing (Reed *et al*., 2008) and shearwaters abundance at sea was decreasing, though this change was not significant (Ainley & Hyrenbach, 2010). Therefore, we interpret PC2 as indicative of seabird population trends, with some demonstrating increasing numbers and others in decline.

Numerical responses

Cross-correlations revealed associations between *T. spinifera* and $PC1_{predators}$ and rockfish abundance (Table 3, Fig. 2a,b). Despite small sample sizes, correlations between *T. spinifera* and predators and rockfish were strong ($P < 0.02$). We also found a strong correlation between rockfish abundance and predators ($P < 0.001$; Fig. 2c). $PC2_{predators}$ was unrelated to any of the krill variables. Path analysis showed that the effect of *T. spinifera* on $PC1_{predators}$ was indirect, operating through juvenile rockfish (standardized direct coefficient = 0.110; sum of indirect coefficients = 0.832). A multiple regression confirmed that in the presence of juvenile rockfish in the model, *T. spinifera* did not have a significant effect on $PC1_{predators}$.

Krill, upwelling, and remote climate forcing

The abundance of *T. spinifera* was correlated to winter NPGO ($\rho = 0.857$, $P = 0.014$; Fig. 2d), but not the winter upwelling index at 39°N ($\rho = -0.179$, $P = 0.702$). *T. spinifera* abundance was also correlated to the NPGO in spring ($\rho = 0.929$, $P = 0.003$), as well as the NPGO in the previous fall and summer (both $\rho = 0.929$, $P = 0.003$). *T. spinifera* was correlated to upwelling in spring of the previous year ($\rho = 0.893$, $P = 0.007$), but unrelated to upwelling in the previous summer or fall. The relationships to spring upwelling lagged by 1 year and this may be related to the production of juveniles that then become adults in the year of observation, but it is beyond the scope of this article to investigate this idea in detail (see also Wells *et al*., 2012). The abundance of *E. pacifica* was not correlated to winter ($\rho = 0.500$, $P = 0.253$) or spring ($\rho = 0.536$, $P = 0.215$) upwelling, nor any seasonal measurements of upwelling or NPGO in the previous year (WJS and SAT, unpublished data).

Change in NPGO and other climate driver variability

Monte Carlo simulations revealed a change in the variance structure of the NPGO through time. Variance in the recent 1985 through 2011 period was significantly greater than from 1950 through 1984 (Fig. 3). Increasing

