THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Di Lorenzo, E., V. Combes, J.E. Keister, P.T. Strub, A.C. Thomas, P.J.S. Franks, M.D. Ohman, J.C. Furtado, A. Bracco, S.J. Bograd, W.T. Peterson, F.B. Schwing, S. Chiba, B. Taguchi, S. Hormazabal, and C. Parada. 2013. Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanography* 26(4):68–81, http://dx.doi.org/10.5670/oceanog.2013.76.

DOI

http://dx.doi.org/10.5670/oceanog.2013.76

Synthesis of Pacific Ocean Climate and Ecosystem Dynamics

BY EMANUELE DI LORENZO, VINCENT COMBES, JULIE E. KEISTER, P. TED STRUB, ANDREW C. THOMAS, PETER J.S. FRANKS, MARK D. OHMAN, JASON C. FURTADO, ANNALISA BRACCO, STEVEN J. BOGRAD, WILLIAM T. PETERSON, FRANKLIN B. SCHWING, SANAE CHIBA, BUNMEI TAGUCHI, SAMUEL HORMAZABAL, AND CAROLINA PARADA

ABSTRACT. The goal of the Pacific Ocean Boundary Ecosystem and Climate Study (POBEX) was to diagnose the large-scale climate controls on regional transport dynamics and lower trophic marine ecosystem variability in Pacific Ocean boundary systems. An international team of collaborators shared observational and eddy-resolving modeling data sets collected in the Northeast Pacific, including the Gulf of Alaska (GOA) and the California Current System (CCS), the Humboldt or Peru-Chile Current System (PCCS), and the Kuroshio-Oyashio Extension (KOE) region. POBEX investigators found that a dominant fraction of decadal variability in basin- and regional-scale salinity, nutrients, chlorophyll, and zooplankton taxa is explained by a newly discovered pattern of ocean-climate variability dubbed the North Pacific Gyre Oscillation (NPGO) and the Pacific Decadal Oscillation (PDO). NPGO dynamics are driven by atmospheric variability in the North Pacific and capture the decadal expression of Central Pacific El Niños in the extratropics, much as the PDO captures the low-frequency expression of eastern Pacific El Niños. By combining hindcasts of eddy-resolving ocean models over the period 1950–2008 with model passive tracers and long-term observations (e.g., CalCOFI, Line-P, Newport Hydrographic Line, Odate Collection), POBEX showed that the PDO and the NPGO combine to control low-frequency upwelling and alongshore transport dynamics in the North Pacific sector, while the eastern Pacific El Niño dominates in the South Pacific. Although different climate modes have different regional expressions, changes in vertical transport (e.g., upwelling) were found to explain the dominant nutrient and phytoplankton variability in the CCS, GOA, and PCCS, while changes in alongshore transport forced much of the observed long-term change in zooplankton species composition in the KOE as well as in the northern and southern CCS. In contrast, cross-shelf transport dynamics were linked to mesoscale eddy activity, driven by regional-scale dynamics that are largely decoupled from variations associated with the large-scale climate modes. Preliminary findings suggest that mesoscale eddies play a key role in offshore transport of zooplankton and impact the life cycles of higher trophic levels (e.g., fish) in the CCS, PCCS, and GOA. Looking forward, POBEX results may guide the development of new modeling and observational strategies to establish mechanistic links among climate forcing, mesoscale circulation, and marine population dynamics.

INTRODUCTION

The POBEX project (http://www.pobex.org, 2008–2012) brought together researchers from North America, Japan, and South America to investigate the mechanisms of climate and ecosystem variability in three Pacific boundary regions: Northeast Pacific (NEP), including the Gulf of Alaska (GOA) and the California Current System (CCS); the Humboldt or Peru-Chile Current System (PCCS); and the Kuroshio-Oyashio Extension (KOE) region.

The main objectives of POBEX were to: (1) understand and quantify how large-scale climate variability drives the regional-scale physical variability that is coherent along the Pacific boundary, and (2) use regional-scale dynamics in combination with existing long-term ecological observations to interpret marine ecosystem processes. Specifically, POBEX quantified how changes in regional ocean processes (e.g., upwelling, transport dynamics, mixing, mesoscale structure) in each Pacific Ocean boundary region control phytoplankton and zooplankton dynamics and the extent to which large-scale climate modes such as the Pacific Decadal Oscillation (PDO; Mantua et al., 1997), the El Niño-Southern Oscillation (ENSO), and the recently discovered North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2008) drive these regional ocean dynamics. The underlying hypothesis of POBEX was that large-scale Pacific climate forcing drives changes in transport dynamics that exert dominant and coherent bottom-up control on coastal ocean ecosystems.

To explore how interannual-to-decadal variations in upwelling and horizontal transport affect the lower trophic levels of the Pacific boundary marine ecosystems, POBEX combined a series of historical (1950–present) eddy-resolving (10 km spatial resolution) ocean simulations at both global and regional scales with model passive tracers to generate temporal indices for transport processes such as upwelling and horizontal advection. The transport indices were then used to test the extent to which observed changes in phytoplankton are connected to modeled changes in the strength, structure, and timing of upwelling and to explore specific hypotheses concerning links between changes in modeled horizontal transport and changes in zooplankton abundance and species diversity. By exploring regional-scale dynamics, POBEX identified the important role of recently identified patterns of climate variability (e.g., central Pacific El Niños and NPGO) and clarified their large-scale and regional-scale dynamics. This has brought improved understanding of the mechanisms of large-scale Pacific climate variability and their regional-scale impacts on the coastal ocean and marine ecosystems.

Here, we report on some of the major accomplishments of the POBEX program in the context of a synthesis of the mechanics of Pacific climate and ecosystem lower trophic variability.

LARGE-SCALE MECHANICS OF PACIFIC CLIMATE AND ECOSYSTEMS

One of the most significant contributions of the POBEX program from a physical standpoint was to improve our understanding of the mechanisms driving decadal variability in the North Pacific. In particular, the models revealed the ocean-atmosphere connections driving the PDO and NPGO. Interannual ENSO fluctuations strongly influence these decadal oceanic responses to atmospheric forcing in the North Pacific (Zhang et al., 1997; Di Lorenzo et al., 2010). ENSO fluctuations propagate through the atmosphere; the ocean ultimately integrates their effects into the observed responses. Two main pathways are apparent, driven by different types of ENSO, and culminating in the PDO and NPGO (Figure 1). In one, an Eastern Pacific ENSO (EP-ENSO) influences the Aleutian Low (AL) atmospheric system to drive the PDO (explains ~ 30% of the variance; Newman et al., 2003; Vimont, 2005). In the other, a Central Pacific ENSO (CP-ENSO) contributes to the low-frequency variability in the North Pacific Oscillation (NPO)—the second dominant mode of atmospheric variability in the North Pacific (Walker and Bliss, 1932; Rogers, 1981), resulting in the NPGO (explains ~ 75% of the variance; Di Lorenzo et al., 2010; Furtado et al., 2012). While ENSO teleconnections play an important role in modulating the low-frequency variability of the atmospheric drivers of the PDO (Figure 1, red path) and NPGO (Figure 1, blue path), these atmospheric drivers are also characterized by significant stochastic high-frequency variability (Figure 1, gray path), which contributes to an equally important fraction of the variability in the oceanic modes. As we show below, PDO and NPGO dynamics drive distinct physical and biological responses, and their relative dominance is changing with time. Interestingly, in the South Pacific, the extremely tight coupling of the oceanic response with ENSO precludes the strong decadal variability seen north of the equator.

Additionally, POBEX researchers showed that the AL/PDO and NPO/NPGO systems drive decadal variations in the North Pacific western boundary (e.g., KOE) that are coherent with those in the eastern boundary. This occurs

A MODEL FOR EXPLAINING PACIFIC DECADAL DYNAMICS

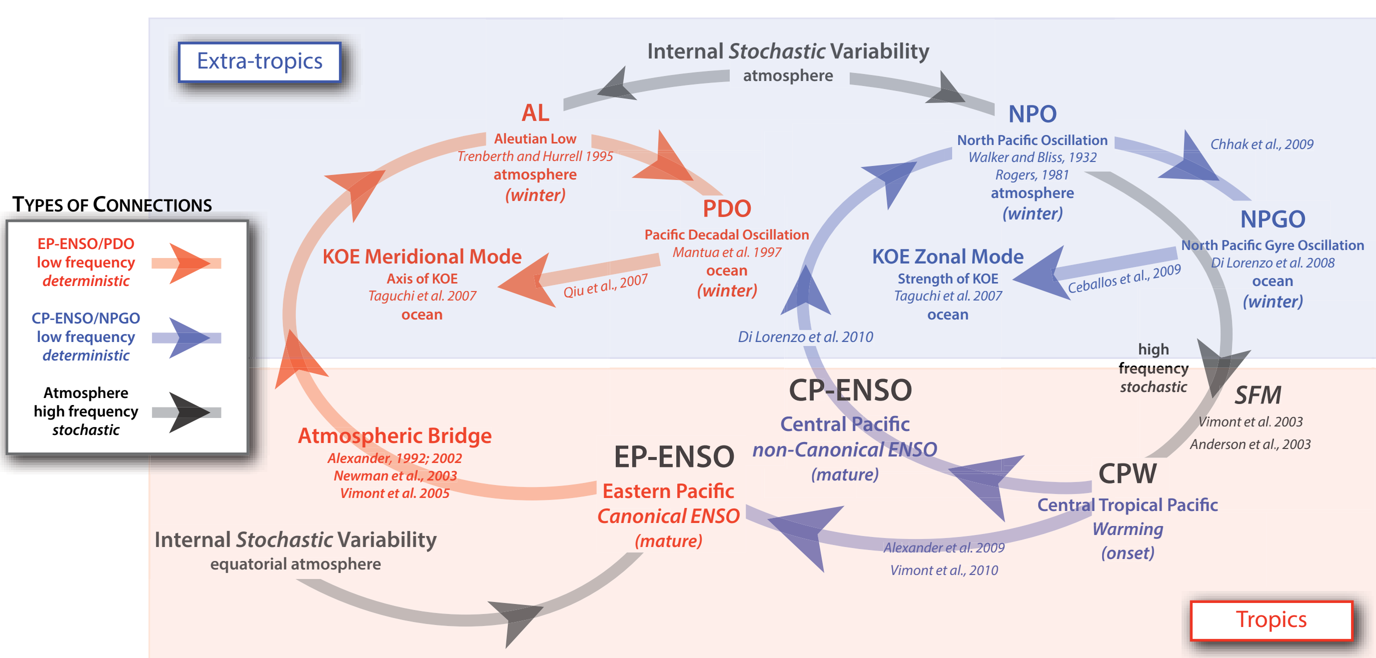

Figure 1. Synthesis of Pacific climate dynamics and teleconnections. The Pacific Decadal Oscillation (PDO; red path) and North Pacific Gyre Oscillation (NPGO; blue path) outline teleconnections at low-frequency time scales. The gray path shows how sources of high-frequency stochastic variability in the atmosphere energize the Aleutian Low (AL), North Pacific Oscillation (NPO), and El Niño-Southern Oscillation (ENSO) systems. In the schematic, NPO low-frequency variability is linked to Central Pacific (CP)-El Niño; however, processes internal to the North Pacific atmosphere appear to drive its high-frequency variability (gray path).

