

A double-integration hypothesis to explain ocean ecosystem response to climate forcing

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Long-term time series of marine ecological indicators often are characterized by large-amplitude state transitions that can persist for decades. Understanding the significance of these variations depends critically on the underlying hypotheses characterizing expected natural variability. Using a linear autoregressive model in combination with long-term zooplankton observations off the California coast, we show that cumulative integrations of white-noise atmospheric forcing can generate marine population responses that are characterized by strong transitions and prolonged apparent state changes. This model provides a baseline hypothesis for explaining ecosystem variability and for interpreting the significance of abrupt responses and climate change signatures in marine ecosystems.

climate variability | ocean climate | zooplankton dynamics | California Current | ecosystem shifts

Long-term time series of marine ecological indicators often are characterized by large-amplitude state transitions that can persist for decades. These transitions have been attributed to nonlinear responses of marine populations to environmental climate forcing (e.g., regime shifts) (1) or to linear tracking of the physical environment (2, 3). However, assessing the significance of these changes relies critically on the type of model characterizing the natural random variability expected in a given ecological ocean time series.

In the climate community the most common null hypothesis used to assess changes in physical ocean variables is an autoregressive model of order 1 (AR-1) (4),

$$\frac{d\phi(t)}{dt} = f(t) - \frac{\phi(t)}{\tau_{ocean}}, \quad [1]$$

where the rate of change of an ocean variable, $\phi(t)$, is forced by white-noise variations of the atmosphere, $f(t)$. The second term on the right-hand side represents damping of the signal associated with the natural dissipation timescale, τ_{ocean} , of the selected variable. A clear example of the applicability of this model (Eq. 1) comes from the Pacific Ocean where the atmospheric variability of the Aleutian Low pressure system drives an oceanic response in the sea surface temperature variability captured by the Pacific Decadal Oscillation (PDO) (5). The decorrelation timescale of the PDO (τ_{ocean}) is ~ 6 mo. By integrating an index of Aleutian Low variability (Fig. 1A), that is, by solving Eq. 1 with the forcing term set to the Aleutian Low index (Methods), we can reconstruct the PDO index with significant correlation of $R = 0.61$ ($>98\%$) (Fig. 1B). The integration associated with the AR-1 model (Eq. 1) filters the high-frequency component of the atmospheric forcing (e.g., white noise) and produces a signal that is characterized by stronger low-frequency variability (e.g., red noise) such as the PDO climate index (6).

Double-Integration Hypothesis to Explain Ecosystem Variability

Although useful, this AR-1 model (Eq. 1) is not necessarily an adequate null hypothesis to explain the variability of marine

populations. Population variability for some marine organisms (e.g., zooplankton or fish species) may not be forced directly by the atmosphere (e.g., white-noise forcing) but rather by changes in ocean conditions (e.g., red-noise forcing),

$$\frac{d\beta(t)}{dt} = \phi(t) - \frac{\beta(t)}{\tau_{bio}}, \quad [2]$$

where the rate of change of an ecological variable, $\beta(t)$, is forced by red-noise variations of the ocean, $\phi(t)$, and τ_{bio} is the natural damping timescale for the selected ecosystem variable (e.g., the lifespan of the species). This hypothesis (Eq. 2) is equivalent to a double integration of the atmospheric white-noise forcing and leads to time series that are characterized by much stronger and smoother low-frequency variability. Fig. 1C shows an example of using Eq. 2 to integrate the PDO index with $\tau_{bio} = 2$ y. This timescale was chosen because it approximates the lifespan of the species *Nyctiphanes simplex*, which we use in the next section to test the double-integration hypothesis with multidecadal zooplankton observations. When $\tau_{bio} > \tau_{ocean}$, time series resulting from double integration of atmospheric forcing exhibit naturally large-amplitude and prolonged state transitions that can emerge from purely random forcing and can exhibit trends when τ_{bio} is sufficiently large compared with the length of the time series.