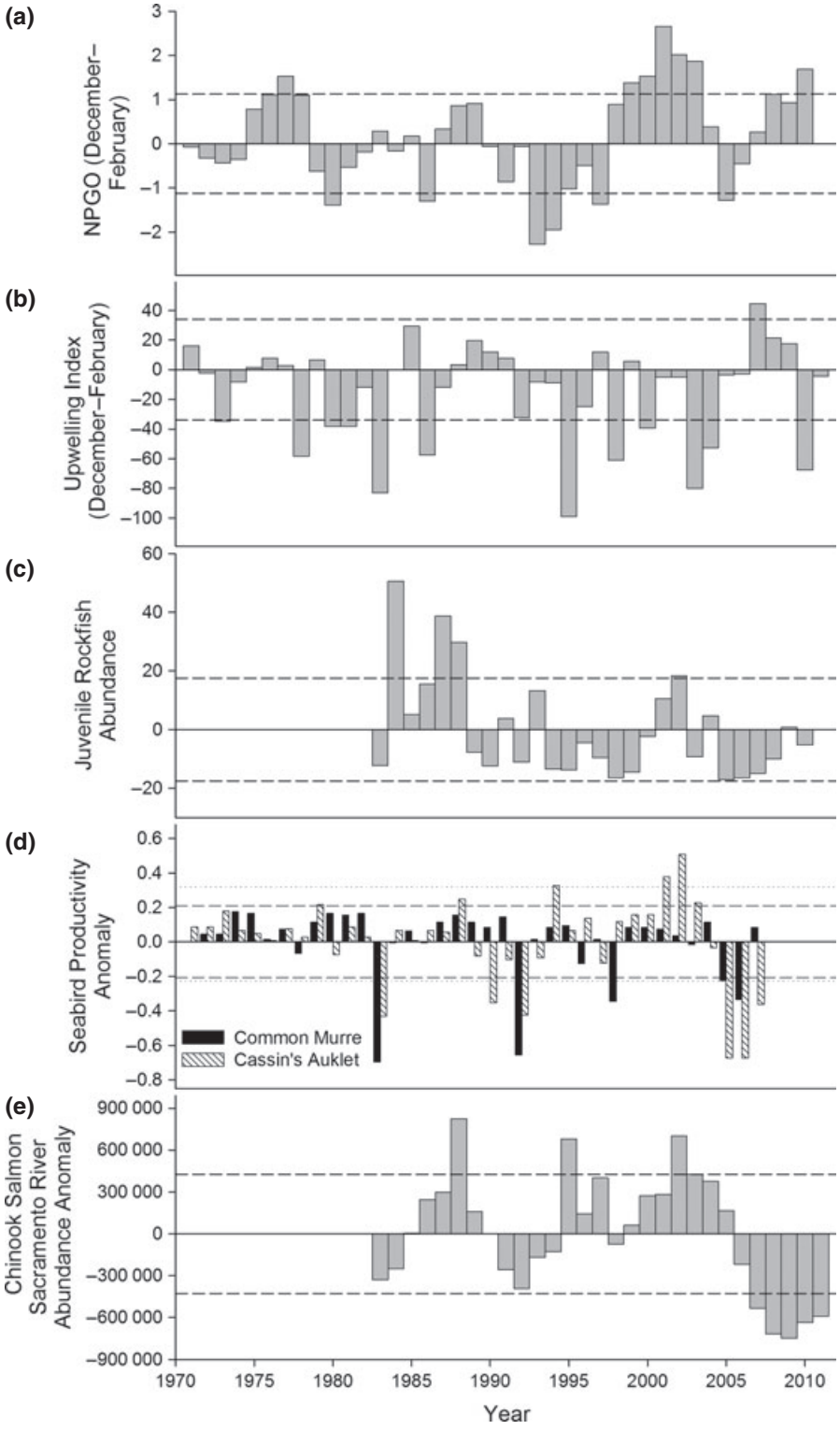

Fig. 1 Time series of interannual variability, 1971–2007. (a) Winter (December-February) North Pacific Gyre Oscillation index (NPGO). (b) Winter Bakun Upwelling Index (December-February) for 39°N, 125°W. (c) Juvenile rockfish productivity (abundance of 10 *Sebastes* species, see Field *et al*. (2010) for details). (d) Productivity anomalies of the seabirds common murre (black) and Cassin's auklet (hatched). (e) Anomalies of Chinook salmon abundance in the Sacramento River. Salmon data were aligned to the year of ocean entry (2-year lag); thus, the time series of returns from 1983–2009 reflects the years of ocean entry 1981–2007. Dashed lines indicate +/− 1 standard deviation of the mean for all variables except Cassin's auklet productivity (dotted line).

Table 3 Cross-correlations (Spearman rank) between krill, juvenile (age-0) rockfish and seabirds and salmon. Note: due to the small sample size of years it was not possible to adjust for autocorrelation. Shown are n, Spearman rho, and *P*-value for each relationship. Bold indicates significance of P < 0.5

	T. spinifera	*E. pacifica*	Acoustic krill index	Salmon, seabirds PC1	Salmon, seabirds PC2
E. pacifica	7				
	0.214				
	0.645				
Acoustic krill index	6	6			
	0.086	0.714			
	0.872	0.111			
Salmon, seabirds PC1	**6**	6			
	0.886	−0.257	0.000		
	0.019	0.623	1.000		
Salmon, seabirds PC2	6	6	7	8	
	−0.143	0.086	0.000	0.048	
	0.787	0.872	1.000	0.911	
Total rockfish	**6**	6	7	**8**	8
	0.886	−0.257	−0.036	**0.929**	−0.117
	0.019	0.623	0.939	**0.001**	0.693

variability was also established by simulation for the Central Pacific Index (Fig. 3), and changes in variance of the NPO, although evident, were not statistically significant. No change in variance was found between time periods for the canonical ENSO, the AL, or the PDO (Fig. 3). To illustrate the changing variability of the NPGO relative to the static variance of the PDO, we plotted 7-year running standard deviations for these variables (Fig. 4). This approach also shows increasing variance in the NPGO ($n = 56$, $\rho = 0.514$, $P = 0.0001$) and no significant change in variance of the PDO ($n = 56$, ρ=0.179, $P = 0.1868$).

