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Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific

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[1] Long-term observations show that fish and plankton populations in the ocean fluctuate in synchrony with large-scale climate patterns, but similar evidence is lacking for estuaries because of shorter observational records. Marine fish and invertebrates have been sampled in San Francisco Bay since 1980 and exhibit large, unexplained population changes including record-high abundances of common species after 1999. Our analysis shows that populations of demersal fish, crabs and shrimp covary with the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO), both of which reversed signs in 1999. A time series model forced by the atmospheric driver of NPGO accounts for two-thirds of the variability in the first principal component of species abundances, and generalized linear models forced by PDO and NPGO account for most of the annual variability of individual species. We infer that synchronous shifts in climate patterns and community variability in San Francisco Bay are related to changes in oceanic wind forcing that modify coastal currents, upwelling intensity, surface temperature, and their influence on recruitment of marine species that utilize estuaries as nursery habitat. Ecological forecasts of estuarine responses to climate change must therefore consider how altered patterns of atmospheric forcing across ocean basins influence coastal oceanography as well as watershed hydrology.

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1. Introduction

[2] An important advance of ocean science has been the discovery that populations of fish and zooplankton fluctuate in synchrony with large-scale climate patterns. Cod recruitment in the North Sea is high when the North Atlantic Oscillation (NAO) is positive [*Stige et al.*, 2006], while salmon stocks in Alaska and California fluctuate inversely with the Pacific Decadal Oscillation (PDO) [*Mantua et al.*, 2002]. Catches from some marine fisheries have been recorded for nearly a century or longer, thereby capturing variability over several cycles of NAO, PDO and other multidecadal climate patterns. This variability includes reorganization of marine communities. For example, starfish, jellyfish, cod and halibut populations increased, while shrimp, forage fish, seabird and marine mammal populations decreased in the Gulf of Alaska after the NE Pacific shifted to its warm (+PDO) phase in 1977 [*Anderson and Piatt*, 1999]. Much of our knowledge of the natural history and community dynamics of marine ecosystems comes from long-term assessments of fish stocks in the sea.

[3] Observational records in the world's estuaries and bays are much shorter and do not provide a comparably robust empirical basis for determining if or how their biological communities are tied to large-scale climate patterns. However, an abrupt change in Pacific climate around 1999 provided a unique natural experiment because of its magnitude ("possibly the most dramatic and rapid episode of climate change in modern times" [*Peterson and Schwing*, 2003]) and its occurrence within the recent period of observation in estuaries such as San Francisco Bay. River flow is generally considered the primary driver of ecological variability in many estuaries, such as Chesapeake Bay [*Kimmel et al.*, 2009], and biological communities in coastal ecosystems have been restructured by nutrient enrichment [*Diaz and Rosenberg*, 2008], fishing [*Casini et al.*, 2009], hydrologic manipulations [*Petersen et al.*, 2008], and introductions of non-native species [*Alpine and Cloern*, 1992]. Therefore, detection of ecological responses to changes in large-scale climate patterns might be difficult at the land-sea interface where atmospheric, oceanographic, watershed and human forcings intersect and can mask climate signals [*Cloern and Jassby*, 2008]. We previously reported population changes at multiple trophic levels in San Francisco Bay (SFB) that occurred after 1999 [*Cloern et al.*, 2007]. Here we present