through Rossby waves that propagate westward from the central and eastern North Pacific and modulate the KOE upon arrival. AL/PDO Rossby waves drive changes in the axis of the KOE (Miller and Schneider, 2000; Qiu et al., 2007; Taguchi et al., 2007), while NPO/NPGO Rossby waves modulate the speed and strength of the KOE (Ceballos et al., 2009). A similar Rossby wave connection has been also isolated in the South Pacific (Holbrook et al., 2011).

Eastern Pacific ENSO and the Pacific Decadal Oscillation

In its positive phase, the "traditional" El Niño is characterized by pronounced warming of the tropical eastern Pacific (e.g., EP-ENSO), weakening trade winds, and positive (negative) atmospherically forced sea level pressure anomalies (SLPa) over the western (eastern) tropical Pacific (Figure 2a). These changes in the tropical atmospheric circulation modify the large-scale Hadley Cell and drive an important fraction of the extratropical variability of the AL through the ENSO atmospheric teleconnection pattern (Figure 2a; Alexander, 1992; Alexander et al., 2002). This teleconnection between EP-ENSO and the AL is evident if we develop an index of the variability of the projection of the EP-ENSO pattern in SLPa in the North Pacific (Figure 2a, black box). This EP-ENSO projection index has significant correlation (R = 0.8) with an index of the AL variability defined as the first principal component of North Pacific SLPa (Figure 3a). The ocean integrates these changes in atmospheric forcing, acting as a filter that enhances the decadal energy of the AL atmospheric forcing and of the ENSO teleconnection. The EP-ENSO-derived variability of the AL drives changes in ocean circulation

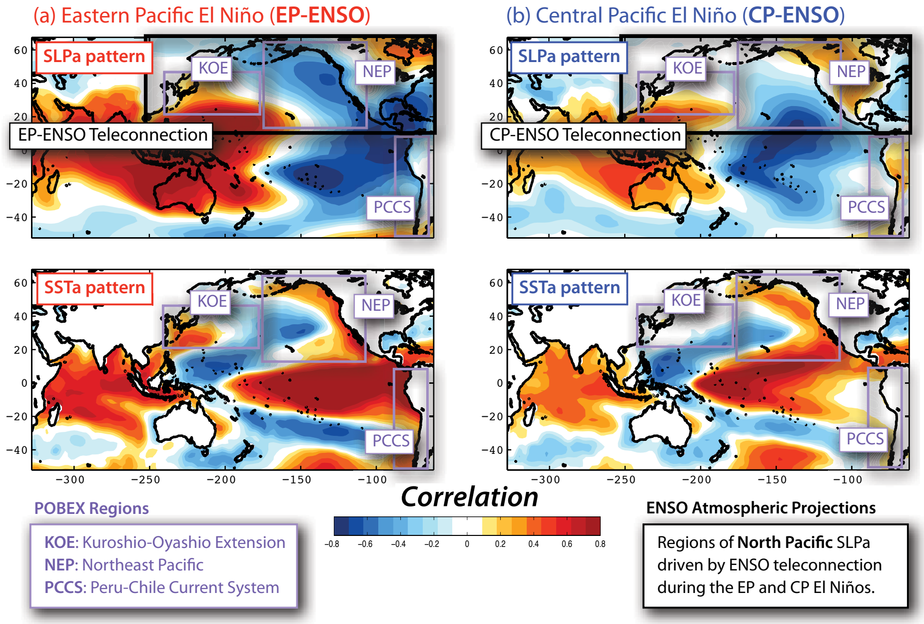

Figure 2. The flavors of ENSO and their teleconnections. Correlation patterns of NOAA sea surface temperature (SST) and National Centers for Environmental Prediction (NCEP) sea level pressure (SLP) monthly anomalies with (a) the eastern Pacific or canonical El Niño index (positive phase of ENSO) and (b) the central Pacific El Niño index. The ENSO indices are from the NOAA climate diagnostic center. Black rectangles show the atmospheric projections of a positive ENSO onto the North Pacific atmosphere, also referred to as the ENSO teleconnection. The purple rectangles shows the geographical domains targeted by the Pacific Ocean Boundary Ecosystem Climate Study (POBEX).

Emanuele Di Lorenzo *(edl@gatech.edu) is Professor of Ocean Sciences, School of Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, GA, USA.* **Vincent Combes** *is Research Associate, College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA.* **Julie E. Keister** *is Assistant Professor, School of Oceanography, University of Washington, Seattle, WA, USA.* **P. Ted Strub** *is Professor, College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA.* **Andrew C. Thomas** *is Professor, School of Marine Sciences, University of Maine, Orono, ME, USA.* **Peter J.S. Franks** *is Professor, Scripps Institution of Oceanography, University of California, San Diego (UCSD), La Jolla, CA, USA.* **Mark D. Ohman** *is Professor, Scripps Institution of Oceanography, UCSD, La Jolla, CA, USA.* **Jason C. Furtado** *is Staff Scientist, Atmospheric and Environmental Research Inc., Lexington, MA, USA.* **Annalisa Bracco** *is Associate Professor, School of Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, GA, USA.* **Steven J. Bograd** *is Oceanographer, National Oceanic and Atmospheric Administration (NOAA), Southwest Fisheries Science Center, Pacific Grove, CA, USA.* **William T. Peterson** *is Oceanographer, NOAA, Northwest Fisheries Science Center, Seattle, WA, USA.* **Franklin B. Schwing** *is Oceanographer, NOAA, Silver Spring, MD, USA.* **Sanae Chiba** *is Senior Scientist, Marine Ecosystem Research Team, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Kanagawa, Japan.* **Bunmei Taguchi** *is Research Scientist, The Earth Simulator Center, JAMSTEC, Kanagawa, Japan.* **Samuel Hormazabal** *is Professor, Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile.* **Carolina Parada** *is Marine Biologist, Departmento de Oceanográfica, Universidad de Concepción, Concepción, Chile.*

and temperature that are captured in the PDO pattern (Figure 3b). These dynamical links allow the PDO to be modeled as a simple integrator of the AL variability and the EP-ENSO teleconnection (Newman et al., 2003; Schneider and Cornuelle, 2005; Vimont, 2005). The EP-ENSO projection index captures both the EP-ENSO and the AL stochastic contributions to North Pacific SLPa variability. A simple integration of the EP-ENSO projection index with an autoregressive model of order-1 (AR1) with a six-month memory time scale leads to a skillful reconstruction of the PDO index (Figure 3b; see Chhak et al., 2009, for details on the AR-1 approach).