Discussion

Studies of climatic impacts on aquatic and terrestrial ecosystems and upper trophic level species are difficult in that climate to prey and predator-prey relationships must be established. Moreover complex, often indirect, multi-species functional relationships may be involved (Sydeman *et al.*, 2012). We found the following key relationships and changes in the pelagic ecosystem: (i) variance in the demography of some components of the pelagic ecosystem has increased, perhaps starting as early as 1990 (see also Sydeman *et al.*, 2006); (ii) over the past 10 years, a period of exceptional variability, krill abundance, particularly that of *T. spinifera*, was indirectly related to seabird and salmon demographic attributes, mostly indirectly via forage fish (age-0 *Sebastes*); (iii) the NPGO, but not regional upwelling, was related to the abundance of *T. spinifera*; and (iv) over the long term (1950–2011), variability of the NPGO increased. Overall, these findings support the need for greater attention to variance in physical and biological attributes, in addition to traditional foci on measures of central tendency, to understand climate-ecosystem variability. This suggestion is not new (Jentsch *et al.*, 2007), nor has it been overlooked in the policy arena (IPCC, 2007), but in practice, ecologists and policy makers still generally neglect variance as a key indicator of climatic impacts on ecosystems. Importantly, the lack of attention on variance may compromise understanding and possibly prediction of ecosystem dynamics; increasing variance has been suggested to be a predictor of phase and regime shifts in a variety of aquatic systems (Scheffer *et al.*, 2009).

While our study supports this perspective, a number of unresolved issues pertaining to both climate-prey and predator-prey relationships remain. Primary questions include the following: (i) given the short time series and correlative approach used in this study, are the reported predator-prey relationships robust?, (ii) how has the NPGO become a dominant mode of ecological variability in the North Pacific over the past two decades?, (iii) why is the NPGO apparently related to krill more than regional upwelling?, and (iv) what are the potential implications of this study with respect to anthropogenic climate change and global warming?

Predator-prey relationships

Determining numerical relationships between prey abundance and predator demography is a key step in resolving how climate variability and change is affecting and will affect upper trophic level taxa, such as seabirds and large predatory fish like salmon (Hunsicker *et al.*, 2011). Previously, using longer time series, relationships between seabird (Field *et al.*, 2010; Cury *et al.*,