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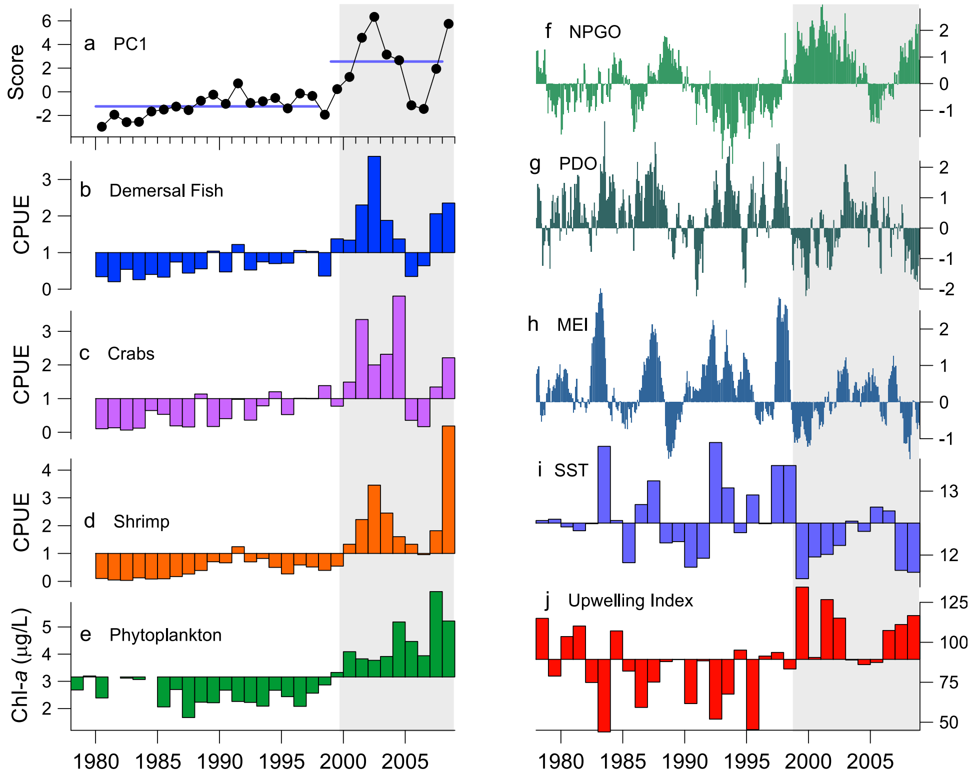

Figure 1. Time series of: (a) PC1 (filled circles) and its mean (blue lines) before and after 1999; (b) mean annual CPUE, normalized to 1980–2008 means, of five species of demersal fish (age-0 English sole, speckled sanddab, plainfin midshipman, bay goby, Pacific staghorn sculpin), (c) three species of crabs (age-0 Dungeness, slender, and brown rock crab), and (d) two species of shrimp (blacktail bay shrimp, Stimpson coastal shrimp), and (e) mean August-December chlorophyll *a* concentration in marine regions of San Francisco Bay. Mean monthly (f) NPGO, (g) PDO, (h) MEI, and (i) mean annual SST (°C) at Farallon Islands and (j) Upwelling Index at 39°N.

analyses showing that populations in this large estuary track variability of North Pacific climate patterns.

2. Data Sources and Analyses

[4] Monthly series of NPGO, PDO and the multivariate ENSO index (MEI) were obtained from http://www.o3d.org/npgo, http://jisao.washington.edu/pdo, and http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/, respectively. We used the monthly NCEP/NCAR Reanalysis 1 sea level pressure (SLP) and NOAA Extended V3b sea surface temperature (SST) anomalies, defined as deviations from the long-term mean (http://www.esrl.noaa.gov/psd/data/gridded). SST measured at Southeast Farallon Island (37°41.8′N, 122°59.9′W) was obtained from the Point Reyes Bird Observatory. The upwelling index at 39°N was obtained from the NOAA Pacific Fisheries Environmental Laboratory.