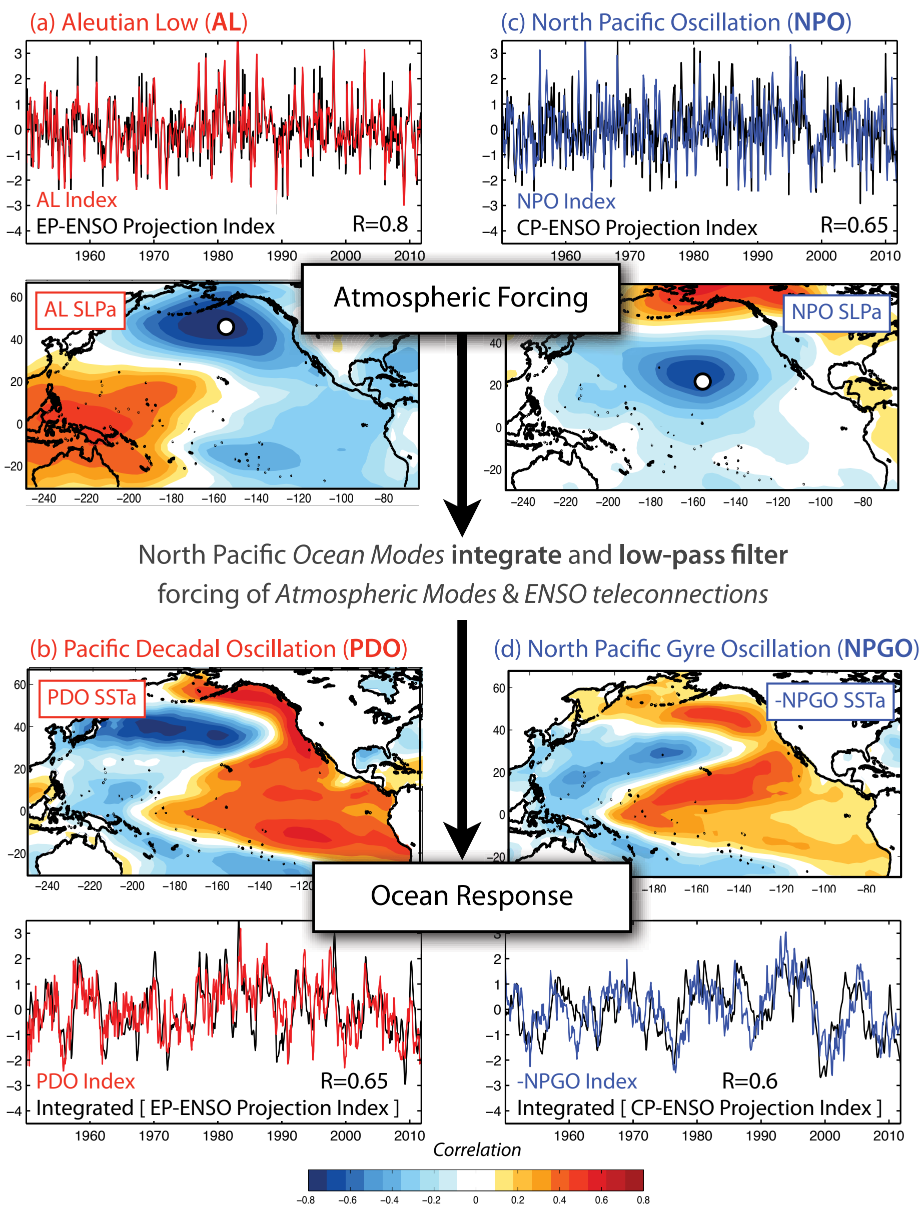

Figure 3. The forcing of the two dominant modes of North Pacific variability. The first (panel a, AL) and second (panel c, NPO) principal components of North Pacific SLP anomalies (SLPa) are compared to indices that track the ENSO atmospheric projections (black line) onto the North Pacific. The ENSO projection indices are derived by projecting the North Pacific SLPa pattern of the EP and CP-ENSO onto the SLPa field. The projection indices capture contributions to SLPa from both ENSO and internal variability in the North Pacific. The spatial correlation of the principal components with SLPa are shown in panels a and c. The AL and NPO drive the oceanic PDO and NPGO (panels b and d show the spatial correlation patterns in the SSTa). The time series of the PDO and NPGO (b and d) can be modeled with a simple auto-regressive model of order-1 forced by the two ENSO projection indices.

Central Pacific ENSO and North Pacific Gyre Oscillation

While many ecosystem fluctuations in the Pacific can be explained within the physical framework of ENSO and PDO variability (e.g., Mantua et al., 1997; Hare and Mantua, 2000), long-term observational time series from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and the Line-P program in the Gulf of Alaska show decadal-scale fluctuations that are not connected to the PDO. Using a set of historical ocean simulations with coupled physical-biological models, POBEX identified a new pattern of North Pacific decadal variability associated with changes in the strength of the subtropical and subpolar gyres—the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2008; Figure 4). Defined as the second dominant mode of SSHa variability in the Northeast Pacific (180°W–110°W, 25°N–62°N), the NPGO explains the dominant decadal fluctuations of salinity, nutrient upwelling, and chlorophyll-*a* (CHL-*a*) in the NEP region (Figure 4; Di Lorenzo et al., 2008, 2009) as well as important state transitions in marine ecosystems (e.g., fish; Sydeman and Thompson, 2010; Cloern et al., 2010). The NPGO signature in SSTa tracks the second dominant mode of North Pacific SSTa (Bond et al., 2003).

Modeling studies conducted within POBEX (Di Lorenzo et al., 2008; Chhak et al., 2009) revealed that the NPGO is the oceanic response to the North Pacific Oscillation (NPO; Figure 3b), a well-known pattern of atmospheric variability. The NPO affects weather patterns, particularly storm tracks, temperatures, and precipitation, over Eurasia and North America (Seager et al., 2005; Linkin and Nigam, 2008, and references therein).

Following previous work on the connection between EP-ENSO and the AL/PDO system, POBEX explored whether the decadal variability of the NPO/NPGO had a tropical, ENSO-like source. This link was found in the recently discovered central Pacific ENSO (CP-ENSO; Ashok et al., 2007; Ashok and Yamagata, 2009). In this ENSO type, or flavor, the El Niño phase, also referred to as the dateline El Niño (Larkin and Harrison, 2005), El Niño Modoki (Ashok and Yamagata, 2009) or warm pool El Niño (Kug et al., 2009; Kao and Yu, 2009), is characterized by peak SST anomalies in the central Pacific capable of modifying the large-scale atmospheric circulation. However, the CP-ENSO signature is different from the EP-ENSO (see SLPa patterns in Figure 2a,b) in that the center of maximum convection is displaced westward with respect to the EP-ENSO. Consequently, the CP-ENSO induces a different pattern of atmospheric teleconnections to the extratropics (Weng et al., 2009). Using an ensemble of coupled ocean-atmosphere simulations, POBEX showed that CP-ENSO teleconnections significantly contribute to the low-frequency variability of the NPO (Figure 3c, compare NPO index with CP-ENSO projection index; see also Supplemental Figure 1 in Di Lorenzo et al., 2010; Furtado et al., 2012). This CP-ENSO/NPO atmospheric variability is then integrated to yield the oceanic NPGO pattern (Figure 3d; Di Lorenzo et al. 2010). The NPGO variance explained by CP-ENSO through this atmospheric teleconnection is significantly higher (~ 75%, time scale > 7 years) in the low frequency than the one associated with EP-ENSO/PDO teleconnection (~ 30%, time scale > 7 years; ~ 40% on interannual time scales of 2–7 years).

CP-ENSOs have become stronger and more frequent in the late twentieth century, possibly a result of climate change (Yeh et al., 2009). Indeed, the variance of the NPGO has increased over time (Sydeman et al., 2013), and there is evidence that over the last two decades, the NPGO, rather than the PDO, drives most of the physical and biological variability of the North Pacific (Cummins and Freeland, 2007; recent work of Patrick Kilduff, University of California, Davis, author Di Lorenzo and colleagues).

A Synthesis of Pacific Climate Variability

The mechanistic relationships between EP-ENSO/AL/PDO and CP-ENSO/NPO/NPGO highlight the significant dynamical linkages between tropical and extratropical modes of climate variability in the Pacific basin and the important role ENSO plays in synchronizing them (Figure 1). The discovery of the new dynamical link between the CP-ENSO ⟶ NPO ⟶ NPGO redefines our physical understanding of how the tropical Pacific climate is coupled to the extratropics and provides the basis

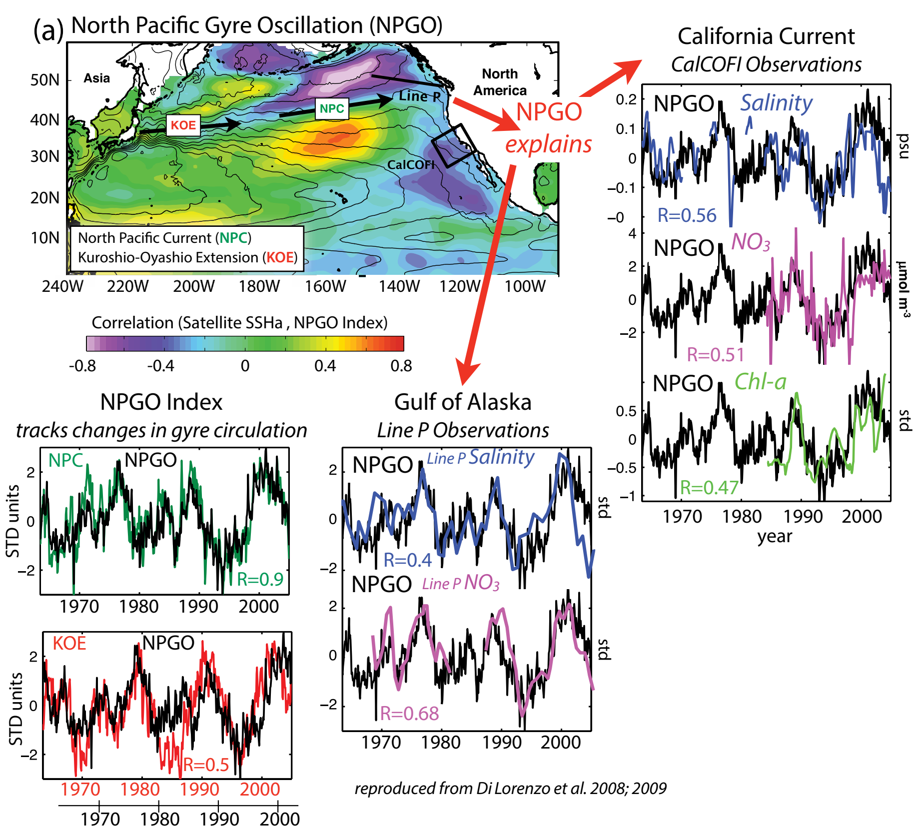

Figure 4. North Pacific Gyre Oscillation. Correlation map between the NPGO index and AVSIO satellite SSHa data (panel a, black contours are the mean dynamic topography; Niiler et al., 2003) showing how the NPGO impacts the mean gyre circulation and captures changes in the strength of the major gyre-scale currents, the North Pacific Current (NPC) and the Kuroshio-Oyashio Extension (KOE). The indices of NPC and KOE strength were computed from the Ocean General Circulation Model for the Earth Simulator (OFES) model (see Di Lorenzo et al., 2009). The NPGO tracks long-term changes in salinity, nutrients, and Chl-*a* observed in the California Current and the Gulf of Alaska (see Di Lorenzo et al., 2009, for a detailed explanation of the data).

for potential positive feedback between tropics and extratropics (Figure 1). While it is well known that ENSO variability can be triggered and energized by stochastic atmospheric variability in the tropics (e.g., westerly wind bursts, Figure 1, gray path), sources of extratropical stochastic variability associated with the NPO are also important in energizing the ENSO system. Past studies on the Seasonal Footprinting Mechanism (SFM; Anderson, 2003; Vimont et al., 2003) show that boreal wintertime variability in the positive phase of the NPO drives warm SST anomalies in the North Pacific that in turn propagate into the central tropical Pacific by the end of spring/summer. Those warm anomalies in the central Pacific weaken the trade winds along the equator (e.g., the Walker Cell) and may trigger a positive ENSO response in the tropics that peaks in the following winter (Alexander et al., 2010). The response can be either an EP-El Niño or CP-El Niño. Although the influence of CP-El Niño on the NPO has only been established for the low frequency, the existence of a high-frequency connection from the CP-El Niño to the NPO could provide the basis for a positive feedback whereby NPO (winter) ⟶ CP-El Niño (next winter) ⟶ NPO (next winter). If this feedback is confirmed, it would provide a longer year-to-year persistence of central Pacific warming in the tropics, which could explain why the CP-ENSO has stronger decadal energy than the EP-ENSO (e.g., Nurhati et al., 2011).