To illustrate further the effects of double linear integration of atmospheric white-noise forcing, we generate three random white-noise time series (Fig. 2A, black lines) in addition to the Aleutian Low index. We then apply the AR-1 model (Eq. 1) to integrate the white noise and generate red-noise time series (Fig. 2B, blue lines). The decorrelation or damping timescale (τ_{ocean}) is set to be the same as the PDO (~ 6 mo). These red-noise time series are characterized by a power spectrum in log space with slope of -2 —that is, stronger power at the low frequency and reduced power at the high frequency. If we integrate again the autogenerated red-noise time series using Eq. 2 with the damping timescale, $\tau_{bio} = 2$ y, we obtain time series that are characterized by a much steeper -4 slope in the power spectrum. This double integration of white noise leads to time series with strong and smooth low-frequency variations (Fig. 2C, red lines) which, when analyzed over selected time periods, can produce regime-like behaviors that are not statistically separable from integrated random noise. Evidence for double-integration effects already has been documented in the ocean for physical variability below the thermocline where wind-driven changes in geostrophic currents along subsurface isopycnals (one integration) drive low-frequency variations in temperature and salinity (e.g., second integration), resulting in a power spectrum slope of -4 (7).

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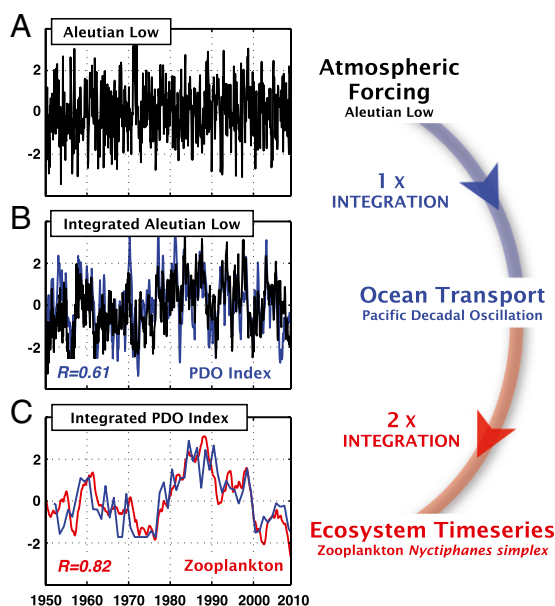


Fig. 1. The effects of double integration. (A) Aleutian Low index. (B) Integrated Aleutian Low index (black) and PDO index (blue). (C) Integrated PDO index (blue) and zooplankton time series of *Nyctiphanes simplex* in the California Current System (red).

Testing the Double-Integration Hypothesis with Ecosystem Observations

Support for the validity of Eq. 2 as a null hypothesis for ecosystem variables that are sensitive to changes in oceanic conditions comes from a 60-y-long time series of zooplankton (*Nyctiphanes simplex*,

a species of krill) in the California Current System (Fig. 3A, blue line). This time series is correlated with the PDO index ($R = 0.41$, $>95\%$) because during the positive phase of the PDO enhanced northward transport along the coast carries *Nyctiphanes simplex* into the California Current from its native breeding center south of the California Current (3, 8). We now model this process using Eq. 2 where the rate of change of the zooplankton [$\beta(t)$] is forced by the PDO [$\phi(t)$], which we use here as an index of changes in ocean transport. The damping timescale, τ_{bio} , is set to the estimated lifespan of the species (~ 2 y). The resulting time series (Fig. 3C, red line showing the integrated PDO index) exhibits a much stronger and significant correlation with the zooplankton time series ($R = 0.82$, $>99\%$) (see *Methods* for the significance test). Such high correlation cannot be achieved by direct comparison between the PDO index and the zooplankton time series even when applying a low-pass filter for the PDO index (e.g., 2-y low-pass $R = 0.52$; Fig. 3B). In fact, the correlations between the zooplankton time series and low-pass versions of the PDO (using a range of different cutoff timescales in the low-pass filter) are insignificant until cutoff timescales of ~ 8 y are reached (Fig. 4). For low-pass filter cutoffs $\gg \tau_{bio}$, the signal (zooplankton) and the forcing (PDO) in Eq. 2 become in phase again; that is, the rate of change in Eq. 2 (e.g., the term on the left-hand side) is negligible compared with the damping term, and the new balance is between the terms on the right-hand side. We also note that the skill of Eq. 2 is not very sensitive to τ_{bio} values within a range of estimated life spans of the species (1–3 y) (Fig. 4). These results suggest that Eq. 2 represents a good process model and null hypothesis to account for natural variability in marine ecosystem variables that are influenced by random fluctuations in ocean climate (red noise) such as changes in geostrophic transport.