[5] We analyzed 1980–2008 catch data from monthly (February–October) bottom trawls taken by the California Department of Fish and Game at 24 sites in the marine regions of San Francisco Bay. Mean annual catch per unit effort (CPUE) was calculated from counts of individual species and age classes of fish, *Cancer* crabs and caridean shrimp collected in 6,085 bottom trawls. We restricted our analyses to the most abundant marine demersal taxa, which included 11 age-0 fishes, 3 age-0 crabs, and 4 shrimp species. We used principal component analysis (PCA) to create a community-level index of temporal change in SFB, where PCA reduced the dimensionality of the 18 fish and crustacean taxa to a single time series. We compiled a 1978–2008 time series of phytoplankton biomass as the August–December mean surface chlorophyll-*a* concentration averaged over marine regions of SFB, using data from the U.S. Geological Survey and Interagency Ecological Program. We emphasize August–December because these were the months of significant phytoplankton biomass increase after 1999 [*Cloern et al.*, 2007]. Additional details about methods and data sources are provided in the auxiliary material.[1]

3. Synchronous Climate and Community Shifts in a Large Estuary

[6] Principal component analysis of the year-by-species matrix of CPUE extracted a first component (PC1) that explained 32% of annual variability and had large positive loadings on 10 common species of fish and crustaceans and large negative loadings on 4 species (Table S1 of the auxiliary material). Regime-shift detection [*Rodionov*, 2004] identified a significant change in the PC1 time series after 1999 (Figure 1a). This shift reflected 3–6 fold increases, and record-high abundances of a group of demersal fish, crab, and shrimp species (Figures 1b–1d). Population increases of these predators after 1999 were followed by population

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2010GL044774.

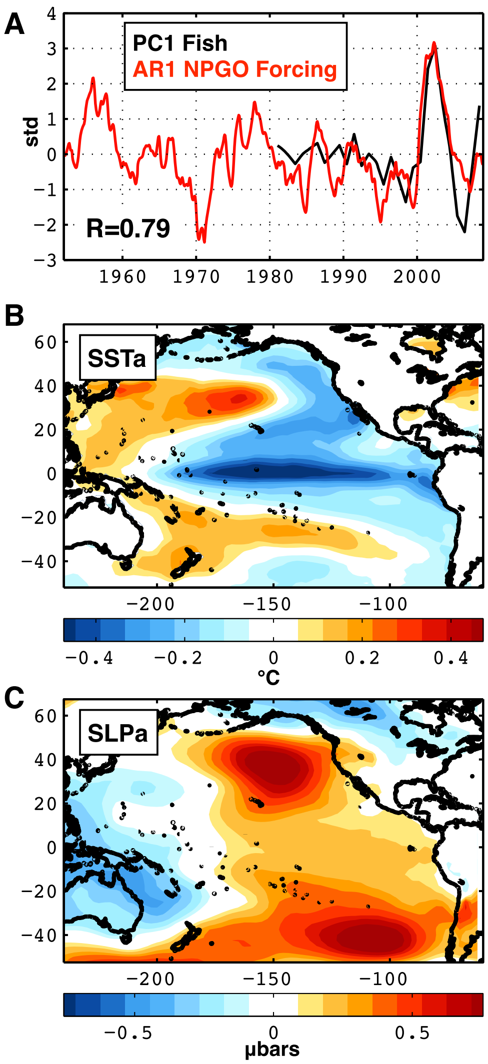

Figure 2. (a) Comparison of observed PC1 (black) with reconstruction of AR1 model (equation (1), red) forced by the atmospheric driver of the NPGO. Regression maps between reconstructed PC1 and (b) SST anomalies and (c) SLP anomalies. Before computing the regression maps with PC1, the SST and SLP fields are filtered using the AR1 model with the same parameters used when reconstructing PC1. This allows extracting the SST and SLP forcing patterns associated with the low-frequency fluctuations of the reconstructed PC1 (see section 4 for more details).

declines of bivalve suspension feeders [*Cloern et al.*, 2007] and increasing phytoplankton biomass that persisted from 2000 through 2008 (Figure 1e). These observations signal a restructuring of biological communities in SFB to a state unseen in the 1980s and 1990s. The community changes followed sign reversals of the Pacific-basin climate indices PDO, MEI, and NPGO after 1998 (Figures 1f–1h).