The synthesis of Pacific climate dynamics presented here focuses on sources of variability internal to the Pacific basin; however, other sources of Pacific climate variability external to the Pacific (e.g., Indian Ocean; Guan and Nigam, 2008; Deser et al., 2010) are also important and need further investigation in the context of the ecosystem dynamics. Although the synthesis of Figure 1 represents a road map of the dynamics of Pacific climate variability, this schematic should not be interpreted as a hard-wired deterministic diagram but rather as the statement of a set of hypotheses that requires further investigation.

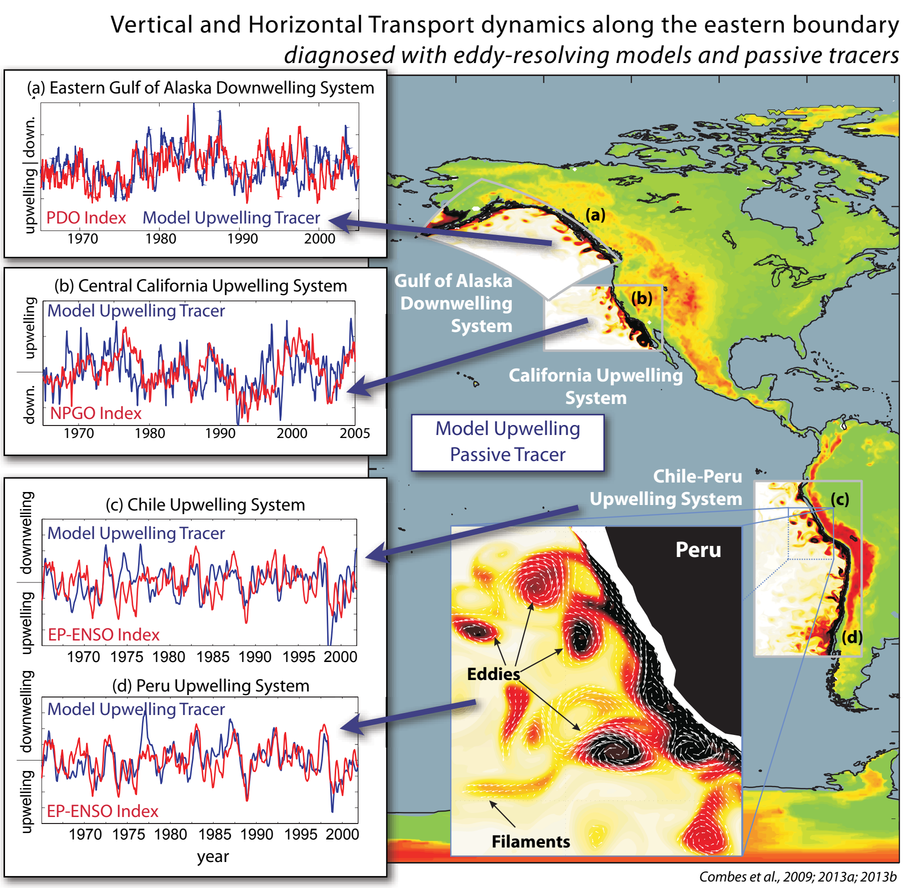

Figure 5. Regional Ocean Modeling System (ROMS) passive tracer transport experiments. Map showing a February 1998 snapshot of passive tracers released from the coast in the nested eddy-resolving ROMS hindcast from 1950 to 2008. The passive tracers were used to study ocean transport dynamics in each of the POBEX regions. The time series panels show how indices of upwelling defined from the passive tracers are linked to different Pacific climate indices in the different POBEX regions (see Combes et al., 2009 and 2013, for details on definitions).

REGIONAL TRANSPORT PROCESSES AND MARINE ECOSYSTEM RESPONSES

To examine how large-scale climate forcing impacts regional transport dynamics and ecosystem processes, the POBEX team ran the regional ocean modeling system (ROMS) for the regions of interest, using the output of the global eddy-resolving OFES (Ocean General Circulation Model for the Earth Simulator) historical hindcast from 1950–2008 (Masumoto et al., 2004; Sasaki et al., 2008) as boundary conditions. The ROMS model historical simulations were combined with passive tracer experiments (Figure 5) that allowed us to (1) diagnose circulation dynamics, such as upwelling, and alongshore and cross-shelf transport, and (2) explore how changes in transport are linked to ecosystem dynamics (e.g., Chhak et al., 2009; Combes et al., 2009, 2013; Keister et al., 2011; Chiba et al. 2013; recent work of author Combes and colleagues).

Large-Scale Climate Controls Coastal Upwelling and Primary Productivity

For each region, we generated indices of coastal upwelling by releasing passive tracers in the model subsurface along the coastline. We found that large-scale climate patterns drive most of the low-frequency variability in upwelling inferred from the passive tracers along the Pacific eastern boundary current system. However, the relative importance and structure of local forcing are different in different regions. In the NEP region south of 38°N, the teleconnections of the CP-ENSO on the NPO dominate the low-frequency modulation of the alongshore winds (Figure 2b), and the decadal upwelling variability mainly tracks the NPGO (–CP-ENSO ⟶ –NPO ⟶ +NPGO ⟶ upwelling; Figure 5b; Di Lorenzo et al., 2008; Combes et al., 2013). Some fraction of interannual variability results from coastally trapped waves excited by EP-ENSO (+waves ⟶ downwelling). North of 38°N, along Northern California and the Gulf of Alaska, the interannual signal of ENSO associated with coastally trapped waves is weaker; the PDO controls most of the upwelling variance +EP-ENSO ⟶ +AL ⟶ +PDO ⟶ downwelling; Figure 5a; Chhak and Di Lorenzo, 2007).

In contrast, in the PCCS, local atmospheric forcing is generally weak, and the upwelling variability inferred from passive tracers (recent work of author Combes and colleagues) is mostly at interannual scales and controlled by the coastally trapped waves generated by EP-ENSO (+waves ⟶ downwelling). Consistent with the findings of author Combes and colleagues, time series of passive tracers in different coastal regions of the PCCS track the EP-ENSO index (Figure 5c,d). The CP-ENSO atmospheric teleconnection (Figure 2) has no projection along the PCCS and therefore the NPGO-equivalent variability is absent.

Large-scale climate control of coastal upwelling is also evident in analyses of satellite Chl-*a* images conducted

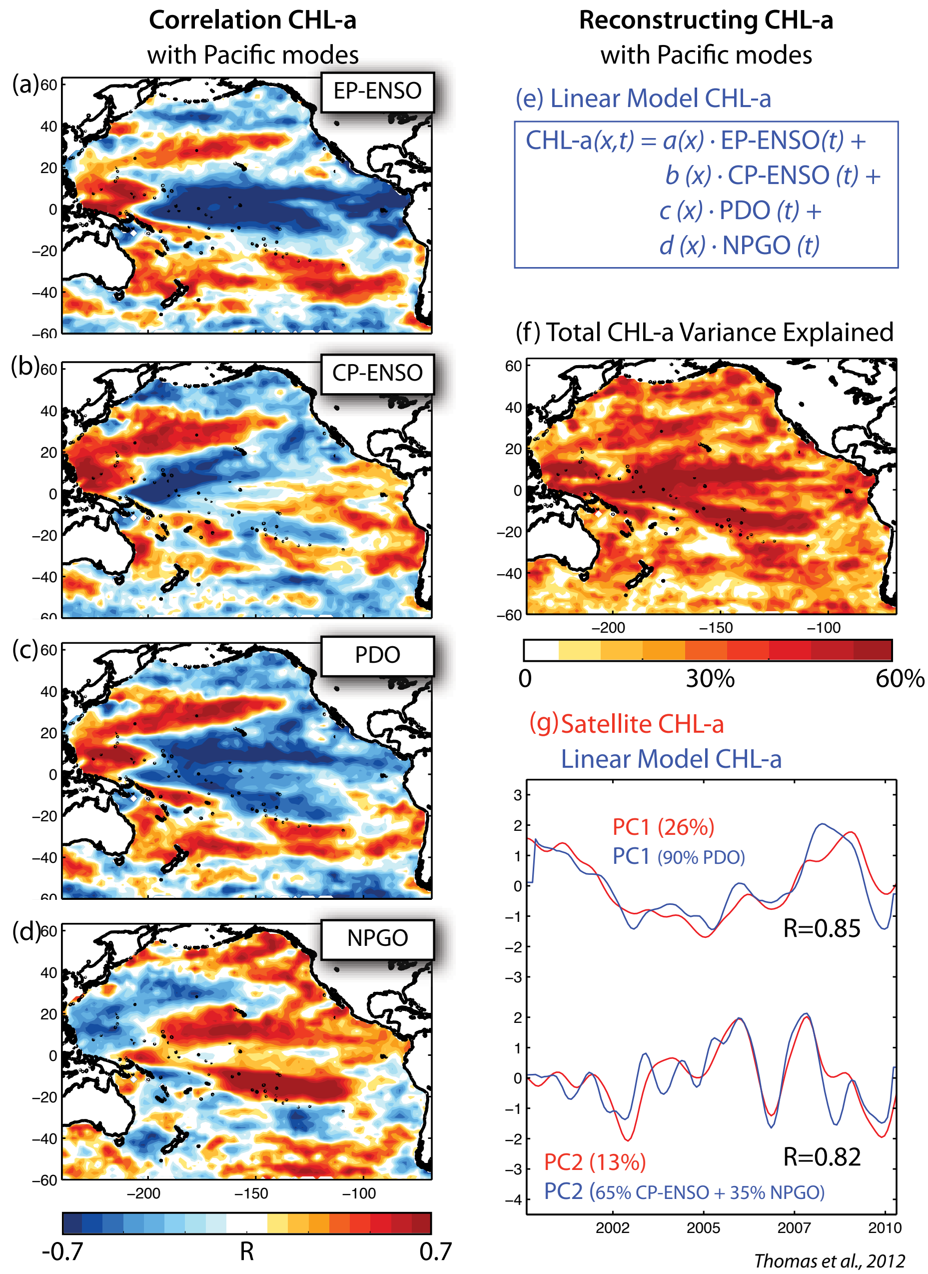

Figure 6. Large-scale climate forcing of chlorophyll-*a*. Correlation maps between climate indices and satellite chlorophyll-*a* (panels a,b,c,d). A simple linear reconstruction of satellite chlorophyll-*a* data using climate modes indices (panel e) captures the largest fraction of the temporal variance at each spatial location (panel f). The principal components of the linear model reconstruction also capture the first two dominant modes of satellite chlorophyll-*a* variability (panel g), which capture in the observations the largest fraction of variance (~ 35%) that is spatially coherent across the Pacific. All data have been smoothed with a one-year running mean prior to the analyses.