Although *Nyctiphanes simplex* provides an example of double-integration effects on a marine population, not all marine

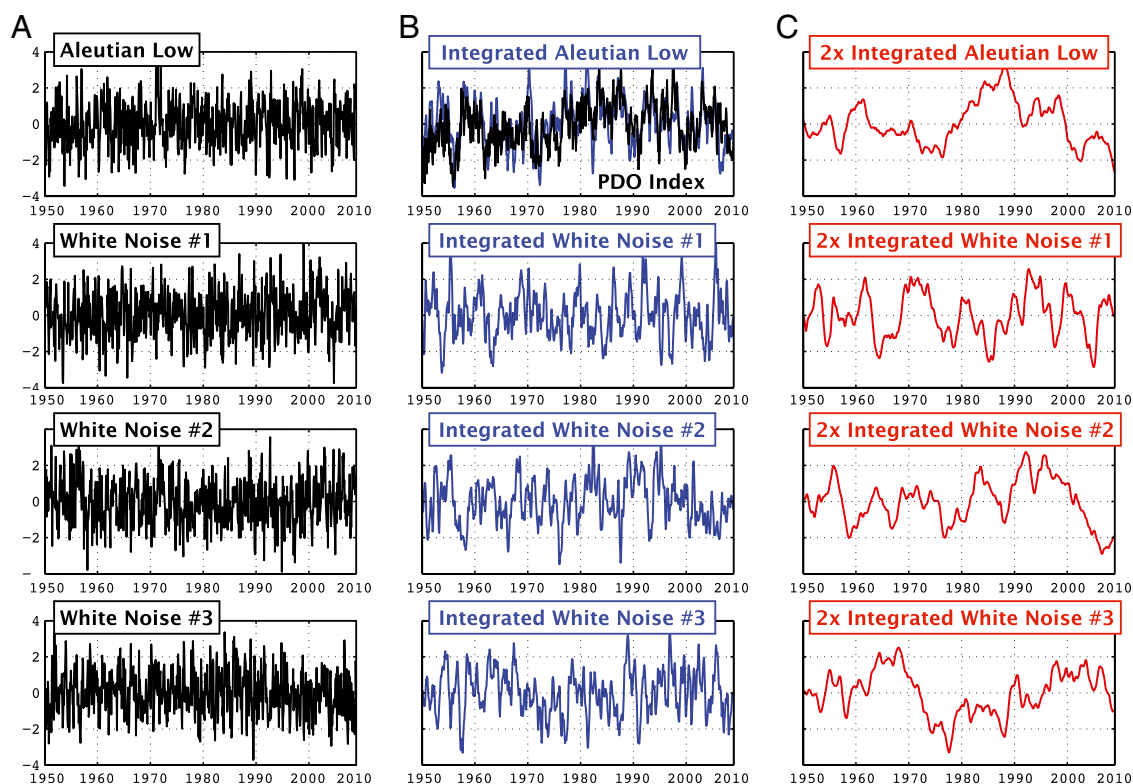


Fig. 2. The emergence of strong and prolonged state transitions from cumulative integrations of white noise. (A) White-noise time series. (B) Integrated white noise (i.e., red noise). (C) Double-integrated white noise (i.e., integrated red noise).