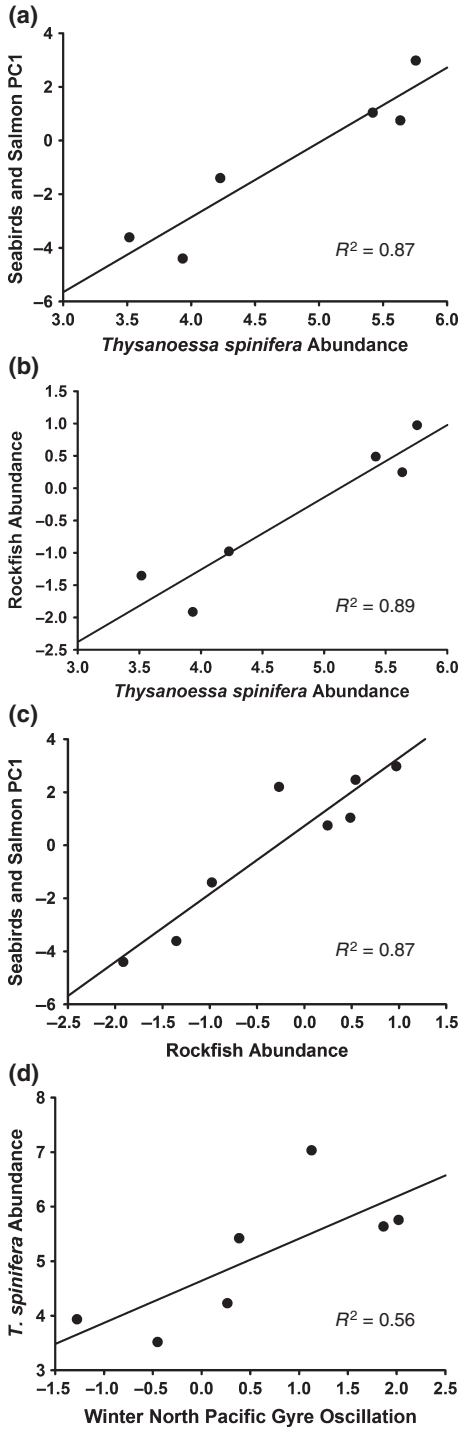

Fig. 2 Bi-variate relationships between (a) CPUE *T. spinifera* and predator abundance and productivity indexed by PC1 (see Table 1), (b) CPUE *T. spinifera* and the abundance of juvenile rockfish, (c) juvenile rockfish abundance and PC1 seabirds and salmon, and (d) winter NPGO and CPUE *T. spinifera*.

2011) and salmon (Thompson *et al*., 2012) productivity and the abundance of juvenile (age-0) rockfish in this system have been established. Seabirds and salmon consume and provision young with substantial quantities of juvenile rockfish (Mills *et al*., 2007; Roth *et al*., 2008), therefore we consider these correlations mechanistically supported. Here, we extend this understanding by providing evidence of indirect linkages between krill, juvenile rockfish, seabirds and salmon (Fig. 3). Substantial amounts of krill are known to be consumed by planktivorous (auklets) and omnivorous (murres, shearwaters) seabirds (Briggs & Chu, 1987; Roth *et al*., 2008) and salmon during their initial time in the ocean (Wells *et al*., 2012). Previously, Abraham & Sydeman (2004) related *E. pacifica* and *T. spinifera* abundance to auklet demographic parameters, but relied on data from southern California, approximately 400 km to the south of their study area (see Brinton & Townsend, 2003). Thus, it is clearly possible both *T. spinifera* and juvenile rockfish play key trophic functions in this region with respect to predator demography. In contrast, *E. pacifica* was not correlated to the predator responses we examined, nor was this species correlated with upwelling or the NPGO. *E. pacifica*, however, has been shown to be important in food web models of the northern CCE (Field *et al*., 2006). In related work, Abraham & Sydeman (2006) showed that *E. pacifica* was taken by auklets early in the summer, whereas *T. spinifera* was consumed later in the summer, suggesting a different functional use for each krill species. Relative to the seabird and salmon parameters examined herein, it appears that *T. spinifera* is the dominant driver of variation for these predator populations. As most of the seabirds and post-smolt salmon inhabit shelf waters in the Gulf of the Farallones (Yen *et al*., 2004; Wells *et al.* 2102) and *T. spinifera* is the more neritic of the two species of euphausiid examined (Santora *et al*., 2012), a likely explanation for the relative importance of this species of krill is greater habitat overlap between predators and prey.

T. spinifera and remote forcing

The NPGO index is calculated as the second empirical orthogonal function of sea surface height (the first mode represents the PDO), and is thought to represent gyre circulation in the North Pacific (Di Lorenzo *et al*., 2008; Ceballos *et al*., 2009), including the California Current. As a large-scale (remote) driver, the NPGO may play a role in nutrient dynamics of the north-central California Current ecosystem (Di Lorenzo *et al*., 2009). The NPGO also has been related to upwelling in the California Current, with stronger effects apparently at lower latitudes (<40°N) than higher ones (>40°N; Di Lorenzo *et al*., 2008). The upwelling index we used (Schwing *et al*., 1996), however, was unrelated to the NPGO (Fig. 2). Sydeman & Thompson (2010) also