during POBEX (Figure 6a–d). Thirteen years of satellite ocean color data (1999–2011) allow visualization of regional ecosystem responses in the CCS, the PCCS, and the KOE (Figure 6; Kahru and Mitchell, 2000; Correa-Ramirez et al., 2007; Thomas et al., 2012). The Pacific climate modes can be linearly combined to reconstruct the satellite Chl-*a* (Figure 6e): Chl-*a*(x,t) = a(x)·EP-ENSO(t) + b(x)·CP-ENSO(t) + c(x)·PDO(t) + d(x)·NPGO (t). This linear model reconstruction of Chl-*a* explains up to 70% of total local satellite Chl-*a* variance (Figure 6). Two principal modes of Chl-*a* appear in the linear model (Figure 6e): the first mode is 90% PDO (decadal, as documented by Martinez et al., 2009), while the second mode is 65% CP-ENSO (interannual) and 35% NPGO (decadal) (Figure 6e). Higher modes in Chl-*a* distributions reflect regional expressions of both large-scale climate modes and local forcing, and need further investigation.

Changes in the timing and amplitude of the seasonal cycle likely exert dominant control on primary productivity. Along the eastern boundary system, POBEX researchers described large, latitudinally dependent, low-frequency changes in the timing, duration, and intensity of coastal upwelling in the California Current (Bograd et al., 2009). An important fraction of these changes in the southern CCS was linked to the NPGO (Chenillat et al., 2012). In the PCCS, changes in seasonal timing are still not well understood but are likely connected to changes in the seasonal cycle of the ENSO system. These phenological changes could be important, as many organisms have life histories that are closely adapted to the strong seasonal cycle (Barth et al., 2007).

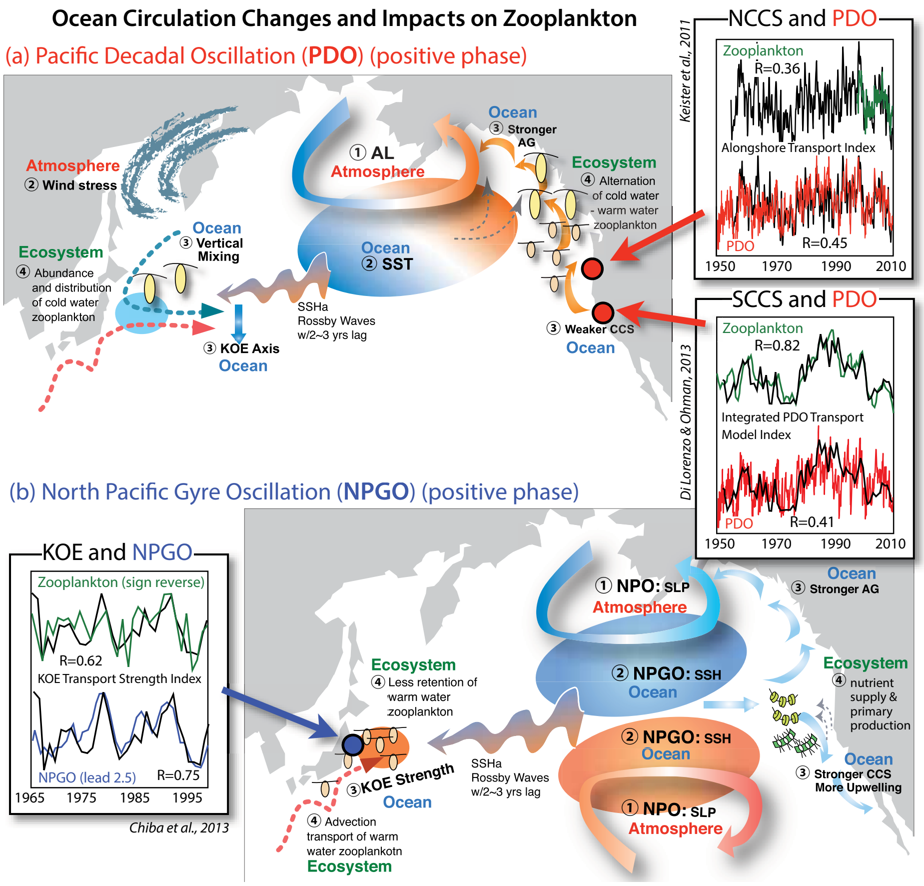

Figure 7. Schematic of ocean transport changes during the PDO (a) and the NPGO (b) and their impacts on zooplankton in the eastern and western boundaries of the North Pacific. The line plots in the Northern (N) and Southern (S) California Currents System (CCS) and the Kuroshio-Oyashio Extension (KOE) compare zooplankton time series (green lines) with zooplankton reconstruction based on indices that capture the changes in local transport (black lines). The local indices of transport in the CCS were connected to the PDO (red lines) and in the KOE to the NPGO (blue line). The definition and the dependence of the transport indices (black lines) on the climate modes are explained in the references placed beside the line plot panels.

Changes in Ocean Horizontal Transport Explain Observed Zooplankton Variability

Large-scale climate forcing was also found to affect regional-scale horizontal circulation, with impacts on lower trophic levels, especially zooplankton species distributions. In the CCS and the KOE where long time series of zooplankton are available, studies during POBEX discovered that changes in basin-scale horizontal advection of surface waters, rather than changes in local upwelling, control a large fraction of decadal variability in zooplankton species composition. This extends to the species composition level. Earlier, Chelton et al. (1982) found that zooplankton total volume in the southern CCS (SCCS) was more strongly correlated with the strength of alongshore transport in the CCS than with the strength of local upwelling. Our initial experiments to test hypotheses about the effects of large-scale forcing on zooplankton were conducted in the northern CCS (NCCS; Figure 7) where zooplankton have been collected approximately biweekly to monthly since 1996 by the National Oceanic and Atmospheric Administration Northwest

Fisheries Science Center off Newport, Oregon. There, zooplankton communities cycle in the relative dominance of cold-water or warm-water species (e.g., Peterson and Keister, 2003) in correlation with the PDO—cold-water species vastly dominate the community during cold (negative) phases of the PDO whereas warm-water species are more important during warm (positive) phases. Passive tracer experiments in ROMS showed that surface current variability associated with the PDO is tightly correlated to the observed changes in copepod species composition (Figure 7, NCCS). Stronger equatorward advection over the shelf during the negative phase of the PDO is reversed during the PDO's positive phase, with anomalously strong poleward currents and downwelling conditions. When smoothed over multiyear time scales, these transport fluctuations explain nearly all of the variance of the copepod community (R = –0.96). Similarly, in the SCCS, a simple PDO-transport model captured almost all of the low-frequency variance in abundances of the euphausiid *Nyctiphanes simplex* (R = 0.82) (Figure 7, SCCS; Di Lorenzo and Ohman 2013). Interestingly, the PDO imprint on the SCCS zooplankton—like the ocean response to atmospheric fluctuations—was best modeled as an integrated response to the physical forcing (e.g., the transport index in Figure 7 for the SCCS is obtained by integrating the PDO; see Di Lorenzo and Ohman, 2013). Note that in Figure 7b, the NPGO mode captures changes in the North Pacific Current and coastal upwelling. However, along the US West Coast, the PDO better captures the strength of the coastal currents. This explains the stronger correlation that exists between zooplankton and PDO in the coastal region.

Similarly, changes in the strength of the KOE control variability in the abundance of warm-water copepods in the Kuroshio-Oyashio Transition (KOT) region (Figure 7; Chiba et al. 2013). Rossby waves excited in the central North Pacific by the NPO/NPGO system drive these changes. The waves arrive in the KOE with an approximate lag of 2.5 years following changes in the central and eastern North Pacific (Figure 7, KOE). Passive tracer experiments show that during years of a weak KOE (–NPGO), warm-water species are transported farther north and are retained in the KOT region (Figure 7), leading to the observed zooplankton anomalies (Chiba et al., 2013).

Together, these studies provide strong evidence that large-scale climate changes affect marine ecosystems coherently around ocean boundaries through changes in ocean transport. This finding, referred to as the "horizontal advection bottom-up forcing hypothesis," was shown to be important in driving marine ecosystem variability in all the US GLOBEC regions (Di Lorenzo et al., 2013, in this issue). In the Pacific, the different lags inherent in the processes complicated the discovery of common signals, but they can provide a degree of predictability to ecosystem changes when the mechanisms are sufficiently well understood.