[7] Climate indices such as PDO and NPGO are powerful because they aggregate changing conditions across ocean basins and can reveal multi-factor influences on marine populations through shifts in ocean currents, temperature, mixing, and primary productivity [*Peterson and Schwing*, 2003]. However, single indices like the PDO provide only a partial view of the basin-scale low frequency variability. *Di Lorenzo et al.* [2008] identified the NPGO as the second dominant mode of sea surface height and temperature variability in the North Pacific. This climate pattern captures the dominant decadal-scale fluctuations of salinity and nutrients in the central and eastern North Pacific [*Di Lorenzo et al.*, 2009]. The PDO and NPGO are forced by changes in large-scale patterns of atmospheric variability. The PDO is driven predominantly by variability in the Aleutian Low (AL), which on interannual timescales is strongly modulated by ENSO through atmospheric teleconnections [*Alexander*, 1992]. The NPGO is driven by variability in the North Pacific Oscillation (NPO) [*Chhak et al.*, 2009], defined as the second dominant mode of North Pacific SLP [*Linkin and Nigam*, 2008] and characterized by a dipole pattern with centers of action over Hawaii and the Aleutians. However, the NPO's low-frequency variability that drives the NPGO is predominantly forced by central tropical Pacific Warming El Niño and exhibits maximum variance only over the Hawaiian region [*Di Lorenzo et al.*, 2010]. During 1999 there was an abrupt transition from a predominantly +PDO/−NPGO to a predominantly −PDO/+NPGO regime (Figures 1f and 1g). Regional manifestations of this change in California coastal waters include strengthening of upwelling-favorable winds (Figure 2c), strengthening of southward transport, cooling of surface waters (Figure 2b), and shoaling of the thermocline. Local observations confirmed an intensification of wind-driven upwelling and cooling of shelf waters adjacent to SFB (Figures 1i and 1j), and satellite imagery measured trends of increasing chlorophyll-*a* in California coastal waters from 1997–2008 [*Kahru et al.*, 2009].

4. Models to Explore Climate-Population Associations

[8] We used two modeling approaches to assess the strength of associations between population variability in SFB and atmosphere-ocean changes represented by the PDO and NPGO. We explored the link between community variability, as captured by the PC1 series, and climate patterns using an auto-regressive model of order 1 (AR1) where the rate of change of PC1 is controlled by the atmospheric forcings that drive either the PDO or NPGO. This approach was motivated by the hypothesis that correlations between PC1 and the ocean climate indices result from sharing the same atmospheric forcings. Under this assumption, the AR1 model should lead to better hindcasts of PC1 because it accounts for different integration timescales of the atmospheric forcing, including the timescale of dissipation of the forced perturbations and lagged population responses to the perturbations. We first tested the effects of the NPGO forcing by formulating an AR1 model for reconstructing PC1 as:

$$\frac{dPC1_{rec}(t)}{dt} = \alpha \mathrm{SLP}_{\mathrm{HI}}(\mathrm{t} - \Delta \mathrm{t}) - \frac{PC1_{rec}(t)}{\tau_{\mathrm{PC1}}} \qquad (1)$$

The $\mathrm{SLP}_{\mathrm{HI}}$ term on the right hand side is a proxy index of the atmospheric forcing of the NPGO, defined as the monthly mean sea-level pressure anomaly over the Hawaiian region (165°W–152°W; 17.5°N–22.5°N) [*Di Lorenzo et al.*, 2010]. The last term represents the dissipation of PC1 and is also referred to as the damping term, where τ_{PC1} is the characteristic damping timescale (~16 months, estimated from the