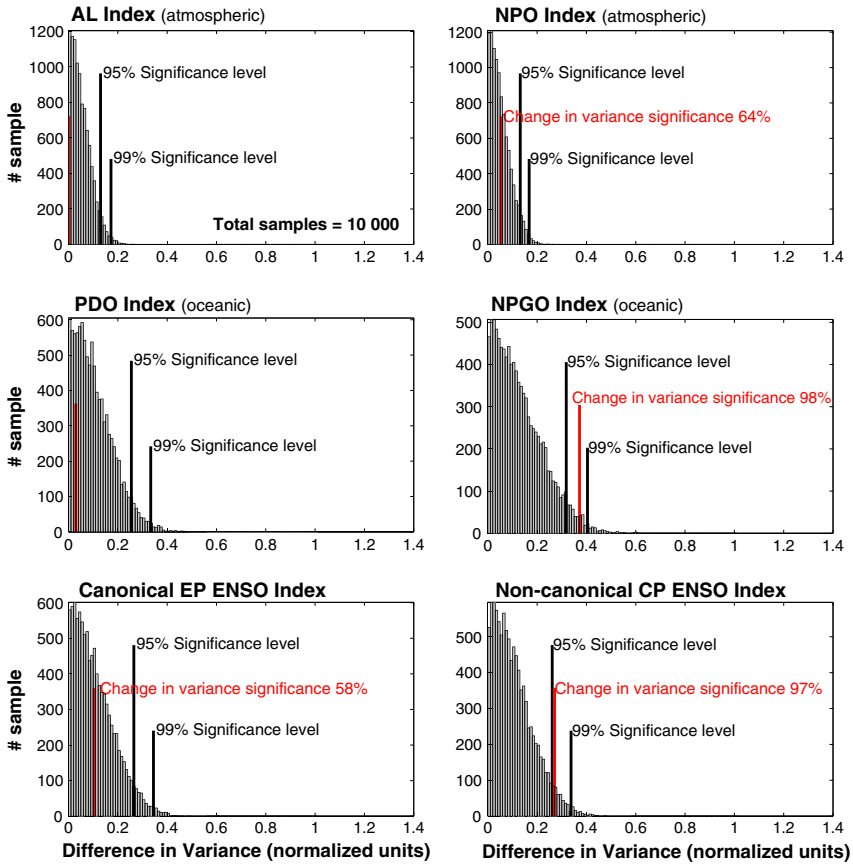

Fig. 3 Significance test for changes in variance for selected Pacific climate indices between 1950 through 1984 and 1985 through 2011. See Methods for a description of the significance test and definition of the climate indices. AL – Aleutian Low (North Pacific), NPO – North Pacific Oscillation (North Pacific), PDO – Pacific Decadal Oscillation (North Pacific), NPGO – North Pacific Gyre Oscillation (North Pacific), Canonical EP ENSO – typical Eastern Pacific ENSO (Tropical Pacific), Non-Canonical CP ENSO – new Central Pacific ENSO.

found weak or nonexistent relationships between proxies of upwelling and the NPGO. Here, we found associations between *T. spinifera* abundance and the NPGO, but no relationship between this krill species and regional upwelling except at a lag of over 1 year. Thus, it appears that remote, rather than regional, forcing mechanisms, possibly reflecting circulation and nutrient transport, are related to variability in the abundance of *T. spinifera* in this region. Process models are needed to confirm this possibility, but to date none have been developed for *T. spinifera* (but see Dorman *et al.*, 2011 for a process model on *E. pacifica*). In a related study, Sydeman *et al.* (2011) demonstrated that when the North Pacific Current is shifted to the north, *T. spinifera* is more abundant, but this study was correlative and based on a small sample of years so further modeling is needed. It is also interesting to consider the biogeographic affinities of *T. spinifera* in this regard. While *T. spinifera* ranges from approximately 25°N to 55°N in the Northeast Pacific, it is distributed primarily in subarctic waters of the northern California Current and Gulf of Alaska (Brinton, 1962). Notably, within our study region, *T. spinifera* is relatively abundant in the Gulf of the Farallones, but not in Monterey Bay, a less subarctic region only approximately 100 km to the south (Brinton & Townsend, 2003; Santora *et al.*, 2012); in addition there is limited shelf habitat for this neritic species in Monterey Bay. It is also well-known that *T. spinifera* becomes considerably less abundant during El Niño and other periods of ocean warming (Brinton, 1981), and that they reproduce vigorously off Oregon when the ocean is cold (Feinberg *et al.*, 2010). Therefore, indicators suggest that *T. spinifera* is influenced by waters with subarctic characteristics either directly or possibly indirectly through upwelling operating on characteristics, such as nutrients, which may be transported into the region.