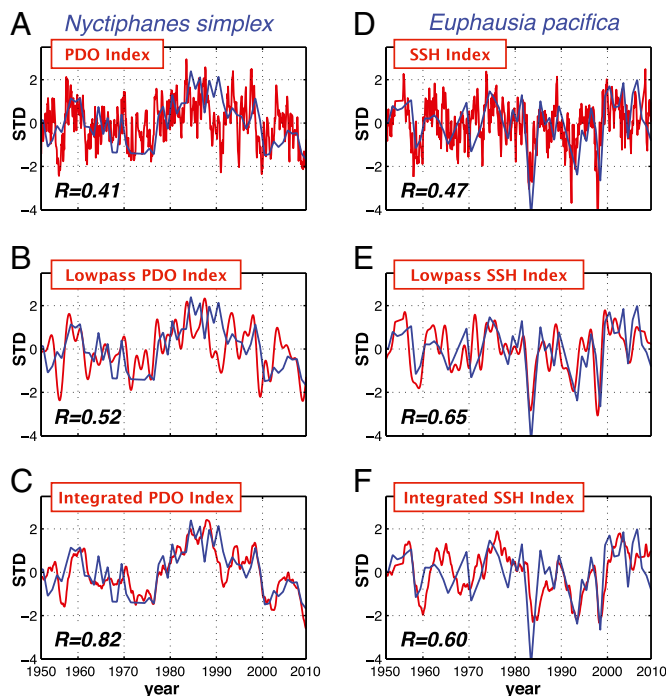


Fig. 3. Reconstruction of zooplankton time series in the California Current. (A–C) Comparison of *Nyctiphanes simplex* (blue line) with PDO index (red line). (A) Monthly data. (B) Two-year low-pass filtering. (C) Integrated PDO index. (D–F) Comparison of *Euphausia pacifica* (blue line) with SSH index (red line). (D) Monthly data. (E) One-year low-pass filtering. (F) Integrated SSH index. The PDO and SSH indices are used as proxies of changes in alongshore transport and in the oceanic response to upwelling, respectively.

populations exhibit persistent state transitions on decadal time-scales that are consistent with the double-integration hypothesis. As an example, we explore the variability of another krill species in the California Current System, *Euphausia pacifica*, which does not exhibit smooth decadal variations but instead is characterized by strong interannual changes (Fig. 3D, blue line). *Euphausia pacifica* is a resident zooplankton species in the region whose variability is thought to be related to changes in local upwelling, which modulate food availability (e.g., via phytoplankton blooms) and thus alter population growth rates (9). The variability in upwelling is controlled by changes in Ekman currents, which are a direct response to changes in the atmospheric forcing. Dynamically the Ekman currents differ from geostrophic currents in that they do not integrate the atmospheric forcing, and their power spectrum is

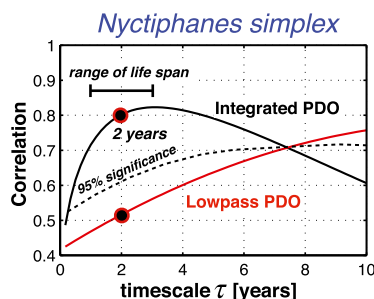


Fig. 4. Sensitivity of *Nyctiphanes simplex* model to biological damping time scale. Correlation skill of integrated PDO (black line) for different values of the damping timescale τ_{bio} in Eq. 2. This model skill is compared with the skill obtained by low-pass filtering the PDO (red line) with different cutoff time scales in the filter.

Types of impacts of climate forcing on ecosystem

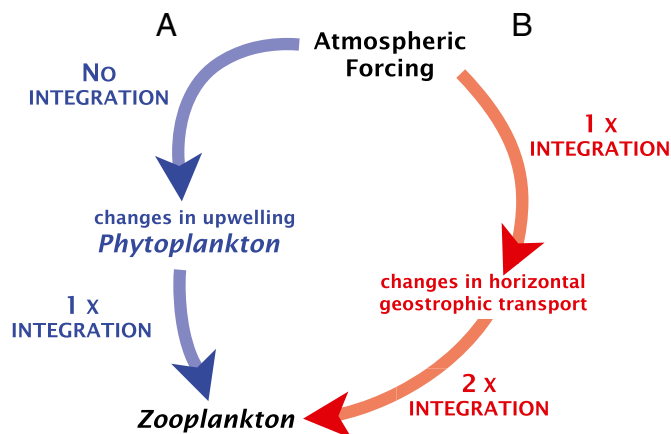


Fig. 5. Schematic of impacts of environmental forcing on zooplankton. (A) Single-integration effects (blue path). (B) Double-integration effects (red path).