Mesoscale Eddies Control Cross-Shelf Exchanges and Impact Fish Habitats

While large-scale climate modes strongly controlled upwelling and alongshore transport variability, the cross-shelf exchanges diagnosed from passive tracers (Combes et al., 2009, 2013) were not as coherent across the POBEX regions. Indeed, they were mostly independent of large-scale climate forcing. Mesoscale features (e.g., eddies and filaments), rather than wind-driven Ekman transport, dominate cross-shelf transport variability along the eastern boundary (Combes et al., 2009, 2013). These structures drive the offshore export of surface waters and subsurface waters of the eastern boundary undercurrents (Combes et al., 2013, for the CCS; Hormazabal et al., 2013, for the PCCS). Although a large fraction of mesoscale variance is internal to the ocean and unpredictable, regional-scale forcings were found to control the statistics of eddies in the Gulf of Alaska and the CCS, especially the anticyclones, which showed stronger low-frequency variability than the cyclones (Combes and Di Lorenzo, 2007; Combes et al., 2009; Davis and Di Lorenzo, in press).

There is growing evidence that mesoscale circulation features strongly impact ecosystem dynamics (e.g., primary productivity; McGillicuddy et al., 2007). POBEX did not fully explore their influence on marine ecosystems due to a lack of adequate long-term observations that resolve eddy-scale processes. Still, studies in the NEP and PCCS suggest strong links between mescoscale circulation and the distribution of zooplankton and higher tropic levels (e.g., fish). Upwelling filaments transport significant portions of coastal zooplankton populations offshore (Keister et al., 2008; recent work of author Keister and Stephen Pierce, Oregon State University), resulting in offshore "hotspots" of upper trophic activity. In the PCCS, a bio-physical modeling study highlighted the potential impact of mesoscale eddies on retention of jack mackerel (*Trachurus murphyi*, Nichols) along the Challenger Plateau and the East Pacific Rise, more than 3,500 km from historically known coastal nursery grounds and ocean spawning regions

(Parada et al., in press). Retention for at least four months in anticyclonic eddies with their associated environmental conditions, such as sea surface temperature, Chl-*a*, wind, and turbulence levels, suggests strong recruitment in these features. Evidence of jack mackerel juveniles in the region for over 20 years, obtained from Russian research vessel logbooks, support the hypothesis (Parada et al., in press).

Similar results emerged from statistical analysis in the NEP, where long-term time series of recruitment data were significantly correlated with indices of mesoscale eddies. For example, sablefish and arrowtooth flounder recruitment time series were found to covary significantly with the formation of large anticyclones in the Gulf of Alaska during strong downwelling events (Andrew Smith, Georgia Tech, and colleagues, *pers. comm.*, 2013; Megan Stachura, University of Washington, and colleagues, *pers. comm.*, 2013). Indices of mesoscale anticyclone activity in model hindcasts were better predictors of fish recruitment data than linear models based on sea surface temperature and wind observations. This finding reinforces the concept that regional model hindcasts provide an important tool for further exploration of the mesoscale dynamics impacting fish and for informing fisheries management strategies.

Although more observations and modeling studies are needed to understand and constrain the mechanics underlying the links among mesoscale dynamics, zooplankton, and fish habitats, these results anticipate a new "ocean mesoscale" phase in joint observational/modeling studies of climate and marine ecosystem dynamics.

DISCUSSION AND FUTURE CHALLENGES

POBEX program investigations provide a mechanistic understanding of the role of bottom-up climate forcing on dynamics of lower trophic levels of Pacific boundary current ecosystems. While the impacts of large-scale climate forcings differ in the various boundary ecosystems (e.g., NEP, KOE, and PCCS), POBEX studies were able to identify common dynamics of ecosystems' responses to climate, in particular, for primary producers and zooplankton. Specifically, while most large-scale and regional-scale variability of primary productivity is linked to changes in upwelling dynamics forced by large-scale climate modes (Figure 6), the low-frequency, bottom-up control of zooplankton does not follow the traditional model where changes in upwelling ⟶ changes in productivity ⟶ changes in zooplankton. Rather, low-frequency variations of zooplankton are more sensitive to changes in large-scale horizontal transport. This finding has important consequences for both our understanding of lower-trophic zooplankton dynamics and the fundamental dynamics of how marine populations respond to climate forcing—"the double integration hypothesis" (Di Lorenzo and Ohman, 2013).

A Double-Integration Hypothesis to Explain Ecosystem Response to Climate

POBEX research shows that ocean decadal fluctuations like the PDO and the NPGO are forced responses of the ocean to atmospheric variability. From a statistical point of view, the ocean response is equivalent to an autoregressive process of order-1 (AR-1) driven by white noise atmospheric forcing (Hasselmann, 1976). For example, if we integrate the Aleutian Low index (first principal component of North Pacific SLPa; Figure 8a) using the AR-1 model formulation, we can reconstruct the PDO index time series with high

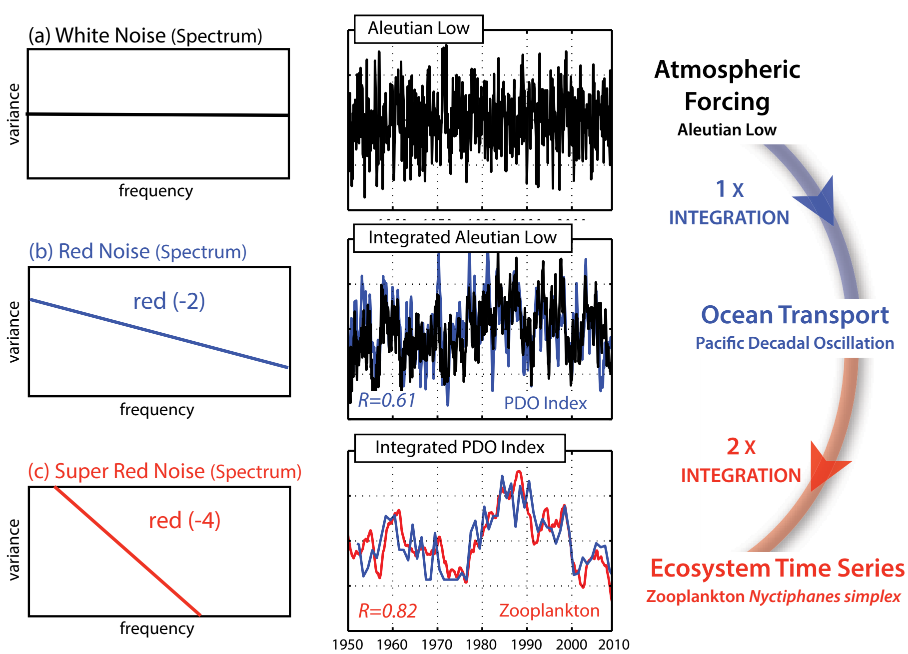

Figure 8. Schematic of the double integration hypothesis. (a) Aleutian Low index. (b) Integrated Aleutian Low index (black) and PDO index (blue). (c) Integrated PDO index (blue) and zooplankton time series of *Nyctiphanes simplex* in the California Current System (red). *Reproduced from Di Lorenzo and Ohman (2013)*

skill (R = 0.6, Figure 8b). This integration by the ocean filters out the high-frequency variability of the white noise atmospheric forcing and enhances the decadal and lower-frequency variability (Figure 8b). Because zooplankton and other marine populations are sensitive to changes in ocean conditions, the ecosystem will integrate the white noise atmospheric forcing a second time—first integration from atmosphere to ocean, and second integration from ocean to marine populations. This double integration allows us to filter away even more high-frequency atmospheric variability and leads to time series of marine ecosystem variability that are dominated by low-frequency fluctuations (Figure 8c) with large-amplitude state transitions that can persist for decades (i.e., a super red power spectrum). Long-term time series of zooplankton in the CCS that are sensitive to PDO-related ocean advection were reconstructed with high skill by integrating the PDO index with an AR-1 model (R = 0.82), supporting the double-integration hypothesis (Di Lorenzo and Ohman, 2013).

These results point to the important need to develop proper null hypotheses of the variability expected in marine populations (e.g., fish) that result from cumulative integration of one or more environmental forcings before interpreting time series of biological or physical variables in terms of (or as indicative of) nonlinear "regime shifts." This need is particularly relevant for correctly assessing the underlying causes and significance of apparent "state transitions" and climate change signatures in marine ecosystems. For example, the double integration of white noise is a linear model that can lead to regime-like variability in ecosystem time series without the need for nonlinear dynamics to be involved.

Climate Change Impacts on Marine Ecosystems

Understanding and modeling the impacts of climate change on marine ecosystems remains an important challenge. Given the important role that Pacific Ocean decadal modes play in driving a large fraction of the low-frequency variability observed in long-term ecological time series (e.g., Mantua and Hare, 2002), it is critical that we understand and constrain the statistics and dynamics of these modes under changing climate conditions. Although International Panel on Climate Change (IPCC)-class climate models provide an important tool for predicting changes in the physical environment, POBEX found that these models are still unable to properly capture the statistics of large-scale Pacific decadal climate modes (Furtado et al., 2011). From a modeling point of view, this finding raises additional challenges and questions about how to properly use IPCC-class models to downscale climate scenarios and examine climate-change impacts on marine ecosystems (e.g., PICES Working Groups 20 and 29; http://www.pices.int). It also points to the important need for advancing our mechanistic understanding of the links between physical climate and ecosystems (e.g., POBEX) that can lead to hypotheses and reduced-order process models of marine ecosystem responses to climate change. These process models offer an alternative approach for exploring the sensitivity of marine ecosystems to climate change (e.g., POBEX, PICES Working Group 27).

In addition to developing proper modeling strategies to address climate change impacts on marine ecosystems, it is also clear that long-term observations of marine ecosystem variability are important. Unfortunately, these long-term observations are rare and often not widely available to researchers because of the nature of the sampling programs that depend on different regional organizations. One path toward accessing and analyzing these data sets is the development of social networks of Pacific scientists from different countries.