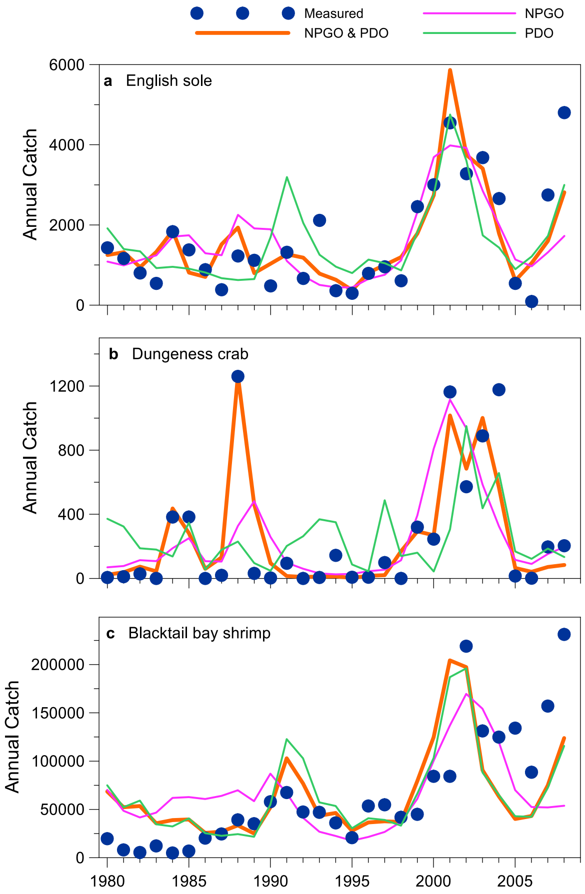

Figure 3. Poisson regression models for (a) English sole, (b) Dungeness crab, and (c) blacktail bay shrimp. Total annual catch of each species is shown for years 1980–2008 (blue circles) and compared to model projections. A model using both NPGO and PDO (red line) was superior to models based on either PDO (green line) or NPGO (purple line) individually.

e-folding timescale of the PC1 auto-correlation function). Physically, τ_{PC1} corresponds to the internal memory timescale of the dynamics governing the evolution of PC1, implying that the effects of forced perturbations on PC1 will only last within the timescale τ_{PC1}. The model includes a delayed response of PC1 to changing atmospheric forcing through inclusion of a lag ($\Delta\tau \sim 2$ years, based on optimizing the fit).

[9] The correlation between reconstructed and observed PC1 was significant (see auxiliary material) at R = 0.79 (Figure 2a), implying that this AR1 model captured 63% of the variance. The reconstructed PC1 showed that the 1999 transition was the strongest in the period 1980–2008. However, comparable extremes occurred in the mid 1950s and early 1970s. The forcing patterns of SLP and SST associated with the low-frequency fluctuations of $\mathrm{PC1}_{\mathrm{rec}}$ were also reconstructed by applying the AR1 model, with identical parameters, to the SST and SLP data at each spatial location and then by regressing the fields against $\mathrm{PC1}_{\mathrm{rec}}$ (Figures 2b and 2c). During times of positive $\mathrm{PC1}_{\mathrm{rec}}$, the SST pattern showed colder than average SST in the California Current system (Figure 2b) and above-average SLP over the NE Pacific (Figure 2c), corresponding to stronger than average upwelling winds off California. We constructed similar AR1 models using the PDO atmospheric forcing and the PDO index. Correlations between observed and reconstructed PC1 obtained by these models were insignificant and never exceeded R = 0.5.

[10] We next explored links between population variability of individual species and the PDO and NPGO using Poisson Generalized Linear Models of annual catch:

$$\log(\mu_t) = \mathbf{x}_t\,\boldsymbol{\beta} + \log(\mathrm{V}_t) \qquad (2)$$