close to white noise. These characteristics suggest that organisms whose populations are controlled by changes in Ekman upwelling will not exhibit double-integration effects, and their variability will be the result of single integrations of the atmospheric forcing. To test this hypothesis, we built an index of the California coastal ocean response to upwelling using the La Jolla sea surface height anomalies (SSH index) from tide gauge data (1× integration of atmospheric forcing). Previous studies (10) have shown that coastal SSH anomalies are a good proxy for biological productivity in the California Current, because they capture the upwelling response to both local and remote forcing (the latter including coastally trapped waves forced by wind changes south of the system). We now compare the SSH index with *Euphausia pacifica* abundance after smoothing the upwelling index with a low-pass filter of 2 y. The resulting correlation ($R = 0.65$, >95%) (Fig. 3E) is significant and shows a strong in-phase relationship between the ocean SSH index and the biological time series. We then perform a second integration of the atmospheric forcing; that is, we integrate Eq. 2 forced with the raw SSH index (i.e., the ocean red-noise forcing) and a decay timescale, τ_{bio} , set to the estimated lifespan of *Euphausia pacifica* (~2 y). The double-integration model does not lead to any significant improvement in the correlation; in fact $R = 0.65$ declines to $R = 0.60$ (<95%; Fig. 3F) and further introduces a slight shift between the phasing of the zooplankton and the integrated SSH index. For *E. pacifica* a low-pass filter of the SSH index performs at least as well as the single integration of Eq. 2, suggesting that this zooplankton time series is mostly in phase with the ocean SSH index (i.e., a single integration of atmospheric forcing).

Although the results for *Euphausia pacifica* support the idea that this species' variability is consistent with a single integration of the atmospheric forcing, as suggested by its upwelling-dependent dynamics, we cannot rule out alternative interpretations of the process dynamics. For example, this species could integrate other sources of oceanic red-noise forcing (e.g., low-frequency changes in the ocean nutricline) and still be characterized by strong interannual power and an in-phase relationship with the ocean forcing. This possibility should be considered for cases in which $\tau_{bio} \leq \tau_{ocean}$, because the species will not integrate the oceanic forcing (Eq. 2) or exhibit double-integration effects.

Types of Ecosystem Response to Climate Forcing

Understanding and explaining the variability of marine ecosystem indicators in response to climate forcing relies critically on the dynamics controlling how marine populations integrate the

variability of the environmental forcing. Two examples of long-term zooplankton observation in the California Current System suggest that, although certain populations (e.g., *Euphausia pacifica*) have strong interannual fluctuations that can be explained by single integrations of white-noise atmospheric forcing (Fig. 5A, blue path, direct response to changes in upwelling), fluctuations in other species (e.g., *Nyctiphanes simplex*) exhibit smooth decadal changes that are consistent with ecosystem dynamics in which the random atmospheric forcing is integrated two times (Fig. 5B, red path showing response to changes in ocean transport).

Taken together, these results suggest that the effects of cumulative integrations of environmental and climate forcing on time series of marine populations (e.g., zooplankton and fish) naturally lead to potentially strong and prolonged apparent state transitions that must be considered carefully when searching for apparent nonlinear responses and climate-change signatures in marine ecosystems.

Methods

The atmospheric Aleutian Low index is defined as the first principal component of monthly sea level pressure anomalies from 20°N–62°N from the National Centers for Environmental Prediction/National Center for Atmospheric Research Reanalysis Project (11).

The PDO index is defined as the first principal component of monthly anomalies of sea surface temperature in the Pacific poleward of 20°N, after removal of the long-term trend (12). The index was downloaded from <http://jisao.washington.edu/pdo/PDO.latest>.

All postmetanaupliar stages of the euphausiid *Nyctiphanes simplex* were enumerated from springtime California Cooperative Oceanic Fisheries Investigations cruises in the southern sector of the California Current System (lines 80–93, from shore to station 70, inclusive; see ref. 13). The net mesh was 0.505 mm, towed from 140–0 m or 210–0 m; only nighttime samples are analyzed to minimize net avoidance and diel vertical migration. Abundances are expressed as anomalies from the long-term log10 mean, standardized by the SD.

The significance of the correlation coefficients is estimated from the Probability Distribution Functions (PDFs) of the correlation coefficient of two red-noise time series with the same autoregression coefficients as estimated from the original signals. The PDFs are computed numerically by generating 10,000 realizations of the correlation coefficient of two random red-noise time series.

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