The success of the POBEX project heavily relied on a prompt exchange of data and methods among the members of the international team. This international collaboration was made successful by prolonged student exchanges (three months to one year) among universities in Japan, Chile, and the United States. In this context, the activities of international organizations such as PICES were invaluable for building the exchange channels that led and maintained POBEX activities. POBEX also leveraged and partnered with the ongoing California Current Ecosystem Long Term Ecological Research (CCE-LTER; http://cce.lternet.edu). This partnership builds on the process studies and modeling activities carried out by CCE-LTER, together with the 65-year CalCOFI time series program. These research collaborations between US GLOBEC and intergovernmental organizations like PICES and US-funded LTERs provide the necessary infrastructure for addressing the scientific and societal issues of climate change impacts on marine resources. While US GLOBEC POBEX was a short-term, four-year project, it was through these partnerships that POBEX scientists were able to conduct a broad range of climate and ecosystem interdisciplinary research (e.g., http://www.pobex.org). As US GLOBEC has ended, it will be critical to find new sources of funding to support science networks like POBEX.

ACKNOWLEDGEMENTS

The Pacific Ocean Boundary Ecosystem and Climate Study (POBEX) was supported by NSF-OCE 0606575 through the GLOBEC program. We would like to thank Nathan Mantua for his very insightful comments in the revision stages of the manuscript. This is US GLOBEC contribution 738.

REFERENCES

Alexander, M.A. 1992. Midlatitude atmosphere–ocean interaction during El Niño. Part I: The North Pacific Ocean. *Journal of Climate* 5:944–958, http://dx.doi.org/10.1175/1520-0442(1992)005<0944:MAIDEN>2.0.CO;2.

Alexander, M.A., I. Blade, M. Newman, J.R. Lanzante, N-C. Lau, and J.D. Scott. 2002. The atmospheric bridge: The influence of ENSO teleconnections on air-sea interaction over the global oceans. *Journal of Climate* 15:2,205–2,231, http://dx.doi.org/10.1175/1520-0442(2002)015<2205:TABTIO>2.0.CO;2.

Alexander, M.A., D.J. Vimont, P. Chang, and J.D. Scott. 2010. The impact of extratropical atmospheric variability on ENSO: Testing the seasonal footprinting mechanism using coupled model experiments. *Journal of Climate* 23:2,885–2,901, http://dx.doi.org/10.1175/2010JCLI3205.1.

Anderson, B. 2003. Tropical Pacific sea-surface temperatures and preceding sea level pressure anomalies in the subtropical North Pacific. *Journal of Geophysical Research* 108, 4732, http://dx.doi.org/10.1029/2003JD003805.

Ashok, K., S.K. Behera, S.A. Rao, H.Y. Weng, and T. Yamagata. 2007. El Niño Modoki and its possible teleconnection. *Journal of Geophysical Research* 112, C11007, http://dx.doi.org/10.1029/2006JC003798.

Ashok, K., and T. Yamagata. 2009. Climate change: The El Niño with a difference. *Nature* 461:481–484, http://dx.doi.org/10.1038/461481a.

Barth, J.A., B.A. Menge, J. Lubchenco, F. Chan, J.M. Bane, A.R. Kirincich, M.A. McManus, K.J. Nielsen, S.D. Pierce, and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ecosystems in the northern California Current. *Proceedings of the National Academy of Sciences of the United States of America* 104:3,719–3,724, http://dx.doi.org/10.1073/pnas.0700462104.

Bograd, S.J., I. Schroeder, N. Sarkar, X. Qiu, W.J. Sydeman, and F.B. Schwing. 2009. The phenology of coastal upwelling in the California Current. *Geophysical Research Letters* 36, L01602, http://dx.doi.org/10.1029/2008GL035933.

Bond, N.A., J.E. Overland, M. Spillane, and P. Stabeno. 2003. Recent shifts in the state of the North Pacific. *Geophysical Research Letters* 30, 2183, http://dx.doi.org/10.1029/2003GL018597.

Ceballos, L.I., E. Di Lorenzo, C.D. Hoyos, N. Schneider, and B. Taguchi. 2009. North Pacific Gyre Oscillation synchronizes climate fluctuations in the eastern and western boundary systems. *Journal of Climate* 22:5,163–5,174, http://dx.doi.org/10.1175/2009JCLI2848.1.

Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research* 40:1,095–1,125.

Chenillat, F., P. Riviere, X. Capet, E. Di Lorenzo, and B. Blanke. 2012. North Pacific Gyre Oscillation modulates seasonal timing and ecosystem functioning in the California Current upwelling system. *Geophysical Research Letters* 39, L01606, http://dx.doi.org/10.1029/2011GL049966.

Chhak, K., and E. Di Lorenzo. 2007. Decadal variations in the California Current upwelling cells. *Geophysical Research Letters* 34, L14604, http://dx.doi.org/10.1029/2007GL030203.

Chhak, K.C., E. Di Lorenzo, N. Schneider, and P.F. Cummins. 2009. Forcing of low-frequency ocean variability in the Northeast Pacific. *Journal of Climate* 22:1,255–1,276, http://dx.doi.org/10.1175/2008JCLI2639.1.

Chiba, S., E. Di Lorenzo, A. Davis, J.E. Keister, B. Taguchi, Y. Sasai, and H. Sugisaki. 2013. Large-scale climate control of zooplankton transport and biogeography in the Kuroshio-Oyashio Extension region. *Geophysical Research Letters* 40:5,182–5,187, http://dx.doi.org/10.1002/grl.50999.

Cloern, J.E., K.A. Hieb, T. Jacobson, B. Sanso, E. Di Lorenzo, M.T. Stacey, J.L. Largier, W. Meiring, W.T. Peterson, T.M. Powell, M. Winder, and A.D. Jassby. 2010. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. *Geophysical Research Letters* 37, L21602, http://dx.doi.org/10.1029/2010GL044774.

Combes, V., F. Chenillat, E. Di Lorenzo, P. Riviere, M.D. Ohman, and S.J. Bograd. 2013. Cross-shore transport variability in the California Current: Ekman upwelling vs. eddy dynamics. *Progress in Oceanography* 109:78–89, http://dx.doi.org/10.1016/j.pocean.2012.10.001.

Combes, V., and E. Di Lorenzo. 2007. Intrinsic and forced interannual variability of the Gulf of Alaska mesoscale circulation. *Progress in Oceanography* 75:266–286, http://dx.doi.org/10.1016/j.pocean.2007.08.011.

Combes, V., E. Di Lorenzo, and E. Curchitser. 2009. Interannual and decadal variations in cross-shelf transport in the Gulf of Alaska. *Journal of Physical Oceanography* 39:1,050–1,059, http://dx.doi.org/10.1175/2008JPO4014.1.

Correa-Ramirez, M.A., S. Hormazábal, and G. Yuras. 2007. Mesoscale eddies and high chlorophyll concentrations off central Chile (29°–39°S). *Geophysical Research Letters* 34, L12604, http://dx.doi.org/10.1029/2007GL029541.

Cummins, P.F., and H.J. Freeland. 2007. Variability of the North Pacific current and its bifurcation. *Progress in Oceanography* 75:253–265, http://dx.doi.org/10.1016/j.pocean.2007.08.006.

Davis, A., and E. Di Lorenzo. In press. The forcing dynamics of mesoscale eddies in the California Current System. *Deep Sea Research Part A*.

Deser, C., M.A. Alexander, S.P. Xie, and A.Z. Phillips. 2010. Sea surface temperature variability: Patterns and mechanisms. *Annual Review of Marine Science* 2:115–143, http://dx.doi.org/10.1146/annurev-marine-120408-151453.

Di Lorenzo, E., K.M. Cobb, J.C. Furtado, N. Schneider, B.T. Anderson, A. Bracco, M.A. Alexander, and D.J. Vimont. 2010. Central Pacific El Niño and decadal climate change in the North Pacific. *Nature Geoscience* 3:762–765, http://dx.doi.org/10.1038/ngeo984.

Di Lorenzo, E., J. Fiechter, N. Schneider, A.J. Miller, P.J.S. Franks, S.J. Bograd, A.M. Moore, A. Thomas, W. Crawford, A. Pena, and A.J. Herman. 2009. Nutrient and salinity decadal variations in the central and eastern North Pacific. *Geophysical Research Letters*, 36, L14601, http://dx.doi.org/10.1029/2009GL038261.

Di Lorenzo, E., D. Mountain, H.P. Batchelder, N. Bond, and E.E. Hofmann. 2013. Advances in marine ecosystem dynamics from US GLOBEC: The horizontal-advection bottom-up forcing paradigm. *Oceanography* 26(4):22–33, http://dx.doi.org/10.5670/oceanog.2013.73.

Di Lorenzo, E., and M.D. Ohman. 2013. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proceedings of the National Academy of Sciences of the United States of America* 110:2,496–2,499, http://dx.doi.org/10.1073/pnas.1218022110.

Di Lorenzo, E., N. Schneider, K.M. Cobb, K. Chhak, P.J.S. Franks, A.J. Miller, J.C. McWilliams, S.J. Bograd, H. Arango, E. Curchister, and others. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35, L08607, http://dx.doi.org/10.1029/2007GL032838.

Furtado, J.C., E. Di Lorenzo, B.T. Anderson, and N. Schneider. 2012. Linkages between the North Pacific Oscillation and central tropical Pacific SSTs at low frequencies. *Climate Dynamics* 39:2,833–2,846, http://dx.doi.org/10.1007/s00382-011-1245-4.

Furtado, J.C., E. Di Lorenzo, N. Schneider, and N.A. Bond. 2011. North Pacific decadal variability and climate change in the IPCC AR4 models. *Journal of Climate* 24:3,049–3,067, http://dx.doi.org/10.1175/2010JCLI3584.1.

Guan, B., and S. Nigam. 2008. Pacific sea surface temperatures in the twentieth century: An evolution-centric analysis of variability and trend. *Journal of Climate* 21:2,790–2,809, http://dx.doi.org/10.1175/2007JCLI2076.1.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103–145, http://dx.doi.org/10.1016/S0079-6611(00)00033-1.

Hasselmann, K. 1976. Stochastic climate models: Part 1. Theory. *Tellus* 28:473–485, http://dx.doi.org/10.1111/j.2153-3490.1976.tb00696.x.