Lastly, while we found no correlations with upwelling or the NPGO and *E. pacifica* in this study, a recent paper (Di Lorenzo & Ohman, 2013) indicates that the

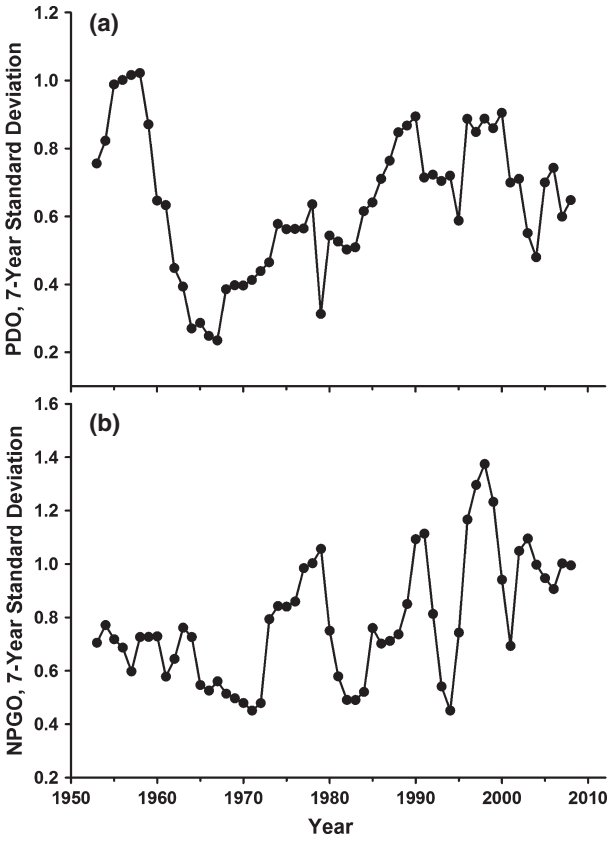

Fig. 4 Variance structure of North Pacific ocean-climate drivers. The 7-year running standard deviations for (a) PDO (Pacific Decadal Oscillation), and (b) NPGO (North Pacific Gyre Oscillation).

abundance of this species off southern California is correlated with sea surface height anomalies (SSHa). SSHa is an excellent indicator of the combined effects of local upwelling and thermocline depth, so perhaps an integrative variable like this is needed to derive relationships with this species of krill (Sydeman & Thompson, 2010).

On changing variance of the NPGO and other climate drivers

To examine if fluctuations in NPGO could be an explanatory factor relative to increasing variability of the pelagic ecosystem we evaluated changes in variance of the NPGO by comparing 1950 through 1984 vs. 1985 through 2011 and by plotting 7-year running standard deviations. Simulations revealed no change in variance of the canonical ENSO nor its drivers, but a significant change in the NPGO and its associated tropical counterpart, the Central Pacific Warming (CPW) index. While changes in the driver of the NPGO, the NPO, were evident, they were not statistically significant, probably because the NPO is an atmospheric index dominated by high frequency variability whereas the NPGO captures the oceanic low-frequency expression of the NPO. Changes in variance in the NPGO could be related to anthropogenic climate change or natural climate variability. Using output from IPCC global climate models, a recent study concluded that changes in variance of the CPW index could be a signature of climate change (Yeh *et al*., 2009). However, this suggestion is challenged by another recent study claiming that variation in the CPW in recent decades is within the range of natural tropical SST variability (Newman *et al*., 2011). Furthermore, the ability of the IPCC models to reproduce the dynamics controlling the low-frequency variation in the North Pacific climate modes is still in question (Furtado *et al*., 2011). Nonetheless, changes in variance of the NPGO are consistent with expectations of climate change impacts on ocean ecosystems. Furthermore, another potential climate change impact revealed from GCM is poleward shifts in the westerly winds, which may cause poleward shifts in gyre-scale currents (Yin, 2005). Thus, it seems possible that climate change could be altering remote forcing of the pelagic ecosystem of the California Current, possibly by changes in circulation transport and nutrient input.