where μ_t is aggregate catch and V_t is aggregate tow area (effort) for year t; $\mathbf{x}_t$ is a vector of climate indices; and $\boldsymbol{\beta}$ is the vector of regression coefficients. Our approach again assumed that populations respond to climate shifts after some lag and integrate effects over some period. We identified values of the lag and integrating period that optimize fit for each species, subject to known life-history constraints. Models using PDO- and NPGO-effects are illustrated for one species of fish, crab, and shrimp (Figure 3). The models explained 69%, 75% and 50% of catch variability (pseudo-R^2 corrected for overdispersion; see auxiliary material) for English sole, Dungeness crab and blacktail bay shrimp, respectively. These models captured responses of individual populations to: the 1999 climate shift (all three species); the temporary reversion back to the +PDO/−NPGO state in 2005 and 2006 (Figures 3a and 3c); and some features of population variability before 1999 (Figure 3b). For Dungeness crab, a model using just NPGO explained approximately 50% of the variance, but a PDO-only model explained only about 25%. A PDO-only model explained 50% of the variability and an NPGO-only model explained 37% of the catch variability of blacktail bay shrimp. Catch variability of English sole was nearly equally explained by models based on either PDO or NPGO effects (57% and 54%, respectively). Therefore, although community variability (PC1) closely tracked the NPGO, populations of individual species had varying degrees of association with the PDO and NPGO.

5. Mechanisms Linking Climate Patterns and Population Variability in an Estuary

[11] The mechanisms linking fluctuations of marine fish and invertebrate populations with climate patterns are not well understood for many species, e.g., Dungeness crab [*Botsford*, 2001]. Most species whose populations increased in SFB after 1999 migrate annually into estuaries, either as ocean-produced juveniles or as adults that reproduce in estuaries. Therefore, we infer that population increases inside SFB represent regional population responses to changes in coastal-ocean habitat quality that promote strong recruitment of this species assemblage. Model results suggest that the relative importance of PDO and NPGO vary among species, so the linkage mechanisms between climate patterns and fish and invertebrate production must also vary with species' life histories. These are predominantly cool temperate species whose biogeographic ranges are centered north of SFB, so cooling and strengthening of southward transport under a −PDO/+NPGO regime would facilitate a southward expansion of adult distributions and increase their reproductive potential in shelf waters near SFB. Secondly, the pelagic larvae of fish and crustaceans have high growth and survival rates when primary productivity is high, and fisheries yields

are strongly correlated with chlorophyll-*a* concentrations [*Ware and Thomson*, 2005] which increased along the California coast between 1997 and 2008 [*Kahru et al.*, 2009]. Finally, separation of the upwelling jet at Point Reyes, north of SFB, creates recirculation in the Gulf of Farallones which retains shelf waters near the mouth of SFB during periods of strong upwelling [*Vander Woude et al.*, 2006]. Collectively, these coastal oceanographic responses to a −PDO/+NPGO regime appear to establish physical conditions in California shelf waters that support high rates of production, growth, survival, and/or retention of early life stages of demersal fish and crustacean species that utilize estuaries as nursery habitat.

6. Implications for Forecasting Estuarine Ecosystem Responses to Climate Change

[12] Three decades of observation reveal that abundances of diverse marine taxa within an estuary track fluctuations of the Pacific Ocean's two dominant climate patterns. Although the linkage mechanisms are unknown, the NPGO and PDO prove to be meaningful indicators of ecological variability in San Francisco Bay. Our results demonstrate a connection between the pattern of atmospheric pressure (winds) across the Pacific basin, its forcing of large-scale oceanic gyre circulations, and responses that cascade to influence coastal oceanographic processes at the regional scale and, then, to the scale of individual estuaries and bays. The ten species highlighted in this study are major components of the epibenthic community and exert a top-down control on herbivores and promote phytoplankton growth through a trophic cascade [*Cloern et al.*, 2007]. Therefore, the PDO and NPGO may provide a basis for forecasting ocean-driven ecological regime shifts in Pacific estuaries and bays. Most projections of climate-change impacts on estuaries take a watershed perspective and assume that altered patterns of precipitation and river inflow will drive ecosystem change [*Najjar et al.*, 2009]. We show here that population fluctuations of key marine species in SFB are tightly tied to climate-driven variability in the coastal ocean. Therefore, ecological forecasts of estuarine responses to climate change must consider how altered patterns of atmospheric forcing across ocean basins will influence both watershed hydrology and coastal oceanography.

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