Holbrook, N.J., I.D. Goodwin, S. McGregor, E. Molina, and S.B. Power. 2011. ENSO to multi-decadal time scale changes in East Australian Current transports and Fort Denison sea level: Oceanic Rossby waves as the connecting mechanism. *Deep Sea Research Part II* 58:547–558, http://dx.doi.org/10.1016/j.dsr2.2010.06.007.

Hormazabal, S., V. Combes, C.E. Morales, M.A. Correa-Ramirez, E. Di Lorenzo, and S. Nuñez. 2013. Intrathermocline eddies in the Coastal Transition Zone off central Chile (31–41°S). *Journal of Geophysical Research* 118:4,811–4,821, http://dx.doi.org/10.1002/jgrc.20337.

Kahru, M., and B.G. Mitchell. 2000. Influence of the 1997–98 El Niño on the surface chlorophyll in the California Current. *Geophysical Research Letters* 27:2,937–2,940, http://dx.doi.org/10.1029/2000GL011486.

Kao, H.-Y., and J.-Y. Yu. 2009. Contrasting Eastern-Pacific and Central-Pacific types of ENSO. *Journal of Climate* 22:615–632, http://dx.doi.org/10.1175/2008JCLI2309.1.

Keister, J.E., E. Di Lorenzo, C.A. Morgan, V. Combes, and W.T. Peterson. 2011. Zooplankton species composition is linked to ocean transport in the Northern California Current. *Global Change Biology* 17:2,498–2,511, http://dx.doi.org/10.1111/j.1365-2486.2010.02383.x.

Keister, J.E., W.T. Peterson, and S.D. Pierce. 2008. Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California Current. *Deep-Sea Research Part I* 56:212–231, http://dx.doi.org/10.1016/j.dsr.2008.09.004.

Kug, J., F. Jin, and S. An. 2009. Two types of El Niño events: Cold tongue El Niño and warm pool El Niño. *Journal of Climate* 22:1,499–1,515, http://dx.doi.org/10.1175/2008JCLI2624.1.

Larkin, N.K., and D.E. Harrison. 2005. On the definition of El Niño and associated seasonal average US weather anomalies. *Geophysical Research Letters* 32, L13705, http://dx.doi.org/10.1029/2005GL022738.

Linkin, M.E., and S. Nigam. 2008. The North Pacific Oscillation–West Pacific teleconnection pattern: Mature-phase structure and winter impacts. *Journal of Climate* 21:1,979–1,997, http://dx.doi.org/10.1175/2007JCLI2048.1.

Mantua, N.J., and S.R. Hare. 2002. The Pacific Decadal Oscillation. *Journal of Oceanography* 58:35–44, http://dx.doi.org/10.1023/A:1015820616384.

Mantua, N., S. Hare, Y. Zhang, J. Wallace, and R. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1,069–1,079, http://dx.doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.

Martinez, E., D. Antoine, F. D'Ortenzio, and B. Gentili. 2009. Climate-driven basin-scale decadal oscillations of oceanic phytoplankton. *Science* 326:1,253–1,256, http://dx.doi.org/10.1126/science.1177012.

Masumoto, Y., H. Sasaki, T. Kagimoto, N. Komori, A. Ishida, Y. Sasai, T. Miyama, T. Motoi, H. Mitsudera, K. Takahashi, and others. 2004. A fifty-year eddy-resolving simulation of the world ocean: Preliminary outcomes of OFES (OGCM for the Earth Simulator). *The Journal of the Earth Simulator* 1:35–56. Available online at: https://www.jamstec.go.jp/esc/publication/journal/jes_vol.1/pdf/JES1-3.2-masumoto.pdf (accessed December 26, 2013).

McGillicuddy, D.J., L.A. Anderson, N.R. Bates, T. Bibby, K.O. Buesseler, C.A. Carlson, C.S. Davis, C. Ewart, P.G. Falkowski, S.A. Goldthwait, and others. 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. *Science* 316:1,021–1,026, http://dx.doi.org/10.1126/science.1136256.

Miller, A.J., and N. Schneider. 2000. Interdecadal climate regime dynamics in the North Pacific Ocean: Theories, observations and ecosystem impacts. *Progress in Oceanography* 47:355–379, http://dx.doi.org/10.1016/s0079-6611(00)00044-6.

Newman, M., G. Compo, and M. Alexander. 2003. ENSO-forced variability of the Pacific decadal oscillation. *Journal of Climate* 16:3,853–3,857, http://dx.doi.org/10.1175/1520-0442(2003)016<3853:EVOTPD>2.0.CO;2.

Niiler, P.P., N.A. Maximenko, and J.C. McWilliams. 2003. Dynamically balanced absolute sea level of the global ocean derived from near-surface velocity observations. *Geophysical Research Letters* 30, 2164, http://dx.doi.org/10.1029/2003GL018628.

Nurhati, I.S., K.M. Cobb, and E. Di Lorenzo. 2011. Decadal-scale SST and salinity variations in the central tropical Pacific: Signatures of natural and anthropogenic climate change. *Journal of Climate* 24:3,294–3,308, http://dx.doi.org/10.1175/2011JCLI3852.1.

Parada, C., A. Gretchina, S. Vásquez, V. Combes, B. Ernst, A. Sepúlveda, and E. Di Lorenzo. In press. Expanding the conceptual framework of the spatial population structure and life history of jack mackerel in the southeastern Pacific off Central Chile: Oceanic seamount region as potential spawning/nursery habitat. *ICES Journal of Marine Science*.

Peterson, W.T., and J.E. Keister. 2003. Interannual variability in copepod community composition at a coastal station in the northern California Current: A multivariate approach. *Deep Sea Research Part II* 50:2,499–2,517, http://dx.doi.org/10.1016/S0967-0645(03)00130-9.

Qiu, B., N. Schneider, and S. Chen. 2007. Coupled decadal variability in the North Pacific: An observationally constrained idealized model. *Journal of Climate* 20:3,602–3,620, http://dx.doi.org/10.1175/JCLI4190.1.

Rogers, J.C. 1981. The North Pacific Oscillation. *International Journal of Climatology* 1:9–57, http://dx.doi.org/10.1002/joc.3370010106.

Sasaki, H., M. Nonaka, Y. Masumoto, Y. Sasai, H. Uehara, and H. Sakuma. 2008. An eddy-resolving hindcast simulation of the quasi-global ocean from 1950 to 2003 on the Earth Simulator. Pp. 157–185 in *High Resolution Numerical Modelling of the Atmosphere and Ocean*. K. Hamilton and W. Ohfuchi, eds, Springer, New York.

Seager, R., N. Harnik, W.A. Robinson, Y. Kushnir, M. Ting, H.P. Huang, and J. Velez. 2005. Mechanisms of ENSO-forcing of hemispherically symmetric precipitation variability. *Quarterly Journal of the Royal Meteorological Society* 13:1,501–1,527, http://dx.doi.org/10.1256/qj.04.96.

Schneider, N., and B.D. Cornuelle. 2005. The forcing of the Pacific Decadal Oscillation. *Journal of Climate* 18:4,355–4,373, http://dx.doi.org/10.1175/JCLI3527.1.

Sydeman, B., J.A. Santora, S.A. Thompson, B. Marinovic, and E. Di Lorenzo. 2013. Increasing variance in North Pacific climate relates to unprecedented marine ecosystem variability off California. *Global Change Biology* 19:1,662–1,675, http://dx.doi.org/10.1111/gcb.12165.

Sydeman, W.J., and M.A. Thompson. 2010. *The California Current Integrated Ecosystem Assessment (IEA), Module II: Trends and Variability in Climate-Ecosystem State*. Final Report to NOAA/NMFS/Environmental Research Division, 59 pp. Available online at: http://www.faralloninstitute.org/Publications/SydemanThompson2010IEA_Module2.pdf (accessed December 26, 2013).

Taguchi, B., S.P. Xie, N. Schneider, M. Nonaka, H. Sasaki, and Y. Sasai. 2007. Decadal variability of the Kuroshio Extension: Observations and an eddy-resolving model hindcast. *Journal of Climate* 20:2,357–2,377, http://dx.doi.org/10.1175/JCLI4142.1.

Thomas, A.C., P.T. Strub, R.A. Weatherbee, and C. James. 2012. Satellite views of Pacific chlorophyll variability: Comparisons to physical variability, local versus nonlocal influences and links to climate indices. *Deep Sea Research Part II* 77–80:99–116, http://dx.doi.org/10.1016/j.dsr2.2012.04.008.

Vimont, D.J. 2005. The contribution of the interannual ENSO cycle to the spatial pattern of decadal ENSO-like variability. *Journal of Climate* 18:2,080–2,092, http://dx.doi.org/10.1175/JCLI3365.1.

Vimont, D.J., J.M. Wallace, and D.S. Battisti. 2003. The seasonal footprinting mechanism in the Pacific: Implications for ENSO. *Journal of Climate* 16:2,668–2,675, http://dx.doi.org/10.1175/1520-0442(2003)016<2668:TSFMIT>2.0.CO;2.

Walker, G.T., and E.W. Bliss. 1932. World Weather V. *Memoirs of the Royal Meteorological Society* 4(36):53–84.

Weng, H., S.K. Behera, and T. Yamagata. 2009. Anomalous winter climate conditions in the Pacific Rim during recent El Niño Modoki and El Niño events. *Climate Dynamics* 32:663–674, http://dx.doi.org/10.1007/s00382-008-0394-6.

Yeh, S.-W., J.-S. Kug, B. Dewitte, M.-H. Kwon, B.P. Kirtman, and F.-F. Jin. 2009. El Niño in a changing climate. *Nature* 461:511–514, http://dx.doi.org/10.1038/nature08316.

Zhang, Y., J. Wallace, and D. Battisti. 1997. ENSO-like interdecadal variability: 1900–93. *Journal of Climate* 10:1,004–1,020, http://dx.doi.org/10.1175/1520-0442(1997)010<1004:ELIV>2.0.CO;2.