Increasing ecological significance of the NPGO

This and other recent studies (Cloern *et al*., 2010; Sydeman & Thompson, 2010) indicate that there has been a shift in the ecological significance of the NPGO relative to other drivers of ecosystem dynamics in the north-central CCE. As shown here, variance in the NPGO has increased, indicating that this mode of variability is now more active than it was in the recent past. The variance explained by the second EOF of sea level in the Northeast Pacific also has increased (Di Lorenzo, unpublished data). The CCE is affected by remote forcing from the tropics (e.g., El Niño) and extratropics (e.g., PDO; Checkley & Barth, 2009), and the tropical drivers also appear to have changed. In particular, the canonical El Niño is no longer the dominant mode of ENSO variability in the tropical Pacific, having been recently replaced by the CPW, which now shows greater spatial correlations on tropical SST than the canonical ENSO does (Newman *et al*., 2011). Finally, as noted above, the NPGO and CPW are related through the atmospheric bridge of the NPO (Di Lorenzo *et al*., 2010; Furtado *et al*., 2012). These changes, however, still do not explain how the ecological significance of the NPGO has become dominant. We think that an indirect effect, increased current flow and transport of nutrients into the CCE, which are then distributed by upwelling, probably explains this new pattern, but this process

remains to be modeled. Alternatively, it may be that NPGO-related currents transport plankton, and perhaps even *T. spinifera* eggs or juveniles into the system, leading to greater variability.

The complexity of competing and perhaps synergistic physical drivers operating on varying spatial scales, coupled with indirect, multi-species predator-prey relationships, makes it difficult to assess how the NPGO is mechanistically related to krill and their predators in the central CCE. However, this study illustrates that changes in the variance of predator demography can be one of the primary responses to variance shifts in the coupled atmospheric-oceanic system. In this case, the biological mechanisms involve predator-prey interactions with euphausiids, primarily *T. spinifera*, and juvenile rockfish as probable trophic connections between the physical and upper trophic level environments. Therefore, this study shows that in addition to the traditional foci on central tendency, greater attention should be paid to shifts in the variance structure of both physical drivers and biological responses. Moreover, as noted by others, changes in variance may afford predictions of ecosystem shifts (Scheffer *et al*., 2009). Finally, we propose that krill could represent key focal taxa for climate-ecosystem studies in many mid- to high-latitude pelagic ecosystems. Given their relative abundance and spatial organization, there is a high level of trophic focusing associated with krill across many coastal and open ocean ecosystems. Overall, we highlight an understudied and perhaps underappreciated ecological response (variance) in studies of climate variability and change. To that end, we support the suggestions of Jentsch *et al*. (2007) and others that assessing changes in variance should become a regular aspect of studies in the incipient field of climate change ecology.

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Author Contributions

WJS, JAS, and SAT conceptualized the paper; WJS, BM, and JAS collected, processed, and contributed data to the analysis; WJS, SAT, and EDL conducted the analyses; WJS, JAS, and EDL wrote the paper; WJS, SAT, JAS, BM, and EDL reviewed, edited, referenced the paper; WJS, JAS, BM, EDL contributed funding for analysis and write-up.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed map of the study region and sampling stations in the Gulf of the Farallones used to develop indices of euphausiid crustacean ('krill'), and juvenile rockfish abundance (CPUE). See Field *et al.* (2010) for details of juvenile rockfish abundance calculations and Santora *et al.* (2011a) for details of acoustic and net sampling and post-processing. The star indicates the location of the seabird breeding colony on Southeast Farallon Island. Data on seabird abundance at sea was obtained while the research vessel was underway between sampling stations. Boundaries of the Monterey Bay, Gulf of the Farallones, and Cordell Bank national marine sanctuaries are illustrated. Inset shows the Gulf of the Farallones relative to the Northeast Pacific Ocean.